Differences in beech (*Fagus crenata*) regeneration between two types of Japanese beech forest

and along snow gradient

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Abstract

Differences in beech (*Fagus crenata*) regeneration were quantitatively investigated using power function analysis for the size-class (diameter at breast height, DBH) distribution and juvenile to canopy tree (J/C) ratio along a snow gradient throughout Japan. In snowy areas, all species combined, as well as *F. crenata* alone, showed constant regeneration, with parameter $b \approx -1.6$ for the power function $y = ax^b$ (x = DBH, y = density), which is related to the DBH-class distribution. A high fit of the data to the function suggests that beech regenerates constantly with self-thinning patch dynamics. Parameter a, which indicates the abundance of small trunks, was high. Furthermore, the mean J/C ratio was ≈ 8, i.e., each parent beech tree produced eight juveniles. These results suggest that beech regenerates constantly with gap dynamics in snowy beech forests on the Japan Sea side of Japan (snowy). However, the fit of *F. crenata* was lower and non-significant in some forests in less snowy areas, despite the high fit of all species combined. In these areas, the mean of a was low, and b was often near zero for *F. crenata* regressions. These results suggest that the abundance of beech was low, and self-thinning was not evident because of the initial low abundance. Moreover, the mean J/C ratio was <1.0, suggesting that juvenile density was lower than that of canopy trees. Thus, the regeneration of *F. crenata* on the Pacific Ocean side of Japan (less snowy) is rather sporadic. Less snowy conditions may promote seed desiccation, predation of beechnuts and seedlings, and water stress. Lower *F. crenata* density may also reduce predator satiation and wind pollination.

Key words: power function analysis, regeneration dynamics, DBH-class distribution, forest structure, global warming.

Introduction

Beech forests are common natural vegetation occurring in the cool temperate zone of Japan. Different types of Japanese beech (*Fagus crenata* Blume) forest occur along a snow accumulation gradient. Sasaki (1970) and Hukushima et al. (1995) divided these forests into two types: Japan Sea (JS) and Pacific Ocean (PO). JS-type beech forests occur in the northwestern part of the Japanese archipelago, facing the Japan Sea, whereas PO types occur in the south, facing the Pacific Ocean. JS-type beech forests are distributed in snowy areas and are associated with some characteristic plants of snowy areas, such as *Aucuba japonica* var. *borealis*, *Hamamelis japonica* var. *obtusata*, *Daphniphyllum macropodum* var. *humile*, *Skimmia japonica* var. *intermedia* f. *repens*, and *Sasa kurilensis* (Sasaki 1970, Hukushima et al. 1995, Shimano 1999). These forest floor shrubs, especially evergreen shrubs, can occur in the

cool temperate zone because the snow cover protects them from cold air temperatures. This type of forest is almost pure beech forest because of the elimination of other trees by snow (Kamitani 1984; Maeda et al. 1985; Onodera et al. 1995; Homma 1997; Shimano 1999, 2002). Consequently, JS-type beech forests are affected by the snow environment. In contrast, PO-type beech forests occur in less snowy areas and have many co-dominant trees (e.g., Shimano & Okitsu 1993, 1994). Other reports have described the differences in forest structure and beech dominance (e.g., Fujita 1987).

Regeneration of natural beech forests has been explained by the gap dynamics theory in Japan (Nakashizuka & Numata 1982a, b; Nakashizuka 1983, 1987; Yamamoto 1989). It is assumed that beech forests have various patches of different developmental stages, resulting in a mosaic pattern; the seedling bank regenerates with canopy gap formation; the growing saplings become canopy trees that undergo competition for space with neighboring trees; and the climax beech forest in a patch mosaic is stable as a regenerating complex. In addition, the importance of beechnut masting, feeding activity on nuts and seedlings by rodents, and simultaneous death of dwarf bamboo has been discussed (Suzuki 1989; Igarashi 1991; Miguchi 1995; Shimano & Masuzawa 1995, 1998; Tanaka 1995a; Ida & Nakagoshi 1996; Homma et al. 1999; Shimano 2002).

Many studies on beech regeneration have been conducted in pure beech forests in snowy areas on the Japan Sea side (Nakashizuka & Numata 1982a, b; Nakashizuka 1983; Yamamoto 1989). However, few quantitative reports of PO-type beech forests are available because of the decreased dominance of beech in these forests (but see Shimano & Okitsu 1993, 1994).

Some studies have indicated that beech on the PO side, i.e., the less snowy area, have low vitality (Ohba 1985; Koizumi et al. 1988). Other reports have pointed out that *F. crenata* forests are mainly distributed in snowy areas or areas that receive heavy winter precipitation (Kojima 1975; Nakanishi & Nishimoto 1981; Kure & Yoda 1984; Uemura at al. 1986; Uemura 1989; Nozaki & Okutomi 1990; Tanaka & Taoda 1996; Yagihashi et al. 2003, 2005; Matsui et al. 2004). Shimano (1998, 2002) reviewed explanations for why beech in less snowy areas does not regenerate constantly. For example, snow accumulation protects beechnuts from consumption by rodents, desiccation, and/or freezing, and snowy areas have lower densities of deer, which consume beech seedlings. Moreover, snow accumulation flattens dwarf bamboo culms, which improves forest floor light conditions for beech seedlings. Shimano (1998, 2002) also proposed two secondary factors related to low *F. crenata* density: seed fertility and

predator satiation. The low density of parent beech trees may result in low seed fertility and cause the failing of predator satiation in mast years.

If beech in less snowy PO-type beech forests does not regenerate constantly because of the above-mentioned reasons, not only beech forests in and around the Kanto District of central Japan (Shimano & Okitsu 1993, 1994), but all beech forests in less snowy areas in Japan, should show the same tendency. Investigations of both types of beech forest throughout Japan should be conducted using the same methods because Shimano and Okitsu (1994) only examined two forests in snowy areas and five in less snowy areas.

I therefore investigated ten JS-type beech forests in snowy areas and 12 PO-type beech forests in less snowy areas throughout Japan and analyzed beech regeneration to determine how snow conditions affect the regeneration of *F. crenata* in Japan. The results support the hypothesis that snow facilitates beech regeneration, whereas the absence of snow accumulation hinders it.

Study areas

I investigated 22 beech forests throughout Japan, including a site near the northern limit (JS type) and a site near the southern limit (PO type; Fig.1, Table 1). The study areas were ordered in a descending sequence of maximum snow depth; when two areas had the same depth, the area that had a greater winter/annual precipitation (W/A) rate was placed in the higher position (Table 1). Ten sites of almost pure JS-type beech forests were distributed in northern and northwestern Japan, facing the Japan Sea. The vegetation was phytosociologically classified as Saso kurilensis-Fagion crenatae (Sasaki 1970; Hukushima et al. 1995). Twelve sites of the PO type were located in southern Japan; these were mixed deciduous forests dominated by *F. crenata*. Both types of beech forest showed good correspondence to the snow conditions, although they were classified only by species composition. The vegetation in all PO-type forests was classified as Sasamorpho-Fagion crenatae (Sasaki 1970; Hukushima et al. 1995).

The mean annual temperature in all 22 forests was 6.9 ± 1.6°C ($\pm$SD; Table 1), which is normal for Japanese *F. crenata* forests (Peters 1997), classifying them as cool temperate forests. Although there was no significant difference in annual precipitation between the two types of beech forest, there was a significant difference in summer (June to August) and winter (December to February) precipitation between the two types (Table 1). In summer, PO-type forests had more precipitation than JS-type forests, but JS-type forests had much more winter precipitation as snow than PO-type forests. All JS-type beech forests were distributed in a region of heavy snow, with snowfall exceeding 100 cm, although the depth varies. All PO-

type forests occurred in less snowy areas, with snowfall <100 cm. Only one PO-type forest had somewhat deep snow accumulation (78 cm) because of its high altitude, but the other 11 had snow accumulation of <25 cm (Table 1). JS-type forests had significantly greater maximum snow depths and up to 10 times more snow than PO-type forests (Table 1).

Methods

Data sampling

Data were collected using the Totaling Method of Patch Sampling (ToMPS, see Shimano 2000a). Cool temperate forests in Japan show patch mosaic structures created by canopy gap formation and subsequent regeneration of cohorts (Nakashizuka & Numata 1982a, b; Tanaka 1985, 1986; Nakashizuka 1987; Ida 2000; Shimano 2000a). Forest structure can be realized by combining data from patches in different developmental stages. In Japanese beech forests, it is difficult to establish large-scale plots in mountainous regions because large (>1 ha) plots tend to include valleys and ridges, and therefore, often incorporate data from other vegetation types.

In all 22 areas, about 40 plots were selected at random per area, and the plots conformed to the shape of each patch (Table 1). Although the shapes of patches were indeterminate, I approximated them as rectangles; consequently, the shapes of the study plots were rectangular or square. The patches were in different developmental stages, from young gaps to mature stands. The mean patch area was 102.7 ± 80.8 m^2 ($\pm$SD; range: 9–625 m^2). Patches that appeared to be in younger developmental phases had cohorts of small trees and covered a small area, whereas later phases had a larger area because small patches merged when neighboring patches developed. The mean study area in the 22 forests was 3918.3 ± 1406.1 m^2.

I recorded the species and diameter at breast height (DBH, 1.3 m) of all stems taller than 2 m; each sprout from one stump was treated individually because each sprout would become a canopy tree. The mean stem number in the ~40 plots was 806.8 ± 371.6, and the total number of stems in all 22 forests was 17749.

Patches in all areas were sampled randomly, although there may have been some bias in the gap to mature rate in each forest. I used a line method to assess the rate of each developmental stage, i.e., gap, developing, and mature; the length of each line in a forest was 200 m in each area. From the results of patch sampling, I previously found that early developmental stages, such as gaps with 0–15 m^2/ha in basal area (BA) have a low canopy height that is <50% of the height of mature patches; intermediate stages with BA of 15–35

m^2/ha are 50–75% of the height of mature patches; and late developmental stages with BA >35 m^2/ha have a canopy height that is >75% that of mature forest (Shimano 2000a). I logged the height of patches crossing the line; the rates of early (gap phase), intermediate (developing phase), and late (mature phase) developmental stages were then estimated using the patch heights. Sampled data from patches at each stage were weighted by the results of the line investigation and combined as forest data for all 22 areas (Shimano 2000a). Using ToMPS, sufficient data can be collected while excluding other communities (Shimano 2000a). Using this method, I recorded the species name and DBH of all stems taller than 2 m.

Analysis

Past studies have conducted qualitative analyses of tree regeneration from DBH-class distributions; for example, the inverse-J shaped distribution implies constant regeneration (Kimmins 1987, Smith et al. 1997). Such analyses using DBH-class distributions are basic and important because trunk diameter is proportional to tree age or the size of the crown that receives sunlight (Shimano 1997).

To analyze beech regeneration in each area, I used the power function $y = ax^b$ to fit the DBH-class distribution curve. A forest that constantly regenerates in gaps with a patch mosaic structure contains several different developmental stages. Such a forest includes a large number of small trees and a small number of large trees because trees acquire lateral spaces for light competition in the regeneration process from gap to mature phases (e.g., Ida 2000). The DBH-class distribution of a forest shows a so-called inverse J shape (Kimmins 1987). The change in stem density with diameter growth can be displayed as a power function ($y = ax^b$, where x = DBH class, y = stem density, and a = a positive constant). The parameter b should be –2 because stem density decreases four-fold as DBH doubles (i.e., the cross-sectional area of the stem correlated to the crown projection area grows four-fold). With this –2 power law for DBH-class distribution (Shimano 2000a), the regeneration patterns of beeches can be confirmed quantitatively in both types of beech forest along the snow accumulation gradient.

Parameter a is related to tree density and parameter b is related to decreasing density when tree size is doubled. For example, low values of a and high values of b (negative, but near zero) are obtained for climax species that have low recruitment rates and high survival rates, whereas high values of a and low values of b (negative and far from zero) are obtained for pioneer species that have high recruitment rates and low survival rates. Thus, a pure forest dominated by only one species would have a b of –2; i.e., density decreases four-fold as DBH doubles. On a log–log coordinate graph, the power function curve will be linear. In this case, the slope equals b and the y-intercept is ln a (= $\log_e a$), allowing for a simple analysis.

Regression analysis was conducted for four categories: all species in each forest; *F. crenata* only; all tree species except *F. crenata*; and all shrub and small tree species that cannot reach the canopy layer, even when they are mature. Because the canopy height ranges from 20 to 25 m in many Japanese beech forests, tree species were defined here as species that can grow taller than 15 m in maximum tree height and can form part of the canopy. Information on the maximum height of each species was acquired from Satake et al. (1989) and confirmed in the field. The relationships of parameters *a* and *b* of *F. crenata* and both winter precipitation and the maximum snow depth were also examined.

To compare the density of juveniles per parent tree, I calculated the juvenile/canopy tree ratio (J/C ratio; Shimano & Okitsu 1994), or the density of juvenile trees per parent tree. For convenience, I considered juvenile trees to be those with DBH <10 cm and parent trees to be those with DBH ≥30 cm (Shimano & Okitsu 1994). The relationships between the J/C ratios and both winter precipitation ratio and the maximum snow depth were also investigated.

Results

Species dominance by basal area

The BA dominance of *F. crenata* was high in snowy areas. On average, the BA of *F. crenata* in JS-type forests made up 86.3 ± 10.6% of the BA of all trunks in the 10 study sites, indicating that these forests are almost exclusively dominated by beech (Table 2). The BA of *F. crenata* on Mt. Garyu (62.3%) and Mt. Akkamori (76.3%), which had comparatively lower snow accumulation, were lower than those of other JS-type beech forests. In contrast, the mean dominance of *F. crenata* in PO-type forests was only 42.9 ± 16.5% in BA in the 12 study sites, which was significantly lower than in JS-type forests ($p < 0.001$; Table 2), and other species sometimes co-dominated (e.g., *F. japonica* [3.1% in average BA], *Acer shirasawanum* [8.4%], *Tilia japonica* [4.2%], *Quercus mongolica* var. *grosseserrata* [5.3%], *Abies homolepis* [2.7%], *Stewartia monadelpha* [3.2%], and *Carpinus japonica* [0.8%]).

Power analysis of DBH-class distribution

Figures 2A and 2B show the regressions for *F. crenata* and for all other tree species, respectively, in all forests; the regressions for all species and shrub species were omitted here because they showed similar patterns in all forests. In all 22 forests, the regressions of DBH against density for all species using the power function were significant ($P < 0.001$ in all forests; Fig. 2A, 2B). The mean of parameter *b* (related to decreasing density as DBH doubles) was −1.943 ± 0.219, and the mean of parameter *a* (related to small trunk density) was 25769.1

± 15174.9 (Table 2). The mean correlation coefficient (*R*) was –0.933 ± 0.037, suggesting good fits.

However, fits of the parameters for *F. crenata* showed a different tendency between snowy and less snowy areas. Coefficients of correlation (*R*) in snowy forests (area 1–10) were near –1, whereas those in less snowy areas showed wide variation. There were no significant regressions for *F. crenata* in five less snowy areas, i.e., Mt. Yamizo, Mt. Kanyudo, Mt. Murone, Men-noki Pass, and Mt. Amagi (area 12–15 and 20, respectively); Mt. Fuji, which had few beech, was omitted. As a result, the beech fit for the power function showed wide fluctuations when it was analyzed throughout Japan. In other words, *F. crenata* only fit the power function well in snowy areas (*R* = –0.530, *P* < 0.05), although all species combined fit it well in all areas.

Figures 3A and 3B show the relationship between snow factors (snow accumulation and winter precipitation ratio) and parameters *a*, *b*, and the coefficient of correlation. The values of parameter *a* of *F. crenata*, which indicates the abundance of beech saplings, significantly increased with maximum snow depth and winter precipitation ratio (max. snow depth: *R* = 0.729, *P* < 0.001; winter precipitation ratio: *R* = 0.489, *P* <0.01). In contrast, the values of parameter *b* significantly decreased (max. snow depth: *R* = –0.654, *P* <0.001; winter precipitation ratio: *R* = –5.48, *P* <0.05) and approached –2 with increased snow.   However, both values of parameter *a* and *b* for all species combined did not show any significant correlation with snow factors, i.e., maximum snow depth (*a: R* = –0.089, *P* > 0.05; *b: R* = 0.110, *P* > 0.05) and winter precipitation ratio (*a: R* = –0.280, *P* > 0.05; *b: R* = 0.29, *P* < 0.05). The fits of *F. crenata* in the power function were high in snowy areas, but low in less snowy areas. For all species combined, the values of parameter *a* were always high and *b* was near –2, and the fits were always good under any snow conditions. These results suggest that forest structure and the regeneration patterns followed the –2 power law for the DBH-class distribution.

J/C ratio

J/C ratios of all species combined in each area did not show any significant trends with snow factors (max. snow depth: *R* = –0.114, *P* > 0.05; winter precipitation ratio: *R* = –0.260, *P* > 0.05; Fig. 4). For *F. crenata* alone, however, the J/C ratio increased with snow factors (max. snow depth: *R* = 0.763, *P* < 0.001; winter precipitation ratio: *R* = 0.519, *P* < 0.05; Fig. 4).

Comparison of snowy and less snowy beech forests

The results of the power function analysis and J/C ratio differed along snow and W/A precipitation ratio gradients; I therefore compared the results between snowy and less snowy forests.

For all species combined, I found no significant differences in parameters a and b between the two types of forest, although the fits for JS-type forests were better than those for PO-type forests (Table 3). For *F. crenata* alone, however, the two types differed significantly. In JS-type forests, all regressions were significant ($P < 0.001$ in all forests, t-test) and correlation coefficients were high (Table 3). The mean b was -1.577 ± 0.402. In contrast, regressions for beech were not significant in five PO-type forests, as mentioned above, and correlation coefficients were low. The mean b was -0.464 ± 0.655, which was far from -2 relative to JS-type forests.

Other tree species showed different tendencies in mean parameters between the two forest types, although the differences were not significant (Table 3, Fig. 2). In the PO type, the means of a and b were both larger than those of the JS type. I found no significant differences in the small tree and shrub species groups between the two forest types. However, these parameters implied somewhat lower density and low survival rates by size in JS-type forests, and higher density and lower mortality in PO-type forests.

The differences in the J/C ratio between the two forests were as follows. The mean J/C ratio of JS-type beech was 8.2 ± 5.4, suggesting that each parent tree produced about eight successors (Table 3). Parent beech density of the PO type was about one-half that of the JS type, and juvenile density was even lower. In the PO type, the mean J/C ratio was about 0.8, which was significantly lower than that of the JS type ($P < 0.001$, U-test). The canopy tree density of other species was comparable to beech, but the J/C ratio was >10.

Discussion

Differences in forest structure and beech dominance between snowy and less snowy areas

The data on 22 beech forests throughout Japan showed good fits to the power function; thus, the DBH-class distributions of the 22 forests showed an inverse-J shape.

In both snowy and less snowy areas, canopy and juvenile tree densities of all species combined were about 150 and 2250 stems/ha, respectively (Table 2). The J/C ratios were also about the same, and there were no significant differences in densities and ratios. In the power analysis, parameters a and b had almost the same values in both forest types, and there were no significant differences between the types (Table 3). Snow factors did not affect the values of all species combined (Fig. 3A, 3B). Thus, both types of beech forest have almost the same

basic forest structure when species composition is disregarded. It seems that trees regenerate constantly and forests are maintained as a whole. The forest structure of Mt. Fuji was the same as that of other beech forests, although the abundance of *F. crenata* was low. The study area on Mt. Fuji may have had fewer *F. crenata* than in some other areas on Mt. Fuji because the altitude of the study area was somewhat higher than typical for cool temperate forests.

Beeches dominate on the snowy JS side because most other species are susceptible to heavy snow loads. Unlike *F. crenata*, other deciduous trees in cool temperate forests tend to weaken with increased snow load (Kamitani 1984; Onodera et al. 1995; Homma 1997; Shimano 1999), restricting their distribution in snowy areas. On the snowy JS side, *F. crenata*, particularly when mature, tends to remain straight, regardless of snow pressure, whereas other species have a tendency to bend at the base, and thus, have difficulty becoming canopy trees. Many studies have indicated that *F. crenata* is resistant to snow pressure and can dominate as a canopy species, unlike other trees (e.g., Kamitani 1984; Maeda et al. 1985; Onodera et al. 1995; Homma 1997; Shimano 1999). The trunks of *Acer amoenum*, *A. japonicum*, *A. mono* var. *mayrii*, and *Acanthopanax sciadophylloides* are easily bent by snow pressure, and they maintain this shape even during the snow-free season. *Acer japonicum* has a straight trunk and grows into the canopy layer on the less snowy Pacific Ocean side, but has a bent trunk and grows like a dwarf shrub on the Japan Sea side (Shimano 1999). This may also explain why immature trees and shrubs have lower densities and higher mortality rates, although some of these species, including evergreen shrubs, are insulated from low temperatures by snow (Shimano 1999).

Beech regeneration

Using power analysis, regeneration traits or conditions can be quantitatively clarified in patch-mosaic forests, where trees regenerate constantly**.**

In snowy areas, beech regenerated constantly with an inverse J-shaped DBH-class distribution, whose curve fit the power function well (Fig. 2). The J/C ratio for beech was ~8 (Table 2), i.e., for each beech canopy tree there were eight juveniles. Over 90% of the canopy trees in these areas were beech (Table 2), indicating that these forests are almost pure beech. Power analysis showed that the values of parameter *b* of *F. crenata* were similar to those of all species combined (Fig. 3), and the mean of parameter *b* for beech was also similar to that of all species combined (Table 3). Regressions for all species combined were not shown (Fig. 2), but were almost the same as for *F. crenata* in snowy forests. This suggests that the density of juveniles decreases with growth, regardless of species, and can be explained by self-thinning (Yoda et al. 1963) and the tile model (Shimano 2000a). In this area, other tree species, small

trees, and shrubs show low densities, and they do not grow large in DBH, unlike those in PO-type forests. This is why the J/C ratio of other species was so high in this type of forest.

Both the parameters and correlation coefficients of all species combined did not show noticeable trends with snow depth and winter precipitation ratios (Fig. 3). In less snowy PO-type beech forest, the mean b for all species was –1.995, which was not significantly different from that for JS-type forests (Table 3). This suggests that trees regenerate constantly, with many juveniles, as predicted by the tile model. However, regeneration of beech alone was different. I was unable to conduct statistical tests for beech in the PO-type forest on Mt. Fuji because of the low density of beech. In less snowy forests, such diminished beech dominance sometimes occurs, although species composition is likely similar to that of other PO-type beech forests. Moreover, I was unable to find a statistically significant regression for beech in five forests because there were few small beech compared to large or intermediate-sized individuals, indicating different regeneration conditions from those of snowy beech forests. In PO-type forests, the mean beech J/C ratio was <1.0 (Table 2), suggesting that juvenile density was lower than canopy tree density, or that sporadic regeneration would require a much longer time in PO-type forests, even though the forest structure was not that different. Beech may regenerate only sporadically in less snowy PO-type forests, and may not necessarily regenerate constantly, as already reported for some forests (Shimano & Okitsu 1993, 1994).

In PO-type beech forests, however, other species may regenerate constantly with an inverse J-shaped DBH-class distribution (Fig. 2) and a high J/C ratio. Parameter b of the power function, –1.588 ± 0.333, was similar to that for *F. crenata* in JS-type forests (–1.577 ± 0.402; Table 3). The power function parameters indicated that these species had high densities of small trees and low mortality rates (Table 2, Fig. 2). The J/C ratio was >10, indicative of many successors. Consequently, tree species other than beech regenerate constantly and maintain the forest structure in PO-type beech forests.

The regeneration characteristics of small trees and shrubs reflect environmental differences between the two types of beech forest, especially snow conditions. In snowy areas, the trunks of other species are easily bent or broken by snow loading and have difficulty growing to large sizes. Therefore, their density and survival rates should be low, with small a and b. It is therefore of interest when small trees and shrubs do not regenerate favorably, even when parameters a and b and J/C ratios are similar to those of *F. crenata*. In contrast, in less snowy forests, other tree species, small trees, and shrubs will have higher densities and lower mortality rates than those in snowy JS-type forests, proportionally decreasing beech dominance.

In the analysis of beech regeneration using the power function for the DBH-class distribution, snow factors were correlated with increased numbers of juvenile beech, as shown by high values of parameter *a*, and pure beech forests, as shown by the value of about –2 of parameter *b*. J/C ratios also increased with snow factor values (Fig. 4), suggesting that snow increases the number of juvenile beech. Beech forests on Mt. Garyu and Mt. Akkamori are phytosociologically classified into JS-type beech forests by their species composition, but parameters similar to those of PO-type forests, probably because the two mountains have less snow accumulation compared to other JS-type forests (Table 1). These results show that *F. crenata* regeneration in more snowy areas is comparatively stable and healthy compared to that in less snowy areas in Japan.

How does snow affect beech regeneration?

Why does *F. crenata* regeneration change along a snow gradient? This study shows that the density of juvenile *F. crenata* is low in less snowy PO-type beech forests. Shimano (1998, 2002) summarized and proposed eight primary factors that are related to the presence or quantity of snow: (1) differential feeding pressure by rodents on seeds (Suzuki 1989; Shimano & Masuzawa 1995, 1998; Irie et al. 1998; Homma et al. 1999), (2) freezing and/or desiccation of nuts (Shimano & Masuzawa 1998; but note that Homma et al. 1999 pointed out less of an effect and Maruta & Kamitani 1996 and Maruta et al. 1997 suggested that only seedlings die because of desiccation), (3) browsing on seedlings by deer (discussed by Maruyama 1981; Takatsuki 1992), (4) light conditions under dwarf bamboo on the forest floor in spring (Shimano 2000b), (5) water stress (Maruyama & Toyama 1987), (6) protection of beech, especially seedlings, from late spring frost (Kashimura 1978), (7) forest fires (Nakashizuka & Iida 1995), and (8) the little ice age (Koizumi et al. 1988). Two secondary factors related to low *F. crenata* density are (9) low seed fertility (Hashizume & Yamamoto 1974; Hashizume & Sugawara 1985; Suzuki 1989; Homma et al. 1999; Ida et al. 2002) and (10) insufficient predator satiation (Kaji & Ohkubo 1995). Although some of these factors were proposed by Shimano (1998, 2002), here, I summarize the discussion with some new reviews for better comprehension.

Factors (9) and (10) are important, especially for mixed *F. crenata* forests of the PO type in Japan. Factors (8) and (9) would not affect the regeneration of American beech (*F. grandifolia*) and European beech (*F. sylvatica*) because *F. sylvatica* forests are usually almost pure, especially in the lowland/colline zone of western and central Europe and in the montane zone of southern Europe, and because *F. grandifolia* regenerates mainly via root suckers (root sprouts; Ellenberg 1988, Peters 1997). However, a positive effect of snow should also be

considered in the regeneration of European and North American beech forests. Power analysis of the DBH-class distribution will be a useful tool for patch-mosaic structured forests such as temperate forests, and the J/C ratio would also be convenient for climax species like beech that produce many shade-tolerant saplings.

In snowy areas, beech regenerates constantly with an inverse J-shaped DBH-class distribution whose curve is well described by a power function. In less snowy areas, beech regenerates sporadically. In these forests, less snowy conditions and low parent tree density make beech regeneration difficult. For beech regeneration, not only the mass of snow accumulation, but also the timing of snowfall, is important for beechnut protection. Such protection is important because many seed predators prefer large beechnuts over the small seeds of other canopy trees. However, only *F. crenata* benefits from snow because other tree species have difficulty dominating because of snow pressure, even though their seeds are also protected.

Fagus crenata can regenerate sporadically in PO-type forests, but this requires mast production, snow cover early in the season, and simultaneous death of dwarf bamboo. Perhaps such desirable conditions arise periodically, maintaining the present PO-type beech forests. Global warming will affect beech regeneration, especially on the less snowy PO side of Japan, if climate change delays the timing of snowfall and reduces snow accumulation, even if total precipitation does not change.

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Figure captions

Fig. 1. Study sites in Japanese beech forests. Ten sites were located in snowy areas that faced the Japan Sea and 12 sites were located in less snowy areas that faced the Pacific Ocean. The white line indicates the boundary; the area to the west of the line experiences heavy snow accumulation in winter (≥50 cm maximum depth).

Fig. 2. The DBH-class distribution of *F. crenata* and all other tree species combined in (A) 10 Japan Sea-type and (B) 12 Pacific Ocean-type beech forests (log–log coordinates).

Fig. 3. Relationships between parameters *a* and *b* of the power function analysis ($y = ax^b$; $x =$ DBH, y = density) and (A) maximum snow depth and (B) the ratio of winter to annual precipitation. Areas 1–10 were located in snowy Japan Sea-Type beech forests; areas 11–22 were located in less snowy Pacific Ocean-type beech forests. Area numbers are as in Table 1.

Fig. 4. Relationships between the juvenile to canopy tree ratio and (A) maximum snow depth and (B) the ratio of winter to annual precipitation. Area numbers as in Fig. 3 and Table 1.

Table 1. Environmental attributes of the study sites (mean values from 1971 to 2000).

	The number of Sampled patches	Altitude (m)	WI	CI	Average temperature ( ) Annual	Monthly Maximum	Monthly Minimum	Maximum snow depth(cm)	Precipitation (mm) and precipitation ratio Annual	Winter	Summer	W/A	S/A
Japan sea type (n=10)													
1 Mt.Kariba	40	800	32.1	- 55.9	3.0	15.4	- 7.7	300.0	1754.4	356.6	404.0	0.203	0.230
2 Mt.Akitakoma	40	1000	46.5	- 50.3	4.7	17.9	- 7.3	209.0	2502.9	413.9	923.5	0.165	0.369
3 Kayanodaira	42	1500	47.5	- 49.7	4.8	18.1	- 7.8	190.0	1808.0	477.4	527.6	0.264	0.292
4 Asahi	20	300	71.1	- 23.2	9.0	22.0	- 2.1	189.0	2843.9	884.7	655.9	0.311	0.231
5 Hinoemata	40	1400	45.7	- 48.1	4.8	17.5	- 7.0	187.0	1508.1	365.0	461.1	0.242	0.306
6 Mt.Tateyama	38	1000	64.0	- 30.2	7.8	20.4	- 3.9	171.0	2884.4	639.8	955.2	0.222	0.331
7 Mt.Hakusan	41	1100	59.7	- 33.6	7.2	19.8	- 4.9	166.0	3317.5	649.5	1066.4	0.196	0.321
8 Mt.Otobe	41	400	53.5	- 39.4	6.2	19.3	- 5.7	166.0	1771.7	338.7	537.5	0.191	0.303
9 Mt.Garyu	39	1100	62.2	- 28.7	7.8	19.6	- 3.4	117.0	2296.0	492.3	838.5	0.214	0.365
10 Mt.Akkamori	38	1000	46.3	- 45.6	5.1	17.9	- 6.6	114.0	1214.0	157.5	411.1	0.130	0.339
Average	38	960	52.9	- 40.5	6.0	18.8	- 5.6	180.9	2190.1	477.5	678.1	0.214	0.309
S.D.	6	381	11.5	11.0	1.9	1.8	2.0	51.9	684.6	204.1	247.2	0.051	0.048
Pacific Ocean type (n=12)													
11 Mt.Fuji	40	1600	53.8	- 27.4	7.2	18.2	- 3.1	78.0	2846.5	404.4	1018.5	0.142	0.358
12 Mt.Yamizo	40	1000	60.9	- 27.8	7.8	19.8	- 3.5	21.0	1558.3	107.7	647.2	0.069	0.415
13 Mt.Kanyudo	40	1400	60.5	- 26.1	7.9	19.4	- 3.3	19.0	1898.1	175.0	726.6	0.092	0.383
14 Mt.Murone	20	800	57.2	- 32.3	7.1	19.6	- 4.1	16.0	1379.2	136.3	492.3	0.099	0.357
15 Men- noki pass	40	1100	62.3	- 27.1	7.9	19.6	- 3.4	15.0	2526.8	223.1	956.1	0.088	0.378
16 Mt.Mito	38	1400	56.0	- 30.5	7.1	18.8	- 4.0	15.0	1525.9	116.6	648.8	0.076	0.425
17 Mt.Ishizuchi	42	1500	50.8	- 36.9	6.2	17.4	- 5.2	14.0	2998.6	338.4	1230.9	0.113	0.410
18 Mt.Kunimi	41	1500	58.2	- 28.7	7.5	18.1	- 3.9	12.0	2802.1	291.3	1395.3	0.104	0.498
19 Mt.Tsurugi	40	1300	55.4	- 30.0	7.1	18.0	- 4.0	12.0	3208.5	333.1	1343.3	0.104	0.419
20 Mt.Amagi	40	1100	67.7	- 16.2	9.3	19.6	- 1.1	11.0	3333.1	291.6	1223.2	0.087	0.367
21 Mt.Misen	41	1500	54.5	- 32.9	6.8	17.8	- 4.2	10.0	2785.0	263.7	1218.6	0.095	0.438
22 Mt.Shiraga	40	1200	73.4	- 18.5	9.6	20.0	- 1.7	8.0	3061.0	261.1	1607.7	0.085	0.525
Average	38	1283	59.2	- 27.9	7.6	18.9	- 3.5	19.3	2493.6	245.2	1042.4	0.096	0.414
S.D.	6	244	6.3	5.8	1.0	0.9	1.1	18.9	707.5	95.0	351.0	0.019	0.053
Difference between two types			ns	p<0.01	p<0.05	ns	p<0.01	p<0.001	ns	p<0.01	p<0.01	p<0.001	p<0.001

Significant differences were detected using t- tests.
WI =   monthly mean temperature - 5   ; in Japan, beech forests are found in areas where WI is 45–85.
CI: coldness index (× month)
Summer: June–August
Winter: November–January
W/A: ratio of winter/annual precipitation
S/A: ratio of summer/annual precipitation

Table 2. Basal area (BA) and juvenile/canopy tree ratio of each species category in all sites.

Japan sea type (n=10)	F. crenata				Other tree species				Total of all species		
	BA %	Juvenils	Canopy trees	J/C ratio	BA %	Juvenils	Canopy trees	J/C ratio	Juvenils	Canopy trees	J/C ratio
1 Mt. Kariba	85.2	1312.8	112.4	11.7	13.1	375.8	13.1	28.7	2479.9	125.5	19.8
2 Mt. Akitakoma	93.8	1790.4	92.1	19.4	5.7	241.0	6.5	37.0	2276.8	98.6	23.1
3 Kayano daira	96.6	1071.4	164.6	6.5	2.1	334.5	1.4	238.7	2074.8	166.0	12.5
4 Asahi	80.9	1281.2	146.9	8.7	17.1	930.8	20.0	46.5	3023.8	166.9	18.1
5 Hinoemata	94.3	1132.8	173.6	6.5	5.3	408.3	3.5	117.4	1880.8	177.1	10.6
6 Mt. Tateyama	92.2	1156.0	123.7	9.3	5.6	416.8	4.2	100.4	2858.4	127.9	22.3
7 Mt. Hakusan	89.9	574.2	192.0	3.0	9.0	389.1	14.9	26.1	1931.8	206.9	9.3
8 Mt. Otobe	91.2	601.0	157.8	3.8	7.9	461.4	3.0	155.7	1496.6	160.8	9.3
9 Mt. Garyu	62.3	101.2	87.9	1.2	32.4	326.0	44.9	7.3	780.0	132.9	5.9
10 Mt. Akkamori	76.3	1970.4	160.1	12.3	21.0	1147.8	20.8	55.1	4091.6	181.0	22.6
Mean	86.3	1099.1	141.1	8.2	11.9	503.2	13.2	81.3	2289.5	154.4	15.4
S.D.	10.6	561.8	35.3	5.4	9.3	293.3	13.2	72.4	906.5	32.4	6.5
Pacific Ocean type (n=12)											
11 Mt. Fuji	5.8	0.0	11.0	0.0	84.1	1378.3	190.7	7.2	2151.8	205.5	10.5
12 Mt. Yamizo	49.2	30.1	80.4	0.4	28.0	279.1	27.7	10.1	2699.2	108.1	25.0
13 Mt. Kanyudo	41.4	7.3	77.5	0.1	28.3	215.9	34.5	6.3	2691.3	115.3	23.3
14 Mt. Murone	55.2	72.6	68.3	1.1	38.7	492.3	49.8	9.9	1344.5	118.1	11.4
15 Mt. Men-noki	51.8	7.7	64.8	0.1	40.2	352.3	44.0	8.0	1428.7	108.8	13.1
16 Mt. Mito	36.0	72.0	67.0	1.1	53.3	835.3	97.7	8.6	2829.8	164.7	17.2
17 Mt. Ishizuhci	71.0	201.8	148.4	1.4	22.8	571.2	32.2	17.7	1678.8	183.1	9.2
18 Mt. Kunimi	50.0	65.7	71.4	0.9	33.4	311.2	17.9	17.3	2415.0	95.1	25.4
19 Mt. Tsurugi	38.2	76.0	46.1	1.6	53.3	825.6	90.1	9.2	2064.7	136.1	15.2
20 Mt. Amagi	54.2	1.7	83.8	0.0	34.0	120.9	42.3	2.9	639.7	133.4	4.8
21 Mt. Misen	27.9	99.9	41.4	2.4	66.0	2513.5	55.4	45.4	3220.3	99.0	32.5
22 Mt. Shiraga	34.6	48.7	65.4	0.7	44.6	804.6	56.9	14.1	3409.9	134.8	25.3
Mean	42.9	57.0	68.8	0.8	43.9	725.0	61.6	13.1	2214.5	133.5	17.7
S.D.	16.5	57.0	32.2	0.7	17.8	665.1	47.0	11.1	825.1	34.5	8.4
Difference between two types	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001	ns	P<0.01	P<0.01	ns	ns	ns

Other tree species are trees that can grow taller than 15 m and reach the canopy layer.
All species combined includes F. crenata, other tree species, small trees, and shrubs. The BA is therefore 100%
Significant differences were detected using t- tests.

Table 3. Mean (± SD) of parameters of the power function $y = ax^b$ and correlation coefficients.

	Total of all species		Fagus crenata		Other tree species		Sub trees and Shrubs	
Coeficient of correlation								
All 22 forests	-0.933 ± 0.037		-0.603 ± 0.439		-0.897 ± 0.107		-0.927 ± 0.072	
Japan Sea types	-0.915 ± 0.040		-0.866 ± 0.054		-0.931 ± 0.019		-0.950 ± 0.059	
Pacific Ocean types	-0.948 ± 0.026	*	-0.384 ± 0.495	**	-0.868 ± 0.138	ns	-0.908 ± 0.076	ns
Parameter a								
All 22 forests	25769.1 ± 15174.9		4617.3 ± 7808.4		4554.5 ± 6065.1		17168.4 ± 16955.2	
Japan Sea types	22146.4 ± 13125.8		9976.3 ± 9023.8		2486.7 ± 1924.9		11582.6 ± 9603.6	
Pacific Ocean types	28788.0 ± 16079.6	ns	151.4 ± 216.0	***	6277.8 ± 7604.0	ns	21823.3 ± 20062.8	ns
Parameter b								
All 22 forests	-1.943 ± 0.219		-0.970 ± 0.772		-1.642 ± 0.302		-2.479 ± 0.626	
Japan Sea types	-1.880 ± 0.239		-1.577 ± 0.402		-1.706 ± 0.245		-2.743 ± 0.783	
Pacific Ocean types	-1.995 ± 0.184	ns	-0.464 ± 0.628	**	-1.588 ± 0.333	ns	-2.258 ± 0.319	ns

Significant differences between Japan Sea and Pacific Ocean types were detected using t-tests. *: p < 0.05; **: p < 0.01; ***: p < 0.001; ns: non-significant.
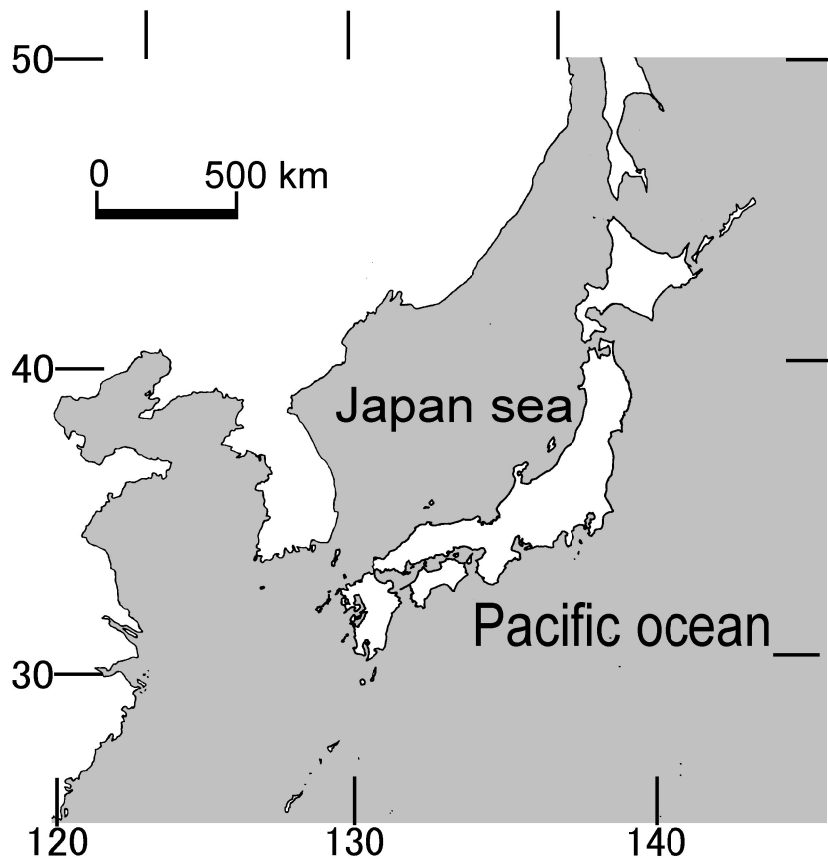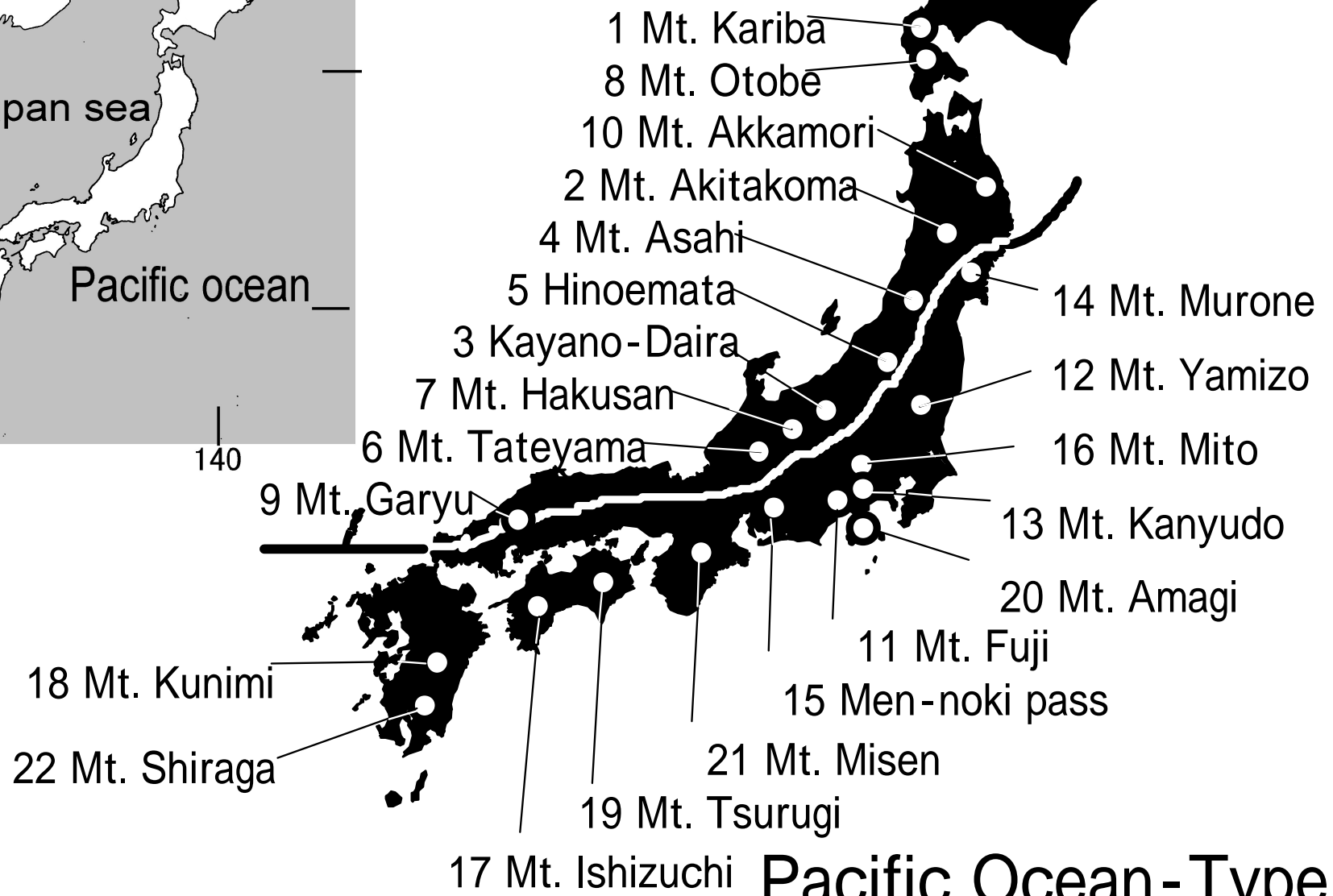
Japan Sea-Type
Beech Forests

1 Mt. Kariba
8 Mt. Otobe
10 Mt. Akkamori
2 Mt. Akitakoma
4 Mt. Asahi
5 Hinoemata
3 Kayano-Daira
7 Mt. Hakusan
6 Mt. Tateyama
9 Mt. Garyu

14 Mt. Murone
12 Mt. Yamizo
16 Mt. Mito
13 Mt. Kanyudo
20 Mt. Amagi
11 Mt. Fuji
15 Men-noki pass
21 Mt. Misen
19 Mt. Tsurugi
17 Mt. Ishizuchi

18 Mt. Kunimi
22 Mt. Shiraga

Pacific Ocean-Type
Beech Forests

Japan sea

Pacific ocean
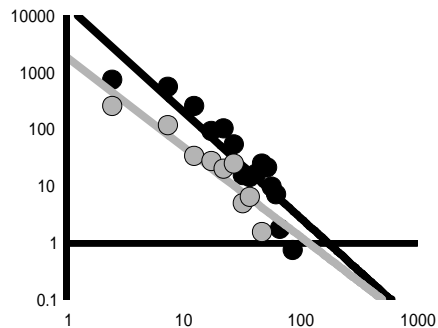
1 Mt.Kariba   2 Mt. Akitakoma   3 Kayano-Daira   4 Asahi
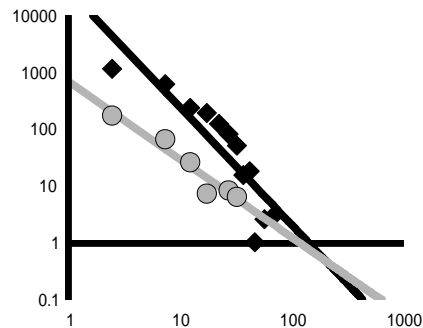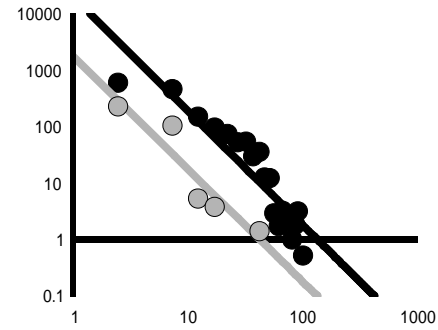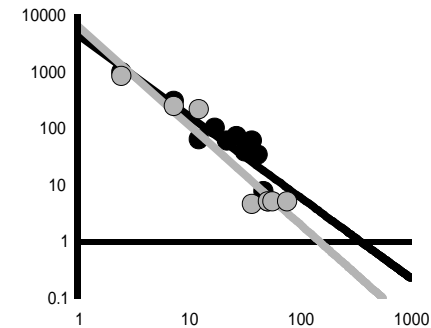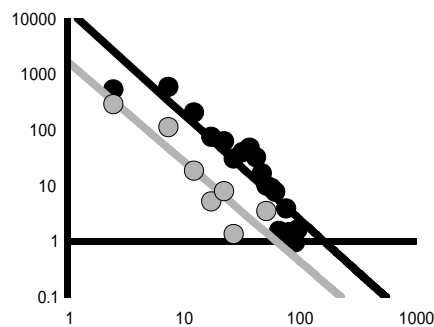
5 Hinoemata   6 Mt. Tateyama   7 Mt. Hakusan   8 Mt. Otobe
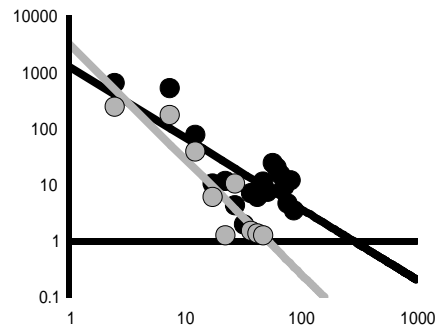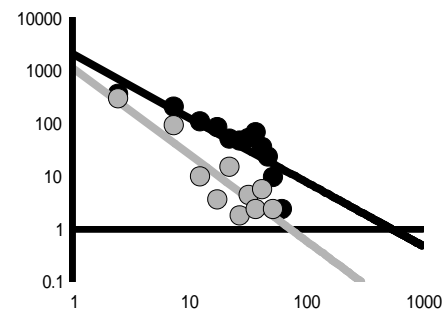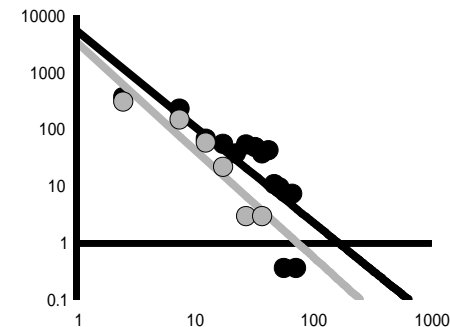
9 Mt. Garyu   10 Mt. Akkamori

ln numer of stems/ha
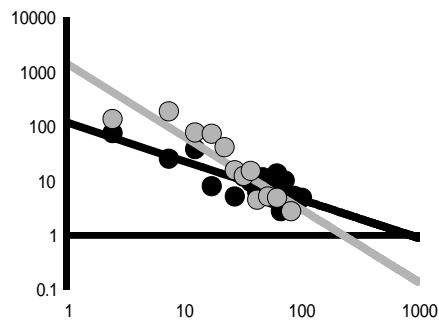
ln DBH class (5cm interval)
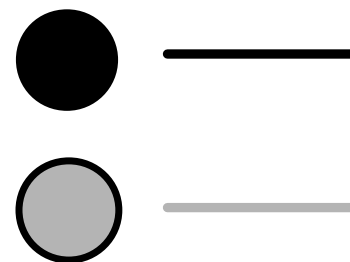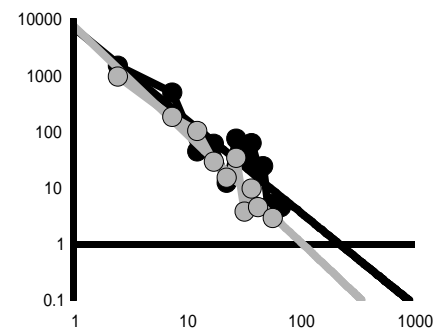
Fagus crenata

Total of other tree species
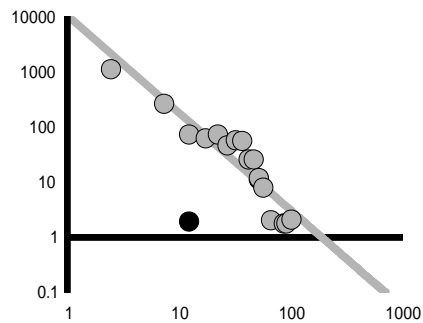
11 Mt. Fuji   12 Mt. Yamizo   13 Mt. Kanyudo   14 Mt. Murone
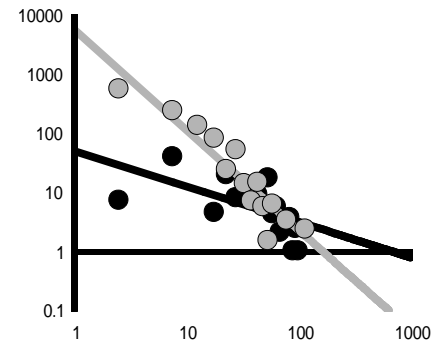15 Men-noki   16 Mt. Mito   17 Mt. Ishizuchi   18 Mt. Kunimi
19 Mt. Tsurugi   20 Mt. Amagi   21 Mt. Misen   22 Mt. Shiraga
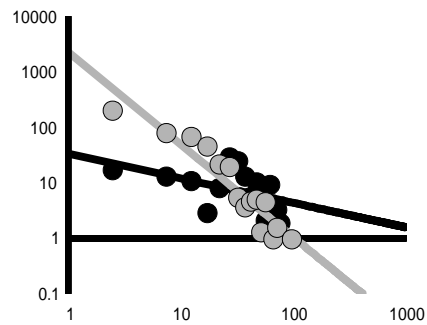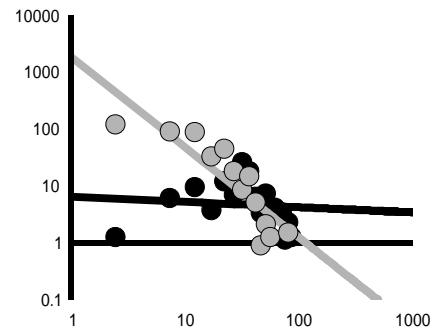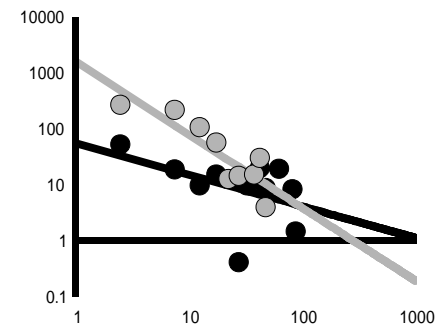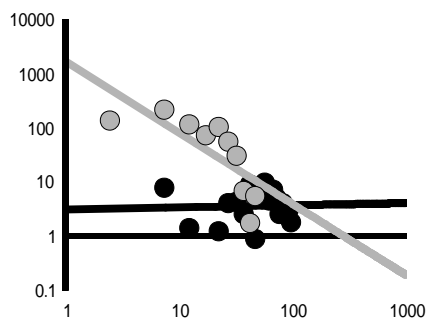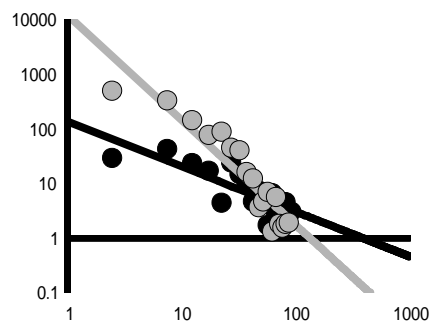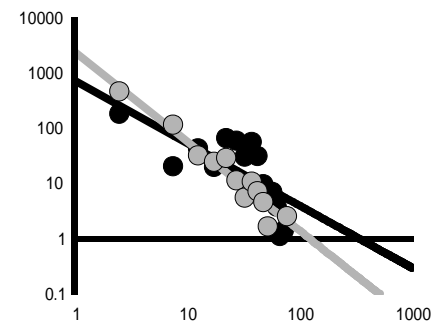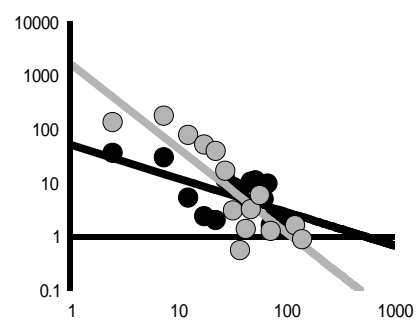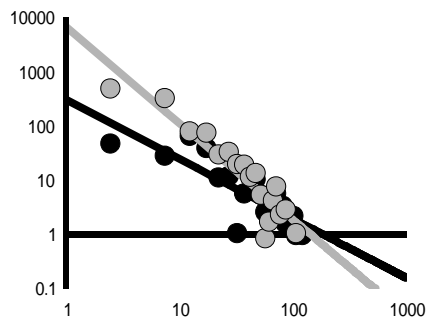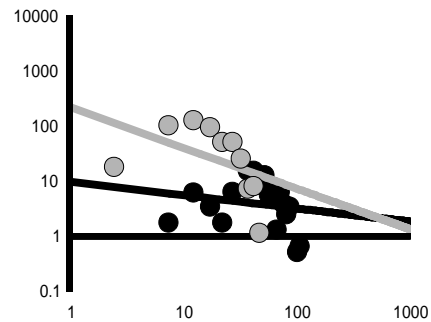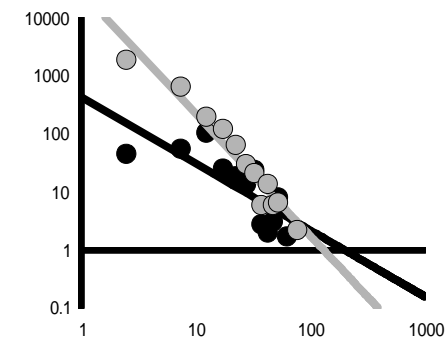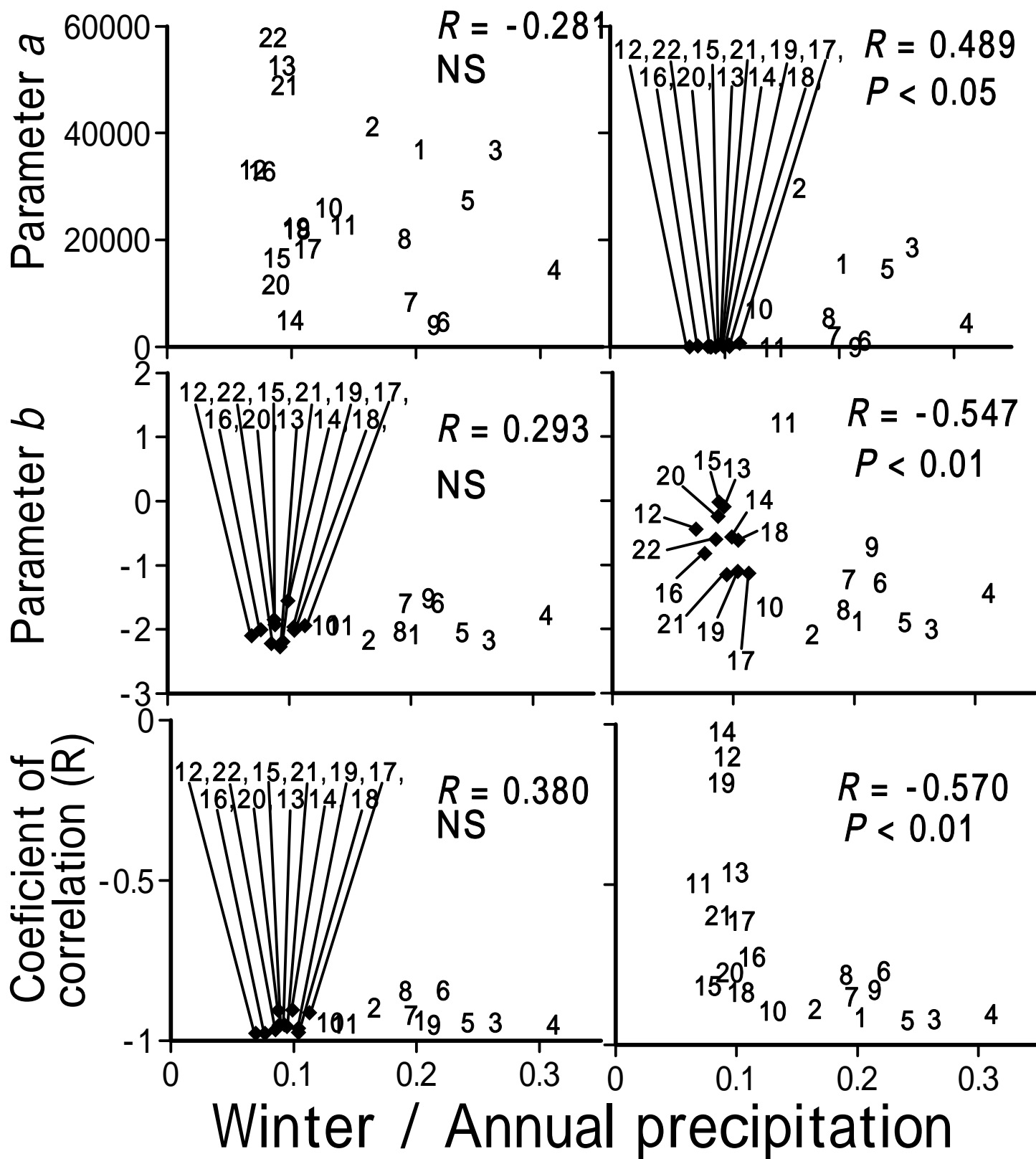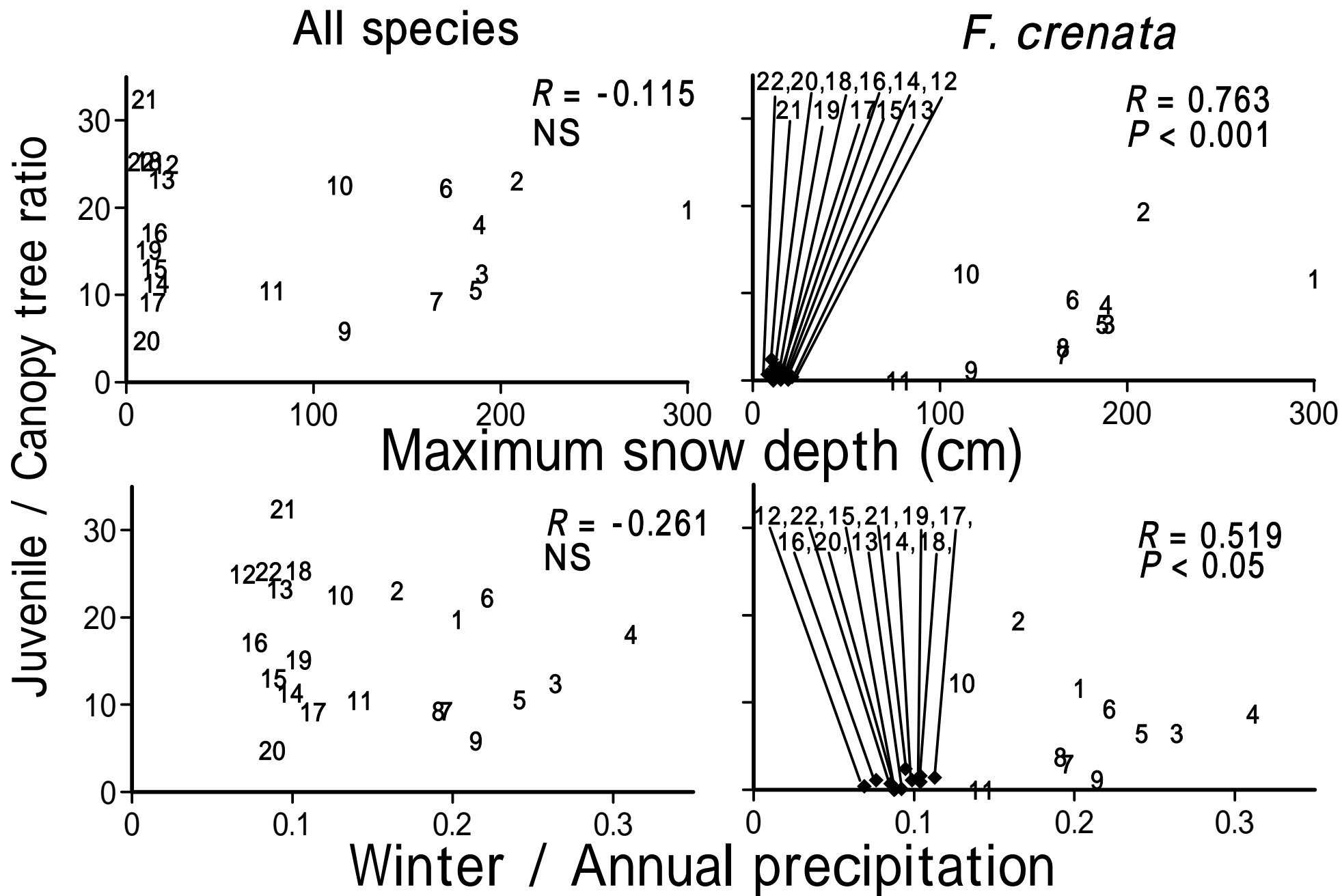
ln numer of stems/ha

ln DBH class (5-cm interval)
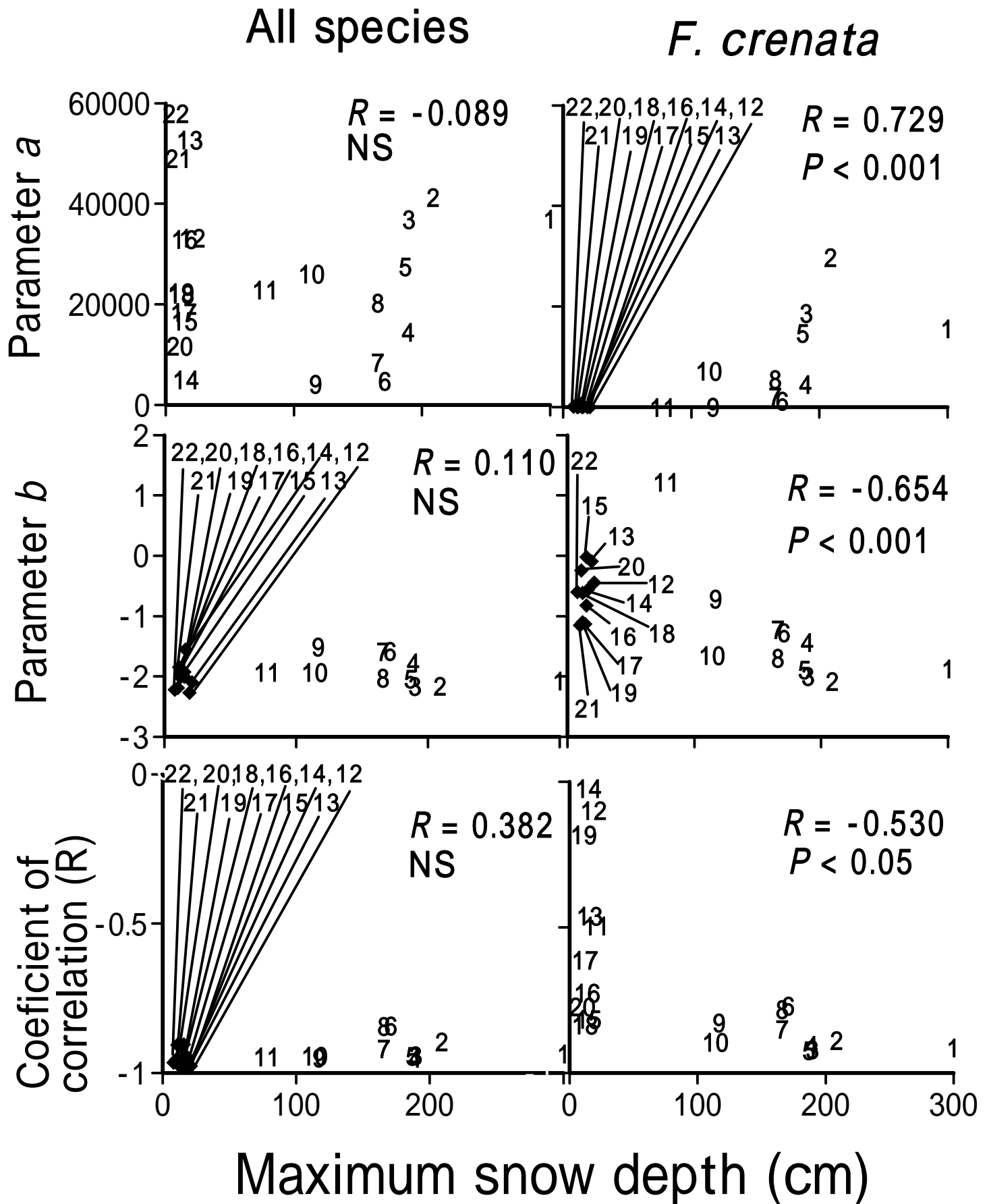
Fig. 3A

Fig. 3B

Fig. 4A (upper), 4B (lower)