# Modeling age-related stand respiration changes in forest stands under the self-thinning law

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A B S T R A C T

There are three different age-related changes in stand respiration (woody + foliage respiration) in an even-aged pure forest stand after canopy closure: (A) monotonous increase (Kira and Shidei, 1967; Odum, 1969), (B) constancy (Oohata and Shidei, 1974; Ogawa et al., 2010), and (C) monotonous decrease (Ryan et al., 1997; Drake et al., 2011). These contrasting views were based on observational data rather than on theoretical arguments. The present study was performed to model age-related changes in stand respiration to elucidate the mechanism of stand respiration dynamics after canopy closure in compliance with three concepts: (i) the self-thinning law, (ii) power scaling between mean individual annual respiration and mean individual mass, and (iii) the logistic function of stand density changes. Simulations showed that although the three hypotheses were tenable theoretically, that proposed by Kira and Shidei is a mathematically special case. Considering these modeling results, age-related stand respiration changes in plantations of hinoki (*Chamaecyparis obtusa*) (Ogawa et al., 1985) can be regarded as decreasing as well as constant after canopy closure. The present modeling revealed that there exists possibility of increasing stand respiration in Kira and Shidei's hypothesis from the theoretical viewpoints, although no observed data support their hypothetical trend. However, from both of the empirical and theoretical viewpoints, we understood that possibilities of stand respiration constancy and decrease in forest stands were regarded to be reasonable after the canopy closure.

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## 1. Introduction

Respiration plays an important role in the carbon balance of a tree and forest stand, because photosynthate is comsumed by respiration for constructing new tissue and maintaining existing tissue (Sprugel and Benecke, 1991; Vogt, 1991). In woody plants, a large portion of respiration is used for maintaining their large phytomass (Jarvis and Leverenz, 1983; Landsberg, 1986; Hagihara and Hozumi, 1991). Because of the large amount of biomass in woody plants, studies and data about stand respiration are still limited despite the abundance of data on net primary production (Kira and Shidei, 1967; Jarvis and Leverenz, 1983; Landsberg, 1986; Hagihara and Hozumi, 1991).

Annual changes in stand respiration have been estimated to integrate stand respiration in sites of different ages as follows. There are three different age-related changes in whole-respiration loss (woody + foliage respiration) in an even-aged pure forest stand, as proposed by (A) Kira and Shidei (1967) and Odum (1969), (B) Oohata and Shidei (1974) and Ogawa et al. (2010), and (C)

Ryan et al. (1997, 2004) and Drake et al. (2011). (A) According to the classical hypothesis developed by Kira and Shidei (1967) and Odum (1969), stand respiration (woody + foliage respiration) in an even-aged pure forest stand increases monotonously with a gradual increase in woody mass, assuming a constant respiration rate per unit mass (Fig. 1A). (B) Oohata and Shidei (1974) and Ogawa et al. (2010) demonstrated the constancy of stand respiration after canopy closure based on the constancy of respiration rate per unit area (Fig. 1B). (C) Möller et al. (1954) first proposed a graphical representation of dry matter production, including loss of respiration in composed organs of European beech (*Fagus silvatica* L.), based on the empirical data. Ryan et al. (1997, 2004) and Drake et al. (2011) reported that trends in stand respiration reached a single peak during stand development and declined thereafter (Fig. 1C) because of the decreasing respiration rate per unit mass.

Although these three different trends in stand respiration appear robust, long-term measurements are needed both to validate the estimates and to determine the effects of variations in site conditions and aging on stand respiration behavior. On the other hand, the lack of a mathematical or theoretical basis is a deficiency in the hypothetical models of age-related stand respiration changes in forest stands. Because woody plant species have such long lives,
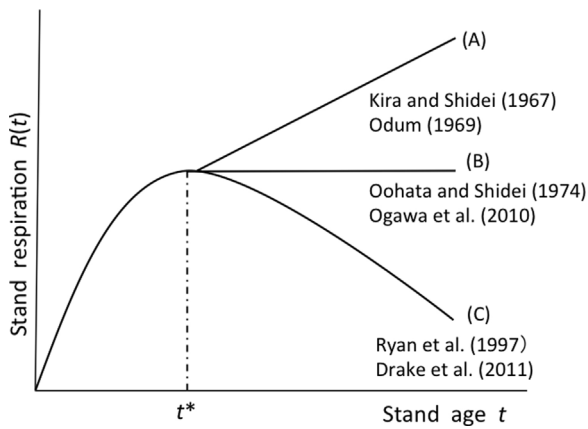
**Fig. 1.** Hypothetical trends of age-related changes in stand respiration (woody + foliage respiration) in a forest stand. (A) Hypothesis proposed by Kira and Shidei (1967) and Odum (1969). (B) Hypothesis proposed by Oohata and Shidei (1974) and Ogawa et al. (2010). (C) Hypothesis proposed by Ryan et al. (1997) and Drake et al. (2011). $t^*$ indicates the time of canopy closure in a forest stand.

mathematical or theoretical models are necessary to elucidate the mechanisms that drive the dynamics of forest systems. Theoretical models are essential for (i) the construction of mechanistic simulations of forest growth, (ii) predicting the responses of forests to changing climates, and (iii) improving our understanding of the productivity and sustainability of commercial forest systems (Ryan et al., 1997). Furthermore, because self-thinning is a common phenomenon during forest development (Perry, 1994; Silvertown and Charlesworth, 2001; Kimmins, 2004; Schulze et al., 2005; Pretzsch, 2009), the leaf biomass in a stand may be influenced by changes in tree density. Ogawa et al. (2010) empirically investigated the relationship between stand density and leaf biomass in a permanent forest plot. Ogawa et al. (2010) mathematically analyzed the hypothetical trends of the relationship between stand density and stand respiration predicted by Oohata and Shidei (1974) and Ogawa et al. (1985) using a dimensional analysis of age-related changes in stand density and stand biomass within even-aged pure forest stands. However, the analysis by Ogawa et al. (2010) was restricted to specific forest types, such tree plantations, and the analysis had few generalities regarding age-related changes in stand respiration in forest stands. Here, a general mathematical model describing age-related changes in forest stand respiration is proposed under the assumptions of the self-thinning law (Yoda et al., 1963; Miyanishi et al., 1979; West et al., 1997; Enquist et al., 1998). This law is widely recognized within the discipline of forest/plant ecology. Since the possibility of leaf biomass constancy in forest stands is not so high, and that forest stand leaf biomass declines after canopy closure (Ogawa, 2016), the present study can provide a main hypothesis that stand respiration declines in aging forest stand, linking well-known concepts of 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. Data sources of stand density

Data on stand density were obtained from previous studies on a *Cryptomeria japonica* D. Don (sugi) plantation (Ogawa and Hagihara, 2003, 2004; Ogawa, 2005b, 2007) and two *Chamaecyparis obtusa* (Zieb. et Zucc.) Endl. (hinoki cypress) plantations (Ogawa et al., 1988, 2010; Sumida et al., 2013). Both species rank 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 ($280\,m^2$) set up 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 applied after planting. Annual counts of all live trees in the plot were conducted in October for 22 years (1983–2004).

The *C. obtusa* field study by Ogawa et al. (1988, 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 $1 \times 1\,m$ cell within a gridded array (190 seedlings in total). Annual counts of all live trees in the plot were conducted in June over 11 years (1986–1996); counts began 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 $ha^{-1}$; plants were not thinned during the observation period. An annual count of all live trees in the plot was conducted in December over 20 years (1977–1996).

### 2.2. Modeling

#### 2.2.1. Stand density model

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

Considering their theoretical backgrounds on stand density, Ogawa (2012) used observational data from two different coniferous plantations to show that the changes in stand density ($\rho(t)$) with stand age ($t$) in a forest undergoing self-thinning can be described by the following logistic equation:

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

where $t$ represents tree age, and $\rho_0$, $m$, and $\alpha$ are positive coefficients. In the present study, Eq. (1) was used to simulate changes in stand density with stand age.

#### 2.2.2. Stand respiration model

In a forest stand undergoing self-thinning, mean individual tree mass ($w$) and mean individual annual respiration rate ($r$) are obtained as functions of time or stand age ($t$) [$w = w(t)$ and $r = r(t)$] under the following assumptions.

**Assumption 1.** The relationship between mean tree mass $w(t)$ and stand density $\rho(t)$ complies with the self-thinning law:

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

where $K$ and $\beta$ are positive coefficients. In both a geometrical analysis (Yoda et al., 1963) and the dimensional rule (Miyanishi et al., 1979), a value of 3/2 was assigned to the $\beta$ coefficient; more recent estimates have been used to assign a value of 4/3 to this coefficient based on the metabolic scaling model and the West/Brown/Enquist (WBE) theory (West et al., 1997; Enquist et al., 1998).

**Assumption 2.** In several even-aged pure forest stands, power functional size dependency was observed between individual tree respiration and mass (Ninomiya and Hozumi, 1981, 1983a, 1983b;