

Article

Allometric Equations for Predicting Culm Surface Area of Three Bamboo Species (*Phyllostachys* spp.)

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Abstract: It is strongly debated whether bamboo forest ecosystems are a carbon sink or a carbon source because of insufficient knowledge regarding carbon loss via CO₂ emissions from these forests. The surface area (*S*) of bamboo culms (stems) is important for estimating culm respiration, a major component of carbon cycling in bamboo forests. However, few studies have attempted to formulate predictive equations for *S*. In this study, we developed allometric equations for predicting *S* in three bamboo species grown in Kyushu Island, western Japan: *Phyllostachys pubescens* Mazel ex Houz., *P. bambusoides* Sieb. et Zucc. and *P. nigra* var. *henonis*. We used a power equation between *S* and diameter at breast height (*D*) and a linear equation between *S* and *D* × total culm length (*H*). The results indicated that *P. bambusoides* and *P. nigra* shared common site-independent equations. In contrast, *P. pubescens* required species-specific equations due to interspecific variation in culm slenderness and tapering. We also found that *D* was a better predictive variable than *DH* when quantifying *S* because of its satisfactory predictive performance and simplicity. These findings will be beneficial for evaluating the contribution of bamboo forest ecosystems to carbon cycling.

Keywords: allometric equation; carbon cycling; culm respiration; culm surface area; *Phyllostachys*

1. Introduction

Bamboo (family: Poaceae, subfamily: Bambusoideae) is a diverse plant group with nearly 1500 species across approximately 119 genera and is native to all continents except Antarctica and Europe [1,2]. Bamboo forests cover roughly 31.5 million hectares worldwide [2,3] and occupy approximately 1% of the total global forested area [4]. International interest in bamboo has rapidly increased because of its highly versatility, fast growth and environmentally friendly characteristics [4–6].

Many studies in the past decade have shown the potential of bamboo forests as a carbon sink (a process that removes carbon dioxide from the atmosphere) [6–11]. Nevertheless, there remains considerable debate whether bamboo forest ecosystems are a carbon sink or a carbon source (a process of releasing carbon dioxide to atmosphere) [12–14]. One possible reason for this uncertainty is insufficient knowledge regarding carbon loss via CO₂ emissions from bamboo forests [14].

Bamboo forests release CO₂ into the atmosphere through respiration of the culm (stem), leaves, branches and soil, including roots [10,14–17]. In particular, culm respiration (*R_C*) is a major component of carbon cycling in bamboo forests, accounting for nearly 30% of aboveground respiration [18,19].

R_C can be quantified by scaling the point-measured respiration rate per unit area (R_{AREA}) up to the individual- or stand-level with the culm surface area (S), i.e., $R_C = S \times R_{AREA}$. This convenient approach is widely used to quantify the stem respiration of a tree as well as R_C [20–23].

During this scaling, errors in S and R_{AREA} can increase errors in the R_C estimate [24]. For bamboo, a reliable R_{AREA} must consider vertical variation, culm size and age, and response to temperature change [14,19]. By contrast, previous studies have not focused on the quantification of S . A previous study assumed cone geometry for culms when estimating R_C in a bamboo forest [19]. However, this simplistic assumption is violated when quantifying S [25]. Because small errors in S could lead to large errors in scaled-up R_C [24], S must be characterized accurately and precisely.

In general, measuring the surface area of a stem or culm requires time and labor-intensive destructive sampling [26]. Therefore, many allometric equations have been developed to estimate stem surface area in various tree species based on commonly measured tree attributes such as diameter at breast height and total tree height [27–31]. Numerous equations have also been derived for estimating culm biomass or volume of bamboo species [11,32–38], but only one study has investigated how S is related to other culm dimensions [39]. In *Phyllostachys pubescens* Mazel ex Houz., a common bamboo species in Asia with high potential for carbon sequestration [6,9,10,40], a power equation described the relationship between S and external culm diameter at breast height (D) [39]. In addition, a linear equation was suitable for representing the relationship between S and the product of D times total culm length (H) [39]. However, to our knowledge, no other allometric equations for predicting S are found in the literature, raising the question whether such predictive equations are site- and species-specific. If they are specific, destructive sampling is required for every site and species for which an equation is developed. In contrast, generic equations can be applied to multiple sites and species, which results in efficient R_C prediction.

The objective of this study was to develop allometric equations for predicting S in three bamboo species grown in Kyushu Islands, southern Japan: *P. pubescens*, *P. bambusoides* Sieb. et Zucc. and *P. nigra* var. *henonis*, which are called the three major useful bamboos in Japan [34,41]. In Japan, bamboo forests are estimated to cover more than 150,000 ha [42,43]; these three species account for more than 99% [44]. Hence, developing allometric equations is helpful to evaluating the potential of the bamboo forests as a carbon sink. The findings obtained in this study will also be beneficial when determining equations for S of other bamboo species in other countries. Specifically, we address the following questions regarding our newly developed allometric equations for S :

- (1) Are the allometric equations site-specific?
- (2) Are the allometric equations species-specific?
- (3) What predictive variable is optimal for S prediction?

2. Materials and Methods

2.1. Study Sites

Data used here were gathered in Kyushu Islands, western Japan, which is situated between latitudes 30°59' N to 33°58' N and longitudes 129°33' E to 132°5' E. *Phyllostachys pubescens* and *P. bambusoides* data were collected in a suburban forest of Toshima Mountain, located in eastern Kumamoto City, Kumamoto Prefecture, western Japan (32°49' N, 130°48' E, 80–90 m a.s.l.; hereafter TO). Average annual temperature and rainfall between 1981 and 2010 at the nearest observatory were 16.9 °C and 1986 mm, respectively [45]. The soil type was classified as ando soil [46]. Stands of both species were located adjacent to each other across an approach to Toshima Shrine at the foot of Mt. Toshima. These sites were originally used for upland farming until a few decades ago and became bamboo stands after the planting of bamboo and subsequent abandonment [33,35,36].

Phyllostachys nigra data were collected from two sites: the campus of Fukuoka University of Education in eastern Munakata City, Fukuoka Prefecture (33°48' N, 130°36' E, 50 m a.s.l.; MU) and the Ito campus of Kyushu University in western Fukuoka City, Fukuoka Prefecture, western Japan (33°36' N, 130°13' E, 60 m a.s.l.; IT). Average annual temperature, rainfall and soil type were, respectively, 15.6 °C, 1640 mm

and a brown forest soil for MU and 16.1 °C, 1677 mm and a gley soil or brown forest soil for IT [45,46]. Both sites were very dense, and no other vegetation was found on their forest floors [34,35].

2.2. Field Measurements

For each site, healthy, living culm samples were felled at ground level after the growing (elongation) period from October to January [47]. In total, 200 culm samples were gathered from each of the *P. pubescens* and *P. bambusoides* stands in TO, while 60 and 110 culms were collected from *P. nigra* stands in MU and IT, respectively. Total culm length (H) and external culm diameter at breast height (D) were directly measured with a tape measure to the nearest 0.1 m and a digital caliper to the nearest 0.1 cm, respectively. To quantify S accurately and efficiently, external culm diameters at 10 successive points were measured with a caliper to the nearest 0.1 cm [25]. The measurement points were located along the culm at equal intervals of one tenth of the direct measured H . It should be noted that the ages of sample culms were not recorded in our sampling. However, this did not distort our results because of the following reasons: (1) the bamboo culms attain maximum total culm length by completing culm elongation [6,48,49], (2) the lack of vascular cambium results in no secondary growth of the culm after the elongation period [50,51], and thus (3) the relationships of S to other culm dimensions do not vary with culm age after completing elongation. The dendrometric parameters of sample culms are shown in Table 1.

2.3. Analyses Methods

For all culm samples, S was calculated from H and successive diameters measured at one-tenth intervals of H using the sectional measurement method [25,39]. Similarly, apparent culm volume (V) [52,53] was computed with the same method [33–36]. To improve the reliability of the allometric equations, we also used published data on D , H , S and V of *P. bambusoides* from three sites [54]: Fukuoka (FU; $n = 122$), Kitakyushu (KI; $n = 102$) and Hisayama (HI; $n = 96$), Fukuoka Prefecture. Therefore, as shown in Table 1, the resulting total number of samples was 890 (200 for *P. pubescens* from one site, 520 for *P. bambusoides* from four sites and 170 for *P. nigra* from two sites). Despite the reliable data of site location, the soil type was estimated to be brown forest soil or ando soil [46]. These data were used previously to develop height-diameter curves, two-way volume equations and one-way volume tables [33–36,55]. Furthermore, a part of the *P. pubescens* data (150 of 200 culms) was used to determine predictive equations for S [39].

For each species and site, samples were randomly split into modeling and validation data. The former was used to develop allometric equations for S , while the latter was used independently to test the predictive performance. Scatterplots of H and D for both datasets were very similar (data not shown), suggesting that robust conclusions could be reached from the validation.

We used the following two allometric equations:

$$S = \alpha D^{\beta}, \quad (1)$$

and

$$S = \gamma DH, \quad (2)$$

where α , β and γ are the parameters [27,39]. *Phyllostachys bambusoides* and *P. nigra* data were gathered from multiple sites, which allowed us to test whether the allometric equations were site-specific. In addition, *P. bambusoides* and *P. nigra* had similar culm taper [34], suggesting that they should share a common allometric equation for S . Furthermore, if the equations for the three species are generic, it is not necessary to develop the equations for each species by tedious destructive sampling. For these reasons, the allometric equations were determined for (1) each species and site (hereafter site-specific equation), (2) each species (species-specific equation), (3) *P. bambusoides* and *P. nigra* (common equation) and (4) all species (generic equation) (see Table 2). Goodness of fit was evaluated with the adjusted coefficient of determination (r^2), root mean square error (RMSE) and Akaike's Information Criteria (AIC).

Table 1. Dendrometric parameters of sample culms ($n = 890$).

| Species | Site ¹ | Number of Samples ² | Soil Type ³ | Total Culm Height (m) ⁴ | Diameter at Breast Height (cm) ⁴ | Culm Surface Area (m ²) ⁴ |
|-----------------------|-------------------|--------------------------------|--------------------------------|------------------------------------|---|--|
| <i>P. pubescens</i> | TO | 200 (100) | Ando soil | 14.1 ± 2.5 | 9.2 ± 2.7 | 2.46 ± 1.01 |
| <i>P. bambusoides</i> | TO | 200 (100) | Ando soil | 11.1 ± 3.0 | 5.0 ± 1.7 | 1.26 ± 0.70 |
| | KI | 102 (51) | Brown forest soil or ando soil | 12.8 ± 3.4 | 6.2 ± 2.1 | 1.77 ± 1.00 |
| | FU | 122 (61) | Brown forest soil or ando soil | 11.8 ± 2.5 | 5.7 ± 1.7 | 1.50 ± 0.81 |
| | HI | 96 (48) | Brown forest soil or ando soil | 9.0 ± 2.1 | 4.1 ± 1.2 | 0.87 ± 0.46 |
| <i>P. nigra</i> | MU | 60 (30) | Brown forest soil | 7.3 ± 2.0 | 2.9 ± 1.1 | 0.50 ± 0.30 |
| | IT | 110 (55) | Gley soil or brown forest soil | 6.2 ± 1.5 | 2.7 ± 0.8 | 0.37 ± 0.19 |

¹ TO: Toshima, KI: Kitakyushu, FU: Fukuoka, HI: Hisayama, MU: Munakata, IT: Ito; ² Values in parentheses are sample sizes of modeling and validation data; ³ The soil type classification is based on website information [46]; ⁴ Average ± S.D.

Table 2. Explanation of the allometric equations developed in this study.

| Equation | Species | Site ¹ | Number of Samples ² |
|------------------|---|---------------------------|--------------------------------|
| Site-specific | <i>P. bambusoides</i> | TO | 200 |
| | | KI | 102 |
| | | FU | 122 |
| | | HI | 96 |
| Species-specific | <i>P. nigra</i> | MU | 60 |
| | | IT | 110 |
| Common | <i>P. pubescens</i> <i>P. bambusoides</i> <i>P. nigra</i> | TO | 200 |
| | | TO, KI, FU and HI | 520 |
| | | MU and IT | 170 |
| Generic | <i>P. bambusoides</i> and <i>P. nigra</i> | TO, KI, FU, HI, MU and IT | 690 |
| Generic | <i>P. pubescens</i> , <i>P. bambusoides</i> and <i>P. nigra</i> | TO, KI, FU, HI, MU and IT | 890 |

¹ TO: Toshima, KI: Kitakyushu, FU: Fukuoka, HI: Hisayama, MU: Munakata, IT: Ito; ² The number of sample culms used for both modeling and validation data.

As a preliminary analysis for examining the validity of Equation (2), we also tested the following three equations:

$$S = \gamma DH + \delta, \quad (3)$$

$$S = \gamma (DH)^\delta, \quad (4)$$

and

$$S = \gamma D^\delta H^\varepsilon, \quad (5)$$

where γ , δ and ε are the parameters. Values of δ in Equations (3) and (4) were not significantly different from zero and unity, respectively. In addition, neither δ nor ε in Equation (5) differed significantly from unity. These facts imply that these three equations are essentially identical to Equation (2), which also exhibited smaller AIC values. Hence, we selected Equation (2) as the predictive equation with two variables (D and H).

Using validation data, S was predicted by substituting measured D and H into the determined equations. Accuracy and precision were then evaluated with average relative error (%AE) and relative root mean square error (%RMSE), respectively. These were defined as:

$$\%AE = 100 \times \sum_n \left\{ \left(S_{\text{predicted}} - S_{\text{observed}} \right) / S_{\text{observed}} \right\} / n, \quad (6)$$

and

$$\%RMSE = 100 \times \sqrt{\sum_n \left(S_{\text{predicted}} - S_{\text{observed}} \right)^2 / n} / S_{\text{average}}, \quad (7)$$

where $S_{\text{predicted}}$ and S_{observed} are predicted and observed S , respectively; n is the number of culm samples; and S_{average} is the average S_{observed} values. Differences between $S_{\text{predicted}}$ and S_{observed} were examined with a Wilcoxon signed rank test.

To compare culm characteristics, height to diameter ratio (HDR) [56] and breast height form-factor for apparent culm volume (λ_b) [57] were calculated from modeling data. The former is known as a slenderness coefficient, whereas the latter is a measure of culm tapering. λ_b was calculated as:

$$\lambda_b = 4V / \pi D^2 H. \quad (8)$$

Culms with higher HDR and λ_b are more slender and non-tapering, respectively. These values were compared using Tukey's HSD test. All statistical analyses were performed using R software version 3.4.3 [58], and $p < 0.05$ was considered significant.

3. Results and Discussion

3.1. Are the Allometric Equations Site-Specific?

Figure 1 shows the relationship between S and D for each species and site. The parameter estimates and fit statistics of the developed equations are summarized in Table 3. The relationship between S and D can be described by a power equation for all species and sites ($r^2 > 0.94$). The relationship between S and DH can also be expressed by a linear equation ($r^2 > 0.99$; Figure 2). For all species and sites, %AE of the site-specific equations was small (less than $\pm 3\%$; Table 4). Hence, Equations (1) and (2) are acceptable as the predictive equations for every species and sites examined in this study.

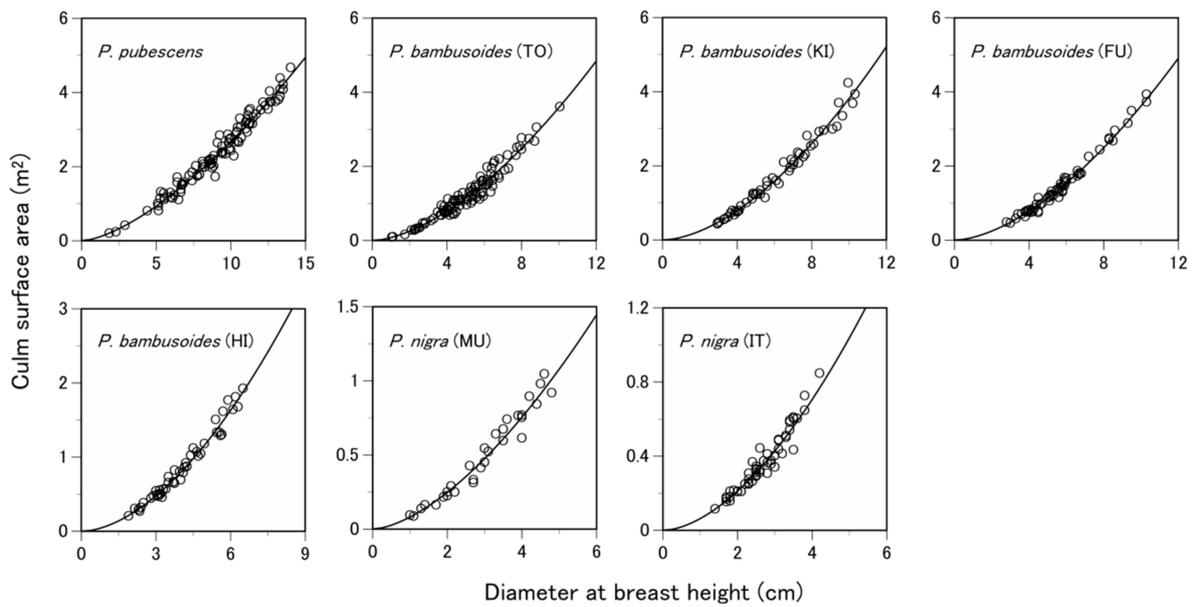


Figure 1. Relationship between culm surface area and diameter at breast height for each species and site. The solid lines represent the power equations detailed in Table 3.

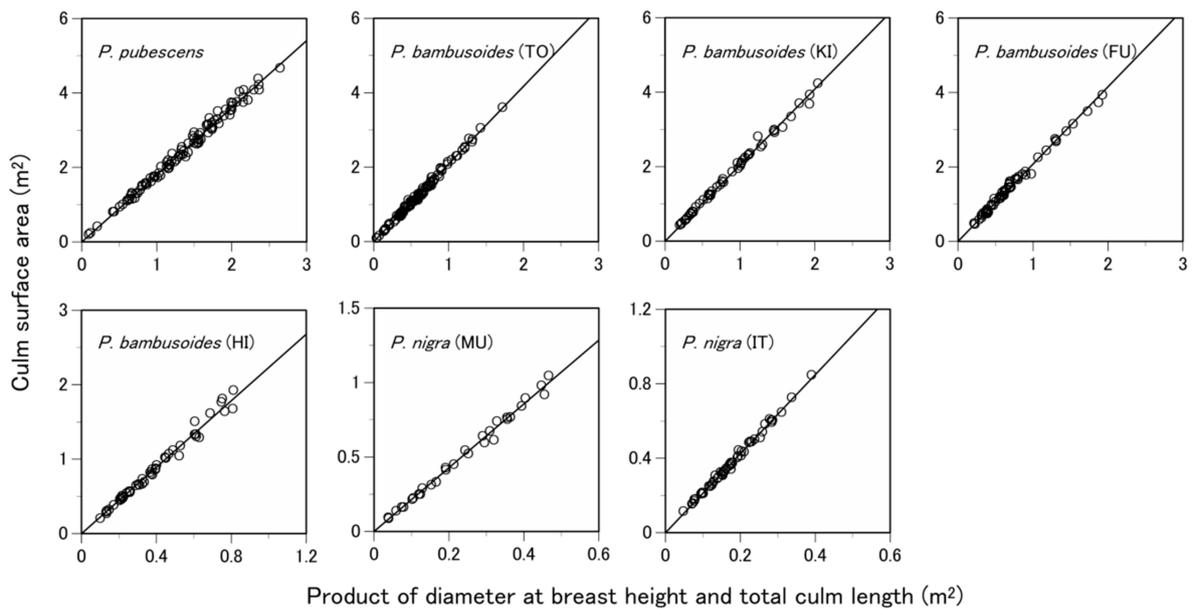


Figure 2. Relationship between culm surface area and product of diameter at breast height and total culm length for each species and site. The solid lines represent the linear equations detailed in Table 3.

Table 3. Parameter estimates of the developed allometric equations and their fit statistics.

| Equation | Species | Site ¹ | Power Equation | | | | Linear Equation | | | | |
|------------------|---|-------------------|----------------|---------|-------|------------------------|-----------------|----------|-------|------------------------|---------|
| | | | α | β | r^2 | RMSE (m ²) | AIC | γ | r^2 | RMSE (m ²) | AIC |
| Site-specific | <i>P. bambusoides</i> | TO | 159.03 | 1.65 | 0.97 | 0.155 | −83.25 | 2.08 | 0.99 | 0.051 | −306.68 |
| | | KI | 178.44 | 1.68 | 0.99 | 0.147 | −46.26 | 2.04 | 0.99 | 0.073 | −120.05 |
| | | FU | 184.19 | 1.70 | 0.98 | 0.089 | −115.35 | 2.07 | 0.99 | 0.068 | −150.95 |
| | | HI | 242.78 | 1.78 | 0.98 | 0.073 | −106.07 | 2.23 | 0.99 | 0.055 | −136.63 |
| | <i>P. nigra</i> | MU | 143.52 | 1.63 | 0.97 | 0.060 | −79.96 | 2.14 | 0.99 | 0.025 | −134.44 |
| | | IT | 263.16 | 1.83 | 0.94 | 0.039 | −191.73 | 2.12 | 0.99 | 0.011 | −322.93 |
| Species-specific | <i>P. pubescens</i> | | 83.21 | 1.49 | 0.98 | 0.174 | −58.68 | 1.80 | 0.99 | 0.101 | −168.49 |
| | <i>P. bambusoides</i> | | 179.50 | 1.69 | 0.98 | 0.131 | −315.58 | 2.07 | 0.99 | 0.069 | −649.89 |
| | <i>P. nigra</i> | | 239.91 | 1.79 | 0.95 | 0.051 | −260.28 | 2.13 | 0.99 | 0.017 | −441.90 |
| Common | <i>P. bambusoides</i> and <i>P. nigra</i> | | 187.66 | 1.70 | 0.98 | 0.118 | −495.65 | 2.08 | 0.99 | 0.061 | −950.25 |
| Generic | All species | | 116.01 | 1.57 | 0.97 | 0.294 | −3.27 | 1.92 | 0.98 | 0.142 | −471.77 |

¹ TO: Toshima, KI: Kitakyushu, FU: Fukuoka, HI: Hisayama, MU: Munakata, IT: Ito.

Table 4. Accuracy (%AE) and precision (%RMSE) of the culm surface area estimated by the developed allometric equations.

| Equation | Species | Site ¹ | Power Equation | | Linear Equation | | |
|------------------|-----------------------|-----------------------|----------------|-----------|-----------------|-----------|-------|
| | | | %AE (%) | %RMSE (%) | %AE (%) | %RMSE (%) | |
| Site-specific | <i>P. bambusoides</i> | TO | −1.45 | 12.04 | −0.55 | 4.04 | |
| | | KI | 2.06 | 6.17 | −1.95 | 2.73 | |
| | | FU | −0.43 | 7.91 | −1.17 | 5.54 | |
| | | HI | 0.95 | 9.44 | 1.12 | 7.86 | |
| | <i>P. nigra</i> | MU | −1.94 | 12.76 | −1.73 | 3.80 | |
| | | IT | −3.09 | 11.06 | −1.31 | 3.33 | |
| Species-specific | <i>P. pubescens</i> | TO | 0.30 | 8.70 | −0.51 | 4.74 | |
| | <i>P. bambusoides</i> | TO | −1.42 | 11.30 | −0.88 | 4.10 | |
| | | KI | 0.05 | 5.78 | −0.28 | 3.16 | |
| | | FU | 0.91 | 8.03 | −1.21 | 5.53 | |
| | | HI | 0.73 | 9.19 | −5.77 | 9.94 | |
| | <i>P. nigra</i> | MU | −10.45 | 14.47 | −2.15 | 3.99 | |
| | | IT | 0.51 | 11.13 | −0.83 | 3.41 | |
| | Common | <i>P. bambusoides</i> | TO | −2.32 | 11.41 | −0.80 | 4.08 |
| | | | KI | −0.46 | 5.91 | −0.20 | 3.21 |
| | | | FU | 0.31 | 8.13 | −1.13 | 5.56 |
| HI | | | −0.48 | 9.25 | −5.70 | 9.89 | |
| <i>P. nigra</i> | | MU | −3.28 | 11.17 | −4.76 | 6.01 | |
| | | IT | 9.08 | 14.06 | −3.47 | 4.01 | |
| Generic | | <i>P. pubescens</i> | TO | 16.54 | 21.75 | 5.81 | 8.41 |
| | | <i>P. bambusoides</i> | TO | −8.39 | 19.40 | −8.48 | 10.30 |
| | KI | | −9.59 | 15.81 | −7.92 | 7.77 | |
| | FU | | −8.32 | 14.42 | −8.78 | 9.06 | |
| | HI | | −4.62 | 14.10 | −12.99 | 16.34 | |
| | <i>P. nigra</i> | MU | −2.28 | 15.18 | −12.12 | 14.02 | |
| | | IT | −10.98 | 13.13 | −10.94 | 11.37 | |

¹ TO: Toshima, KI: Kitakyushu, FU: Fukuoka, HI: Hisayama, MU: Munakata, IT: Ito.

In *P. bambusoides* and *P. nigra*, a single, site-independent power equation represented the relationship between *S* and *D* (Figure 3). The values of r^2 and RMSE of the power equation were, respectively, 0.98 and 0.131 m² for *P. bambusoides* and 0.95 and 0.051 m² for *P. nigra*. The relationship between *S* and *DH* was fitted by a single linear equation for both species, with $r^2 = 0.99$ for both species (Figure 4). RMSE was 0.069 m² for *P. bambusoides* and 0.017 m² for *P. nigra*. Site- and species-specific equations for both species had comparable fit statistics and predictive performance, suggesting that separate equations are not necessary for different *P. bambusoides* and *P. nigra* sites. Therefore, the answer to the first question is that allometric equations for *P. bambusoides* and *P. nigra* are not site-specific. However, further studies are necessary to verify whether equations for *P. pubescens* are site-specific, as our data were insufficient to clarify this point.

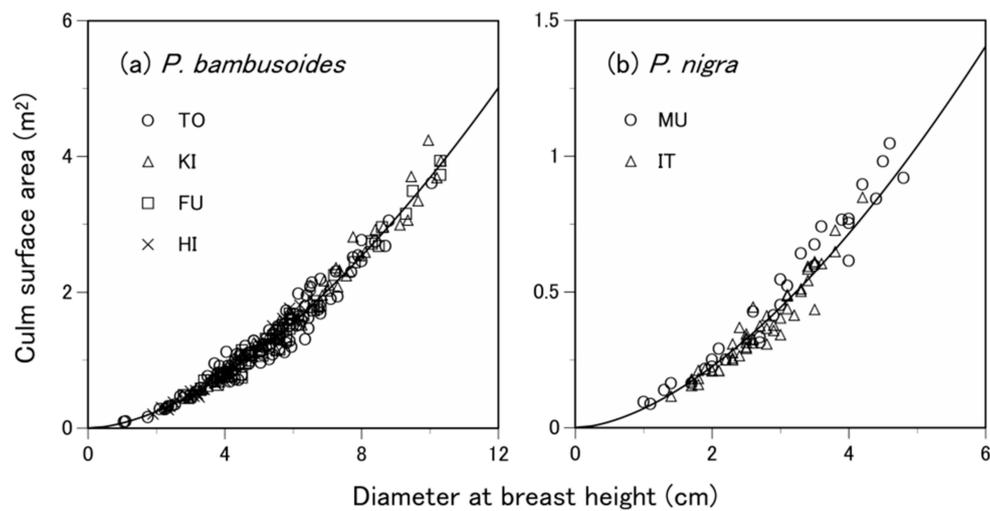


Figure 3. Relationship between culm surface area and diameter at breast height in (a) *Phyllostachys bambusoides* and (b) *P. nigra*. The solid lines represent the power equations detailed in Table 3.

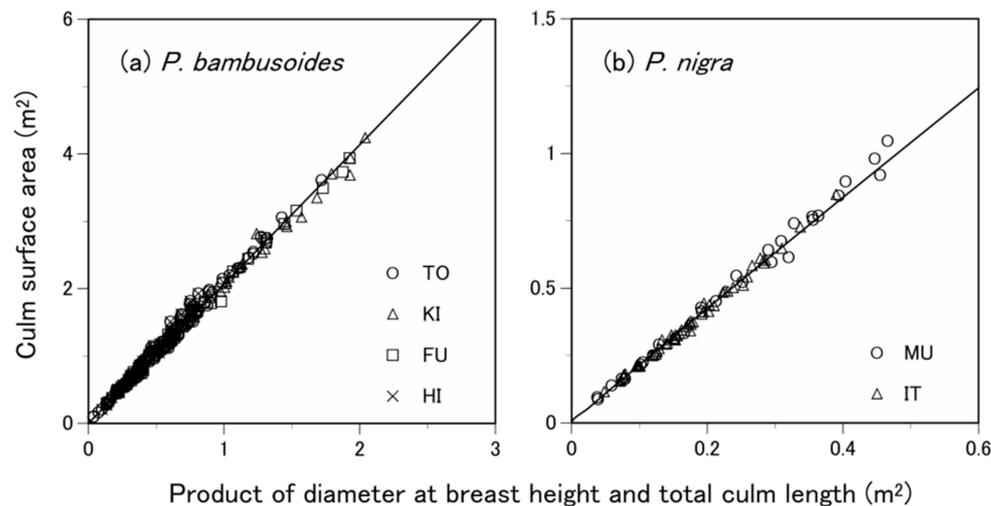


Figure 4. Relationships between culm surface area and product of diameter at breast height and total culm length in (a) *Phyllostachys bambusoides* and (b) *P. nigra*. The solid lines represent the linear equations detailed in Table 3.

3.2. Are the Allometric Equations Species-Specific?

Figure 5 depicts the relationships of S to D and DH for *P. bambusoides* and *P. nigra*. Similar to the two-way volume equations for these species [33,34], the relationships were well expressed by the common power and linear equations with $r^2 = 0.98$ for the former and $r^2 = 0.99$ for the latter. Common equations had intermediate RMSEs compared to site- and species-specific equations. The relationships of S to D and DH for all three species are shown in Figure 6. Although the generic power equation for all three species was significant ($r^2 = 0.97$), S and D scatterplots indicate a clear separation of *P. pubescens* and the other two species; for the same D , *P. pubescens* had a smaller S than *P. bambusoides* and *P. nigra* (Figure 6a). Similarly, the relationship between S and DH for the three species could be fitted by the single linear equation ($r^2 = 0.98$). However, for the same DH , S was slightly smaller in *P. pubescens* than in the other two species (Figure 6b). In both generic equations, %AE was positive for *P. pubescens*, but negative for *P. bambusoides* and *P. nigra*. Therefore, when applying the generic equations, R_C will be overestimated for *P. pubescens* and underestimated for the other two species. Moreover,

the generic equations had larger %RMSEs than the other equations. These results indicate that generic equations are inappropriate when estimating S , and the predictive equations for *P. pubescens* should be species-specific. For these reasons, the optimal equations for predicting S are as follows:

$$S = 83.21D^{1.49}, \tag{9}$$

$$S = 1.80DH, \tag{10}$$

for *P. pubescens* (species-specific equations) and

$$S = 187.66D^{1.70}, \tag{11}$$

$$S = 2.08DH, \tag{12}$$

for *P. bambusoides* and *P. nigra* (common equations).

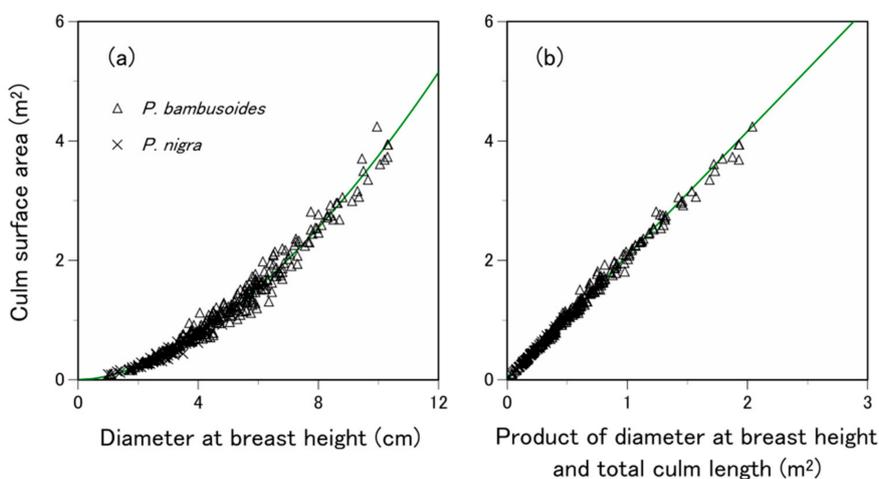


Figure 5. Relationships of culm surface area to (a) diameter at breast height and (b) product of diameter at breast height and total culm length for *Phyllostachys bambusoides* and *P. nigra*. The solid lines represent the power and linear equations detailed in Table 3.

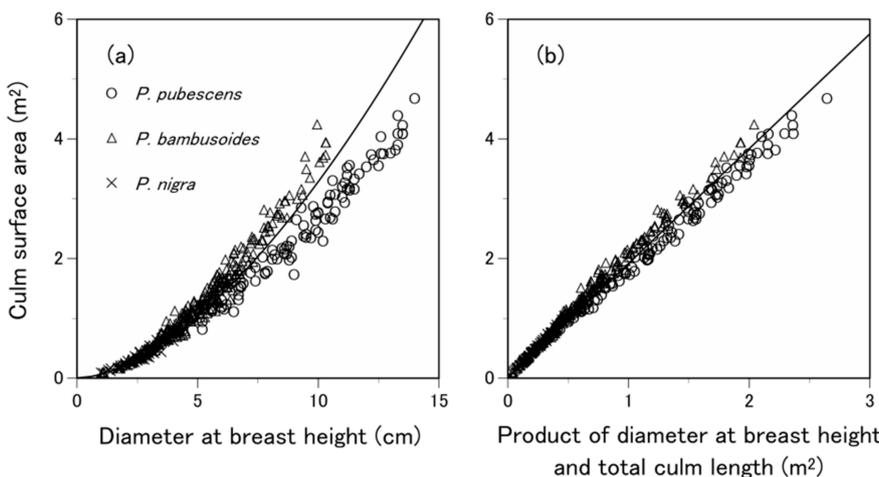


Figure 6. Relationships of culm surface area to (a) diameter at breast height and (b) product of diameter at breast height and total culm length for three *Phyllostachys* species. The solid lines represent the power and linear equations detailed in Table 3.

For *P. pubescens*, both power and linear equations had %AE less than $\pm 0.5\%$, with no significant differences between $S_{\text{predicted}}$ and S_{observed} . Generally, $S_{\text{predicted}}$ of *P. bambusoides* from power and linear common equations did not differ significantly from S_{observed} , with %AE less than $\pm 1.2\%$ for all sites and equations except for $S_{\text{predicted}}$ in the TO from the power equation (%AE = -2.3%) and in the HI from the linear equation (-5.7%). For *P. nigra*, a significant difference was found between $S_{\text{predicted}}$ and S_{observed} at both sites; %AE from the power equation was relatively large for IT (9.1%), but less than $\pm 5\%$ for other sites and equations. It should be noted that the common power equation in MU had smaller %AE than the species-specific power equation. Therefore, the predictive performance of common equations is not inferior to that of species-specific equations. However, common equations have broader application than species-specific equations, even if they are not relevant for *P. pubescens*.

Why are the predictive equations different between *P. pubescens* and the other two species? Figure 7a compares HDR computed from modeling data across species and sites. *P. pubescens* had significantly lower HDR, and therefore shorter culm length, than *P. bambusoides* and *P. nigra*. Hence, *P. pubescens* has a relatively smaller S for the same D than the other species. Moreover, *P. pubescens* had lower λ_b (Figure 7b), indicating a more tapered culm. A tapered culm results in smaller S for the same D and H . These facts indicate that interspecific variation in culm slenderness and tapering explains differences in allometric power equations, while only variation in culm tapering explains differences in the linear equation. Therefore, the answer to the second question is that species-specific predictive equations are required for *P. pubescens*, but not for *P. bambusoides* and *P. nigra*, because of interspecific variation in culm characteristics.

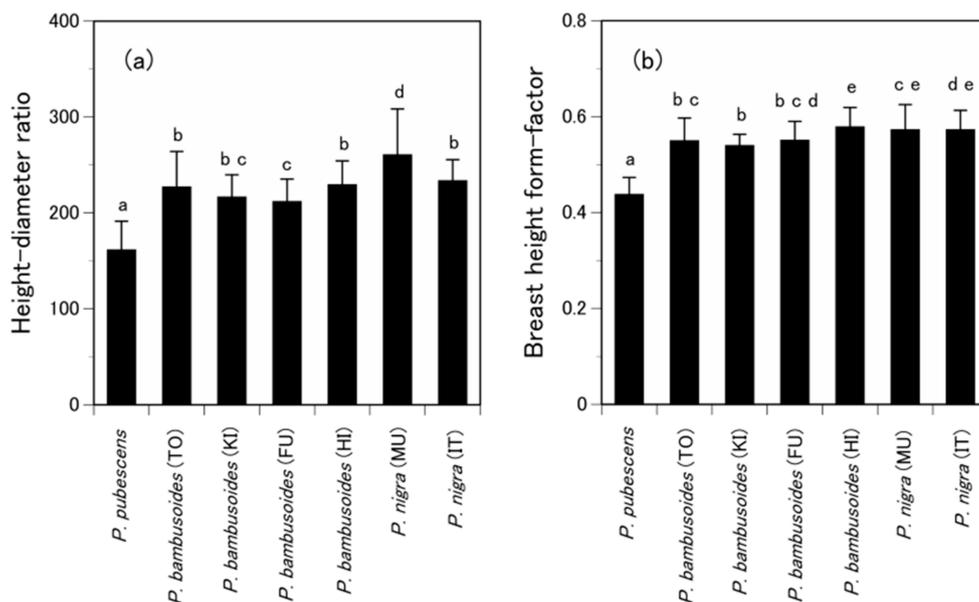


Figure 7. Comparisons of (a) height-diameter ratio and (b) breast height form-factor for each species and site. Error bars indicate the standard deviation. Values labeled with the same lower case letter are not significantly different according to Tukey's HSD test.

3.3. What Predictive Variable Is Optimal for S Prediction?

We compared two allometric equations for predicting S with the different variables, i.e., D and DH . Which predictive variable is better? We found that the DH -based equation, Equation (2), showed slightly higher r^2 and smaller RMSE and AIC than the D -based equation, Equation (1) (Table 3). However, %AE and %RMSE magnitudes exhibited inter-site and inter-specific variation (Table 4), suggesting that the inclusion of the additive variable H does not improve the predictive performance. Diameter at breast height and tree height are easy measurable dendrometric variables of trees [28]. D of bamboo is also the most easily measured culm attribute. In contrast, it is difficult to measure H of

standing bamboo culm, since the culm tip is generally bent askew [35,52,59]. Equations (10) and (12) clearly demonstrated that inaccurate measurement of H causes errors in S prediction, which results in uncertain R_C prediction. Similar arguments are found in estimating V or biomass of tree species [60–62]. For these reasons, our answer to the third question is that D is the optimal variable for estimating S of the three examined bamboo species.

4. Conclusions

In this study, we developed allometric equations for predicting S in three *Phyllostachys* species grown in Kyushu Island, western Japan. We demonstrate that *P. bambusoides* and *P. nigra* share the common site-independent equations, whereas *P. pubescens* requires species-specific equations because of interspecific variation in culm slenderness and tapering. We also conclude that D is the optimal variable when predicting S of all three species. These equations enable us to scale point-measured R_{AREA} up to R_C at individual- or stand-levels efficiently through simple measurement of D . Therefore, the equations developed here will be beneficial for evaluating R_C , and bring a consensus regarding the contribution of bamboo forest ecosystems to the carbon cycle. In future, it is necessary to examine whether the equations vary with culm sizes, climatic conditions and soil properties.

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