

1 **Mathematical consideration of the age-related decline in leaf biomass in**
2 **forest stands under the self-thinning law**

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17 **Abstract:** In addition to the hypothetical trends proposed by Kira and Shidei (1967), Odum
18 (1969) and Ryan *et al.* (1997, 2004), Oshima *et al.* (1958) observed a complicated
19 age-related change in stand leaf biomass in *Abies* forests. To explain this change in stand
20 leaf biomass theoretically, the age-related change in leaf biomass was modeled based on the
21 following three assumptions after canopy closure: (i) the self-thinning law; (ii) expanded
22 allometric scaling between the mean individual leaf mass and mean individual total mass;
23 and (iii) the formulation of a logistic function for stand density change. The model
24 successfully explained these three trends in forest stand leaf biomass and introduced
25 expanded allometric scaling including the properties of the model based on simple
26 allometric scaling proposed by Ogawa (2017). Therefore, the model developed here can
27 generalize age-related changes in forest stand biomass better than the model proposed by
28 Ogawa (2017).

29

30 *Keywords:* *Abies* forests, Allometric scaling, Canopy closure, Hypothetical trends, Logistic
31 function, Stand density

32

33 **1. Introduction**

34 Contrasting the classical hypothesis of stand leaf biomass constancy proposed by
35 Kira and Shidei (1967) and Odum (1969), Ryan *et al.* (1997, 2004) hypothesized that there
36 was an age-related decline in stand leaf biomass after forest canopy closure (cf. Fig. 1).
37 These two hypotheses were based on observations of *Cryptomeria japonica* plantations in
38 Japan (Ando *et al.*, 1968, Fig. 2A) and *Pinus sylvestris* plantations in England (Ovington
39 1957, Fig. 2B), as summarized by Tadaki (1977). However, no mathematical or
40 theoretical models explain why leaf biomass should remain constant or decline after canopy
41 closure.

42 Recently, Ogawa (2008) demonstrated the theoretical constancy of stand leaf
43 biomass after canopy closure for the first time, by scaling up from the shoot level to the
44 stand level based on assumptions such as the leaf mass/number (leafing intensity) trade-off
45 at the shoot level (Kleiman and Aarssen, 2007). According to this model, leaf biomass
46 constancy is constrained by the following assumptions: (1) the mean individual tree leaf
47 mass is inversely proportional to the mean leafing intensity (Kleiman and Aarssen, 2007);

48 (2) crown depth is proportional to tree height; and (3) leaf biomass is proportional to tree
49 height. Considering Ogawa's theory, the constancy of leaf biomass depends on several
50 assumptions, and empirical confirmation is necessary to test which of these assumptions are
51 valid.

52 Following his study, Ogawa *et al.* (2010) developed a hypothetical model of stand
53 leaf biomass changes based on the effects of self-thinning of a stand on the mean leaf mass
54 of a tree. In their analysis, the mean leaf mass of a tree remains essentially constant and
55 then increases because of space produced by self-thinning within the stand; the rapid
56 increase in leaf mass of a tree is referred to as a growth shift (Hozumi, 1985, 1987). A
57 growth shift occurs when a plant resumes more vigorous growth after the removal of
58 inhibitory effects, such as the reduction in light intensity caused by the growth of adjacent
59 plants.

60 Ogawa (2012) developed a mathematical model to describe how leaf biomass varies
61 as a function of stand density, using empirical data from permanent plot studies. Ogawa
62 (2017) also derived the age-related changes in leaf biomass of forest stands theoretically

63 under the following three assumptions: (1) the self-thinning law (Yoda *et al.*, 1963;
64 Miyanishi *et al.*, 1979; West *et al.*, 1997; Enquist *et al.*, 1998); (2) the allometric scaling
65 relationship between the mean individual leaf mass and mean individual total mass (Ogawa
66 and Kira, 1977; Niklas, 1994); and (3) the formulation of a logistic function for stand
67 density change (Ogawa, 2012). As a result, Ogawa (2017) proposed a functional model of
68 the age-related changes in forest stand leaf biomass and found that the forest stand leaf
69 biomass may decline or remain constant after canopy closure, depending on the values of
70 the model parameters. According to Ogawa's (2017) model, the possibility of leaf
71 biomass constancy in forest stands is low and stand leaf biomass declines after canopy
72 closure.

73 However, the model proposed by Ogawa (2017) cannot be used to predict the
74 pattern of age-related changes in stand leaf biomass for a given forest stand, because there
75 are no methods for setting model parameters based on the current state of a forest stand due
76 to a lack of observed data. In addition, the complicated age-related change in stand leaf

77 biomass in *Abies* forests on Mt. Shimagare, Japan (Oshima *et al.*, 1958, Fig. 2C) has not yet
78 been explained theoretically by constructing a reasonable mathematical model.

79 Therefore, this study delineated the domain of model application based on the above
80 three assumptions, which are rearranged herein; our rearrangement of the assumptions
81 clarifies the domain of model application proposed by Ogawa (2017), and leads to a new
82 realistic model of the age-related changes in forest stand leaf biomass under the assumption
83 of the self-thinning law (Yoda *et al.*, 1963; Miyanishi *et al.*, 1979; West *et al.*, 1997;
84 Enquist *et al.*, 1998).

85

86 **2. Materials and methods**

87 *2.1. Stand density*

88 Data on stand density were obtained from studies of a *Cryptomeria japonica* D. Don
89 (sugi) plantation (Ogawa and Hagihara, 2003, 2004; Ogawa, 2005, 2007) and two
90 *Chamaecyparis obtusa* (Sieb. et Zucc.) Endl. (hinoki cypress) plantations (Ogawa *et al.*,

91 1988, 2010; Sumida *et al.*, 2013). The two species are among the most important trees in
92 the Japanese forestry industry (Yato, 1978; Hayashi, 1988).

93 The *C. japonica* field study was conducted in a permanent experimental plot (280
94 m²) established in a 23-year-old stand located in the Nagoya University Experimental
95 Forest at Inabu (35°11'N, 137°33'E), *ca.* 55 km east of Nagoya (Aichi Prefecture, central
96 Japan). This plantation is located at an elevation of 960 m on an east-facing slope with a
97 23° gradient. Two-year-old seedlings were planted in a geometrical pattern at an initial
98 density of 6,000 trees ha⁻¹; no thinning was performed after planting. Annual counts of
99 all live trees in the plot were conducted in October for 22 years from 1983 to 2004.

100 The *C. obtusa* field study by Ogawa *et al.* (1988, 2010) was conducted in an
101 experimental plot (171 m²) within the grounds of the Graduate School of Bioagricultural
102 Sciences, Nagoya University, Japan (35°09'N, 136°58'E). This plot was 50 m above sea
103 level. Each seedling was planted in a separate 1 × 1 m cell within a gridded array (190
104 seedlings in total). All live trees in the plot were counted in June over 11 years from 1986
105 to 1996, beginning when the stand reached 3 years of age.

106 The *C. obtusa* field study by Sumida *et al.* (2013) was conducted in a permanent
107 experimental plot (191 m²) containing a 21-year-old stand of trees; the plot was located in
108 the Nagoya University Experimental Forest at Inabu (35°12'N, 137°33'E), *ca.* 55 km east of
109 Nagoya (Aichi Prefecture, central Japan). This plantation grew on a northwest-facing
110 slope with a 37° gradient; the plot elevation was 970 m. The 2-year-old seedlings were
111 planted geometrically at an initial planting density of 8,000 ha⁻¹; the plants were not
112 thinned during the observation period. All live trees in the plot were counted annually in
113 December over 20 years (1977–1996).

114

115 2.2. *Stem volume*

116 A monthly census was conducted of all *C. obtusa* trees in the stand for 11 years
117 beginning when the stand was 3 years old (in 1986) and ending when the stand was 13
118 years old (in 1996) (Ogawa *et al.*, 1988, 2010). From 1986 to 1988, when the stand was at
119 the seedling stage, the stem diameter at the crown base was measured. From 1989 to 1996,
120 stem girth was measured at the crown base.

121 To estimate stem volume each year from 1986 to 1988, seedling height (H) and
122 stem diameter at 10% of seedling height ($D_{0.1H}$) were measured. Ogawa (1989) examined
123 an allometric relationship involving stem volume, v ($\text{cm}^3 \text{ tree}^{-1}$), and the seedling height
124 times the square of stem diameter at 10% of seedling height, $D_{0.1H}^2 H$ (mm^3), for 254
125 destructively sampled hinoki cypress seedlings and found a strong relationship,
126 $v = 0.000528(D_{0.1H}^2 H)^{0.955}$ ($R^2 = 0.969$, $P < 0.001$, Ogawa, 2010). This relationship was
127 used to estimate the stem volume of individual trees. In addition, from 1989 to 1996, stem
128 height and stem girth at 50-cm intervals starting from the base of the stem were measured
129 (Yokota *et al.*, 1994; Yokota and Hagihara, 1995, 1996, 1998; Adu-Bredu and Hagihara,
130 1996, 2003; Adu-Bredu *et al.*, 1996*a, b*, 1997*a-c*). From the measurements, stem volume
131 was calculated using Smalian's formula (*e.g.*, Avery and Burkhart, 1994), with the tree top
132 being regarded as a cone.

133

134 *2.3. Stand leaf biomass*

135 According to pipe model theory (Shinozaki *et al.*, 1964a, b), the leaf mass of
136 individual trees is proportional to the stem cross-sectional area at the crown base in any
137 stand, regardless of age or habitat. This relationship was confirmed by Ogawa *et al.*
138 (2010) and Ogawa (2015) ($R^2 = 0.71$, $P < 0.001$). Therefore, we used the stem
139 cross-sectional area at the crown base to determine the time course of leaf biomass changes.
140 We measured the stem diameters of *C. obtusa* seedlings (3–5 years old) and the crown base
141 stem circumferences of trees that were 4–13 years old.

142

143 2.4. Modeling

144 2.4.1. Ogawa's (2017) case

145 **Assumption 1 (stand density model)**

146 According to Hozumi (1973), the changes in stand density (ρ) with stand age (t) in a
147 forest undergoing self-thinning are generally expressed by a logistic model, based on
148 Shinozaki's (1962) logistic theory of plant growth. Considering the theoretical
149 background on stand density, Ogawa (2012, 2017) used observational data from three

150 different coniferous plantations to show that the changes in stand density ($\rho(t)$) with stand
151 age (t) in a forest undergoing self-thinning can be described by the following logistic
152 equation (Fig. 3):

$$153 \quad \rho(t) = \frac{\rho_0}{1 + me^{\alpha t}} \quad (1)$$

154 where t represents tree age, and ρ_0 , m , and α are positive coefficients (Table 1). Here, we
155 use Eq. (1) to simulate the changes in stand density with stand age.

156

157 **Assumption 2 (self-thinning model)**

158 Following the first study of the relationship between stand density and average tree
159 size (stem diameter at breast height) by Reineke (1933), the relationship between mean tree
160 mass, $w(t)$, and stand density, $\rho(t)$, complies with the self-thinning law:

$$161 \quad w(t) = K\rho(t)^{-\beta} \quad (2)$$

162 where K and β are positive coefficients, and t is stand age. A geometrical analysis (Yoda
163 *et al.*, 1963) and the dimensional rule (Miyanishi *et al.*, 1979) both assigned a value of 3/2
164 to the coefficient β , while more recent estimates assigned a value of 4/3 to this coefficient

165 based on a metabolic scaling model, the West/Brown/Enquist theory (West *et al.*, 1997;
 166 Enquist *et al.*, 1998).

167

168 **Assumption 3 (allometric scaling model)**

169 The allometric relationship between mean leaf mass, $w_L(t)$, and mean tree mass, $w(t)$,
 170 is described by the following equation:

$$171 \quad w_L(t) = gw(t)^h \quad (3)$$

172 where g and h are positive coefficients (Ogawa and Kira, 1977; Niklas, 1994).

173 As stand leaf biomass $y_L(t)$ is defined as $y_L(t) = w_L(t)\rho(t)$, Assumptions 2 and 3

174 predict the following relationship between $y_L(t)$ and stand density $\rho(t)$:

$$175 \quad y_L(t) = gK^h \rho(t)^{1-\beta h} \quad (4)$$

176 Substituting Eq. (1) into Eq. (4), we obtain the following expression describing stand leaf

177 biomass $y_L(t)$ as a function of stand age t ,

$$178 \quad y_L(t) = gK^h \left(\frac{\rho_0}{1 + me^{at}} \right)^{1-\beta h} \quad (5)$$

179

180 2.4.2. *The present case*

181 In the model we develop here, Ogawa's (2017) third assumption was modified as
 182 the following expanded allometric scaling function (Ogawa and Kira, 1977):

$$183 \quad \frac{1}{w_L(t)} = \frac{1}{gw(t)^h} + \frac{1}{w_L^*} \quad (6)$$

184 If w_L^* is infinitely large, Eq. (6) becomes identical to Eq. (3); that is, the latter equation (Eq.
 185 3) is included in the former (Eq. 6) as a special case. In addition, as $w(t)$ becomes
 186 sufficiently large in Eq. (6), $w_L(t)$ approaches the upper limit of w_L^* .

187 By combining Eqs. (2) and (6), an equation for stand leaf biomass $y_L(t)$ can be
 188 derived as

$$189 \quad y_L(t) = w_L(t)\rho(t) = \frac{gK^h w_L^* \rho(t)^{1-\beta h}}{gK^h \rho(t)^{-\beta h} + w_L^*} \quad (7)$$

190 Substituting Eq. (1) into Eq. (7), we obtain the following expression describing stand leaf
 191 biomass $y_L(t)$ as a function of stand age t ,

$$192 \quad y_L(t) = \frac{gK^h w_L^* \left(\frac{\rho_0}{1 + me^{at}} \right)^{1-\beta h}}{gK^h \left(\frac{\rho_0}{1 + me^{at}} \right)^{-\beta h} + w_L^*} \quad (8)$$

193

194 *2.4.3. Non-linear regression analysis*

195 The coefficients of the nonlinear equations (α , ρ_0 , and m in Eqs. 1 and 6) were
 196 determined using KaleidaGraph (ver. 4.1.2; Synergy Software, Reading, PA, USA), which
 197 is based on the Levenberg–Marquardt algorithm (Press *et al.*, 1992) and an algorithm that
 198 measures the goodness of fit by the coefficient of determination (R^2).

199

200 **3. Results**

201 *3.1. Growth stage*

202 Combining the stand density (Eq. 1) and self-thinning (Eq. 2) models leads to the
 203 following growth equation for mean tree mass $w(t)$:

$$204 \quad w(t) = K \rho_0^{-\beta} (1 + me^{\alpha t})^{\beta} \quad (9)$$

205 which indicates that the mean tree mass $w(t)$ increases exponentially because coefficients α
 206 and β are positive.

207 Since the stand biomass $y(t)$ is defined as the product of $w(t)$ and $\rho(t)$, the function
 208 $y(t)$ can be expressed as an exponential equation, as follows:

209
$$y(t) = w(t)\rho(t) = K\rho_0^{1-\beta} (1 + me^{at})^{\beta-1} \quad (10)$$

210 where $\beta = 3/2$ or $4/3$ in the present study, so that $\beta-1 > 0$ and then $y(t)$ increases
211 exponentially.

212 Equations (9) and (10) indicate that the domain of model application is restricted to
213 the exponential growth stages or premature forest stands, that is, to those stands that have
214 not yet reached their peak growth rate.

215

216 *3.2. Application of an expanded allometric scaling relationship between leaf mass and tree*
217 *mass*

218 Kira and Shidei (1967) found the relation in Eq. (6) between leaf mass and stem and
219 branch mass in a cool temperate deciduous forest, and Ogawa and Kira (1977) reported the
220 same relationship between leaf mass and stem mass in a mixed evergreen forest. Since the
221 tree mass is proportional to the stem volume (White, 1981), the stem mass is assumed to be
222 proportional to the tree mass.

223 Based on a dataset of the mean stem cross-sectional area at the crown base and
224 mean stem volume in a *C. obtusa* plantation (Ogawa *et al.*, 2010), Eq. (6) is suitable for
225 describing the expanded allometric scaling relationship between leaf mass and tree mass in
226 a forest undergoing self-thinning (Fig. 4). The values of g , h , w_L^* , and R^2 in Eq. (6) are
227 $30.91 \text{ cm}^2 \text{ dm}^{-3h}$, 0.9685, 26.39 cm^2 , and 0.9965, respectively.

228

229 3.3. Properties of the present model

230 Since the coefficients g , K , h , and w_L^* are constants in Eqs. (7) and (8) of the stand
231 leaf biomass model, both equations may be applied to three cases with different values of
232 $1 - \beta h$ ($\beta h = 1$, $\beta h < 1$, or $\beta h > 1$). According to the geometric (Yoda *et al.*, 1967;
233 Miyanishi *et al.*, 1979) and metabolic scaling (West *et al.*, 1997; Enquist *et al.*, 1998)
234 theories, the values of β (Eq. (2)) are $3/2$ and $4/3$, respectively. Consequently, the values
235 of h (Eq. 3) are (i) $h = 2/3$ or $h = 3/4$, (ii) $h < 2/3$ or $h < 3/4$, or (iii) $h > 2/3$ or $h > 3/4$,
236 respectively.

237 When $\beta h = 1$ ($\beta = 3/2, h = 2/3$, or $\beta = 4/3, h = 3/4$), the stand leaf biomass $y_L(t)$ is
 238 essentially constant regardless of stand age t , and then decreases with stand age t (Fig. 5A
 239 or B). When $\beta h < 1$ ($\beta = 3/2, h < 2/3$ or $\beta = 4/3, h < 3/4$), or $\beta h > 1$ ($\beta = 3/2, h > 2/3$ or $\beta =$
 240 $4/3, h > 3/4$), the value of $y_L(t)$ in Eq. (8) was simulated (with βh as a parameter) by fixing
 241 the values of gK^h , m , α , ρ_0 , and w_L^* at $1.0 \text{ ha}^{-1}\beta^h$, 0.0501 , $0.0.823 \text{ yr}^{-1}$, 6491 ha^{-1} , and 26.39
 242 cm^2 , respectively (Figs. 5A, B). Here, the values of m , α , and ρ_0 correspond to the values
 243 determined for a *C. japonica* plantation (cf. Table 1). The stand leaf biomass $y_L(t)$
 244 decreases monotonously with stand age t when $\beta h < 1$, but shows complicated, unrealistic
 245 changes with stand age t when $\beta h > 1$.

246

247 3.4. Interpretation of the models

248 The developmental stage of a forest in the present model is restricted to the time
 249 ($t > t^*$) after full canopy closure, when the self-thinning rule (Eq. 2) is operational (Fig. 5).
 250 During the period before full canopy closure, stand leaf biomass increases with stand age t
 251 because large areas of illuminated space are available. In the model, stand leaf biomass (i)

252 remains constant and then decreases or (ii) decreases monotonously with stand age t after
253 the forest closes fully.

254 Although this model is related only to the development process after canopy closure,
255 future studies should focus on linking processes before and after the closure event. A
256 linked model would contribute to the development of predictions of the overall future
257 dynamics of stand leaf biomass.

258

259 **4. Discussion**

260 *4.1. Interpreting the cases in the stand leaf biomass model*

261 In assumption 3 of the allometric scaling model (Eq. 3), the leaf mass ratio
262 ($w_L(t)/w(t)$) of an average tree increases with tree mass ($w(t)$) or tree age (t) when $h > 1$.
263 This trend in the leaf mass ratio is not biologically reasonable because trees commonly
264 accumulate woody tissues in their trunks, branches, and roots as they age. From this
265 biological viewpoint, Ogawa (2017) suggested that the predicted increases in stand leaf

266 biomass $y_L(t)$ with age t are not tenable. Therefore, the increasing trend of stand leaf
267 biomass $y_L(t)$ with age t observed in the model (Fig. 5B) is also considered untenable.

268 Consequently, the two alternative cases [(i) decreasing $y_L(t)$, and (ii) constant and
269 then decreasing $y_L(t)$] are considered to be more biologically reasonable. Case (i) fits the
270 hypothetical trend proposed by Ryan *et al.* (1997), and case (ii) corresponds to the trend in
271 *Abies* forests observed by Oshima *et al.* (1958). Although the hypothetical trend proposed
272 by Kira and Shidei (1967) and Odum (1969) is realized under the assumption of the simple
273 allometric scaling model of Eq. (3) (Ogawa, 2017), the leaf biomass constancy was rejected
274 under the expanded allometric scaling model of Eq. (6) in the present analysis.

275 Many studies have suggested that these coefficients of Eq.(2) or (3) are not stable
276 even though West/Brown/Enquist imply that the scaling exponent is centered on 4/3 or
277 3/4. Some examples of papers (Pretzsch, 2006; Ducey, 2012; Lines *et al.*, 2012; Sileshi,
278 2014; Forrester *et al.*, 2017) with large empirical data sets showed these departures from
279 West/Brown/Enquist.

280

281 *4.2. Age-related decline of stand leaf biomass*

282 Equation (8), which is derived under the assumption of an expanded allometric
283 scaling relationship of Eq. (7), is so complicated that the model deals with Eq. (7) to
284 understand the age-related changes in forest stand leaf biomass $y_L(t)$.

285 In Eq. (7), when $w(t)$ becomes maximal or the time t progresses fully, $w_L(t)$
286 approaches an upper limit of w_L^* (cf. Fig. 2). Thus, the stand leaf biomass $y_L(t)$ can be
287 expressed as

$$288 \quad y_L(t) = w_L^* \rho(t) = \frac{w_L^* \rho_0}{1 + m e^{ct}} \quad (11)$$

289 Equation (11) indicates that the stand leaf biomass $y_L(t)$ decreases exponentially as stand
290 age increases.

291 The developmental stage of a forest in the model is restricted to the time after full
292 canopy closure, when the self-thinning rule (Eq. 2) is operational. In this stage, the
293 domain of model application is restricted to the exponential growth stage or premature
294 forest stands (cf. Eq. 10). Therefore, the decreasing $y_L(t)$ in the model results mainly from
295 the property reflected in Eq. (11).

296 During the period before full canopy closure, stand leaf biomass increases with
297 stand age t because large areas of illuminated space are available. In the model, stand leaf
298 biomass decreases exponentially with stand age t after the forest closes fully. As a result,
299 the age-related changes in forest stand leaf biomass $y_L(t)$ show a single peak during the
300 entire development stage of forest stands.

301

302 *4.3. Generality of the present leaf biomass model*

303 Ogawa (2017) proposed a leaf biomass model in which stand leaf biomass decreases,
304 increases monotonously with stand age, and then remains constant regardless of stand age
305 after canopy closure. The leaf biomass model given by Eq. (8) can cover all of the cases
306 of age-related changes in leaf biomass shown by Ogawa (2017). In addition to the three
307 cases proposed by Ogawa (2017), the model revealed that another complicated leaf biomass
308 change observed in *Abies* forests (Oshima *et al.*, 1958, Fig. 2C) can be explained
309 mathematically by replacing the simple allometric scaling (Eq. 3) with expanded allometric
310 scaling (Eq. 6) between the mean individual leaf mass and entire-tree mass.

311 Since the model based on a simple allometric scaling (Eq. 3) proposed by Ogawa
312 (2017) cannot explain the leaf biomass changes in *Abies* forests (Fig. 2C), the present
313 model introduced expanded allometric scaling (Eq. 6) and is considered to be useful for
314 explaining age-related changes in forest stand leaf biomass. Oshima *et al.* (1958) also
315 provided experimental evidence that with increasing tree age, the dry mass of leaves on a
316 standard tree increased, and reached a maximum in mature trees. This trend in individual
317 leaf mass corresponds to the trend in expanded allometric scaling (Eq. 6) between the mean
318 individual leaf mass and entire-tree mass.

319 As a result, the model that introduced expanded allometric scaling includes the
320 properties of the model based on the simple allometric scaling proposed by Ogawa (2017).
321 Therefore, the model developed here has generality for expressing age-related changes in
322 forest stand biomass, unlike the model proposed by Ogawa (2017).

323

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328

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458 hinoki cypress (*Chamaecyparis obtusa*) on tree size. Tree Physiol. 14, 467-479.
- 459
- 460

461 **Figure legends**

462 **Fig. 1.** Hypothetical trends in age-related changes in leaf biomass in a forest stand.

463 (A) Hypothesis proposed by Kira and Shidei (1967) and Odum (1969). (B) Hypothesis
464 proposed by Ryan *et al.* (1997, 2004). t^* is the time of canopy closure in a forest stand.

465

466 **Fig. 2.** Examples of age-related changes in stand leaf biomass in even-aged pure stands.

467 (A) *Cryptomeria japonica* plantations in Japan (Ando *et al.*, 1968). (B) *Pinus sylvestris*
468 plantations in England (Ovington, 1957). (C) *Abies veitchii*/*A. mariesii* forests on Mt.
469 Shimagare (Oshima *et al.*, 1958) (cited from Tadaki (1977)).

470

471 **Fig. 3.** Logistic curves describing the trends in stand density (ρ) with stand age (t) in a

472 young *Chamaecyparis obtusa* plantation (squares, Ogawa *et al.*, 1988, 2010), mature

473 *Cryptomeria japonica* plantation (triangles, Ogawa and Hagihara 2003, 2004), and mature

474 *C. obtusa* plantation (circles, Sumida *et al.*, 2013). The curves were fit using Eq. (1) and

475 KaleidaGraph statistical analysis software. See Table 1 for the values of the coefficients.

476

477 **Fig. 4.** Relationship between the mean stem cross-sectional area at the crown base $w_L(t)$ and
478 mean stem volume $w(t)$ in a *Chamaecyparis obtusa* plantation (Ogawa *et al.*, 2010). The
479 smooth curve is the expanded allometric scaling function of Eq. (6).

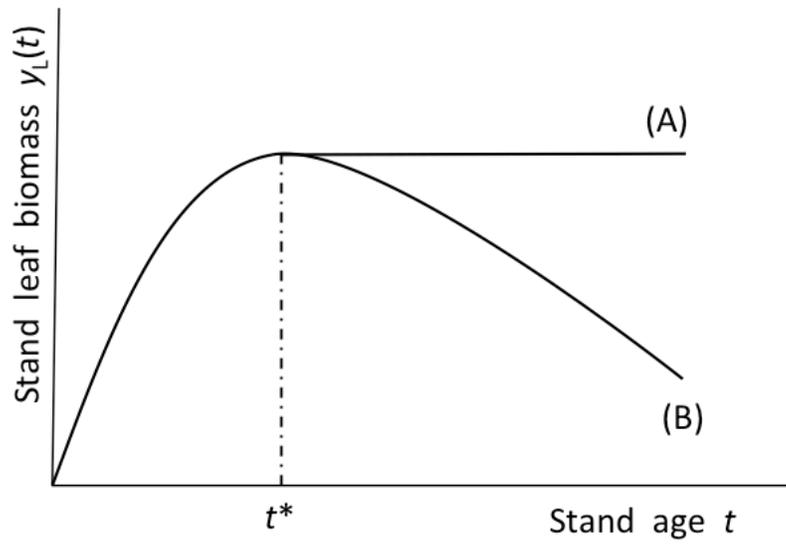
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481 **Fig. 5.** Age-related changes in leaf biomass $y_L(t)$ in Eq. (8), with βh as parameter, on fixing
482 the values of gK^h , m , α , ρ_0 , and w_L^* at $1.0 \text{ ha}^{-1}\beta^h$, 0.0501 , $0.0.823 \text{ yr}^{-1}$, 6491 ha^{-1} , and 26.39
483 cm^2 , respectively, for the cases (A) $\beta h < 1$ and (B) $\beta h > 1$.

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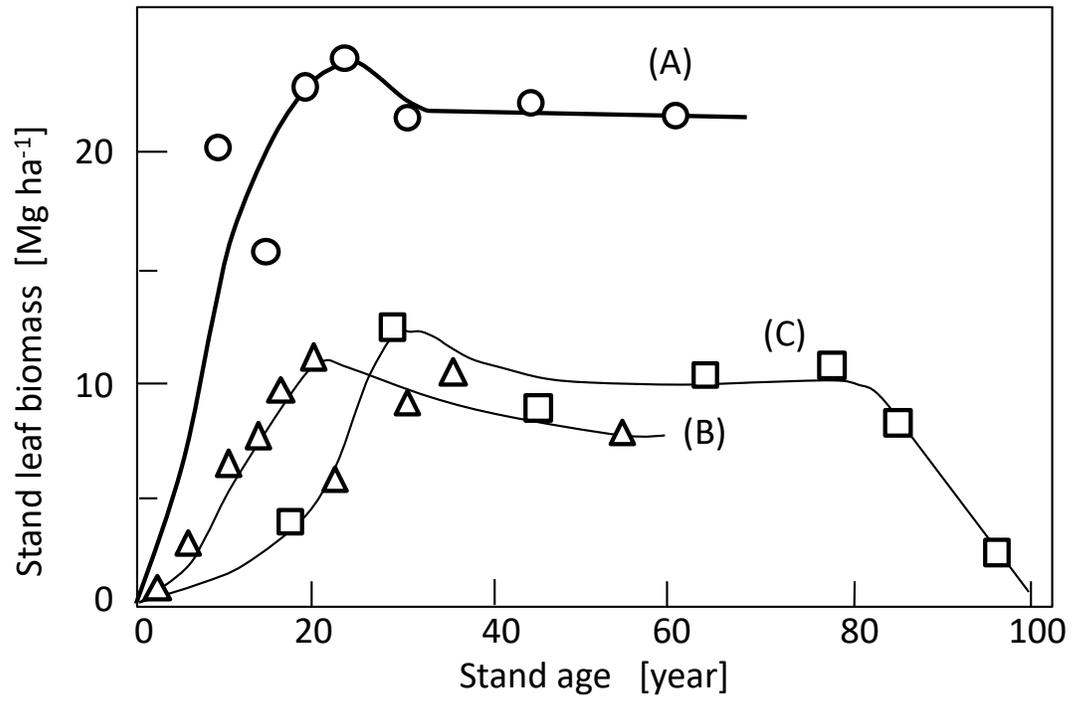
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488 Fig. 1

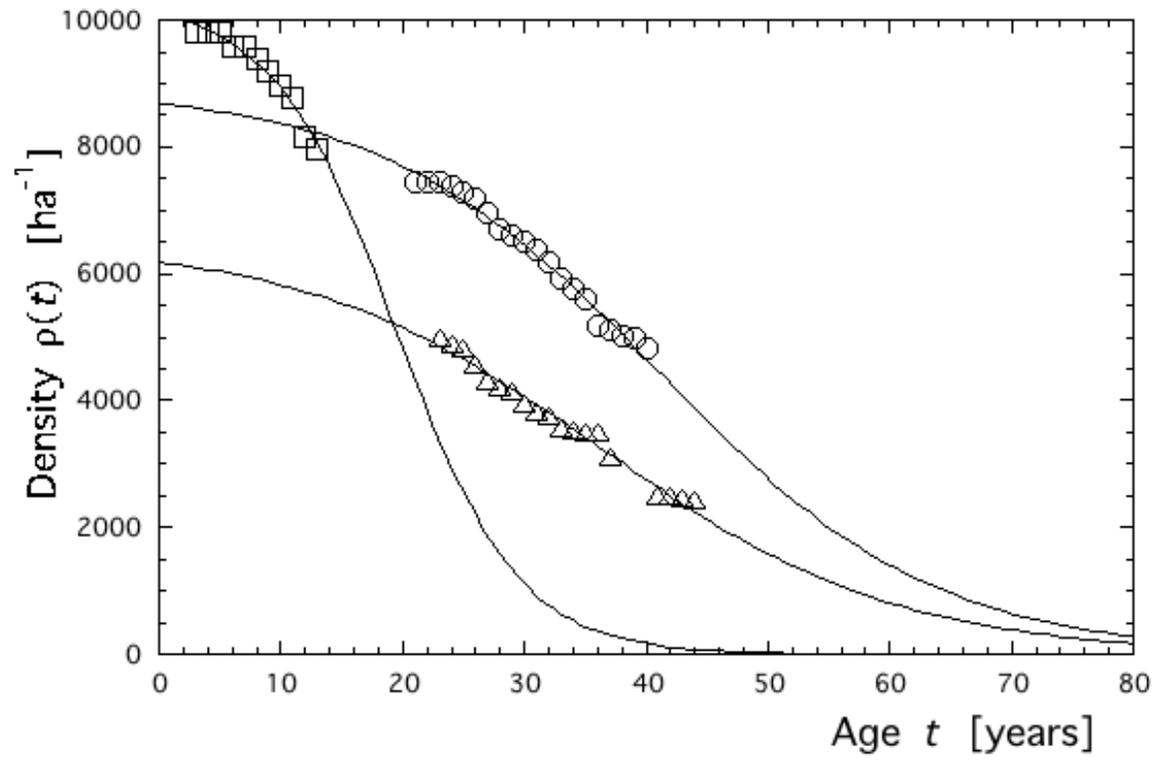
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491 Fig. 2

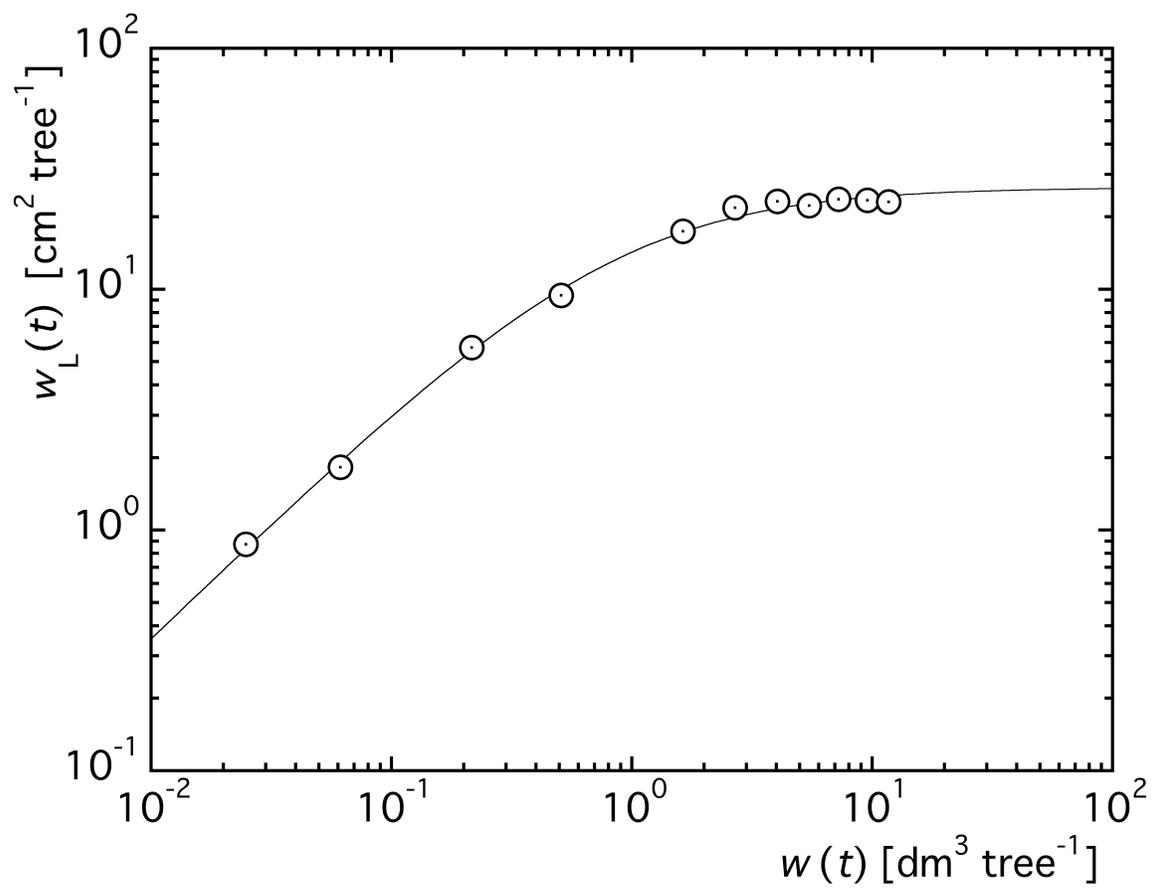
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494 Fig. 3

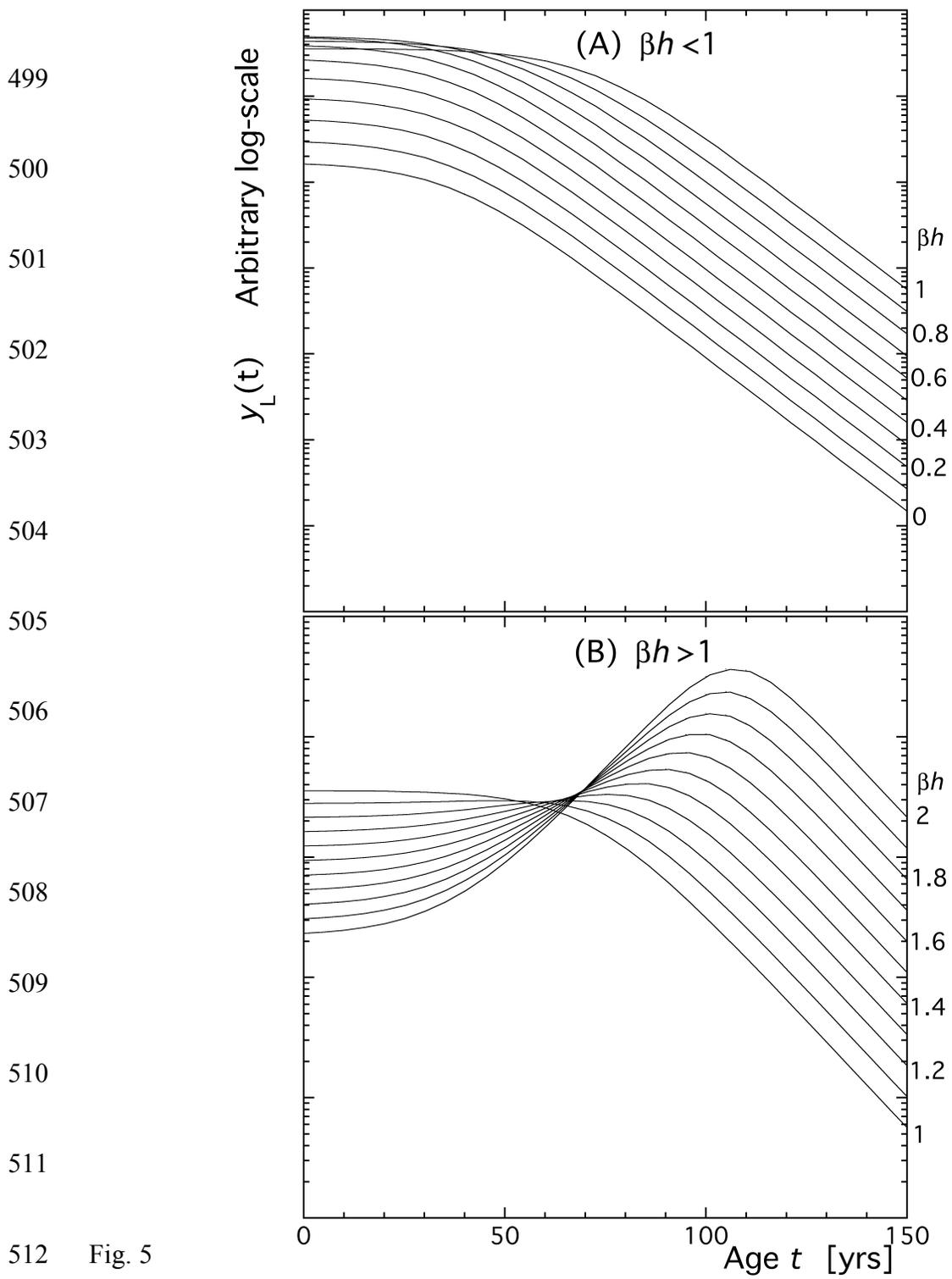
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496

497 Fig. 4

498



512 Fig. 5

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