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

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ABSTRACT

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

1. Introduction

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

Recently, Ogawa (2008) demonstrated the theoretical constancy of stand leaf biomass after canopy closure for the first time, by scaling up from the shoot level to the stand level based on assumptions such as the leaf mass/number (leafing intensity) trade-off at the shoot level (Kleiman and Aarssen, 2007). According to this model, leaf biomass constancy is constrained by the following assumptions: (1) the mean individual tree leaf mass is inversely proportional to the mean leafing intensity (Kleiman and Aarssen, 2007); (2) crown depth is proportional to tree height; and (3) leaf biomass is proportional to tree height. Considering Ogawa's theory, the constancy of leaf biomass depends on several assumptions, and empirical confirmation is necessary to test which of these assumptions are valid.

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

Ogawa (2012) developed a mathematical model to describe how leaf biomass varies as a function of stand density, using empirical data from permanent plot studies. Ogawa (2017) also derived the age-related changes in leaf biomass of forest stands theoretically under the following three assumptions: (1) the self-thinning law (Yoda et al., 1963; Miyanishi et al., 1979; West et al., 1997; Enquist et al., 1998); (2) the allometric scaling relationship between the mean individual leaf mass and mean individual total mass (Ogawa and Kira, 1977; Niklas, 1994); and (3) the formulation of a logistic function for stand density change (Ogawa, 2012). As a result, Ogawa (2017) proposed a functional model of the age-related changes in forest stand leaf biomass and found that the forest stand leaf biomass may decline or remain constant after canopy closure, depending on the values of the model parameters. According to Ogawa's (2017) model, the possibility of leaf biomass constancy in forest stands is low and stand leaf biomass declines after canopy closure.

However, the model proposed by Ogawa (2017) cannot be used to predict the pattern of age-related changes in stand leaf biomass for a given forest stand, because there are no methods for setting model parameters based on the current state of a forest stand due to a lack of observed data. In addition, the complicated age-related change in stand leaf biomass in *Abies* forests on Mt. Shimagare, Japan (Oshima et al.,

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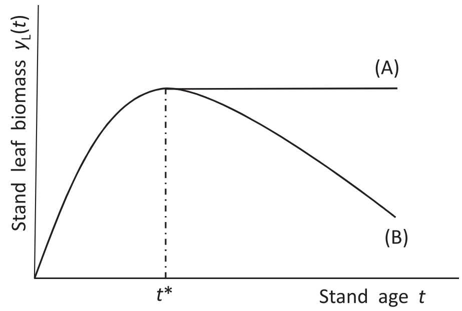

Fig. 1. Hypothetical trends in age-related changes in leaf biomass in a forest stand. (A) Hypothesis proposed by Kira and Shidei (1967) and Odum (1969). (B) Hypothesis proposed by Ryan et al. (1997, 2004). t^* is the time of canopy closure in a forest stand.

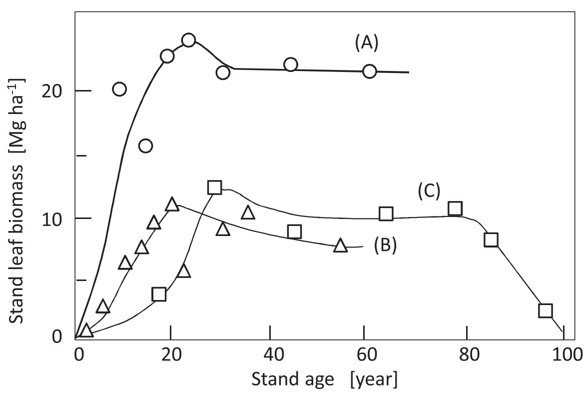

Fig. 2. Examples of age-related changes in stand leaf biomass in even-aged pure stands. (A) *Cryptomeria japonica* plantations in Japan (Ando et al., 1968). (B) *Pinus sylvestris* plantations in England (Ovington, 1957). (C) *Abies veitchii/A mariesii* forests on Mt. Shimagare (Oshima et al., 1958) (cited from Tadaki (1977)).

1958, Fig. 2C) has not yet been explained theoretically by constructing a reasonable mathematical model.

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

2. Materials and methods

2.1. Stand density

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

The *C. japonica* field study was conducted in a permanent experimental plot (280 m^2) established in a 23-year-old stand located in the Nagoya University Experimental Forest at Inabu (35°11′N, 137°33′E), *ca.* 55 km east of Nagoya (Aichi Prefecture, central Japan). This plantation is located at an elevation of 960 m on an east-facing slope with a 23° gradient. Two-year-old seedlings were planted in a geometrical pattern at an initial density of 6000 trees ha^{-1}; no thinning was performed after planting. Annual counts of all live trees in the plot were conducted in October for 22 years from 1983 to 2004.

The *C. obtusa* field study by Ogawa et al., 1988, Ogawa et al., 2010 was conducted in an experimental plot (171 m^2) within the grounds of the Graduate School of Bioagricultural Sciences, Nagoya University, Japan (35°09′N, 136°58′E). This plot was 50 m above sea level. Each seedling was planted in a separate 1 × 1 m cell within a gridded array (190 seedlings in total). All live trees in the plot were counted in June over 11 years from 1986 to 1996, beginning when the stand reached 3 years of age.

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

2.2. Stem volume

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

To estimate stem volume each year from 1986 to 1988, seedling height (H) and stem diameter at 10% of seedling height ($D_{0.1H}$) were measured. Ogawa (1989) examined an allometric relationship involving stem volume, v (cm^3 tree^{-1}), and the seedling height times the square of stem diameter at 10% of seedling height, $D_{0.1H}{}^2H$ (mm^3), for 254 destructively sampled hinoki cypress seedlings and found a strong relationship, $v = 0.000528(D_{0.1H}{}^2H)^{0.955}$ ($R^2 = 0.969$, $P < .001$, Ogawa et al., 2010). This relationship was used to estimate the stem volume of individual trees. In addition, from 1989 to 1996, stem height and stem girth at 50-cm intervals starting from the base of the stem were measured (Yokota et al., 1994; Yokota and Hagihara, 1995, Yokota and Hagihara, 1996, Yokota and Hagihara, 1998; Adu-Bredu and Hagihara, 1996, Adu-Bredu and Hagihara, 2003; Adu-Bredu et al., 1996a,Adu-Bredu et al., 1996b, Adu-Bredu et al., 1997a, Adu-Bredu et al., 1997b,Adu-Bredu et al., 1997c). From the measurements, stem volume was calculated using Smalian's formula (*e.g.*, Avery and Burkhart, 1994), with the tree top being regarded as a cone.

2.3. Stand leaf biomass

According to pipe model theory (Shinozaki et al., 1964a, Shinozaki et al., 1964b), the leaf mass of individual trees is proportional to the stem cross-sectional area at the crown base in any stand, regardless of age or habitat. This relationship was confirmed by Ogawa et al. (2010) and Ogawa (2015) ($R^2 = 0.71$, $P < .001$). Therefore, we used the stem cross-sectional area at the crown base to determine the time course of leaf biomass changes. We measured the stem diameters of *C. obtusa* seedlings (3–5 years old) and the crown base stem circumferences of trees that were 4–13 years old.

2.4. Modeling

2.4.1. Ogawa's (2017) case

Assumption 1. (stand density model)

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

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