

Applicability of the pipe-model theory to seedlings of hinoki cypress (*Chamaecyparis obtusa*)

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Research Article

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Abstract

According to the pipe-model theory, the relationship between the cumulative mass of leaves [$F(z)$] and the density of non-photosynthetic organs [$C(z)$] at depth z from the crown surface is linear for adult trees. However, the present study of seedlings of *Chamaecyparis obtusa* demonstrates that the $F(z)-C(z)$ relationship can be approximated as a non-rectangular hyperbola with convexity (θ) between 0 and 1. For $\theta=1$, the $F(z)-C(z)$ relationship is linear, in accordance with adult trees. Therefore, the basic concept of pipe-model theory regarding the $F(z)-C(z)$ relationship can be generalized as a non-rectangular hyperbola for both growth stages (i.e., seedlings and adult trees). The difference between linearity ($\theta = 1$) and curvilinearity ($\theta \neq 1$) in the $F(z)-C(z)$ relationship corresponds to the difference in proportional area of sapwood in the studied seedlings. Thus, the proportional sapwood area is larger for seedlings with a linear $F(z)-C(z)$ relationship than for seedlings with a curvilinear $F(z)-C(z)$ relationship. The relationship between convexity and the square of stem diameter at the crown base showed scatter in terms of both season and seedling size, indicating that the size dependence of the degree of curvature in the $F(z)-C(z)$ relationship for seedlings remains unclear. The allometric relationship between leaf mass and the square of stem diameter at crown base tended to separate seedlings from adult trees. Seedlings have more leaves per stem cross-sectional area at crown base than adult trees, as seedling stems are mostly composed of sapwood, which functions as an assemblage of living pipes connected to the leaves. Greater scattering of data for seedlings than adult trees in the allometry between leaf mass and the square of stem diameter at crown base could be explained by the non-rectangular hyperbola of the $F(z)-C(z)$ relationship.

Introduction

Shinozaki et al. (1964a, b) proposed an elegant conceptual framework that interprets the linear relationship between the observed amount of stem tissue and the corresponding quantity of supporting leaves using the specific pipe length, a constant of proportionality, which is the basic concept of pipe-model theory. Thus, the leaf mass of an individual tree is proportional to the cross-sectional area of the stem at the crown base or to the square of the stem diameter at the crown base, indicating that the stem diameter at the crown base is useful for estimating the leaf mass of a tree.

During the period of more than a half century since its introduction, pipe-model theory has been reinterpreted and used for various applications, and undoubtedly represents an important milestone in the mathematical interpretation of plant form and function (cf. the review by Lehnebach et al. 2018). Several models have been developed for distinguishing between active and disused pipes to elucidate the significance of specific pipe length in the context of pipe-model theory (e.g., Whitehead et al. 1984; Chiba et al. 1988; Mäkelä et al. 1995; Mäkelä and Vanninen 1998; Kershaw and Maguire 2000; McDowell et al. 2002; Schneider et al. 2011). In such models, foliage mass should be most closely related to sapwood area, as the sapwood area can be considered equivalent to the active pipe area. As a result, a novel pipe model ratio, the ratio of foliage mass to the sapwood area at the crown base, was proposed in lieu of the specific pipe length (cf. Lehnebach et al. 2018).

The pipe-model theory has been refined and applied to sapwood area–leaf area and sapwood area–water flow relationships (Mäkelä et al. 1995; Mencuccini and Grace 1995; Berninger and Nikinmaa 1997; McDowell et al. 2002). Sone et al. (2009) studied the mechanisms through which pipe model relationships are maintained in the crown. Mäkelä (2002), Berninger et al. (2005) and Mäkelä and Valentine (2006) further developed the allometric scaling theory (cf. West et al. 1997, 1999; Enquist 2002) for woody plants based on the pipe model using the approach of West et al. (1999). The pipe-model theory has also been used to formulate hypotheses about crown structure and development based on the assumption of an allometric scaling relationship between foliage mass and crown length (Ilomäki et al. 2003; Kantola and Mäkelä 2006). Aye et al. (2022) mentioned that the non-linearity of the trunk shape is explained by the combination of active and disused pipes. The model builds upon merging the branch thinning theory (Hellström et al. 2018) with the pipe model and indirectly accounts for the leaf area and crown shape.

The pipe-model theory is one of the most important models explaining the hydraulic architecture of trees. However, this theory has major limitations, including the suggestion that pipe structures such as those proposed by Shinozaki et al. (1964a, b) cannot be found in actual trees. The most critical assumption of the model relies on the basic element of the plant vascular system, the pipe, being cylindrical (i.e., the diameter of the conduit does not vary axially). However, a major characteristic of tree hydraulic systems is that the conduits exhibit tip-base widening (e.g., West et al. 1999; Anfodillo et al. 2006; Petit and Anfodillo 2009; Savage et al. 2010; Olson et al. 2014, 2018, 2021; Koçillari et al. 2021). This universal and non-negligible pattern undoubtedly has a significant influence on the relationship between leaf mass and stem diameter.

Recently, Ogawa (2015) studied the variations in specific pipe length among several forest trees and documented the size dependence of specific pipe length. Based on those observations, he analyzed the proportional relationship between leaf mass and stem cross-sectional area at the crown base of trees, and thereby developed an alternative interpretation of specific pipe length. He found that the scaling exponent is controlled by the size dependence of specific pipe length, which is related to competition among forest trees and can be used as an indicator of the degree of suppression by large trees. Ogawa (2022) provided a simple allometric scaling model of leaf mass based on leaf mass and stem diameter at the crown base, accounting for hydraulic vessel systems such as sapwood area fraction and conduit diameter, and identified factors controlling the isometric exponent of leaf mass in the pipe model.

However, previous studies of the pipe-model theory have focused on adult trees as research material (cf. Lehnebach et al. 2018). Therefore, little information is available about the pipe-model theory in relation to seedlings at the early stages of stand development. As tree height becomes much greater after the seedling stage, seedlings do not require a fully developed hydraulic architecture, such as the tip-base widening of conduits present in adult trees (e.g., West et al. 1999; Anfodillo et al. 2006; Petit and Anfodillo 2009; Savage et al. 2010; Olson et al. 2014, 2018, 2021; Koçillari et al. 2021). In terms of hydraulic architecture, the proportions of sapwood and heartwood in total woody tissues are considered to differ between seedlings and adult trees. Therefore, the proportion of sapwood area was considered for application of the pipe-model theory to seedlings in the present study. Due to the differences in the

hydraulic systems of seedlings and adult trees, such as conduit diameter and sapwood area, the purposes of this study were to examine the applicability of the pipe-model theory to seedlings and to generalize the pipe-model theory to seedlings as well as adult trees.

Materials and methods

Data source

The data used in the present study were related to 1-year-old (April 1985 to March 1986) and 2-year-old (October 1981 to October 1982) seedlings of hinoki cypress (*Chamaecyparis obtusa* [Sieb. et Zucc.] Endl.) growing at Midorigaoka Nursery, Gifu District Forest Office, Minokamo, Gifu Prefecture, central Japan (cf. Ogawa 1989). The planted seedling density was 60 seedlings m⁻² for 1-year-old seedlings and 62 seedlings m⁻² for 2-year-old seedlings.

The nursery is situated at an elevation of 84 m above sea level. The meteorological records from the nursery show that the mean annual precipitation, annual air temperature, warmth index, and coldness index values over the five years between 1981 and 1985 were 1,785 mm yr⁻¹, 14.1°C, 116.1°C month, and - 7.1°C month, respectively.

Seedling size and mass measurement

Sampling of seedlings was conducted monthly from April 1985 to March 1986 for 1-year-old seedlings, and at semi-monthly intervals from October 1981 to October 1982 for 2-year-old seedlings. In total, 25 individuals were harvested at each sampling time from the seedbed, totaling 300 1-year-old seedlings and 618 2-year-old seedlings.

After harvesting of the sample seedlings, the seedling height, crown base height, stem diameter at ground level, stem diameter at one-tenth of the height, and stem diameter at the crown base were measured (Table 1).

At each harvest, the seedlings were divided into leaves, roots, and stems. All parts of the sampled seedlings were oven-dried at 85°C for 24 h, transferred to desiccators, and weighed after cooling.

Stratified clipping method

The stratified clipping method (Monsi and Saeki 1953) was applied to 2-year-old seedlings from October 28, 1981, through October 18, 1982, on a total of 24 occasions. Stratified clipping was conducted at monthly intervals in October 1981 and 1982 and at semi-monthly intervals from November 1981 to September 1982. Overall, 10 seedlings were subjected to stratified clipping at each sampling time from October 1981 to September 1982, and 15 seedlings were harvested in October 1982, totaling 256 seedlings.

At each clipping time, the above-ground parts of the sampled seedlings were divided into leaves, stems, and branches in each 4-cm (from October 1981 to June 1982) or 6-cm (from July 1982 to October 1982) horizontal layer. The sorted plant parts collected in each horizontal layer were oven-dried at 85°C for 24 h, transferred to desiccators, and weighed after cooling.

Model descriptions

Relationships of the cumulative leaf mass $[F(z)]$ with the density of non-photosynthetic organs $[C(z)]$ and sapwood area $[S_s(z)]$

The pipe-model theory proposed by Shinozaki et al. (1964a, b) empirically demonstrated that the $C(z)$ (mass tree⁻¹ length⁻¹; i.e., stems and branches) per tree in terms of biomass above the level at a certain distance (length) from the top of the crown $[z]$ is proportional to the $F(z)$ (mass tree⁻¹) above the z horizon.

In the present model, the relationship between $F(z)$ and $C(z)$ is fitted to a non-rectangular hyperbola, which is often used to describe the rate of single-leaf gross photosynthesis (Thornley 1976; Johnson and Thornley 1984). The non-rectangular hyperbola is expressed as the lower root of the quadratic equation:

$$\theta F(z)^2 - (\alpha C(z) + F_{max}) F(z) + \alpha C(z) F_{max} = 0$$

1

for which:

$$F(z) = \frac{1}{2\theta} \left(\alpha C(z) + F_{max} - \sqrt{(\alpha C(z) + F_{max})^2 - 4\theta \alpha C(z) F_{max}} \right)$$

2

where α is the initial slope of the curve (cm), F_{max} is the limiting value of $F(z)$ at the saturation limit of $C(z)$ (g seedling⁻¹), and θ is a dimensionless parameter indicating the convexity of the curve ($0 \leq \theta \leq 1$). Ogawa (2015) successfully described the $F(z)$ – $C(z)$ relationship given by Eq. (4) for adult trees of several different species by using Eq. (2). In this study, whether Eq. (2) is also applicable to tree seedlings will be examined, including another case such as Eqs. (3) as well as Eq. (4).

For $\theta = 0$, Eq. (1) reduces to the rectangular hyperbola:

$$F(z) = \frac{\alpha C(z) F_{max}}{\alpha C(z) + F_{max}} = \alpha \left(1 - \frac{F(z)}{F_{max}} \right) C(z) \quad (3)$$

In the special case in which the curve of the non-rectangular hyperbola (Eq. 2) does not converge to fit the data, Eq. (2) for $\theta = 0$ or the rectangular hyperbola (Eq. 3) was fitted rather than the non-rectangular hyperbola for $0 < \theta < 1$.

When $\theta = 1$, the following limiting response is obtained:

$$F(z) = \begin{cases} \alpha C(z), & 0 \leq C(z) \leq \frac{F_{max}}{\alpha} \\ F_{max}, & C(z) > \frac{F_{max}}{\alpha} \end{cases}$$

4

Intermediate values of θ generate response curves lying between these two extremes. The extreme case of Eq. (4) corresponds to the basic concept of the pipe-model theory proposed by Shinozaki et al. (1963a), with α and F_{max} defined as the specific pipe length and the total leaf mass of a tree, respectively.

According to Ogawa (2015), the $C(z)$ at a given depth z is expressed as follows:

$$C(z) = \sigma(z) S(z)$$

5

where $S(z)$ and $\sigma(z)$ are the cross-sectional area of the non-photosynthetic organs and the wood density at depth z , respectively.

If the proportion of bark area at depth z is assumed to be negligible and the sapwood area and the proportional heartwood area are represented by $S_S(z)$ and $\eta(z)$, respectively, $S(z)$ is determined as:

$$S(z) = \frac{1}{1 - \eta(z)} S_S(z)$$

6

After combining Eqs. (5) and (6), Eq. (4) can be rewritten as:

$$F(z) = \alpha \sigma(z) \frac{1}{1 - \eta(z)} S_S(z)$$

7

Eq. (7) indicates that $F(z)$ is proportional to $S_S(z)$, as in Eq. (4), if $\eta(z)$ is constant, whereas $F(z)$ is not proportional to $S_S(z)$ if $\eta(z)$ is not constant.

Allometric relationship between leaf mass (m_L) and the square of stem diameter at the crown base (D_B^2)

As $S(z)$ is the cross-sectional area of the non-photosynthetic organs at depth z , $S(z) = S(z^*)$ at a depth of z^* from the top of the crown (i.e., the crown base height), which can be expressed as follows:

$$S(z^*) = \frac{\pi}{4} D_B^2$$

8

where D_B is the stem diameter at the crown base.

Considering Eqs. (5) and (8), the following relationship between tree $m_L (= F(z^*))$ and D_B^2 can be derived from the two extremes of Eq. (3) for $\theta = 0$ and Eq. (4) for $\theta = 1$:

$$m_L = \frac{\pi}{4} \alpha \left(1 - \frac{m_L}{F_{max}} \right) \sigma(z^*) D_B^2$$

9

$$m_L = \frac{\pi}{4} \alpha \sigma(z^*) D_B^2$$

10

where α in Eq. (10) is equal to the specific pipe length (L) because the $F(z)-C(z)$ relationship described by Eq. (4) is linear. At intermediate values of θ , namely $0 < \theta < 1$, Eq. (2) is rewritten as the following $m_L-D_B^2$ relation:

$$m_L = \frac{1}{2\theta} \left(\frac{\pi}{4} \alpha \sigma(z^*) D_B^2 + F_{max} - \sqrt{\left(\frac{\pi}{4} \alpha \sigma(z^*) D_B^2 + F_{max} \right)^2 - \pi F_{max} \alpha \sigma(z^*) D_B^2} \right)$$

11

If the terms $\alpha \left(1 - \frac{m_L}{F_{max}} \right) \sigma(z^*)$ in Eq. (9) and $\alpha \sigma(z^*)$ in Eq. (10) are constant, m_L scales as D_B^2 . In contrast, in the range of θ between 0 and 1, the allometric scaling relation between m_L and D_B^2 is not represented by Eq. (11).

Regression analysis

The bivariate relationship, of $m_L-D_B^2$ (Eq. 9 or 10) was analyzed with standardized major axis (SMA) regression (Warton et al. 2006) and ordinary least squares (OLS) regression using the smatr package of R (v. 4.1.2, R Core Development Team, 2021). Significant differences among power (i.e., scaling) exponents were based on 95% confidence intervals (CIs).

Fitting of the nonlinear equation (Eq. 2) to the data was performed using KaleidaGraph software (v. 5.0.2, Synergy Software, Reading, PA), which is based on the Levenberg-Marquardt algorithm (Press et al. 1992), and the coefficient of determination (R^2) was used to test for goodness of fit.

Results

F(z)–C(z) relation

Over the one-year experimental period, $F(z)–C(z)$ relations for 2-year-old seedlings were fitted ($R^2 = 0.783–0.993$) to a non-rectangular hyperbola using Eq. (2) across the total range of convexity θ , including the two extremes expressed in Eq. (3) for $\theta = 0$ and Eq. (4) for $\theta = 1$ (Fig. 1), while approximation for adult trees employs only Eq. (4) (cf. Ogawa 2015). The relationship between θ and D_B^2 showed scatter in both season and seedling size (Fig. 2), and thus whether the degree of curvature in Eq. (2) depends on seedling size remains unclear.

m_L–D_B² allometry

The allometric relationship between m_L and D_B^2 can be regressed as a single line on log-log coordinates for the whole dataset including both 1-year-old and 2-year-old seedlings (Ogawa 1989) along with adult trees (Hagihara et al. 1993) (Fig. 3). The scaling exponent is 1.155 with a 95% CI of 1.144 to 1.166 for SMA and 1.142 with a 95% CI of 1.131 to 1.153 for OLS regression, which are significantly higher than unity.

When regressing the $m_L–D_B^2$ allometry solely for adult trees, in contrast, the regression line had a scaling exponent of 1.273 with a 95% CI of 1.179 to 1.375 for SMA and 1.226 with a 95% CI of 1.128 to 1.324 for OLS, and was situated below the observed data for seedlings. The higher values of m_L per D_B^2 observed in seedlings indicates that seedlings have more leaves per stem cross-sectional area at the crown base than adult trees, as the stems of seedlings are mostly composed of sapwood, which is related to the assemblage of living pipes connected to the leaves.

The difference in $m_L–D_B^2$ allometry between seedlings and adult trees indicates that the applicability of the pipe-model theory to seedlings may differ from that for adult trees. In addition to the allometric regression, the scatter of the observed data is higher for seedlings than adult trees, although the number of data points is much greater for seedlings ($n = 918$) than young and adult trees ($n = 52$). If the pipe-model theory was common to both seedlings and adult trees, no such differences in the allometric regression and data scattering would be observed.

Discussion

Generalization of the pipe-model theory

The basic concept underlying the pipe-model theory is proportionality between $F(z)$ and $C(z)$, as expressed in Eq. (4) (Shinozaki et al. 1963a). For seedlings of *C. obtusa*, some seedlings exhibit the proportionality represented by Eq. (4), while others show no such proportionality, indicating that the pipe-model theory does not cover the specific properties of seedlings. The $F(z)–C(z)$ relation in adult trees is

expressed as Eq. (4) (Ogawa 2015), and the present study clarifies that the $F(z) - C(z)$ relationship can be represented by a non-rectangular hyperbola (Eq. 2) for adult trees as well as seedlings over the whole range of θ from 0 to 1.

As the degree of the curvature described in Eq. (2) did not depend on seedling size (Fig. 2), the change trends of θ may not explain the process of crown development. However, considering that the present values of θ covered the full range from 0 to 1, a simple example can be explored by varying θ values (= 0, 0.5, 0.7, 0.9, 0.95, and 1) while the values of α and $F_{\max}$ are fixed to 100 cm and 10 g seedling⁻¹, respectively (Fig. 4). Thus, as the crown develops during seedling growth, the θ of the curve approaches unity, as described for adult trees (Shinozaki et al. 1963a, b).

As $S(z)$ is proportional to $C(z)$ if $\alpha(z)$ is constant (Eq. 5), the difference between the linear ($\theta = 1$) and curvilinear ($\theta \neq 1$) in $F(z) - C(z)$ relationships corresponds to the difference in the proportion of sapwood area in the studied seedlings (Fig. 5). Thus, the proportional sapwood area is larger for seedlings with linear $F(z) - C(z)$ relationships than seedlings with curvilinear $F(z) - C(z)$ relationships.

The proportional sapwood area directly influences the $F(z) - C(z)$ relationship, as indicated by Eq. (7). Even if the $F(z) - C(z)$ relationship is linear (Eq. 4), that between $F(z)$ and $S_S(z)$ becomes curvilinear if the proportional sapwood area $\eta(z)$ is not constant but varies through the tree crown (cf. Eq. 7). The proportional sapwood area varied vertically within the tree (Longuetaud et al. 2006). Whitehead et al. (1984) reported that the relationship between $F(z)$ and $S_S(z)$ throughout the tree crown is somewhat curvilinear for both Sitka spruce (*Picea sitchensis* [Bong.] Carr.) and lodgepole pine (*Pinus contorta* Dougl.).

Eq. (7) indicates that even if the $F(z) - C(z)$ relation is linear (Eq. 4), that between $F(z)$ and $S_S(z)$ becomes curvilinear when the proportional sapwood area $\eta(z)$ is variable. In this case, where $\eta(z)$ is non-constant, the same phenomenon of non-linear relationship found in the trunk diameter profile can be explained (Aye et al. 2022). Previous studies have observed that sapwood remains alive for decades (cf. Lehnebach et al. 2018). As it seems unlikely that there would be heartwood in seedlings, the $F(z) - C(z)$ relationship tends to become curvilinear based on Eq. (7). Therefore, curvilinearity in the $F(z) - C(z)$ relationships expressed in Eqs. (2) and (3) appears to reflect variations in the sapwood proportion through the seedling crown.

Scattering of data in the allometric scaling of leaf mass for tree seedlings

Ogawa (2015) reported that m_L scales with D_B^2 for adult trees of *C. obtusa*, assuming that the term $\alpha \sigma(z^*)$ is constant in Eq. (10). However, the present study showed that the $m_L - D_B^2$ relation is represented by three functions for seedlings of *C. obtusa*, namely the scaling relations of Eqs. (9) and (10) and the non-rectangular equation of Eq. (11). If the term $\alpha \left(1 - \frac{m_L}{F_{\max}}\right) \sigma(z^*)$ is constant, Eq. (9)

represents an isometric function of $m_L - D_B^2$ relation equivalent to Eq. (10), while Eq. (11) does not show isometry between m_L and D_B^2 . Therefore, seedlings showed greater scatter than adult trees in the diagram of $m_L - D_B^2$ allometry (Fig. 3).

Ogawa (2022) proposed an allometric scaling model for m_L based on the assumption of size dependence in the proportion of sapwood area at the crown base. According to his model on allometric scaling of m_L , the scatter of data in the present study results from differences in proportional sapwood area at the crown base among seedlings.

From the perspective of tree hydraulic architecture, the classical pipe-model theory developed by Shinozaki et al. (1964a, b) relies on the assumption that the basic pipe element of the plant vascular system is cylindrical (i.e., the conduit diameter does not change axially). However, a major characteristic of tree hydraulic systems is tip-base widening of the conduits, which has been established both theoretically (West et al. 1999; Koçillari et al. 2021) and experimentally (Anfodillo et al. 2006; Petit and Anfodillo 2009; Savage et al. 2010; Olson et al. 2014, 2018, 2021). This universal pattern is likely to have a significant impact on the relationship between m_L and stem diameter. However, the pattern in which juvenile wood above the crown base transitions into mature wood near or below the crown base is notably complex (Burkhart and Tomé 2012).

Declarations

Conflict of interest

None declared.

Author Contribution

The author (K.O.) designed the research, performed the experiments, collected and analyzed the data, and wrote the paper.

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Tables

Table 1 is available in the Supplementary Files section.

Figures

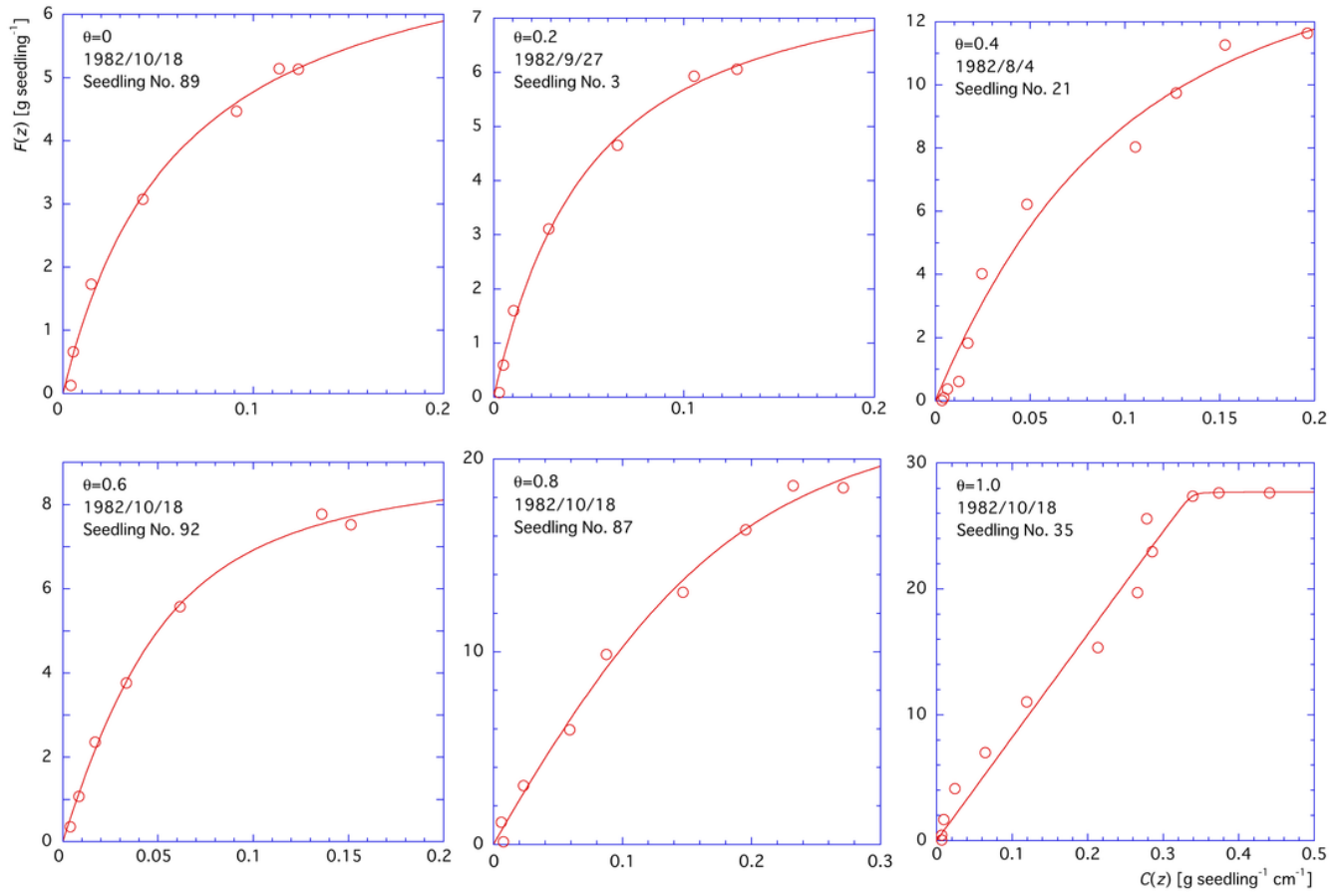


Figure 1

Examples of $F(z) - C(z)$ relationships at $q = 0, 0.2, 0.4, 0.6, 0.8$, and 1.0 obtained using Eq. (2) for two-year-old seedlings. The extremes of $q = 0$ and $q = 1.0$ are presented in Eqs. (3) and Eq. (4), respectively.

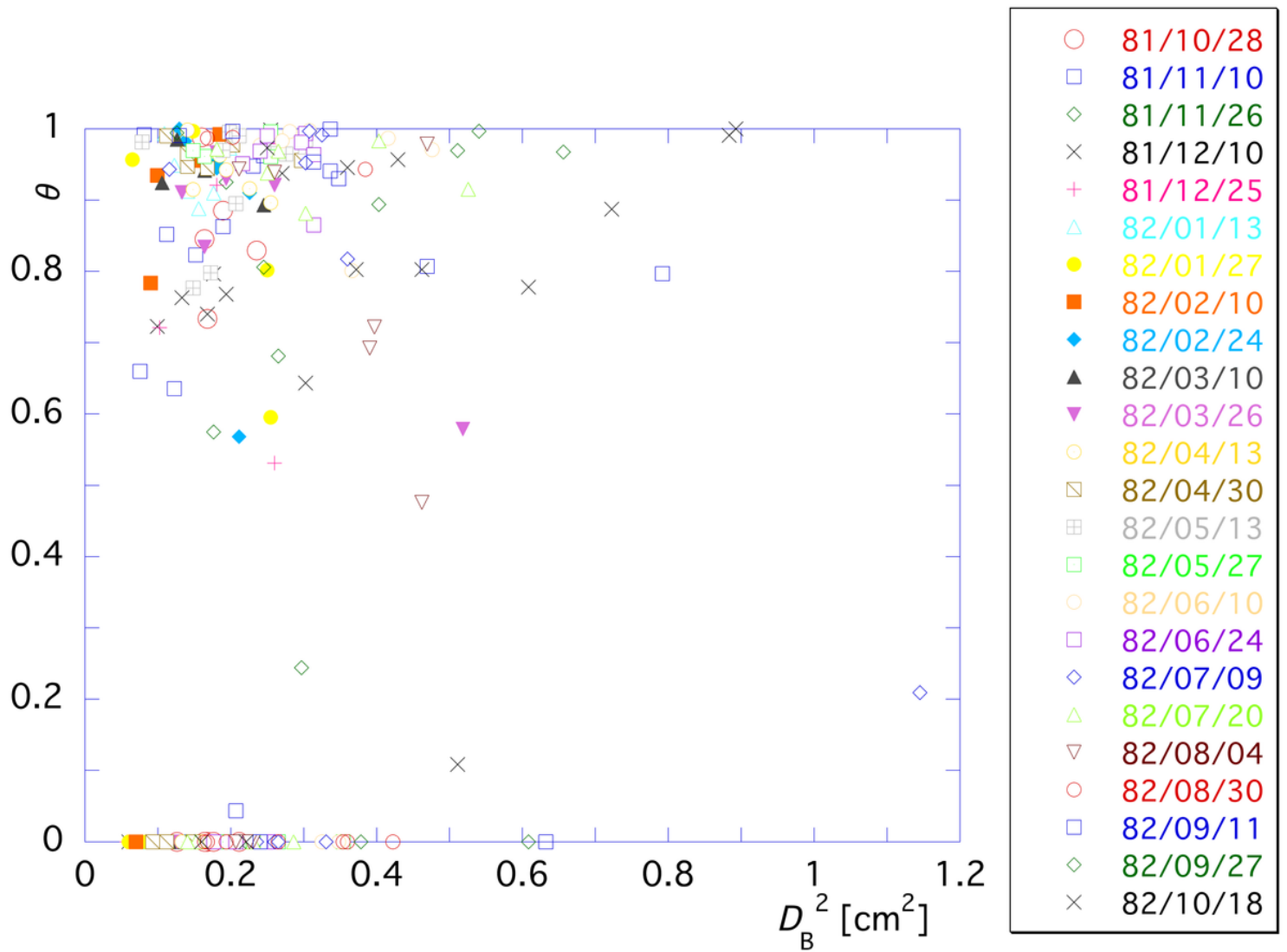


Figure 2

Scattered relationship between q in Eq. (2) and D_B^2 over the one-year experimental period of Oct. 28, 1981, to Oct. 18, 1982, for two-year-old seedlings ($n = 256$).

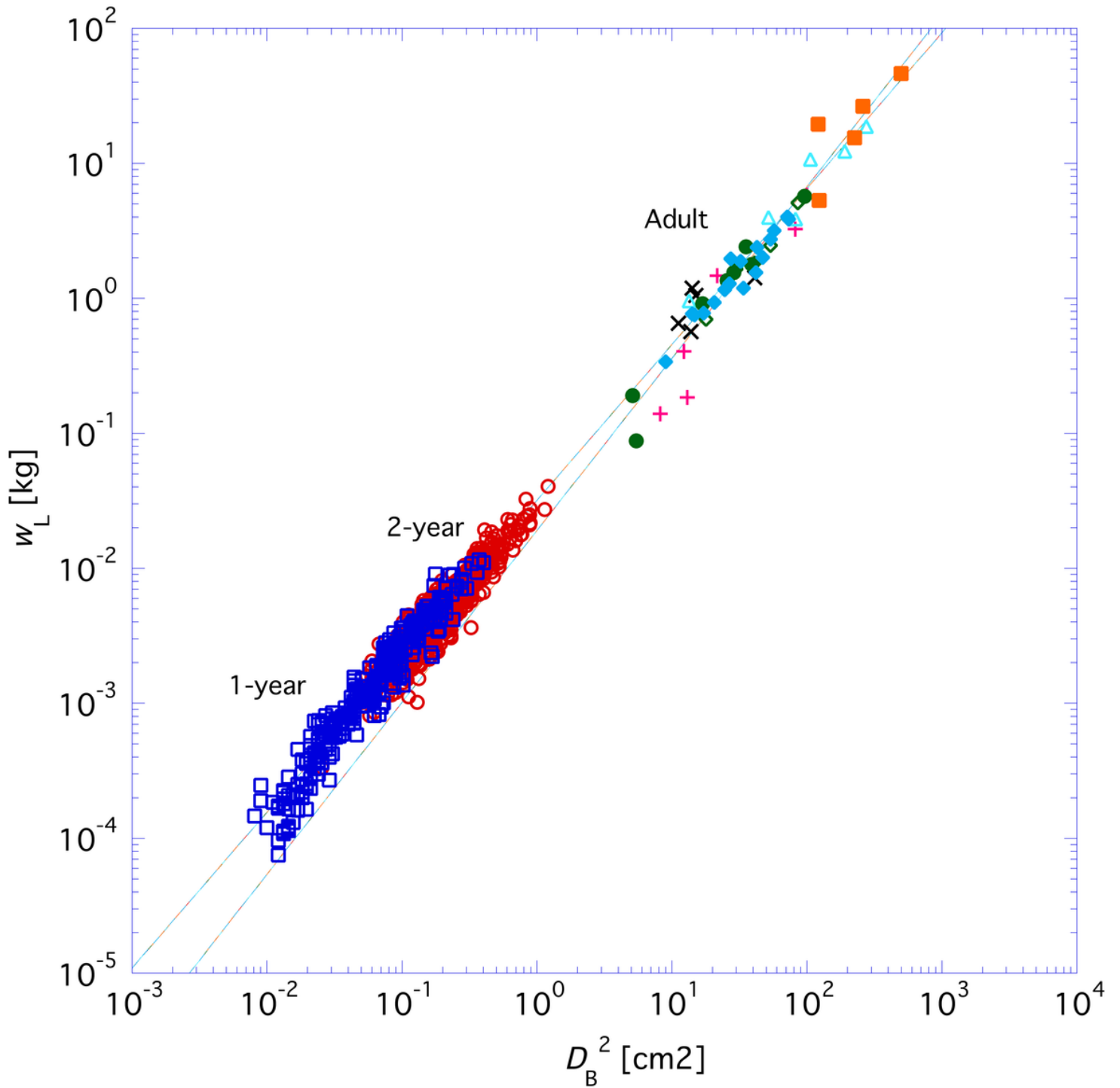


Figure 3

Allometric relationships between m_L and D_B^2 for one-year-old ($n = 300$) and two-year-old ($n = 618$) seedlings and adult trees ($n = 52$; Hagihara et al. 1993). The regression line in the diagram follows the equation $y = 0.0319x^{1.155}$ (scaling exponent 95% CI, 1.144–1.166; $R^2 = 0.978$; $P < 0.001$) for the SMA regression method. The equation obtained using the OLS regression method is $y = 0.0311x^{1.142}$ (scaling exponent 95% CI, 1.131–1.153; $R^2 = 0.978$; $P < 0.001$). The regression equation for only adult trees is $y = 0.0191x^{1.273}$ (scaling exponent 95% CI, 1.179–1.375; $R^2 = 0.927$; $P < 0.001$) for the SMA regression

method (Ogawa 2022). The equation obtained with the OLS regression method for only adult trees is $y = 0.0125x^{1.206}$ (scaling exponent 95% CI, 1.091–1.333; $R^2 = 0.875$; $P < 0.001$).

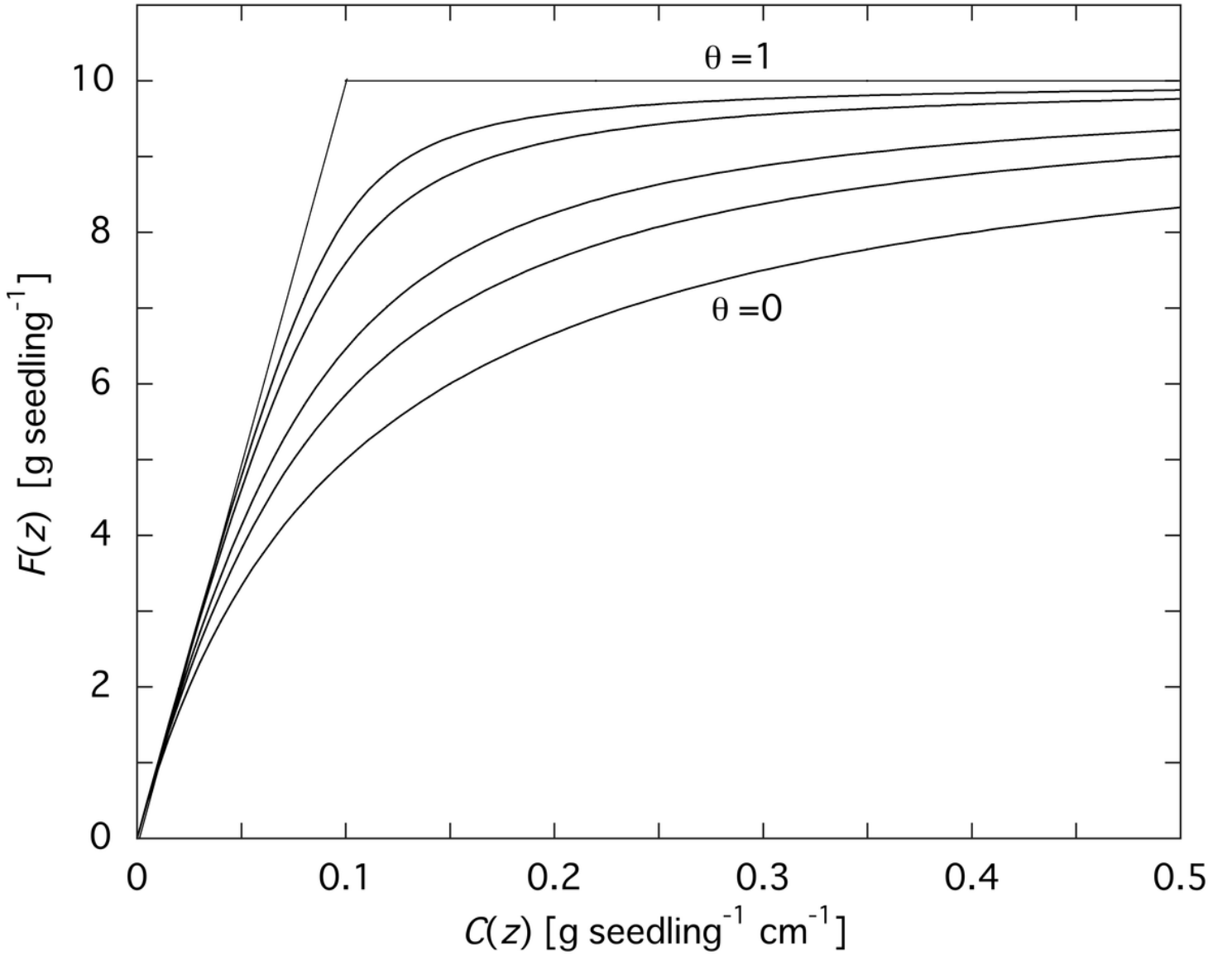


Figure 4

Non-rectangular hyperbola describing the $F(z) - C(z)$ relationship at various values of q in Eq. (2). $q = 0$ (rectangular hyperbola, Eq. 3) and $q = 1$ (Eq. 4) are labeled and the intermediate curves show $q = 0.5, 0.7, 0.9$, and 0.95 . Parameters are $a = 100$ cm and $F_{\max} = 10$ g seedling⁻¹.

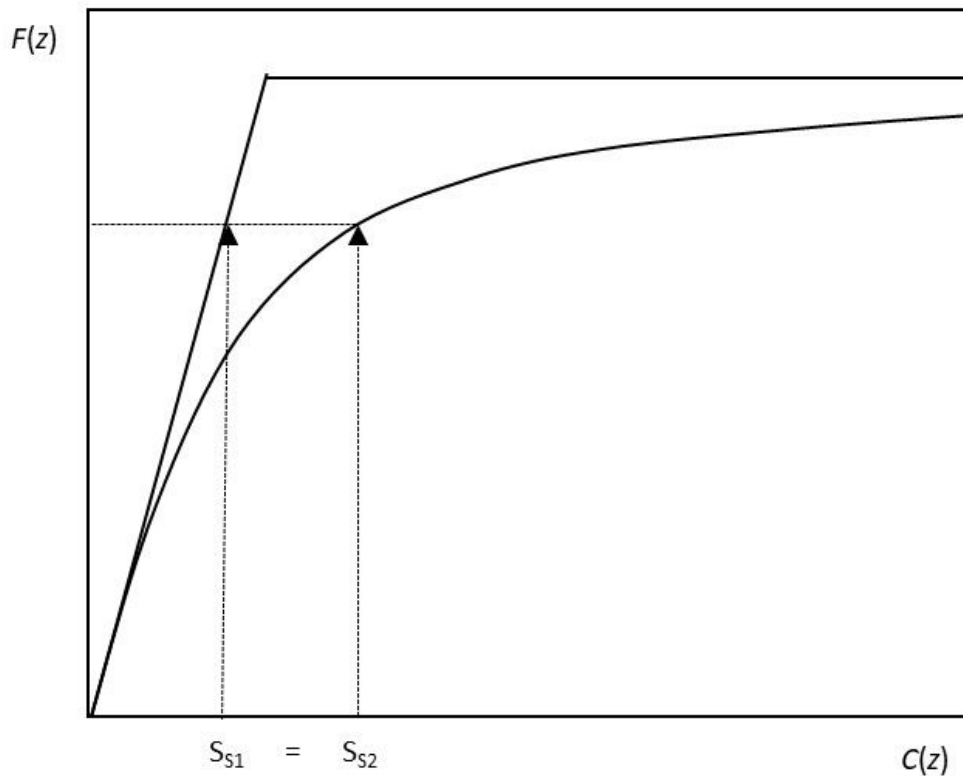


Figure 5

Diagrammatic representation of the difference between linear ($\theta = 1$) and curvilinear ($\theta \neq 1$) in $F(z) - C(z)$ relationships for differences in proportional sapwood area. The symbol S_s indicates the cross-sectional area of sapwood, as $C(z)$ corresponds to the cross-sectional area of woody organs such as stems and branches (cf. Ogawa 2015).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [PipeModelSeedlingTable1.xlsx](#)