1	Allometric scaling of leaf mass based on the pipe model theory for woody
2	plant species
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### 26 Abstract

27 There is an exceptional case in which Shinozaki's pipe model predictions should not explain that 28 the allometric scaling exponent between foliage mass and stem diameter at the crown base is 29 bigger than 2 empirically. This study proposes an allometric scaling model with components f30 and b, which are the scaling exponent between the sapwood area and stem cross-sectional area 31 and foliage mass and the stem cross-sectional area at crown base, respectively. The scaling 32 exponent f of sapwood area vs. stem diameter at the crown base has no effect on leaf mass vs. 33 stem diameter at the crown base, while the scaling exponent b has effects on leaf mass vs. stem diameter at the crown base. Because the value of b is greater than unity, this scaling model 34 35 predicts that the diameters of conduits at the crown base widen with tree size, indicating tip-base 36 widening of conduits. Because the proportion of sapwood area remains constant (or f=0) across 37 sizes, the assumption of Shinozaki's pipe model theory appears to apply to the case *f*=0. 38 39 Keywords allometric scaling, conduit diameter, leaf mass, pipe model theory, stem diameter at 40 crown base, sapwood area 41 42 Author Contribution Statement: The author (KO) designed research, collected the data, 43 analyzed them, and wrote the paper. 44 45 **Conflict of Interest:** The author (KO) declares that he has no conflict of interest.

### 47 Introduction

48 According to the classical pipe model theory developed by Shinozaki et al. (1964a, b), the leaf mass of individual trees is closely related to the stem diameter at the crown base, which is 49 50 therefore a useful metric for estimating the leaf mass. Based on the pipe model theory, the 51 allometric scaling exponent between leaf mass and stem diameter at the crown base is 52 theoretically 2. However, there is an exceptional case when the allometric scaling exponent is 53 greater than 2, which occurs when the proportionality of leaf mass to the square of the stem 54 diameter at the crown base tends to segregate canopy trees from suppressed trees (Shinozaki et 55 al. 1964b). Therefore, the present models have a limited (Kobayashi and Maskawa 1973) ability 56 to express the mechanism of the allometric scaling between leaf mass and stem diameter at the 57 crown base.

58 Several subsequent models have been developed by distinguishing between active and 59 disused pipes, and by considering sapwood area equivalent to active pipe area, since the foliage mass should be closely related to the sapwood area (as reviewed by Lehnebach et al. 2018). As a 60 61 result of these approaches, the allometric scaling exponent becomes unity in the leaf mass-62 sapwood area relationship, in which the pipe model ratio, or the ratio of foliage mass to the 63 sapwood ratio at the crown base, which was proposed in lieu of the specific pipe length 64 (Shinozaki et al. 1964a), should be constant (e.g. Whitehead et al. 1984, Shelburne et al. 1993, Mencuccini and Grace 1995, Mäkelä et al. 1995, Vanninen et al. 1996, Meadows and Hodges 65 2002). 66

The pipe model theory is one of the most important approaches for understanding the 67 68 hydraulic architecture of trees. However, it has major limitations that suggest that the pipe 69 structure as proposed by Shinozaki et al. (1964a, b) cannot be found in an actual tree. The most 70 critical assumption relies on the fact that the pipes of the basic elements of the plant vascular 71 system are cylindrical, i.e., the conduit diameter does not change axially. However, the main 72 property of the hydraulic system of trees is to have tip-base widening of the conduits (e.g., West 73 et al. 1999; Anfodillo et al. 2006; Petit and Anfodillo 2009; Savage et al. 2010; Olson et al. 2014, 2018, 2021; Koçillari et al. 2021). Therefore, this universal, but ineludible, pattern has a 74 75 profound effect on the relationship between foliage mass and stem diameter.

Recently, Ogawa (2015) examined the allometric scaling exponent between leaf mass and stem diameter at the crown base among several forest trees, and reported values greater than 2 for all species. Ogawa (2015) applied the stratified clipping method (Monsi and Saeki 1953) to conduct a mathematical analysis of the mechanism that causes the scaling exponent to exceed 2, and found that the scaling exponent is controlled by the size dependence of the specific pipe length, which is related to competition among forest trees and can be used as an index of the degree of suppression by larger trees.

83 However, it is not known how the pipe model ratio (cf. Lehnebach et al. 2018) is related 84 to the allometric scaling exponent between leaf mass and stem diameter at the crown base in 85 classical pipe model theory (cf. Shinozaki et al. 1964a, b). That is, if the pipe model ratio is 86 constant, under what conditions does the classical pipe model theory hold? Because the pipe 87 model ratio is related to the stem sapwood area, while the classical pipe model theory is related 88 to the stem cross-sectional area, the proportion of sapwood area might explain why the 89 allometric scaling exponent exceeds 2 by linking the pipe model ratio and classical pipe model 90 theory. In addition to the sapwood area proportion, tip-to-base xylem conduit widening should be 91 considered for the exceptional cases in which the pipe model predictions should not explain the 92 correlation between leaf mass and diameter of the stem using experimental data.

The stratified clipping method is a time- and labor-intensive approach, especially for trees, for which relevant data are very limited. Therefore, to clarify the factors that control the allometric scaling exponent of leaf mass in the pipe model, the present study provides a simple allometric scaling model of leaf mass based on the leaf mass and stem diameter at the crown base, considering the hydraulic vessel system, such as the proportion of sapwood area, and the conduit diameter.

All data used in this study were collected from four stands of hinoki cypress
(*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) located in Aichi Prefecture, central Japan (Table
1, cf. Hagihara et al. 1993), as follows:

Nagoya. This stand was established in an experimental forest of Nagoya University on flat
 terrain at 50 m a.s.l.. No artificial management has been performed since the plantation was
 established. Since the canopy was fully closed, undergrowth vegetation was nearly absent.

105 2) Inabu. This stand is located at Nagoya University Forest on a 35° north-facing slope at an
 106 elevation of 500 m a.s.l.. Artificial management was performed only immediately after the
 107 plantation was established. Undergrowth vegetation was nearly absent.

3) Hourai. This stand is located at the Aichi Prefectural Forest Research Institute on an 18.5°
 northwest-facing slope at 435 m a.s.l. No artificial management was performed in the stand
 within the 20 years preceding the survey. Undergrowth vegetation was nearly absent.

4) Dando. This stand is located in a national forest administered by the Shinshiro District Forest
 Office and Nagoya Regional Forest Office on a 25° west-facing slope at 900 m a.s.l.

113 Thinning was performed 4 years prior to the survey. Ground vegetation consisted of a dense

114 population of suzudake (*Sasamorpha borealis* [Hack.] Nakai) that was ca. 2 m tall.

115

# 116 Measurement of tree size and mass

117 After the sample trees were felled, the tree height, crown base height, stem diameter at a height 118 of 1.3 m above the ground (DBH), and stem diameter at the crown base ( $D_B$ ) were measured.

Following the tree size measurements, the stratified clipping method (Fig. 1) was applied to the felled trees (Monsi and Saeki 1953). The trees were stratified into several vertical strata defined at 0–0.3, 0.3–1.3 m, and then 1.0 m intervals from ground level to the top of the crown. The stems, branches, and leaves from each stratum were clipped separately from all layers. The stems, branches, and leaves in each stratum were weighed. The roots were washed and weighed following excavation.

Samples were collected from each stratum to estimate the dry/fresh mass ratio for each organ, including the roots. The samples were dried in ventilated ovens at 85°C for a few days, desiccated at room temperature, and then weighed. Fresh mass was converted to dry mass to obtain stem, branch, leaf, and root values per tree using their respective ratios.

129

### 130 Measurement of sapwood area at the crown base

131 Measurements of sapwood area at the crown base (Adu-Bredu and Hagihara 1996) were

132 performed using 12-year-old *C. obtusa* trees (Table 1) as follows: 13 trees were harvested, and

133 stem discs were removed from the crown base (thickness, 1.5–4.0 cm). Sapwood was

differentiated from heartwood by color and staining with ferric chloride solution (e.g., Ryan1989).

The disc circumference was measured using a steel measuring tape, and the heartwood circumference was measured using a Digital Curvimeter (S-880; Uchida, Tokyo, Japan). The sapwood cross-sectional area was calculated as the difference between the stem and heartwood cross-sectional areas, and the proportion of sapwood area was determined as the ratio of the sapwood cross-sectional area to the stem cross-sectional area.

141

### 142 *Model descriptions*

Allometric scaling of leaf mass: Assuming that the pipe model ratio is constant at the crown base, i.e., an allometric scaling exponent of unity between the leaf mass and the sapwood area at the crown base, the leaf mass is not proportional to the sapwood area at the crown base as long as the proportion of the sapwood area is greater in larger trees than in smaller trees. Under this condition, the following model supports  $m_L-D_B^2$  allometry, with a scaling exponent that tends to be greater than unity in several woody species (Ogawa 2015).

According to traditional pipe model theory (cf. Lehnebach et al. 2018), the stem crosssectional area at the crown base and the sapwood area are denoted as  $A_{\rm B} \left(=\frac{\pi}{4}D_B^2\right)$  and  $A_{\rm S}$  (cm<sup>2</sup>), respectively, where the leaf mass  $m_{\rm L}$  (kg) is assumed to be proportional to  $A_{\rm S}$  as follows:

152

$$153 mtextbf{m}_L = aA_s. (1)$$

154

where *a* is a constant equivalent to the pipe model ratio at the crown base. This model has more generality in the  $m_L$ - $A_s$  relation of Eq. (1), so that the leaf mass  $m_L$  (cm<sup>2</sup>) scales as  $A_s^b$ ,

157

$$m_L = a A_S^b. \tag{2}$$

159

158

160 If the relationship between the proportion of sapwood area at the crown base  $\frac{A_S}{A_B}$ 161 (dimensionless) and  $A_B$  (cm<sup>2</sup>) satisfies the following scaling relation,

163 
$$\frac{A_S}{A_B} = eA_B^f, \tag{3}$$

165 then the relationship between  $m_{\rm L}$  (kg) and  $A_{\rm B}$  (cm<sup>2</sup>) is derived as

166

167 
$$m_L = ae^b A_B^{(1+f)b}$$
. (4)

168

169 Therefore, the scaling exponent of  $m_{\rm L}$ – $D_{\rm B}^2$  allometry is controlled by the values of coefficients *b* 170 and *f* in Eqs. (2) and (3).

171 Specifically, if f=0 means that sapwood fraction remains constant across sizes in Eq. (2), 172 then the  $m_L-A_B$  allometry in Eq. (5) is simplified as the following scaling equation with the 173 exponent of *b*:

174

 $m_L = a e^b A_B^b. (5)$ 

176

177 Therefore, the scaling exponent of Eq. (5) is determined by the scaling exponent of  $m_L$ -As allometry of Eq. (2) in the special case f=0. If the scaling exponent of  $m_L-A_S$  allometry (Eq. 2) is 178 179 larger than unity, the scaling exponent of  $m_L$ - $A_B$  allometry (Eq. 4 or 5) is larger than unity. The case when the scaling exponent of  $m_{\rm L}$ – $D_{\rm B}^2$  allometry becomes unity is generally b =180  $\frac{1}{1+f}$  in Eq. (4). Therefore, Eq. (5) indicates that even if f=0, that does not necessarily mean only 181 b=1 or the proportionality of  $m_{\rm L}$  and  $D_{\rm B}^2$  from Eqs. (4). Equation (4) suggests that the leaf mass 182 per unit sapwood area at the crown base  $m_L/A_S$  (kg cm<sup>-2</sup>) depends on the sapwood area  $A_S$  (cm<sup>2</sup>) 183 184 as follows:

185

$$\frac{m_L}{A_S} = aA_S^{b-1} \tag{6}$$

187

188 If the number of conduits per unit sapwood area is assumed to be constant,  $m_L/A_S$  is regarded as 189 an index of conduit diameter. That is, the larger  $m_L/A_S$  is, the larger the conduit diameter is, and 190 vice versa. Based on Eq. (6), Eq. (1) corresponds to the case when the conduit diameter is

- 191 constant irrespective of tree size because the value of b is unity. In addition, the conduit diameter
- 192 increases in larger trees compared to smaller trees if the value of *b* is greater than unity.
- 193

## 194 *Regression analysis*

195 Bivariate relationships, i.e., the  $\frac{A_s}{A_B}$   $D_B^2$  (Eq. 3),  $m_L$   $-A_s$  (Eq. 2), and  $m_L$   $-D_B^2$  (Eq. 4) relationships,

- 196 were analyzed using standardized major axis (SMA) regression (Warton et al. 2006) and
- 197 ordinary least squares (OLS) regression, using the smatr package of R (v. 4.1.2, R Core
- 198 Development Team, 2021). Significant differences among power (i.e., scaling) exponents were
- 199 based on 95% confidence intervals (CIs).

In the present analysis, Inabu had 36 individuals whereas the other sites have six individuals on average (Table 1). Therefore, a mixed-effects linear regression model was performed in the  $m_L-D_B^2$  allometry (Eq. 4) to evaluate whether there is autocorrelation between data points from the same site, using the ImerTest package of R.

204

205 **Results** 

# 206 Allometric scaling of leaf mass

207 The allometric relationship between leaf mass  $(m_L)$  and the square of the stem diameter at the crown base  $(D_{\rm B}^2)$  was approximated by a single regression line on log-log coordinates, applying 208 209 to all stands (Fig. 2). The scaling exponent was 1.273 (95% CI, 1.179–1.375) in SMA and 1.226 210 (95% CI, 1.128–1.324) in the OLS regression, both of which were significantly greater than 211 unity. Performing a mixed-effects linear regression model, the scaling exponent was calculated 212 to be 1.160 (95% CI, 1.006–1.314), which was significantly higher than unity, as with the SMA 213 and OLS regression methods. Therefore, there is no profound autocorrelation between data 214 points from the same site.

215

## 216 Allometry of leaf mass to sapwood area at the crown base

- 217 The allometric relationship between leaf mass  $m_{\rm L}$  and sapwood area at the crown base  $A_{\rm s}$
- satisfied Eq. (2) for 12-year-old *C. obtusa* (Adu-Bredu and Hagihara 1996) (Fig. 3). The value of
- scaling exponent *b* is significantly higher than unity (1.448, 95% CI = 1.126 1.862) in the SMA

- regression. Because the isometric relation between  $w_L$  and  $A_s$  given by Eq. (1) is not valid, the pipe model ratio at the crown base is not constant among trees. In constrast, the value of *b* is not significantly different from unity (1.337, 95% CI = 0.970–1.706) in the OLS regression. This method (OLS) at least covers isometry for the allometry of leaf mass to sapwood area at the crown base.
- 225

# Relationship between the proportion of sapwood area at the crown base and the square of the stem diameter at the crown base

In a *C. obtusa* plantation, 12-year-old trees (Adu-Bredu and Hagihara 1996) had a negative

229 correlation between the proportion of sapwood area  $\frac{A_s}{A_B}$  at the crown base and tree size  $D_B^2$ , as

230 given by Eq. (3) (Fig. 4). However, the *p*-value of the linear regression between the logarithm of

these two terms is too high (0.892) in both the SMA and OLS regression methods. This indicates

that the available data do not show that the scaling exponent is significantly different from 0.

233 Therefore, the proportion of sapwood area at the crown base is independent of tree size, although

the proportion of sapwood area varied vertically within the tree (Longuetaud et al. 2006).

235

# 236 **Discussion**

# 237 Allometric scaling relation of leaf mass

The allometric scaling relationships of  $m_{\rm L}$  to  $D_{\rm B}^2$  (Fig. 2) suggest that the amount of foliage per tree should be most closely correlated with the sum of the cross-sectional areas of the living pipes supporting them, which in turn is thought to be well approximated by the cross-sectional area of the trunk at the crown base. These relationships support fundamental concepts related to active and disused pipes within the pipe model theory (Shinozaki et al. 1964a, b); therefore, the stem diameter at the crown base  $D_{\rm B}$  can serve as an overall basis for foliage amount estimation in any stand, regardless of the tree age or habitat.

In the present study, a scaling model is used (Eq. 4) to explore the underlying causes of an exponent that might increase above a value of 2. According to studies of plant hydraulic adaptation (Savage et al. 2010; Olson et al. 2014, 2018, 2021; Kocillari et al. 2021), natural 248 selection operates on allometric scaling exponents between sapwood area and stem cross-

sectional area (Eq. 2) and foliage mass and stem cross-sectional area at the crown base (Eq. 4).

Because the scaling exponent of  $m_L - D_B^2$  allometry is controlled by the *f* value of the coefficient in the case b=1 in Eq. (4) or Eq. (1), the scaling exponent of Eq. (4) is unity because the value of *f* in Eq. (3) is regarded as zero (Fig. 4). Therefore, this case cannot be applied to the present result of  $m_L - D_B^2$  allometry (Fig. 2). We conclude that the pipe model ratio at the crown base is not constant irrespective of tree size, and varies among individual trees. In fact, the allometric scaling exponent between leaf mass  $w_L$  and sapwood area at the crown base  $A_s$  is significantly higher than unity in SMA regression (Fig. 2).

257 According to Shelburne et al. (1993) and Mäkelä and Albrektson (1992), the foliage area to sapwood area ratio is lower in suppressed trees than in dominant trees, indicating that the 258 259 constant pipe model ratio given by Eq. (1) is not applicable to a wide range of tree sizes. Shinozaki et al. (1964b) stated that the proportionality of  $w_{\rm L}$  to  $D_{\rm B}^2$  tends to segregate canopy 260 261 trees from suppressed trees with less foliage. In suppressed trees, the scaling exponent (1+f)b of the  $m_{\rm L}$ - $D_{\rm B}^2$  relationship (Eq. 4) becomes greater than unity, resulting in a positive scaling with 262 the specific pipe length L (m) (Shinozaki et al. 1963a), namely  $L \propto (D_R^2)^{\xi}$ , where  $\xi$  is a positive 263 264 scaling exponent. Thus, it is reasonable that L is related to competition among forest trees and is used as an index of the degree of suppression (Ogawa 2015). 265

However, the present  $w_{\rm I}$  – $D_{\rm B}^2$  allometry with a scaling exponent greater than unity can be 266 267 explained based on the more general scaling relation given by Eq. (4) and the sapwood area 268 proportion relation given by Eq. (3). If the value of f in Eq. (3) is zero because the correlation between the proportion of sapwood area  $\frac{A_S}{A_B}$  at the crown base and tree size  $D_B^2$  is not significant 269 (Fig. 4), the value of the scaling exponent of  $m_{\rm L} - D_{\rm B}^2$  allometry equals the value of the scaling 270 exponent of  $m_L - A_s$  allometry. Therefore, the scaling exponent of  $m_L - D_B^2$  allometry can be 271 determined by factors such as the size dependency of the pipe model ratio (Eq. 4) and constancy 272 273 of the sapwood area proportion (Eq. 3) at the crown base.

### 275 Hydraulic architecture

From the perspective of the hydraulic architecture of trees, Eq. (1) is based on the assumption that the basic pipe elements of the plant vascular system are cylindrical, i.e., the conduit diameter does not change axially. However, the main property of the hydraulic system of trees is to have tip-base widening of the conduits theoretically (West et al. 1999; Koçillari et al. 2021) and experimentally (Anfodillo et al. 2006; Petit and Anfodillo 2009; Savage et al. 2010; Olson et al. 2014, 2018, 2021). Therefore, this universal, includible pattern is considered to have a profound effect on the relationship between foliage mass and stem diameter.

Based on SMA regression in Eq. (2), the conduit diameter is higher in larger trees than in smaller trees because the scaling exponent of b is greater than unity (Eq. 7). In contrast, the OLS regression in Eq. (2) indicates that the conduit diameter is constant irrespective of tree size because the value of b did not differ significantly from unity. However, considering the result of the scaling exponent between leaf mass and the square of stem diameter at the crown base (Fig. 2), it is reasonable to consider that the diameter of conduits widens with tree size.

Shinozaki's pipe model theory (1964a, b) assumes that plants do not have heartwood, or wood that is not conducting water to the foliage above the crown base. In the present study, the proportion of sapwood area  $\frac{A_S}{A_B}$  is constant (or *f*=0) irrespective of tree size (Eq. 3) and in turn  $\frac{A_S}{A_B}$ did not affect the allometric scaling relation in Eq (4). In this case (*f*=0 in Eq. 4), the allometric scaling of  $m_L - D_B^2$  is operated only by the scaling exponent of *b* in the allometry of leaf mass  $m_L$ to sapwood area  $A_S$  (Eq. 2). Therefore, the assumption of Shinozaki's pipe model theory seems to apply to the case *f*=0 in Eq. (4).

296

### 297 Conclusions

The present scaling model (Eq. 5) can cover an exceptional case in which Shinozaki's pipe model predictions (1964a, b) should not explain that leaf mass vs. stem diameter at the crown base has an exponent greater than 2. The scaling exponent f of sapwood area vs. stem diameter at the crown base has no effect on leaf mass vs. stem diameter at the crown base, while the scaling exponent b of leaf mass vs. sapwood area at the crown base affects leaf mass vs. stem diameter at the crown base. Because the value of b is higher than unity, the present scaling model predicts that the diameter of conduits at the crown base widens with tree size, indicating tip-basewidening of xylem conduits.

306

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311 University of Arizona, for their invaluable comments.

312

# 313 Figure legends

Fig. 1 Diagram of the stratified clipping method (Monsi and Saeki 1953). In the practical

315 experiment, the trees were stratified into several vertical strata defined at 0–0.3, 0.3–1.3, and

316 subsequent 1.0 m intervals from ground level to the top of the crown.

317

318 Fig. 2 Allometric scaling relationships between the total leaf mass  $m_{\rm L}$  and the square of the stem diameter at the crown base  $D_{\rm B}^2$  in 52 *Chamaecyparis obtusa* trees at four study sites. Circles, 319 Nagova; squares, Inabu; triangles, Hourai; crosses, Dando. The regression line in the diagram is 320 the equation  $y = 0.0191x^{1.273}$  (scaling exponent 95% confidence interval [CI], 1.179–1.375;  $R^2 =$ 321 0.927; P < 0.001) for the SMA regression method. The respective equations with the OLS 322 regression method and linear mixed model are  $v = 0.0125x^{1.206}$  (scaling exponent 95% CI, 1.091– 323 324 1.333;  $R^2 = 0.875$ ; P < 0.001) and  $y = 0.0322x^{1.160}$  (scaling exponent 95% CI, 1.006–1.314; P < 0.001) 325 0.001).

326

**Fig. 3** Allometry between the total leaf mass  $m_L$  and sapwood area at the crown base  $A_s$  in 12-

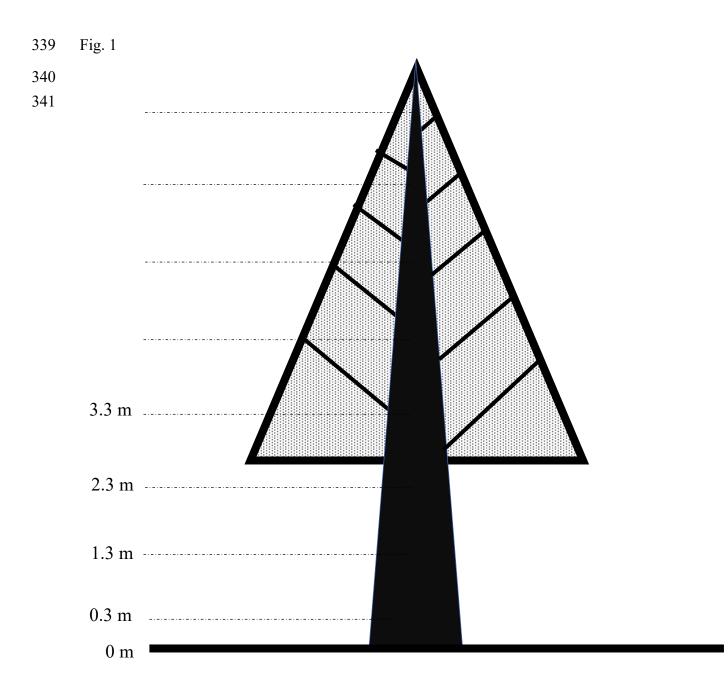
328 year-old C. obtusa trees. The regression line in the diagram is an approximation of y =

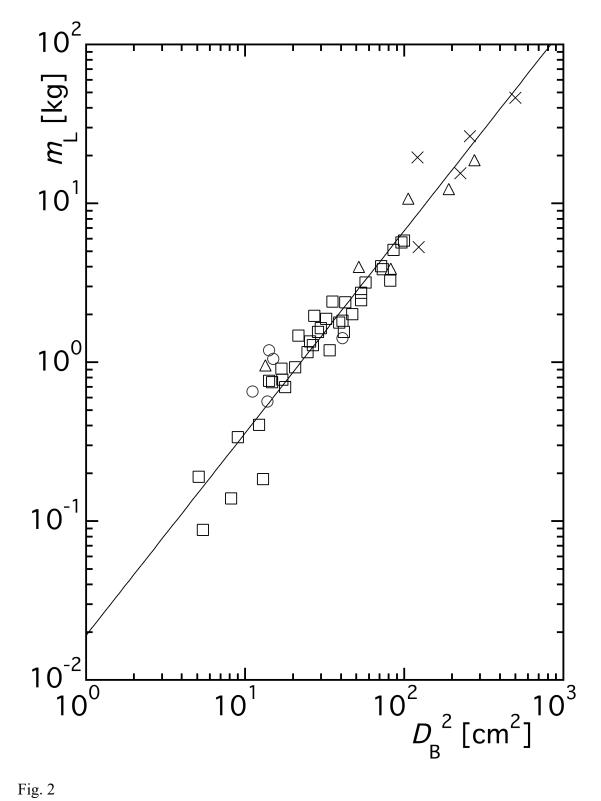
329  $0.0218x^{1.448}$  (scaling exponent 95% CI, 1.126 - 1.448;  $R^2 = 0.854$ ; P < 0.001) for SMA

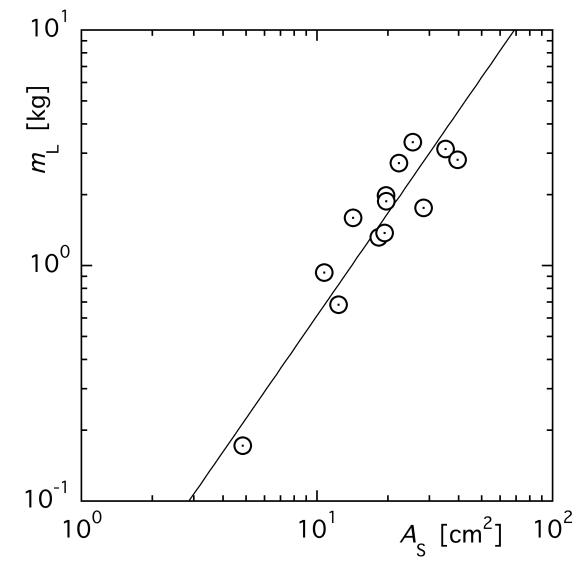
regression method. The equation with the OLS regression method is  $y = 0.0301x^{1.338}$  (scaling

331 exponent 95% CI, 0.970–1.706;  $R^2 = 0.854$ ; P < 0.001).

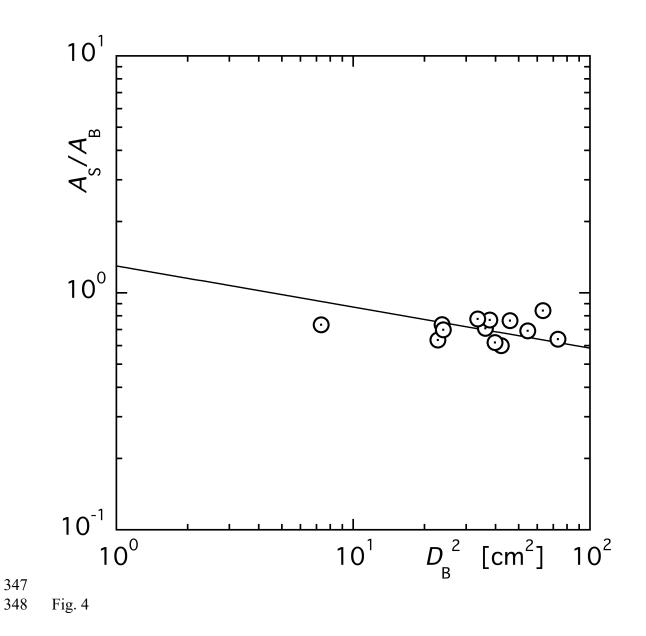
- Fig. 4 Relationship between the sapwood area proportion at the crown base  $\frac{A_S}{A_P}$  and the square of
- the stem diameter at the crown base  $D_{\rm B}^2$  in 12-year-old *C. obtusa*. The regression line in the
- 335 diagram is an approximation of  $y = 1.299x^{-0.173}$  ( $R^2 = 0.00176$ ; P = 0.892) for the SMA
- regression method. The OLS regression equation is  $y = 0.723x^{-0.00727}$  (scaling exponent 95% CI, -
- 337  $0.122-0.108; R^2 = 0.00176; P = 0.892)$
- 338











Nagoya\$		Stand density [ha <sup>-1</sup> ]	Tree height [m]	Crown base height [m]	DBH [cm]	D <sub>B</sub> [cm]	n
	12	15000	3.3 - 5.7	n/a	2.90 - 8.28	2.71 - 8.56	13
Nagoya	12 - 16	15000	4.67 - 7.55	2.10 - 4.55	4.77 - 7.35	3.34 - 6.40	5
Inabu	16 - 25	6000 - 7500	4.73 - 12.1	1.25 - 6.00	3.47 - 13.4	2.26 - 9.99	36
Hourai	26 - 27	2281	7.92 - 12.2	5.06 - 5.90	8.02 - 23.1	3.66 - 16.6	6
Dando	58 - 59	2700	16.1 - 20.1	9.60 - 13.1	16.6 - 29.3	11.0 - 22.3	5
stem diameter a	at crown base	e.					