

1 **Modeling age-related leaf biomass changes in forest stands under the assumptions of**
2 **the self-thinning law**

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1 **Abstract**

2 ***Key message*** The present model indicates that possibility of leaf biomass constancy
3 in forest stands is not so high, and that forest stand leaf biomass declines after
4 canopy closure.

5 *Abstract* Kira and Shidei (1967) and Odum (1969) proposed a classical hypothetical
6 trend that leaf biomass of a forest stand shows a more or less constant level after the
7 initial peak maximum, with the result of constant GPP after canopy closure. On the
8 contrary, Ryan et al. (1997, 2004) proposed a hypothetical trend that stand leaf biomass
9 shows a singular peak maximum of leaf biomass, coinciding with canopy closure, with
10 the result of singular peak of GPP. However, neither the hypothesis of leaf biomass
11 constancy or the hypothesis of a leaf biomass maximum explicitly states why leaf
12 biomass should remain constant or decline after canopy closure from the mathematical or
13 theoretical models. Therefore, age-related change in leaf biomass was modeled on the
14 basis of the following three assumptions after canopy closure: (i) self-thinning law, (ii)
15 allometric scaling between mean individual leaf mass and mean individual total mass,
16 and (iii) formulation of a logistic function in stand density change. In the present
17 modeling, both hypotheses can exist theoretically, but hypothesis by Kira and Shidei
18 (1967) and Odum (1969) holds only in a case limited mathematically. Using the reliable
19 data on leaf biomass, leaf biomass constancy was also discussed by fitting mathematical
20 model. From the empirical and theoretical viewpoints, possibility of leaf biomass

1 constancy in forest stands is not so high, and it is reasonable that the forest stand leaf

2 biomass declines after the canopy closure.

3

4 **Keywords** Age-related changes • Canopy closure • Mathematical model • Self-thinning law •

5 Stand leaf biomass • Stand density

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1 **Introduction**

2 Primary production by the foliage of terrestrial vegetation is a globally significant
3 biosphere-to-atmosphere carbon flux. Forest foliage will certainly play an important role
4 in the absorption of atmospheric CO₂ as concentrations rise within the next century from
5 the current level of 380 parts per million (ppm) to a predicted 700–1000 ppm (Conway et
6 al. 1994; Matthews 2005; Schellnhuber et al. 2006). Leaf biomass is the most important
7 forest system index used for analyzing stand production capacity and production
8 processes (Tadaki 1977; Satoo and Madgwick 1982); hence, accurate estimates of stand
9 leaf biomass are critical for assessments of global carbon fluxes.

10 According to a classical hypothesis developed by Kira and Shidei (1967) and
11 Odum (1969), leaf biomass in an even-aged pure forest stand reaches a maximum after
12 canopy closure and is maintained at a more or less constant level thereafter (Fig. 1).
13 Several studies have shown that leaf biomass and the leaf area index (LAI) are relatively
14 constant over considerable periods of time during forest stand development (Kira and
15 Shidei 1967; Ogawa et al. 2010). Ogawa (2008) detected a theoretical constancy in stand
16 leaf biomass after canopy closure by scaling up from the shoot level to the stand level;
17 this work was based on several assumptions, such as the leaf mass/number (leafing
18 intensity) trade-off at the shoot level (Kleiman and Aarssen 2007). Assuming a constant
19 gross photosynthetic rate per unit leaf mass or area, Kira and Shidei (1967) also
20 postulated a similar trend for gross primary production (GPP) throughout stand

1 development. Thus, stand leaf biomass estimates are important indicators of GPP in tracts
2 of forest. Barnes et al. (1998) extended the general model of Kira and Shidei (1967) in a
3 study of variation in factors controlling the carbon balance in forest ecosystems.

4 In contrast to the classical model, Ryan et al. (1997, 2004) demonstrated that
5 trends in leaf biomass and GPP reached a single peak during stand development and
6 declined thereafter (Fig. 1) because of long-term trends in diminishing nutrient
7 availability (Binkley et al. 1995; Schulze et al. 1995), increased mechanical abrasion in
8 tree crowns (Putz et al. 1984; Long and Smith 1992), and increased mortality among
9 mature individuals that are not replaced by the recruitment of new seedlings (Spies et al.
10 1990).

11 However, neither the hypothetical model of leaf biomass constancy (Kira and
12 Shidei 1967) nor the hypothetical model of a single leaf biomass peak (Ryan et al. 1997,
13 2004) incorporates mathematical or theoretical explanations for the constancy of or
14 reduction in leaf biomass after canopy closure. Ogawa et al. (2010) developed a
15 hypothetical model of GPP based on the effects of stand self-thinning on the mean leaf
16 mass of an individual tree. In their analysis, the mean leaf mass of a single tree was
17 maintained at a more or less constant level and then increased when space was made
18 available by self-thinning within the stand. A rapid increase in the leaf mass of a single
19 tree is referred to as a growth shift (Hozumi 1985, 1987). This shift occurs when a plant
20 resumes more vigorous meristematic activity after the removal of inhibitory effects, such

1 as the reduction in light intensity caused by the growth of neighboring plants. Many
2 regeneration processes initiated after gap formation relate to the growth shift (Suzuki
3 1979, 1980, 1981a,b; Kohyama 1982; Nakashizuka and Numata 1982a,b; Nakashizuka
4 1983, 1984).

5 The lack of a mathematical or theoretical basis is certainly a deficiency in the
6 hypothetical models of Kira and Shidei (1967), Ryan et al. (1997, 2004), and Ogawa et al.
7 (2010). Because woody plant species have such long lives, mathematical or theoretical
8 models are necessary to elucidate the mechanisms that drive the dynamics of forest
9 systems. Theoretical models are essential for (i) the construction of mechanistic
10 simulations of forest growth, (ii) predicting the responses of forests to changing climate,
11 and (iii) improved understanding of the productivity and sustainability of commercial
12 forest systems (Ryan et al. 1997). Furthermore, because self-thinning is a common
13 phenomenon during forest development (Perry 1994; Silvertown and Charlesworth 2001;
14 Kimmins 2004; Schulze et al. 2005), the leaf biomass in a stand may be influenced by
15 changes in tree density. The relationship between stand density and leaf biomass was
16 investigated empirically in a permanent forest plot by Ogawa et al. (2010).

17 In an investigation of the relationship between stand density and leaf biomass,
18 Ogawa (2012) mathematically analyzed the hypothetical trends predicted by Kira and
19 Shidei (1967) and Ryan et al. (1997, 2004) using empirical data on age-related changes in
20 stand density and leaf biomass within even-aged pure forest stands. However, Ogawa's

1 (2012) analysis was restricted to specific forest types, such tree plantations, and his
2 analysis had few generalities about age-related changes in leaf biomass in forest stands.
3 Here, I propose a general mathematical model describing age-related changes in forest
4 stand leaf biomass under the assumptions of the self-thinning law (Yoda et al. 1963;
5 Miyanishi et al. 1979; West et al. 1997; Enquist et al. 1998). This law is widely
6 recognized within the discipline of forest/plant ecology.

7

8 **Materials and methods**

9 Stand density

10 Data on stand density were obtained from previous studies of a *Cryptomeria japonica* D.
11 Don (sugi) plantation (Ogawa and Hagihara 2003, 2004; Ogawa 2005, 2007) and two
12 *Chamaecyparis obtusa* (Zieb. et Zucc.) Endl. (hinoki cypress) plantations (Ogawa et al.
13 1988, 2010; Sumida et al. 2013). Both species rank among the most important trees in the
14 Japanese forestry industry (Yato 1978; Hayashi 1988).

15 The field study of *C. japonica* was conducted in a permanent experimental plot
16 (280 m²) set up in a 23-year-old stand located in the Nagoya University Experimental
17 Forest at Inabu (35°11'N, 137°33'E), ca. 55 km east of Nagoya (Aichi Prefecture, central
18 Japan). This plantation is located at an elevation of 960 m on an east-facing slope with a
19 23° gradient. Two-year-old seedlings were planted in a geometrical pattern at an initial
20 density of 6000 ha⁻¹; no thinning procedures were applied after the initial planting.

1 Annual counts of all live trees in the plot were conducted in the month of October for the
2 22 years between 1983 and 2004.

3 The field study of *C. obtusa* by Ogawa et al. (1988, 2010) was conducted in an
4 experimental plot (171 m²) within the grounds of the Graduate School of Bioagricultural
5 Sciences, Nagoya University, Japan (35°09'N, 136°58'E). This level plot was 50 m above
6 sea level. Each seedling was planted in a separate 1 × 1-m cell within a gridded array
7 (190 seedlings in total). Annual counts of all live trees in the plot were conducted in June
8 over 11 years (1986–1996); counts began when the stand was 3 years old.

9 The field study of *C. obtusa* by Sumida et al. (2013) was conducted in a
10 permanent experimental plot (191 m²) containing a 21-year-old stand of trees; the plot
11 was located in the Nagoya University Experimental Forest at Inabu (35°12'N, 137°33'E),
12 ca. 55 km east of Nagoya (Aichi Prefecture, central Japan). This plantation grew on a
13 northwest-facing slope with a 37° gradient; the plot elevation was 970 m. The 2-year-old
14 seedlings were planted geometrically at an initial planting density of 8000 ha⁻¹; plants
15 were not thinned during the observation period. An annual count of all live trees in the
16 plot was conducted in December over 20 years (1977 to 1996).

17

18 Stand leaf biomass

19 According to the pipe model theory (Shinozaki et al. 1964a,b), the leaf mass of individual
20 trees is proportional to the stem cross-sectional area at the crown base in any stand

1 regardless of age or habitat. This relationship was confirmed in later studies of the
2 relationship by Ogawa et al. (2010) and Ogawa (2015) ($R^2 = 0.71$, $P < 0.001$). Thus, we
3 used stem cross-sectional area at the crown base to determine the time course of leaf
4 biomass changes. We measured the stem diameters of seedling-stage *C. obtusa* plants (3–
5 5 years old) and the crown base stem circumferences of trees that were 4–13 years old.

6

7 **Modeling**

8 Stand density model

9 According to Hozumi (1973), changes in stand density (ρ) with stand age (t) in a forest
10 undergoing self-thinning are generally expressed by the logistic model (based on
11 Shinozaki's [1962] logistic theory of plant growth).

12 Ogawa (2012) used observational data from two different coniferous
13 plantations to show that the changes in stand density ($\rho(t)$) with stand age (t) in a forest
14 undergoing self-thinning are described by the following logistic equation:

15

$$16 \quad \rho(t) = \frac{\rho_0}{1 + me^{\alpha t}} \quad (1)$$

17

18 where t represents tree age, and ρ_0 , m , and α are positive coefficients. In the present study,
19 I used Eq. (1) to simulate changes in stand density with stand age.

20

1 Leaf biomass model

2 In a forest stand that is undergoing self-thinning, mean individual tree mass (w) and mean
 3 individual leaf mass (w_L) are obtained as functions of time or stand age (t) [$w = w(t)$ and
 4 $w_L = w_L(t)$] under the following assumptions.

5 *Assumption 1:* Following the first study on the relationship between stand density and
 6 average tree size (stem diameter at breast height) by Reineke (1933), the relationship
 7 between mean tree mass $w(t)$ and stand density $\rho(t)$ complies with the self-thinning law:

8

$$9 \quad w(t) = K\rho(t)^{-\beta} \quad (2)$$

10

11 where K and β are positive coefficients. Geometrical analysis (Yoda et al. 1963) and the
 12 dimensional rule (Miyanishi et al. 1979) have both assigned a value of $3/2$ to the β
 13 coefficient; more recent estimates have assigned a value of $4/3$ to this coefficient based
 14 on the metabolic scaling model, namely the WBE (West/Brown/Enquist) theory (West et
 15 al. 1997; Enquist et al. 1998).

16 *Assumption 2:* The allometric relationship between mean leaf mass $w_L(t)$ and mean tree
 17 mass $w(t)$ is described by the following equation:

18

$$19 \quad w_L(t) = gw(t)^h \quad (3)$$

20

1 where g and h are positive coefficients (Ogawa and Kira 1977; Niklas 1994). Equation
 2 (3) leads to the following relationship between leaf mass ratio $w_L(t)/w(t)$ and $w(t)$:

3

$$4 \quad \frac{w_L(t)}{w(t)} = gw(t)^{h-1} \quad (4)$$

5

6 When $h = 1$, the expression $w_L(t)/w(t)$ is constant; when $h < 1$, $w_L(t)/w(t)$ decreases as
 7 values of $w(t)$ increase; and when $h > 1$, $w_L(t)/w(t)$ increases as values of $w(t)$ increase.

8 As stand leaf biomass $y_L(t)$ is defined as $y_L(t) = w_L(t)\rho(t)$, *Assumptions 1* and

9 *2* predict the following relationship between $y_L(t)$ and stand density $\rho(t)$:

10

$$11 \quad y_L(t) = gK^h \rho(t)^{1-\beta h} \quad (5)$$

12

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

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

15

$$16 \quad y_L(t) = gK^h \left(\frac{\rho_0}{1 + me^{at}} \right)^{1-\beta h} \quad (6)$$

17

18 *Non-linear regression analysis*

1 We determined the coefficients of the nonlinear equations (α , ρ_0 , and m in Eq. (1)) using
2 KaleidaGraph ver. 4.1.2 statistical software (Synergy Software, Reading, PA, USA),
3 which is based on the Levenberg–Marquardt algorithm (Press et al. 1992); this algorithm
4 measures the goodness of fit by the coefficient of determination (R^2).

5

6 **Results**

7 Application of the stand density model

8 Equation (1) (proposed by Ogawa 2012) was applied to two different forest stands: a
9 young *C. obtusa* plantation (Ogawa et al. 1988, 2010) and a mature *C. japonica*
10 plantation (Ogawa and Hagihara 2003, 2004; Ogawa 2005, 2007). Sumida et al. (2013)
11 published a dataset that included tree density measurements collected over 20 years in an
12 even-aged *C. obtusa* stand. These data can also be fitted with Eq. (1) (Fig. 2), showing
13 that this equation is suitable for describing the age-related changes in stand density in
14 forests undergoing self-thinning. The values of ρ_0 , m , α , and R^2 in Eq. (1) are listed in
15 Table 1.

16

17 Properties of the leaf biomass model

18 Since the coefficients g , K , and h are constants in Eqs. (5) and (6) of the stand leaf
19 biomass model, both equations may be applied to three cases that differ in the value of $1-$
20 βh ($\beta h = 1$, $\beta h < 1$, or $\beta h > 1$). According to the geometric (Yoda et al. 1967; Miyanishi

1 et al. 1979) and metabolic scaling (West et al. 1997; Enquist et al. 1998) theories, the
 2 values of β (Eq. (2)) are $3/2$ and $4/3$, respectively. Thus, the h values (Eq. (3)) are (i) $h =$
 3 $2/3$ or $h = 3/4$, (ii) $h < 2/3$ or $h < 3/4$ or (iii) $h > 2/3$ or $h > 3/4$, respectively.

4 When $\beta h = 1$ ($\beta = 3/2, h = 2/3$, or $\beta = 4/3, h = 3/4$), stand leaf biomass $y_L(t)$ is
 5 constant regardless of any function of $\rho(t)$, which is evident from Eq. (5). When $\beta h < 1$
 6 ($\beta = 3/2, h < 2/3$ or $\beta = 4/3, h < 3/4$), or $\beta h > 1$ ($\beta = 3/2, h > 2/3$ or $\beta = 4/3, h > 3/4$), the
 7 value of $y_L(t)$ in Eq. (6) was simulated (with βh as a parameter) by fixing the values of
 8 gK^h , m , α , and ρ_0 at 1.0 Mg ha^{-1} , 0.0501 , $0.0.823 \text{ yr}^{-1}$, and 6491 ha^{-1} , respectively (Figs.
 9 3A, B). Here, the values of m , α and ρ_0 correspond to the values determined for a *C.*
 10 *japonica* plantation (cf. Table 1). Stand leaf biomass $y_L(t)$ monotonously decreases with
 11 stand age t when $\beta h < 1$, but monotonously increases with stand age t when $\beta h > 1$.

12

13 Interpretation of the models

14 The developmental stage of a forest in the present model is restricted to the time ($t > t^*$)
 15 after full canopy closure, when the self-thinning rule (Eq. (2)) is operational (Fig. 3).
 16 During the period before full canopy closure, stand leaf biomass increases with stand age
 17 t because large areas of illuminated space are available. In the present model, stand leaf
 18 biomass is (i) maintained at a more or less constant level, (ii) decreases, or (iii) increases
 19 monotonously with stand age t after the forest fully closes.

20 Although the present model is only related to development process after canopy

1 closure, future studies should focus on linking processes before and after the closure
2 event. A linked model would contribute to the development of predictions on the overall
3 future dynamics of stand leaf biomass.

4

5 **Discussion**

6 Interpreting the cases in the stand leaf biomass model

7 According to the model, the leaf mass ratio ($w_L(t)/w(t)$) of an average tree increases with
8 tree mass ($w(t)$) or tree age (t) when $h > 1$ (Eq. (3)). This trend in leaf mass ratio is not
9 biologically reasonable because trees commonly accumulate woody tissues in their trunks,
10 branches, and roots as they age. According to Ogawa (2001), the value of h in Eq. (3) is
11 <1 in a tree seedling population of *C. obtusa* undergoing self-thinning. This experimental
12 finding suggests that predicted increases in stand leaf biomass $y_L(t)$ with age t (Fig. 3B) in
13 the present model are not tenable. Thus, the two alternative cases [(i) constant $y_L(t)$ and
14 (ii) decreasing $y_L(t)$] are considered to be more biologically reasonable. Case (i) fits the
15 hypothetical trend proposed by Kira and Shidei (1967) and Odum (1969), and case (ii)
16 corresponds to the hypothetical trend proposed by Ryan et al. (1997). Ogawa (2012)
17 demonstrated that the growth curve of average leaf mass on a tree is expressed by several
18 logistic equations that represent growth phase shifts. According to this interpretation,
19 there is a single peak in stand leaf biomass that is coincident with canopy closure. The
20 present model also shows that constancy in stand leaf biomass is possible during the

1 self-thinning process, in agreement with Ogawa's (2012) mathematical analysis.

2

3 Growth and mortality

4 By substituting Eq. (3) into Eq. (2) and by differentiating both sides with respect to t , the

5 relationship between the relative growth rate of leaf mass and the relative mortality rate is

6 obtained:

7

$$8 \quad \frac{1}{w_L(t)} \frac{dw_L(t)}{dt} = \beta h \left(-\frac{1}{\rho(t)} \frac{d\rho(t)}{dt} \right) \quad (7)$$

9

10 From Eq. (7), we can deduce the following three cases: (i) when $\beta h = 1$, the relative

11 growth rate in leaf mass is equivalent to the relative mortality rate; (ii) when $\beta h < 1$, the

12 relative growth rate in leaf mass is lower than the relative mortality rate; (iii) when $\beta h > 1$,

13 the relative growth rate in leaf mass exceeds the relative mortality rate. However, case

14 (iii) is not tenable because the inequalities $h > 2/3$ and $h > 3/4$ are not possible in the

15 present model analysis. Because the self-thinning rule is satisfied in all cases, the

16 relationship between the relative growth rate of a whole tree and the relative mortality

17 rate is derived directly from Eq. (2) as follows:

$$18 \quad \frac{1}{w(t)} \frac{dw(t)}{dt} = \beta \left(-\frac{1}{\rho(t)} \frac{d\rho(t)}{dt} \right) \quad (8)$$

1 where β is equal to either $3/2$ (Yoda et al. 1967; Miyanishi et al. 1979) or $4/3$ (West et al.
2 1997, Enquist et al. 1998) in compliance with the self-thinning rule.

3

4 Constancy of stand leaf biomass

5 As for the parameter h of Eq. (3) in the present model, if $\beta h=1$ ($\beta = 4/3$ and $h = 3/4$) in Eq.
6 (5), stand leaf biomass is constant. This is included in the derivation of the WBE model
7 (Enquist et al. 1998), where it is assumed that, in a closed forest, stand leaf biomass
8 remains constant.

9 Following Ogawa's (2008, 2010, 2012) modeling analyses of leaf biomass
10 constancy in forest stands, Sumida et al. (2013) reported the age-related changes in leaf
11 biomass in a 20-year dataset assembled for an even-aged *C. obtusa* stand. In agreement
12 with the interpretations of Ogawa et al. (2010), Sumida et al. (2013) concluded that stand
13 leaf biomass was maintained at a constant level within the 20-year dataset, fitting the
14 predictions of the pipe model theory (Shinozaki et al. 1964*a,b*), i.e., the leaf mass of
15 individual trees was proportional to the stem cross-sectional area at the crown base
16 (Ogawa 2015). Self-thinning occurred in the stand studied by Sumida et al. (2013), but no
17 large canopy gaps formed during whole observational period (personal observation; K.
18 Ogawa).

19 According to Ogawa's (2012) modeling of forest foliage dynamics, stand leaf
20 biomass remains constant in two cases; one of these is related to the common

1 self-thinning case (Model I), and the other is related to the special circumstances of gap
2 formation (Model II). In the self-thinning case, stand leaf biomass is not constant and
3 peaks just once during stand development. Ryan et al. (1997, 2004) proposed a
4 hypothetical trend in forest leaf biomass with a single peak during stand development.
5 The present model predicts both of the previously proposed age-related changes in stand
6 leaf biomass, i.e., (i) constancy in stand leaf biomass and (ii) a single peak during stand
7 development. Within this context, I interpret the statement of Sumida et al. (2013) as an
8 indicator of the limitations in Ogawa's (2008, 2012) models of leaf biomass constancy
9 (Model II).

10 To examine leaf biomass constancy *vs.* age-related changes in leaf biomass, I
11 applied Ogawa's (2012) model (Model I) to the dataset on stand leaf biomass provided by
12 Sumida et al. (2013) (Fig. 4A), together with the dataset on a dense young tree plantation
13 of *C. obtusa* (Fig. 4B) observed by Ogawa et al. (1998, 2010). The graphical plot (Fig. 4)
14 shows that the constancy of stand leaf biomass is not fully stable in both datasets.
15 Consideration of the theoretical growth curve of stand leaf biomass leads to the
16 conclusion that a constant leaf biomass was realized over a relatively short period (20
17 years).

18

19 **Author Contribution Statement:** The author (KO) designed research, collected the data,
20 analyzed them, and wrote the paper.

1

2 **Acknowledgements**

3 I thank the staff of the Nagoya Regional Forest Office and the Midorigaoka Nursery
4 attached to the Gifu District Forest Office for providing the seedlings, and my colleagues
5 for their assistance during field work.

6

7 **Conflict of Interest:** The author (KO) declares that he has no conflict of interest.

8

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1 **Figure legends**

2 **Fig. 1** Hypothetical trends of age-related changes in leaf biomass in a forest stand. (A)
 3 Hypothesis proposed by Kira and Shidei (1967) and Odum (1969). (B) Hypothesis
 4 proposed by Ryan et al. (1997, 2004). t^* stands for the time of the canopy closure in a
 5 forest stand.

6

7 **Fig. 2** Logistic curves describing trends in stand density (ρ) with stand age (t) in young
 8 *Chamaecyparis obtusa* plantation (square, Ogawa et al. 1988, 2010), mature *Cryptomeria*
 9 *japonica* plantation (triangle, Ogawa and Hagihara 2003, 2004), and mature *C. obtusa*
 10 plantation (circle, Sumida et al. 2013). The curves were fit using Eq. (1) and
 11 KleidaGraph statistical analysis software. See Table 1 for values of coefficients.

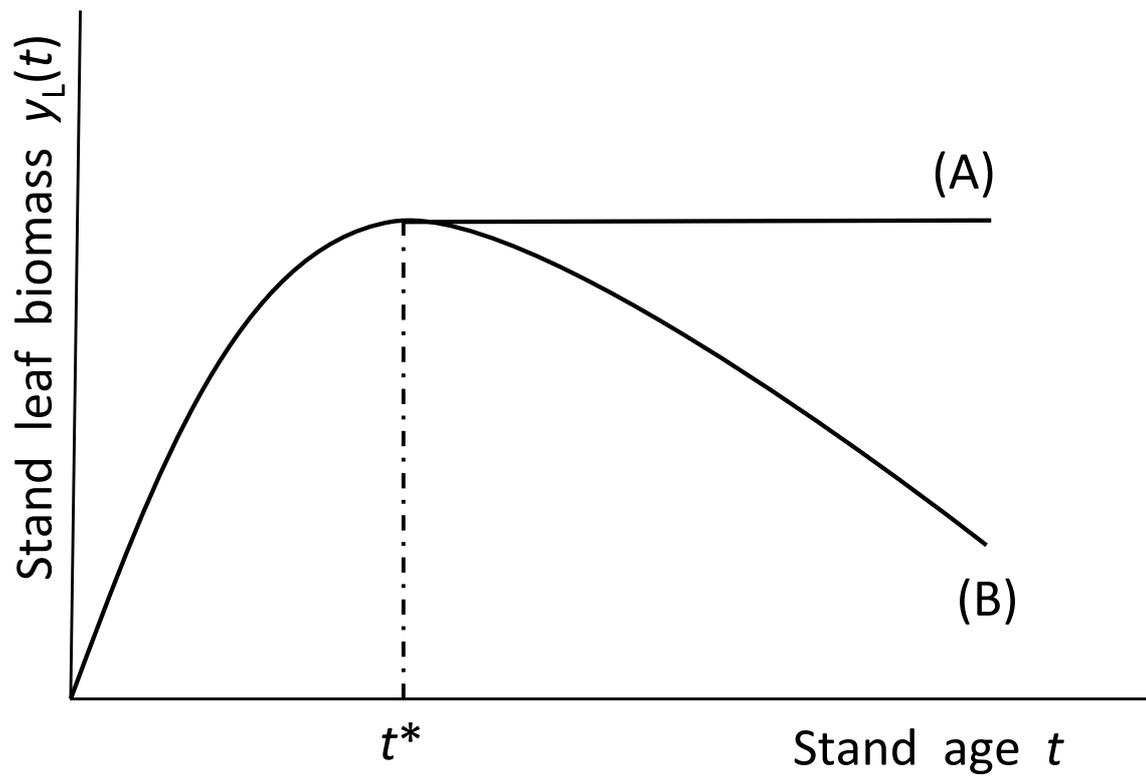
12

13 **Fig. 3** Age-related changes in leaf biomass $y_L(t)$ in Eq. (6), with βh as parameter, by
 14 fixing the values of gK^h , m , α and ρ_0 as 1 Mg ha^{-1} , 0.0501 , 0.0823 yr^{-1} and 6491 ha^{-1} ,
 15 respectively, for the cases of (A) $\beta h < 1$ and (B) $\beta h > 1$.

16

17 **Fig. 4** Application of Ogawa's (2012) model (Model I) to the leaf biomass data on mature
 18 (A, Sumida et al. 2013) and young (B, Ogawa et al. 1988, 2010) *Chamaecyparis obtusa*
 19 stands.

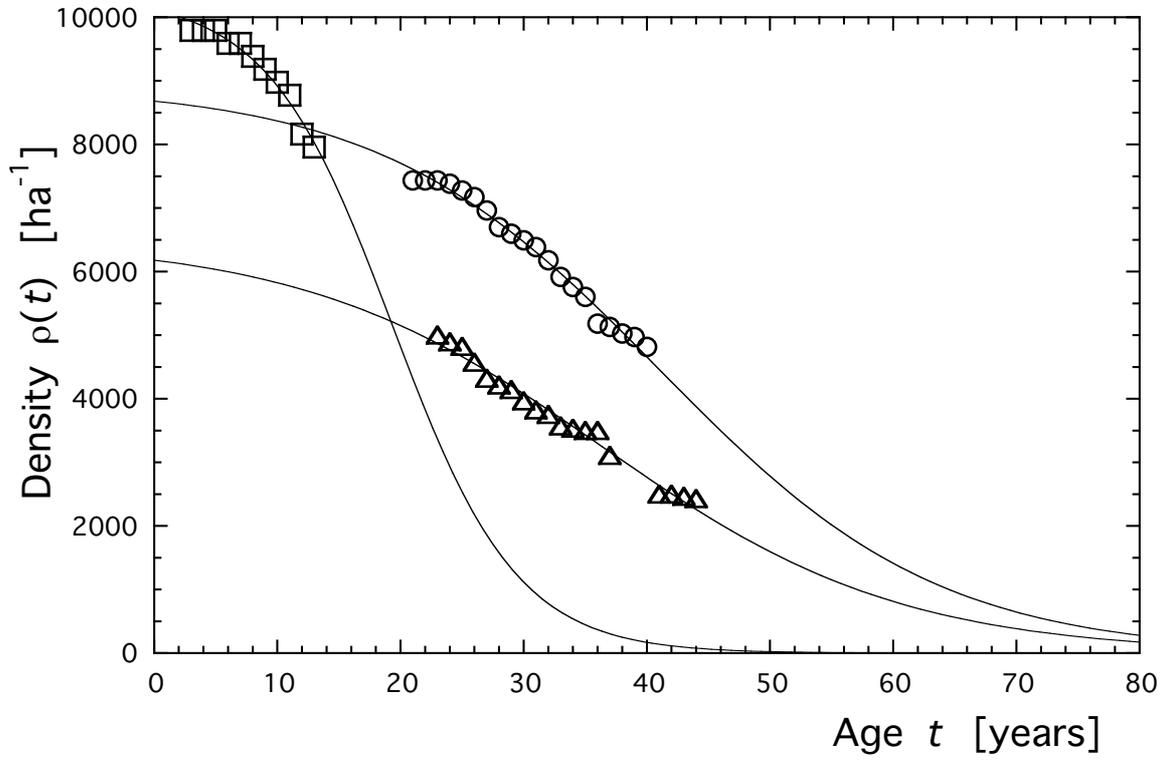
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1

2 Fig. 1.

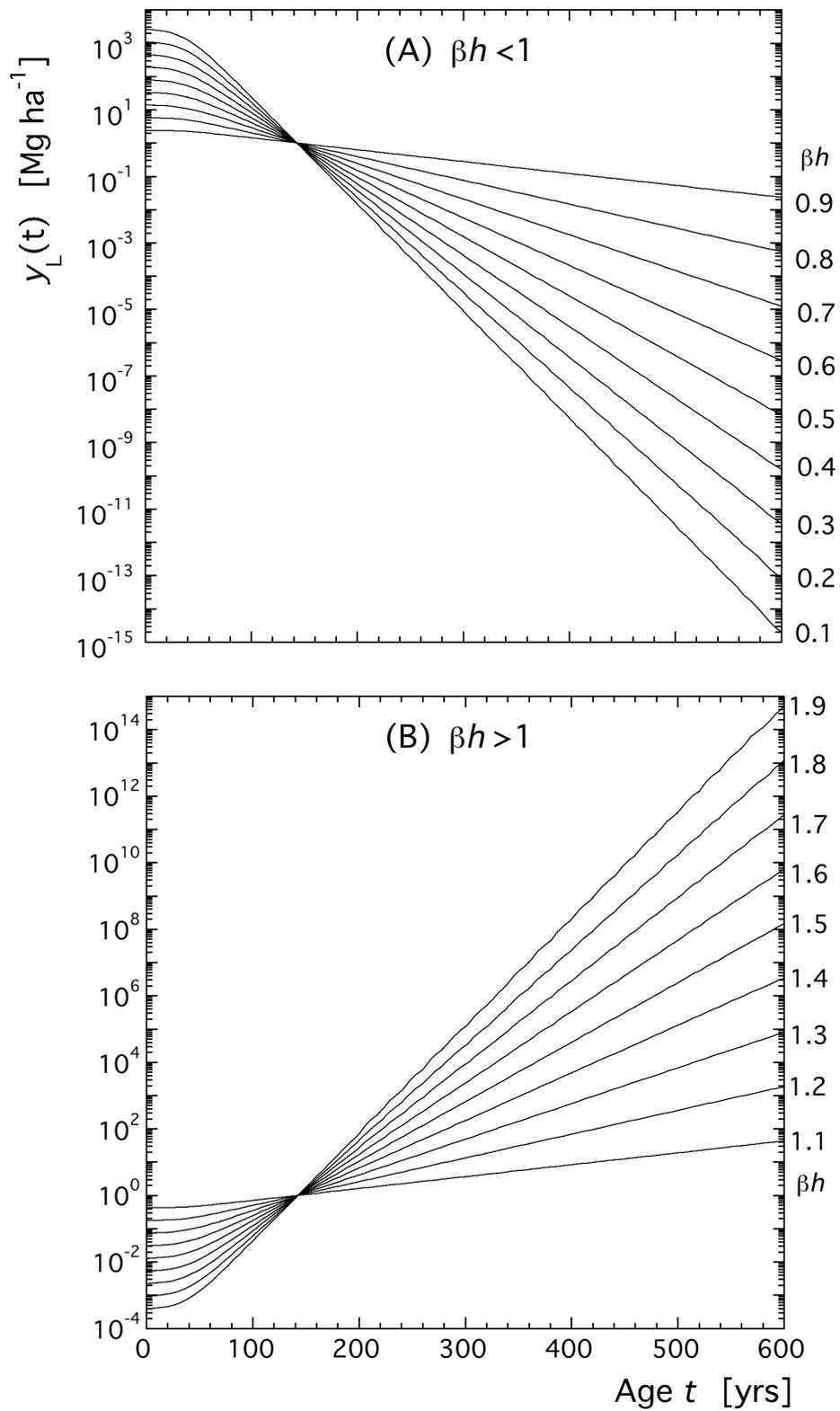
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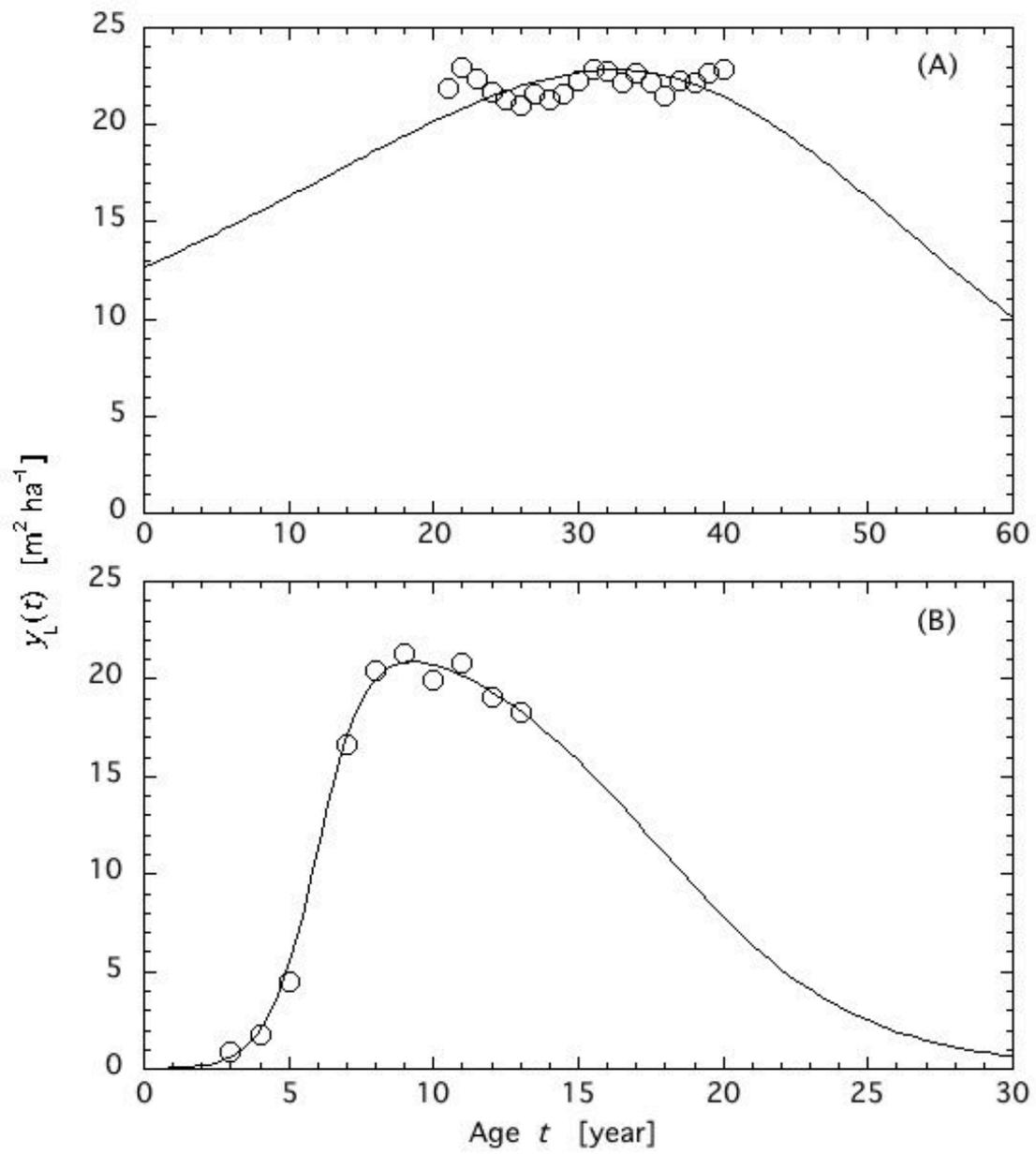
2 Fig. 2

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2 Fig. 3.



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2 Fig. 4.

3

1

Table 1 The values of coefficients (ρ_0 , m , α) and the standard error, and coefficient of determination (R^2) in Eq. (1) for *C. obtusa* and *C. Japonica* plantations.

Species	Coefficient			R^2	Localities	Authority
	ρ_0 ha ⁻¹	m	α yr ⁻¹			
<i>C. obtusa</i>	10006 ± 104	0.00654 ± 0.00315	0.286 ± 0.036	0.988	Nagoya/Aichi, central Japan	Ogawa et al. (1988, 2010)
<i>C. obtusa</i>	8622 ± 89.7	0.0181 ± 0.00257	0.0965 ± 0.0032	0.987	Inabu/Aichi, central Japan	Sumida et al. (2013)
<i>C. Japonica</i>	6491 ± 730	0.0501 ± 0.0348	0.0823 ± 0.0127	0.981	Inabu/Aichi, central Japan	Ogawa and Hagihara (2003, 2004), Ogawa (2005, 2007)