

1 **An allometric study of the contribution of prostrate stems to belowground development of**
2 **juvenile *Fagus crenata***

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15 **Abstract:** Prostrate stems represent an important morphological component of *Fagus*
16 *crenata* (Siebold’s beech). This unique stem-bending growth strategy has led to the
17 dominance of this tree species in regions with heavy snowfall along the Sea of Japan. We
18 investigated the early-stage aboveground–belowground dynamics of *F. crenata* by
19 applying allometric scaling theory to analyze morphological development in saplings
20 (aged 3–20 years). Samples were collected from 25 trees in three forests in Nagano,
21 central Japan. The scaling exponent (b) demonstrated an increase in the fraction of
22 aboveground biomass (i.e., dry mass) in relation to the overall surface area (aboveground,
23 $b = 0.748$; belowground, $b = 0.626$) and biomass (aboveground, $b = 1.087$;
24 belowground, $b = 0.983$). These values are highly consistent with recent field
25 observations by other researchers. Aboveground biomass growth was supported by the
26 increasing role of prostrate stems in belowground development ($b = 1.114$). Despite its
27 extension belowground, the growth properties of the prostrate stem may be identical to
28 those of shoots, as both are directly influenced by nutrient sources above the germination
29 point. Our findings highlight the significance of the prostrate stem in supporting beech
30 survival in areas with heavy snowfall.

31 **Keywords:** allometric scaling theory; prostrate stems; beech sapling; biomass allocation;
32 snowfall tolerance

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34 Introduction

35 Prostrate stems are a unique morphological trait of Siebold's beech (*Fagus crenata* Blume),
 36 which bends its trunk in response to heavy snowfall along the coasts of the Sea of Japan
 37 (Shimano 2006). Mature beech trees have relatively high flexural strength against bending stress
 38 (Miyashita et al. 2020), enabling them to deform their trunks against high snow pressure that
 39 other species fail to tolerate. In juvenile beech trees, the trunk can bend below the snow line and
 40 rise again as the snow melts the following spring. This seasonal bending causes the trees to
 41 develop a permanent curvature at the base of the trunk. Other tall deciduous tree species do not
 42 develop this bending morphology, and therefore break upon exposure to high snowfall pressure
 43 near the Sea of Japan (Homma 1997). Therefore, forest ecologists have treated prostrate stems
 44 as a potential mechanism explaining the dominance of *F. crenata* in beech forests along the Sea
 45 of Japan (Shimano 2006). Despite accumulating studies on prostrate stems in mature stands,
 46 their development in the early life stages of beech trees has not been studied extensively.

47 Allometric scaling theory is an emerging method in ecology that systematically
 48 describes the transformation of body or plant parts across life stages (West et al. 1997). This
 49 method permits analysis of the scaling of plant organ size (Y) with overall plant mass (X),
 50 through the formula $Y = aX^b$, where a is a normalization constant and b is a scaling exponent.
 51 This theory was pioneered through the analytical and empirical demonstration of an
 52 interspecific scaling relationship of biomass partitioning into leaves, stems, and roots across
 53 nine orders of magnitude of plant mass across diverse communities (Enquist and Niklas 2002).
 54 The authors predicted and observed that shoot vs. root distribution in woody angiosperms was
 55 allometrically related, with a scaling exponent of $b = 1.10 \pm 0.019$ (Enquist and Niklas
 56 2002). Positive allometry among angiosperms suggests that trees older than one year devote
 57 more resources to aboveground growth as they mature (Poorter et al. 2012). The scaling
 58 exponent has been shown to be largely consistent across sites with differential selection for
 59 adaptations to diverse environmental conditions (e.g., site age, absolute latitude, elevation, or
 60 number of species within the community). Scaling theory is founded on the first principles of

statistical mechanics and has been thoroughly tested through field observation; it complements traditional shoot:root ratios by capturing the actual functional relationships characterizing biomass allocation among organ types. The theory is based on a rigorous theoretical underpinning and provides a viable exponent baseline for the analysis of biomass partitioning trends in *F. crenata* (Marquet et al. 2014).

Kurosawa et al. (2023) applied allometric scaling to demonstrate that *F. crenata* allocates metabolic products to its roots during early growth, gradually shifting allocation towards shoots over time; when the whole plant fresh mass exceeded 0.00108 kg, the scaling exponent b for shoots increased from 0.09 to 1.13, whereas that for roots decreased from 2.5 to 0.825. Thus, *F. crenata* initially invests metabolic production into root growth to enhance water uptake and minimize seedling death (Kurosawa et al. 2021). As the plant matures, it shifts energy allocation to shoot growth to transition energy intake from roots to photosynthesis.

Morphological indicators of plants can also be used to analyze the unique survival strategy by which juvenile beech trees persist through the critical early growth period (Bardgett et al. 2014). In this study, we applied allometric scaling methods to analyze biomass partitioning across shoots, prostrate stems, and belowground roots in beech saplings by systematically comparing scaling exponents for juvenile *F. crenata* morphometrics based on samples collected in this study and previous field observations of juvenile beech growth.

Methods

In October and November 2017, we collected a total of 25 *F. crenata* saplings (height, 8.5–58 cm; age, 2–17 years) from three mature beech stands in Nagano Prefecture, central Japan. The first stand is located in Karayama (36°59'N, 138°27'E, 540 m a.s.l.), with a maximum snow depth (MSD) of 304 cm, calculated as an average of measurements taken by H. Ida from 2004 to 2017; the second stand is located on Mt. Hijiri (36°29'N, 138°02'E, 1180 m a.s.l.), with an MSD of 86 cm; and the third stand is in Ohbora (36°30'N, 138°19'E, 1253 m a.s.l.), with an MSD of 59 cm. We collected 15 saplings in Karayama and 5 saplings each on Mt. Hijiri and in

Ohbora. Due to low sapling density and isolation, we refrained from extensive sampling in the latter two stands for conservation reasons. We selected the Mt. Hijiri and Mt. Karayama stands because they are representative of haplotype B populations, which receive heavy snowfall near the Sea of Japan, whereas the Ohbora stand belongs to haplotype F, which inhabits low-snowfall regions near the Pacific Ocean (Koyama et al. 2012). Initially, we aimed to consider the effects of genetic differences on divergent morphological adaptation by *F. crenata* to different maximum snow depths. However, due to our limited sample sizes, data collected from all sites were pooled for analysis.

We used a high-resolution digital caliper to measure the following aboveground traits during sample collection: stem length, stem height, stem inclination, and stem diameter at ground level. We also recorded the direction and angle of the terrain. Following these measurements, we excavated each sample from the ground, including the main roots. All samples were transported to the laboratory for air-drying at room temperature, and then we removed all leaves and recorded the belowground morphology and age of each sample. For each sample, laboratory measurements included that from the tip of the stem to the end of the taproot, the length of the taproot along the slope, the length of the taproot perpendicular to the slope, and the average stem diameter at the germination point, calculated as the average of length in two orthogonal directions. We determined the germination point by visually identifying the taproot thickness and shape, and the presence of fine roots. Based on measurements of the stem and root length and diameter at the origin, we computed the cylindrical surface area of the shoots, prostrate stems, and roots (Mori and Hagihara 1988).

Next, we cut the samples into three parts (shoots, prostrate stems, and roots below the germination point) and measured the dry mass of each part. Subsequently, we dried one sample from each site at 80°C for 72 hours to measure the dry mass and determine the average moisture content. Finally, we calculated the dry mass of all samples by multiplying the wet mass by the average moisture content.

In addition, we counted bud scale scars and tree rings to infer the ages of the whole tree and each organ. We estimated the age of the whole tree by counting the scars and rings at the

germination point, and we measured the age of shoots with reference to the scars and rings at the ground origin. As scars were not present on prostrate stems, we inferred their ages by subtracting the ring counts between the ground origin and germination point.

We used R Studio v4.1.3 to plot the ranged major axis regression to evaluate the scaling relationships between the biomass of each plant part and the whole-plant biomass, as well as the derived surface area (Sibly et al. 2012). We also simulated coefficients (1000 iterations per value) to calculate confidence intervals to quantify the level of uncertainty for exponents and normalization constants (King et al. 2000).

Result

[Table 1 near here]

All samples were collected in the early stage of transition from seedlings to mature trees, with a median age of 12 years (range, 3–20 years). Whole-plant dry mass ranged from 0.0001169 to 0.0194953 kg ($n = 25$; Table 1).

[Figure 1 near here]

[Table 2 near here]

Biomass and surface area partitioning between above- and belowground plant parts are illustrated in Figure 1, and the data are presented in Table 2. The surface area scaling of both above- and belowground surface area showed negative allometric relationships with whole-plant mass (i.e., $b < 1$; aboveground, $b = 0.748$; belowground, $b = 0.626$), whereas biomass scaled nearly isometrically (i.e., $b = 1$; aboveground, $b = 1.087$; belowground, $b = 0.983$). For both surface area and biomass, aboveground scaling was significantly higher than belowground scaling, based on a 95% confidence interval (CI). The normalization constants for surface area and biomass were higher in magnitude for belowground plant parts than for aboveground parts.

Prostrate stems constituted a significant portion of the belowground mass of young beech trees (Figure 1c). Compared to roots, prostrate stems alone produced a higher log (a) intercept and scaling exponent b . The biomass of shoots and prostrate stems showed

consistently positive allometric scaling (shoots, $b = 1.087$, 95% CI = 0.982–1.206, $R^2 = 0.946$; prostrate stems, $b = 1.114$, 95% CI = 0.956–1.293, $R^2 = 0.892$), whereas that of roots showed a lower scaling exponent ($b = 0.860$, 95% CI = 0.717–1.032, $R^2 = 0.851$). There were no significant differences in shoot and prostrate stem biomass scaling, based on the 95% CI. The normalization constants of prostrate stems and shoots were very similar (prostrate stems, $a = -0.174$; shoots, $a = -0.126$), which indicated their matched growth across whole-plant size. The scaling exponents indicated isometric scaling of shoots and prostrate stems, and that a dominant portion of the whole-plant dry mass was below the germination point (Figure 1c). The negative allometric relationship between root and whole-plant mass indicated that roots continually decrease their fraction as trees grow larger. This decreasing root fraction is compensated by consistent growth of the prostrate stem fraction. This significant scaling relationship is the main contributing factor to the apparently higher proportions of belowground surface area and biomass in young beech trees.

Discussion

We confirmed that the prostrate stems previously reported among mature beech trees are also present in young *F. crenata* trees. When we decomposed the belowground component further into roots and prostrate stems, we found that such stems constitute a large portion of beech belowground development. The scaling exponent of these stems ($b = 1.114$) was significantly higher than that for roots ($b = 0.860$), which suggests that in addition to root growth below the germination point, submersion of the trunk within the soil is essential to the belowground support of *F. crenata* trees. Furthermore, the allometric relationship between shoots and prostrate stems showed no significant difference at the 95% confidence interval (shoots, $a = -0.174$, $b = 1.087$; prostrate stems, $a = -0.125$, $b = 1.114$). This suggests that despite their growth belowground, prostrate stems may share key developmental traits with shoots. Kurosawa et al. (2023) reported similar results, with shoot mass exhibiting a much higher scaling exponent than root mass after a critical metabolic transition (shoots, $b = 1.13$;

170 roots, $b = 0.825$). After consuming seed nutrients, the beech seedling first undergoes rapid root
 171 expansion to forage water and nutrients from the soil, and then develop shoots that rely
 172 primarily on photosynthesis. When the beech bends its stem into the soil, it rapidly develops
 173 adventitious roots around the ground origin to counteract additional pressure caused by
 174 deformation. This rapid growth pattern is strikingly different from that of the original roots.
 175 Similarly, our results suggest that prostrate stems maintain an identical growth pattern to shoots,
 176 which markedly differs from that of roots. The consistent positive allometric relationship
 177 detected in this study contributes a significant portion of the belowground composition of the
 178 whole plant, supporting the belowground development of young beech trees.

179 Young beech trees in high snowfall regions are resilient against snow pressure due to
 180 their unusually soft trunks, which are easily deformed (Meguro et al. 2015). However, as trees
 181 mature through secondary growth, they become less flexural, and prostrate stems reform within
 182 straight bark (Higuchi and Onodera 1993). Therefore, the soft bark of young trees molds an
 183 initial morphological foundation for the mature trees to also deform when exposed to high snow
 184 pressure. In addition, trees are relatively small in the early growth stage, and become larger
 185 (Weiner and Thomas 2001). Potentially, young beech trees cope with this drastic aboveground
 186 mass increase by bending growing shoots back into the soil to reinforce their physical
 187 foundation.

188 Given the small sample sizes that we collected in Nagano, increasing the number of
 189 samples across haplotypes would illuminate the role of prostrate stems under contrasting snow
 190 conditions. Furthermore, developing better methods to exhaustively collect the total biomass of
 191 samples is critical to the integrity of future aboveground–belowground analyses. The
 192 belowground biomass of our samples was approximately the same as that determined by
 193 Kurosawa et al. (2023), although our samples were older, which suggests that we may have
 194 missed some fine roots in our sample collection. Another important consideration is the
 195 inclusion of leaf surface area and mass. Leaves are fundamental components of allometric
 196 scaling analysis, as their photosynthetic role significantly shapes the overall growth of plants.

197 In summary, our findings demonstrate the important role of prostrate stems in the
198 overall biomass and surface area of *F. crenata* during early maturity. Despite their extension
199 underground, these stems exhibited identical growth properties to shoots, possibly because they
200 are influenced by nutrient sources above the germination point. Our results highlight the key
201 morphology of prostrate stems in supporting *F. crenata* survival in forest near the Sea of Japan.
202 Elucidating the aboveground–belowground dynamics of young *F. crenata* trees will contribute
203 to the formulation of a mechanistic understanding of the dominance of *F. crenata* in coastal
204 regions of Japan.

205

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211

212 **Disclosure statement**

213 The authors report there are no competing interests to declare.

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215 **Data availability statement**

216 The data that support the findings of this study are openly available in Figshare at
217 <https://figshare.com/s/19ea87265ff95fb9c4cd>.

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219 **References**

220 Bardgett RD, Mommer L, De Vries FT. 2014. Going underground: root traits as drivers of
221 ecosystem processes. *Trends Ecol Evol.* 29(12):692–699. doi: [10.1016/j.tree.2014.10.006](https://doi.org/10.1016/j.tree.2014.10.006).

222 Chapman N, Miller AJ, Lindsey K, Whalley WR. 2012. Roots, water, and nutrient acquisition:
223 let's get physical. *Trends Plant Sci.* 17(12):701–710. doi:
224 doi.org/10.1016/j.tplants.2012.08.001.

225 Enquist BJ, Niklas KJ. 2002. Global allocation rules for patterns of biomass partitioning in seed
226 plants. *Science*. 295(5559):1517–1520. doi: doi.org/10.1126/science.1066360.

227 Higuchi H, Onodera H. 1993. The snow hardness of deciduous tree species (I) Characteristics
228 of basal bending of several deciduous trees. *J Jpn For Soc.* 75(1):56–59. doi:
229 [10.11519/jjfs1953.75.1_56](https://doi.org/10.11519/jjfs1953.75.1_56).

230 Homma K. 1997. Effects of snow pressure on growth form and life history of tree species in
231 Japanese beech forest. *J Veg Sci.* 8(6):781–788. doi: [/10.2307/3237022](https://doi.org/10.2307/3237022).

232 King G, Tomz M, Wittenberg J. 2000. Making the most of statistical analyses: Improving
233 interpretation and presentation. *Am J Polit Sci.*:347–361. doi: [10.3886/icpsr01255](https://doi.org/10.3886/icpsr01255)

234 Koyama Y, Takahashi M, Murauchi Y, Fukatsu E, Watanabe A, Tomaru N. 2012. Japanese
235 beech (*Fagus crenata*) plantations established from seedlings of non-native genetic
236 lineages. *J For Res.* 17(1):116–120. doi: [10.1007/s10310-011-0262-9](https://doi.org/10.1007/s10310-011-0262-9).

237 Kurosawa Y, Mori S, Wang M, Ferrio JP, Yamaji K, Koyama K, Haruma T, Doyama K. 2021.
238 Initial burst of root development with decreasing respiratory carbon cost in *Fagus crenata*
239 Blume seedlings. *Plant Species Biol.* 36(2):146–156. doi: [10.1111/1442-1984.12305](https://doi.org/10.1111/1442-1984.12305).

240 Kurosawa Y, Mori S, Wang M, Pedro Ferrio J, Nishizono T, Yamaji K, Koyama K, Haruma T,
241 Doyama K. 2023. Ontogenetic changes in root and shoot respiration, fresh mass and
242 surface area of *Fagus crenata*. *Ann Bot.* 131(2):313–322. doi: [10.1093/aob/mcac143](https://doi.org/10.1093/aob/mcac143).

243 Marquet PA, Allen AP, Brown JH, Dunne JA, Enquist BJ, Gillooly JF, Gowan PA, Green JL,
244 Harte J, Hubbell SP, others. 2014. On theory in ecology. *BioScience*. 64(8):701–710. doi:
245 [10.1093/biosci/biu098](https://doi.org/10.1093/biosci/biu098).

246 Meguro S, Suzuki S, Hayashi H. 2015. Dynamic characteristic of tree in snowy
247 environments. *Eco-Habitat: JISE Reaserch.* 21(1): 57-67. doi:
248 [10.24600/ecohabitat.21.22.1_57](https://doi.org/10.24600/ecohabitat.21.22.1_57).

249 Miyashita A, Minamino R, Sawakami K, Katsuhima T, Tateno M. 2020. Monitoring bending
250 stress of trees during a snowy period using strain gauges. Bull Glaciol Res. 38:25–38. doi:
251 [10.5331/bgr.20a01](https://doi.org/10.5331/bgr.20a01).

252 Mori S, Hagihara A. 1988. Respiration in stems of hinoki (*Chamaecyparis obtusa*) trees. J Jpn
253 For Soc. 70(11):481–487. doi: [10.1007/bf00204336](https://doi.org/10.1007/bf00204336).

254 Paz H. 2003. Root/Shoot allocation and root architecture in seedlings: Variation among forest
255 sites, microhabitats, and ecological groups1. Biotropica. 35(3):318–332. doi:
256 [10.1646/02120](https://doi.org/10.1646/02120).

257 Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to
258 leaves, stems and roots: meta-analyses of interspecific variation and environmental control.
259 New Phytol. 193(1):30–50. doi: [10.1111/j.1469-8137.2011.03952.x](https://doi.org/10.1111/j.1469-8137.2011.03952.x).

260 Shimano K. 2006. Differences in beech (*Fagus crenata*) regeneration between two types of
261 Japanese beech forest and along a snow gradient. Ecol Res. 21:651–663. doi:

262 Sibly RM, Brown JH, Kodric-Brown A. 2012. Metabolic Ecology: A Scaling Approach.
263 Hoboken (NJ): John Wiley & Sons. doi: [10.1007/s11284-006-0172-z](https://doi.org/10.1007/s11284-006-0172-z).

264 Weiner J, Thomas SC. 2001. The nature of tree growth and the "age-related decline in forest
265 productivity". Oikos. 94(2):374–376. doi: [10.1034/j.1600-0706.2001.940219.x](https://doi.org/10.1034/j.1600-0706.2001.940219.x).

266 West GB, Brown JH, Enquist BJ. 1997. A general model for the origin of allometric scaling
267 laws in biology. Science. 276(5309):122–126. doi: [10.1126/science.276.5309.122](https://doi.org/10.1126/science.276.5309.122).

269 **Figure and table captions**

270 Figure 1. Above- and belowground partitioning of (a) surface area and (b) fresh biomass. (c)
271 Scaling relationships among shoots, prostrate stems, and root mass in response to whole-plant
272 fresh mass. Straight lines represent the ranged major axis regression fit for each plant part.

273 Table 1. Mass, surface area, and age profile of the collected samples.

274 Table 2. Scaling exponents and normalization constants for above- and belowground biomass
275 partitioning. Belowground biomass is further partitioned into prostrate stems and roots below

276 the germination point.

