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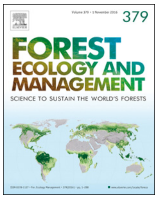

Maximum size-density relationship in bamboo forests: Case study of *Phyllostachys pubescens* forests in Japan

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ABSTRACT

Bamboo forests are likely to be subjected to self-thinning due to their rapid growth rate. In fully stocked bamboo forests, the stand density (ρ) was suggested to be inversely proportional to the square of mean diameter at breast height (D) ($\rho \propto D^{-2}$), differing from the conventional power-law for trees, i.e., Reineke equation ($\rho \propto D^{-1.6}$). Nevertheless, the validity and mechanism of the inverse-square law remained unclear, despite its significance for managing bamboo forests. In this study, we derived an allometric model that predicts the slope of the maximum size-density relationship (MSDR) between D and ρ on double logarithmic coordinates based on well-known ecological laws. The model indicates that the slope of -2 for bamboo is theoretically valid, with the difference in the slope between bamboo and trees being caused by their differences in inner-culm (or inner-stem) structure. We also determined the MSDR empirically by compiling data of 415 *Phyllostachys pubescens* Mazel ex Houz. pure stands across Japan. The obtained MSDR describes the upper boundary of the D-ρ relationship well, with a slope of -1.996 that is very close to -2. We further established a stand density management diagram of *P. pubescens* stands based on the MSDR. This diagram allows forest managers to regulate ρ depending on D as well as management purposes (production of bamboo shoot, bamboo charcoal and culm wood).

1. Introduction

The maximum size-density relationship (MSDR) is widely used to express the upper boundary of the combination of variables between size and density that appears as a consequence of self-thinning (VanderSchaaf and Burkhart, 2012; Condés et al., 2017). The MSDR reflects the boundary site occupancy or carrying capacity (Condés et al., 2017; Yang and Burkhart, 2017). It also provides a criterion that indicates the population density at which self-thinning occurs at high rates, making it a useful tool for regulating plant density (Drew and Flewelling, 1979; VanderSchaaf and Burkhart, 2012). Therefore, the MSDR is of ecological and economic significance.

The Reineke equation (Reineke, 1933) is a well-established MSDR between quadratic mean diameter (D_q) and stand density (ρ) of fully stocked tree populations as:

$$\rho \propto {D_q}^{\alpha}, \tag{1}$$

where α is the slope of the MSDR on the double logarithmic coordinates. Reineke (1933) found that the slope was fairly consistent at -1.605 for all species of trees and locations. After Reineke's work, many studies have revealed that the slope varied within a relatively narrow band around -1.6 (e.g., Inoue et al., 2004; Zeide, 2010; Condés et al., 2017).

The MSDR is expected to be highly useful for regulating ρ not only in tree populations but also in bamboo forests (Uchimura, 1973; Watanabe, 1985; Liu et al., 2016). Bamboos are a group of large woody grasses belonging to the family Poaceae and subfamily Bambusoideae (Scurlock et al., 2000; Clark et al., 2015). They are long-lived clonal plants that produce vegetative units (ramets) by vigorous rhizomatous growth (Banik, 2015; Liu et al., 2016). There are nearly 1500 bamboo species across approximately 119 genera, which are native to all continents except Antarctica and Europe (Scurlock et al., 2000; Clark et al., 2015). Bamboo forests cover roughly 31.5 million hectares worldwide (Clark et al., 2015; Kuehl, 2015) and represent approximately 1% of the total forested area globally (Song et al., 2011). Because of their highly versatile, fast-growing and environmentally-friendly characteristics, bamboos have received increasing attention over the last two decades (Song et al., 2011, 2016; Yen, 2016).

It is important to implement MSDR to bamboo stands because of an urgent demand of bamboo forest management. In Japan, bamboo forests are estimated to cover more than 150,000 ha (FAO, 2010), of which

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99% are composed of *Phyllostachys pubescens* Mazel ex Houz. and *Phyllostachys bambusoides* Sieb. et Zucc. at a 3:1 ratio (Torii and Isagi, 1997). *Phyllostachys pubescens* was introduced from China to Japan in the 1700s for its edible shoots (Scurlock et al., 2000; Uchimura, 2009). However, cheaper bamboo imports, the widespread use of alternative materials and heavy labor costs caused the Japanese bamboo industry to decline in the 1970s (Shibata, 2003; Takano et al., 2017). Consequently, many *P. pubescens* forests have been abandoned, and are expanding their range by invading neighboring stands or farms (Torii and Isagi, 1997; Suzuki, 2015). Moreover, Takano et al. (2017) suggested that *P. pubescens* forests could expand their potential habitat in association with recent climate warming.

Because of the rapid growth rate of bamboo forests (Song et al., 2016; Yen, 2016), they are likely to be subjected to self-thinning (Liu et al., 2016). If bamboo stands are not thinned, their asexual reproduction capacity declines at high stand densities (Yen et al., 2010; Yen and Lee, 2011). Furthermore, abandonment and expansion of bamboo forests might ultimately affect ecosystem services (Shinohara et al., 2014). Therefore, the management of bamboo forests implemented by thinning of old culms and harvesting bamboo shoot is required to prevent the decline of bamboo forests and their ecosystem services (Suzuki and Nakagoshi, 2008; Yen, 2015). The management of bamboo forests should be focused on reliable data and information (Kleinn and Morales-Hidalgo, 2006).

MSDR provides important information for regulating ρ in bamboo stands (Uchimura, 1973; Watanabe, 1985; Liu et al., 2016). When examining MSDR in bamboo forests, diameter is useful as a measure of culm size (Liu et al., 2016), since it is the most easily and accurately measured culm attributes (Suga et al., 2011). Uchimura (1973) demonstrated the intra-species MSDR between mean culm diameter at breast height (D) and ρ of *P. bambusoides* stands across Japan. The author found that

$$\log \rho = 6.033 - 1.971 \log D, \tag{2}$$

of which slope was close to -2. Following this work, Watanabe (1985) also formulated the MSDR of *P. pubescens* stands as:

$$\log \rho = 6.157 - 2 \log D, \tag{3}$$

where $\alpha = -2$ was assumed without theoretical basis. At first glance, these studies seem to be useful in regulating ρ of bamboo forests, but two questions arise:

(1) Does ρ scale to D^{-2} in fully stocked bamboo populations?
(2) If so, why does the slope of MSDR differ between bamboo ($\alpha \approx -2$) and tree ($\alpha \approx -1.6$)?

The purpose of this study is to determine the MSDR between D and ρ of *P. pubescens* stands in Japan. First, we derived an allometric model that estimates the slope of MSDR based on well-known ecological laws to answer the two questions. Next, we determined the MSDR empirically by compiling data on the relationship between D and ρ for pure stands of *P. pubescens* across Japan from the published literature. Finally, we constructed a stand density management diagram (SDMD) for *P. pubescens* stands based on the determined MSDR.

2. Theoretical considerations

2.1. Does ρ scale to D^{-2} in fully stocked bamboo populations?

Uchimura (1973) addressed the first question using an isometric model (Yoda et al., 1963; Miyanishi et al., 1979). For bamboo, the mean area occupied by an individual (S) was assumed to be inversely proportional to ρ as:

$$S \propto \rho^{-1}. \tag{4}$$

It was also assumed that S scales to the square of D as:

$$S \propto D^2. \tag{5}$$

Inserting Eq. (4) into Eq. (5) yields:

$$\rho \propto D^{-2}. \tag{6}$$

Based on this model, Uchimura (1973) presumed that ρ of bamboo forests scales to D^{-2}. However, it should be emphasized that the isometric model fails to predict MSDR, since bamboo does not grow isometrically, but allometrically (e.g., Inoue, 2013). Therefore, the presumption using an isometric model by Uchimura (1973) is violated.

As a refinement, we propose an allometric model by referring to Satoo (1962) and Long and Smith (1984). First, we assume that total foliage mass in a fully stocked stand is almost constant independent of ρ, i.e., the law of foliage mass constancy (Kira and Shidei, 1967; Tadaki, 1976). Then, we have

$$F\rho = \text{const.}, \tag{7}$$

where F is the average foliage mass per individual. This assumption has been widely accepted when developing self-thinning models (e.g., Satoo, 1962; Osawa, 1995; Osawa and Kurachi, 2004). The second assumption is the pipe model theory (Shinozaki et al., 1964): given an individual, the ratio of foliage mass (f) to conductive sapwood cross-sectional area is a constant throughout plant development. Watanabe and Oohata (1984) showed that the pipe model theory holds true for *P. bambusoides*. Accordingly, f is assumed to be linearly proportional to culm sapwood cross-sectional area (cross-sectional area of culm wall: a_c):

$$f \propto a_c. \tag{8}$$

Third, we assume the following allometric relationship between a_c and culm diameter at breast height (d) at the individual-level:

$$a_c \propto d^{\beta}, \tag{9}$$

where β is an allometric exponent (Kume et al., 2010; Ichihashi et al., 2015). The value of β should be a constant independent of culm aging, since bamboo culm exhibits no secondary growth due to the lack of vascular cambium (Ahmad and Kamke, 2005; Wang et al., 2011). Finally, we suppose that variations in f, a_c and d in a fully stocked population are represented by the $-3/2$ power distributions (Hozumi et al., 1968; Osawa et al., 2001) with different parameters. Then, the relationships at the individual-level, i.e., Eqs. (8) and (9), could both be considered identical to those at the stand-level (Osawa and Kurachi, 2004; see Appendix A), as follows:

$$F \propto A_c \tag{10}$$

and

$$A_c \propto D^{\beta}, \tag{11}$$

where A_c is the average a_c in a stand. Eliminating F and A_c from Eqs. (7), (10) and (11), we have

$$\rho \propto D^{-\beta}. \tag{12}$$

When comparing Eq. (1) with Eq. (12) under the assumption of $D \propto D_q$, it is inferred that the slope of MSDR is determined by the allometric power exponent between A_c and D (or between a_c and d), i.e., $\alpha = -\beta$.

For *P. pubescens*, Inoue et al. (2011a) found that a_c scales linearly with the cross-sectional area of whole culm (a_w) as:

$$a_c \propto a_w. \tag{13}$$

The same relationship was found to exist in other bamboo species such as *P. bambusoides* (Shiga, 1899; Aoki, 1987; Inoue et al., 2011b, 2018). In theory, a_w scales to d^2, i.e., $a_w = \pi(d/2)^2$, which results in $\beta = 2$. Inserting $\beta = 2$ into Eq. (12), we obtain the following MSDR for bamboo populations:

$$\rho \propto D^{-2}. \tag{14}$$