

REGENERATION DYNAMICS, CAUSAL FACTORS, AND CHARACTERISTICS OF PACIFIC OCEAN-TYPE BEECH (*FAGUS CRENATA*) FORESTS IN JAPAN: A REVIEW

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Abstract: This paper reviews the differences in the distribution and regeneration of *Fagus crenata* between two types of Japanese beech forests, the Japan Sea (JS)-type and the Pacific Ocean (PO)-type, and discusses the causal factors and characteristics of these forests, particularly the PO-type. *F. crenata* in PO-type forests regenerates sporadically rather than constantly, whereas regeneration in the JS-type forests is relatively constant with gap dynamics. *F. crenata* has dominated in snowy areas both in the past, after the last glacial age, when there was less human disturbance, and in the present. Snow accumulation facilitates beech regeneration in snowy JS-type forests, but not in the less snowy PO-type. Snow protects beechnuts from damage caused by rodents, desiccation, and freezing. In addition, snow suppresses dwarf bamboo in the spring, thus increasing the amount of sunlight available for beech seedlings on the forest floor. Snow also supplies melt water during the growing season and limits the distribution of herbivores. Moreover, snow reduces the number of forest fires during the dry winter and early spring seasons. The low densities of *F. crenata* impede its regeneration, because disturbed wind pollination lowers seed fertility and predators are less effectively satiated. In snowy JS-type beech forests, *F. crenata* dominates both at the adult and the juvenile stages because it regenerates well, while other species are eliminated by heavy snow pressure. On the less snowy PO-side, deciduous broad-leaved forests with various species are a primary feature, although *F. crenata* dominates because of its large size and long lifespan.

INTRODUCTION

Two types of beech forest in Japan

Siebold's beech, *Fagus crenata* (*Fagaceae*), is the most common tree in deciduous broad-leaved forests of the Japanese cool temperate zone; consequently, this zone is also known as the *F. crenata* zone. In this zone, the mean annual temperature ranges from 6 °C to 13 °C (YAMANAKA 1979). Kira's warmth index (KIRA 1949), which is the summation of average monthly temperatures minus five for months in which the average temperature exceeds 5 °C (PETERS 1997), ranges from 45 °C to 85 °C × month. This zone lies about 700–1500 m a.s.l. in central Japan.

Japanese beech forests are classified into two types, the Japan Sea (JS)-type and the Pacific Ocean (PO)-type, based on physiognomy and phytosociology. Phytosociologically, the JS-type beech forest is defined as *Saso kurilensis-Fagion crenatae*, while the PO-type is defined as *Sasamorpho-Fagion crenatae* (SAKAKI 1970, HUKUSHIMA et al. 1995, Table 1). *Saso kurilensis-Fagion crenatae*, the JS-type beech forest, is characterized by *Cephalotaxus harringtonia* var. *nana*, *Daphniphyllum macropodum* var. *humile*, *Ilex leucoclada*, and

Table 1. Characteristics of Japan Sea-type and Pacific Ocean-type beech forests.

Characteristics	Japan Sea (JS)-type beech forests	Pacific Ocean (PO)-type beech forests	notes
Distributed in snowy area (the maximum snow depth is more than 50 cm)		less snowy area	
Phytosociological classification	<i>Saso kurilensis-Fagion crenatae</i>	<i>Sasamorpha-Fagion crenatae</i>	
	characterized by <i>Cephalotaxus harringtonia</i> var. <i>nana</i> , <i>Daphniphyllum macropodum</i> var. <i>humile</i> , <i>Ilex leucoclada</i> , <i>Aucuba japonica</i> var. <i>borealis</i> (evergreen shrubs)	characterized by <i>Acer shirasawanum</i> , <i>Stewartia pseudo-camellia</i> , <i>Symplocos coreana</i> , <i>Acer palmatum</i> var. <i>amoenum</i>	from SAKAKI 1970 and HUKUSHIMA et al. 1995
Species richness and diversity			
total number of species	22.3 ± 7.3	33.8 ± 13.0	$P < 0.05$, <i>t</i> -test, SHIMANO (1996). Trees larger than 2 m in height in 10 sites of JS-type and 12 sites of PO-type throughout Japan
tree species that can grow more than 15 m in height	10.5 ± 3.4	15.8 ± 5.2	$P < 0.05$, SHIMANO 1996, 1998
Shannon-Wiener index (bit)	0.93 ± 0.11	2.73 ± 0.55	$P < 0.05$, SHIMANO 1998

Aucuba japonica var. *borealis*, which are evergreen shrubs that escape cold temperatures in winter under thick snow cover. In contrast, *Sasamorpha-Fagion crenatae*, the PO-type beech forest, is characterized by *Acer shirasawanum*, *Stewartia pseudo-camellia*, *Symplocos coreana*, *Acer palmatum* var. *amoenum*, and several other species, many of which are deciduous broad-leaved trees.

Table 1 shows the differences in species richness and diversities in both types of beech forests. *F. crenata* dominates physiognomically in JS-type beech forests, but many different canopy trees co-dominate with *F. crenata* in PO-type. Since *F. crenata* dominates JS-type beech forests, species richness and diversity are lower than in PO-type forests, where *F. crenata* is less dominant. As for dominance, more than 80% of the basal area is occupied by *F. crenata* in the JS-type and about 50% in the PO-type (from SHIMANO 1996). Several studies have shown that twice the number of species grow 15 m tall in PO-type forests than in the JS-type (TAKAHASHI 1962, FUJITA 1986, OHSAWA & TAKIGUCHI 1987, HUKUSHIMA et al. 1995). In summary, both species richness and diversity are relatively high in PO-type forests and low in JS-type forests.

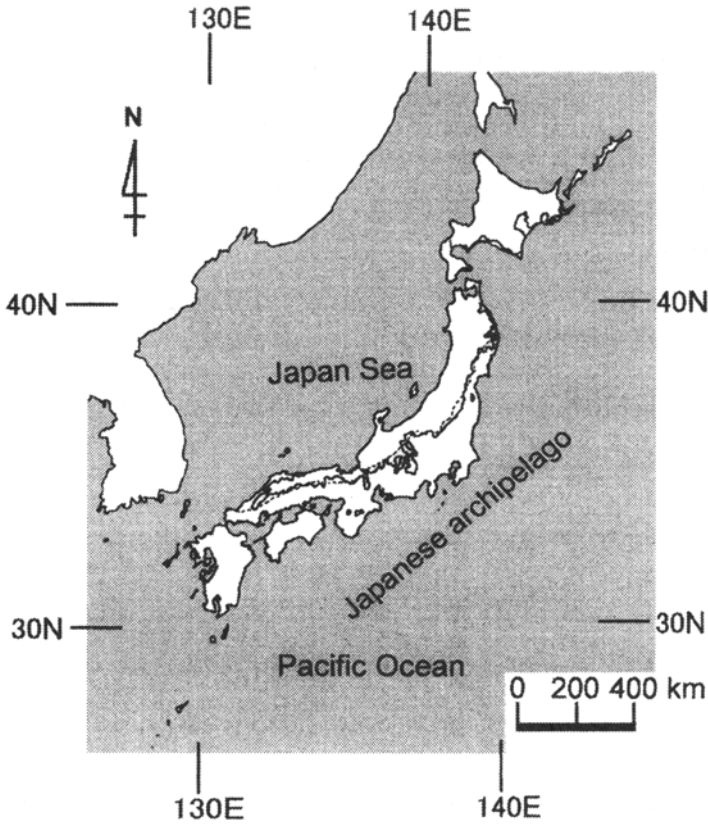


Fig. 1. Distribution of Japan Sea (JS)-type beech forests and snowy area. Japan Sea type beech forests and snowy area, where the maximum snow depth is equal or more than 50 cm, are distributed in western part of dotted line and north-western part of solid line in Japanese archipelago, respectively.

SHIMANO (1998) suggested that the major difference in the environmental factors affecting the two types was snow condition. JS-type beech forests occur in areas where maximum snow depth exceeds 50 cm (Table 1, Fig. 1) and is typically as deep as two or three meters in the mountains. Time of snowfall is also different between the two types. In JS-type beech forests, snow falls in mid-November and covers the ground throughout the winter. In PO-type forests, however, there is little snowfall in November and December, and even if snow does fall during this time, much of it disappears. In this area, snow cover occurs in January or February. SHIMANO (1996) reported mean annual temperatures and precipitation both in JS-type (ten sites) and PO-type (twelve sites) forests. Winter precipitation (including both snow and rainfall) was greater in JS-type forests (450.1 ± 219.9 mm) than in the PO-type (190.6 ± 62.5 mm; $P < 0.01$, t -test). As discussed below, some aspects of snow, including pressure and protection, affect the differences in species composition, regeneration, and *F. crenata* dominance between the two types of beech forest.

The Japanese archipelago has two different types of beech forests; that comes from different climates caused by backbone mountains. The objective of this paper is to review the

differences in *F. crenata* regeneration between the two types of Japanese beech forest, and to discuss causal factors and characteristics of vegetation in Japanese beech forests, particularly in the PO-type. Here, snow conditions have the most important influence on beech regeneration because it is the major environmental difference between the two types. Beech distribution in other countries will also be discussed and compared to Japanese beech forests.

Nomenclature of taxa in this paper follows OHWI (1972).

***Fagus crenata* regeneration, particularly in JS-type beech forests**

Some aspects of *F. crenata* regeneration dynamics, such as fruiting behavior, seedling establishment, growth, and forest structure, have been studied mainly in JS-type beech forests. It is known that *F. crenata* masts every five to eight years (MAEDA 1988), and that *F. crenata* growing in sunny locations produce many nuts (HASHIZUME & YAMAMOTO 1974a, HASHIZUME 1979, KAMITANI 1986). Nut fertility (i.e., the probability that nuts germinate into seedlings) is high where *F. crenata* is highly dominant (HASHIZUME & YAMAMOTO 1974b), but many seedlings die within the germination year due to shading (HASHIZUME & YAMAMOTO 1975, HASHIZUME & NOGUCHI 1977). Not only canopy trees, but also dwarf bamboo on the forest floor obstruct seedling establishment (KIKUCHI 1935, YANAGITANI et al. 1971, TANIMOTO et al. 1983); therefore, the synchronous death of dwarf bamboo and the period it requires to recover are important in beech regeneration (NAKASHIZUKA & NUMATA 1982, NAKASHIZUKA 1987) because *F. crenata* seedlings are released by gap formation. Damage by insects and rodents can affect the survival of beech seedlings (TANIMOTO 1994, IDA & NAKAGOSHI 1996), and it is known that *F. crenata* does not tolerate water stress very well.

Following these studies, NAKASHIZUKA & NUMATA (1982), NAKASHIZUKA (1984, 1987), HARA (1983), TANAKA (1986), and YAMAMOTO (1989) described the entire regeneration cycle of *F. crenata* from the viewpoint of gap dynamics. These studies showed that *F. crenata* forests of the JS-type have a patch mosaic structure with different developmental stages caused by gap formation, as demonstrated by WATT (1947). Dead beech trees cause canopy gaps, and beech seedlings released in the gaps grow to become canopy trees, while reducing their density by self-thinning. NAKASHIZUKA (1987) reported changes in *F. crenata* density and biomass during patchy cohort regeneration. First, beech seedlings and saplings under the canopy layer were released by gap formation, and both density and biomass increased sharply, suggesting Watt's gap phase. Then, during the build-up phase after the crowns of the saplings had closed, their biomass increased but their density decreased sharply because of self-thinning. The relationship between density and biomass followed the $-3/2$ power law proposed by YODA et al. (1963). In the mature phase, the cohort reached the canopy layer and no longer followed the $-3/2$ power law. As a result, density decreased less rapidly and biomass continued to increase. A series of studies by Nakashizuka (e.g., NAKASHIZUKA 1984, 1987, NAKASHIZUKA & NUMATA 1982) quantitatively demonstrated that Japanese beech forests have a patch mosaic structure composed of cohorts in different developmental stages. These detailed studies were conducted in JS-type beech forests, and showed patterns of regeneration typical of pure beech forests.

Beech regeneration in PO-type forests

It has recently been suggested that, in contrast to JS-type forests, *F. crenata* regeneration in the PO-type is not necessarily constant. SHIMANO & OKITSU (1993, 1994) conducted studies in and around the Kanto area of Japan to compare changes in *F. crenata* density between the two types during the different developmental stages, from the viewpoint of gap dynamics. In gap-dynamic forests, tree density will increase in gaps and decrease in intermediate and mature phases due to competition with neighboring trees (i.e., self-thinning, YODA et al. (1963), WHITE (1981), SILVERTOWN (1982), WESTOBY (1984), and SHIMANO (2000a)). In the JS-type, *F. crenata* density increased during the early or intermediate developmental stages, and decreased in the late stages. In the PO-type forests, however, the density was high in the late stages, but low in the early and intermediate stages. The phenomenon observed in the JS-type of forest is similar to density changes reported in previous investigations (e.g., NAKASHIZUKA 1987), indicating that *F. crenata* regenerates constantly with enough saplings released by gap formation. However, density changes in the PO-type beech forests differ from such typical *F. crenata* regeneration patterns. SHIMANO & OKITSU (1993, 1994) showed that density changes of other tree species in the PO-type beech forests were similar to *F. crenata* in the JS-type forests, and suggested that these species, but not *F. crenata*, would regenerate constantly in those areas.

Subsequently, SHIMANO (1996) used a power function analysis of diameter-at-breast-height (DBH) class distribution, which shows size class and density relationships, to demonstrate that *F. crenata* regeneration in PO-type forests is sporadic. This method was based on the following principle: DBH-class distributions of trees that regenerate constantly show an inverse J-shape (KIMMINS 1987). When such trees regenerate in a patch mosaic forest, the distribution pattern of the DBH-classes should follow a power function curve ($y = ax^b$, where x = DBH class, y = density, a and b = constants), in which the parameter b should be -2 for all trees in the forest (SHIMANO 2000a). He showed that DBH-class distributions of *F. crenata* in JS-type forests fit the power function well, and that the mean of parameter b was about -1.6, suggesting a constant regeneration of beech with an inverse J-shaped DBH-class distribution. On the other hand, the size distribution of *F. crenata* did not fit the power function well, suggesting that beech regeneration was not necessarily constant. Furthermore, he compared the ratio of juvenile to canopy trees (J/C ratio) of *F. crenata* in both types. The mean J/C ratio was about 8 in the JS-type, and 0.8 in the PO-type. This implies that for each parent tree there were eight juveniles in the ten sampled JS-type forests, whereas juvenile density was lower than parent tree density in the twelve PO-type forests sampled. These results suggested that in PO-type forests, *F. crenata* does not regenerate constantly (i.e., sporadic regeneration) because of the low juvenile density, but that instead, other tree species do regenerate constantly.

Reported densities of *F. crenata* seedlings also differed between the two types of beech forest in Japan. HASHIZUME (1991) reported that *F. crenata* seedling density on the JS side ranged from tens of thousands to several millions. On the PO side, SHIMANO & OKITSU (1993) reported a density of 375 seedling ha⁻¹ (individuals < 2 m in height) on Mt. Mito, and SHIMANO (1999a) reported a density of 37 seedling ha⁻¹ (same criteria) in the Tanzawa Mountains, both in central Japan. IMAI (1996) reported that a density of 2300 *F. crenata*

seedlings ha^{-1} in the germination year decreased to 60 seedling ha^{-1} in the next year. *F. crenata* seedling density tends to be considerably lower on the PO side, which likely influences the sporadic regeneration of *F. crenata* in that area.

FAVOURABLE ENVIRONMENT FOR *FAGUS CRENATA* DISTRIBUTION AND REGENERATION

Why does *F. crenata* not regenerate constantly in PO-type beech forests? The environment in the PO-type may simply not be suitable for *F. crenata*. In this paper, I shall consider snow conditions to be “the environment”, because the snow condition is the main environmental difference between the two types of forest.

Correlation between snowfall and the present distribution of *Fagus crenata* forests

Snow abundance and the present distribution of *F. crenata* are correlated. NAKANISHI & NISHIMOTO (1981) studied the vertical distribution of *F. crenata* on the Chugoku Mountains in western Japan. These authors found that *F. crenata* forests occurred up to the lower limits of deciduous broad-leaved forests, and that their distribution overlapped with that of evergreen *Quercus* forests on the snowy JS side. In the inland sea (“Setouchi”) area, which experiences little snow, the lower boundary of *F. crenata* forest distribution was higher, and a zone of *F. japonica* was found in between the *F. crenata* zone and the evergreen *Quercus* forest zone. The authors suggested that the winter precipitation of < 600 mm (December to February) restricts the distribution of *F. crenata*. TANAKA & TAODA (1996) also showed that the elevational distribution of *F. crenata* is wider on the JS side than on the PO side. KURE & YODA (1984) reported a lower distribution limit of *F. crenata* on the JS side of the Kinki district, and indicated that this lower limit was related to the number of days with snow cover. Many studies have suggested that the vertical distribution of *F. crenata* is narrower on the less snowy PO side than on the snowy JS side. In addition, KOJIMA (1975) investigated the relationship between vegetation types and climatic factors with multivariate analysis and concluded that *Cryptomeria japonica*-*F. crenata* forests are not suited to areas where the maximum snow depth is < 100 cm. In studies of *F. crenata*-restricting factors, such as warmth index, precipitation, and days of snow cover depth ≥ 50 cm, UEMURA et al. (1986) and UEMURA (1989) reported that *F. crenata* occurred primarily where there was much precipitation, especially snowfall. SHIMANO (1998) also suggested that the distribution of JS-type beech forests correlated well with snowy areas where the maximum snow depth was ≥ 50 cm. NOZAKI & OKUTOMI (1990) concluded that the distribution of *F. crenata* was narrower than many studies previously suggested, and was inclined toward the snowy JS side; they also suggested that beech distribution in cool temperate zones was limited in less snowy areas.

Correlation between snowfall and the past distribution of *Fagus crenata* forests

Although the relationship between beech distribution and snow conditions is thought to be important, as mentioned above, vast areas of beech forests have been lost as a result of human disturbances, such as land-use changes and forestry. Therefore, it is necessary to confirm this

relationship by analyzing past distributions that were free from large-scale effects of human disturbance. Furthermore, it is well documented that snowfall in Japan was less severe during the last glacial age than it is at present, although there were vast regions with suitable temperature conditions. Therefore, the importance of snow will be clearer if we correlate snow to the past distribution of *F. crenata*.

During the coldest era of the last glacial age, in the period from 17,000 to 20,000 years ago, both air and seawater temperatures were 5 °C–7 °C lower than they are now (YASUDA & NARITA 1981, ARAI et al. 1981), although YASUDA (1987) suggested that at that time biota were more affected by precipitation than by temperature. In those days, there was less snowfall, despite the cold winters. The factor regulating snowfall on the JS side of Japan is the Tsushima warm current. This current flows into the Japan Sea through the Tsushima Strait between western Japan and the Korean Peninsula, and vapor from the warm current creates snow clouds on the JS side of Japan. During the ice age, however, seawater levels dropped about 100 m (80–140 m, KAIZUKA & NARUSE 1977, KAIZUKA 1980, MOGI 1981, OHSHIMA 1980a,b, 1982, 1990, OHNISHI 1990) and reduced the flow of the Tsushima warm current; as a result, the amount of snowfall was reduced (KAIZUKA 1980). ONO (1984) assumed that snowfall during this time was about 20–30% or less of the current levels. SHIMANO (1996) showed that mean winter precipitation (including both snow- and rainfall) in twelve PO-type beech forests was 42.4% of the precipitation measured in ten JS-types. If we consider Ono's assumption and the present difference in winter precipitation between the two types, then we can infer that snowfall in the past was roughly the same as that measured on the PO side in modern times.

YASUDA & NARITA (1981) showed that in the past the lowland areas of western Japan were occupied by a cool temperate zone that had an area almost the same as that of the present-day warm temperate zone. In this area, however, there appears to have been little *F. crenata* pollen during that time, whereas the pollen of deciduous species, such as *Quercus*, *Acer*, *Tilia*, *Carpinus*, etc., was plentiful (YASUDA 1978, FURUTANI 1979). In the glacial age, when there was less snowfall, *F. crenata* tended to be less dominant in the cool temperate zone (KAMEI et al. 1981, TSUKADA 1984, 1988). *F. crenata* expanded its range between 12,000 (FURUTANI 1979, TSUKADA 1981, YASUDA 1983) and 8,500 years ago (YASUDA 1978, HATANAKA & MIYOSHI 1980, TAKAHARA et al. 1989). During that time, the Tsushima warm current began flowing into the Japan Sea, bringing snowy conditions to the JS side of Japan. Therefore, YASUDA (1978, 1985, and 1987) suggested that snow, which increased after the last glacial age, influenced the expansion of *F. crenata*.

A similar tendency has also been confirmed in eastern Japan. In the past, sub-boreal species like *Pinus koraiensis*, *Picea* sect. *Picea*, *Larix kaempferi*, and the *Abies* species dominated, followed by deciduous *Quercus*, before *F. crenata* expanded its range 8,500–6,500 years ago (TSUJI et al. 1983, MORITA & AIZAWA 1986, MORITA 1987, 1992). As discussed earlier, snow conditions have greatly influenced *F. crenata* distribution, not only in the present but also in the past, when there was less human disturbance. Furthermore, the dominant species in the cool temperate zone during the last glacial age were essentially the same deciduous species (i.e., *Quercus*, *Carpinus*, *Tilia*, etc.) that now co-dominate PO-type beech forests. Although it is known that such species sometimes dominate after

human disturbance of natural beech forests, in past eras they have also dominated in less snowy areas with less human activity. Consequently, it is possible that mixed deciduous broad-leaved forests with fewer *F. crenata* occurred in less snowy areas without the destruction of natural beech forests. Furthermore, we can imagine that PO-type climate conditions are not necessarily suitable for *F. crenata*, because snow assists in the regeneration of *F. crenata*, as discussed below.

Factors impeding the constant regeneration of *F. crenata* in PO-type beech forests

SHIMANO (1998) considered the factors restricting beech regeneration that are affected by snow accumulation to be the following (Fig. 2): (1) seed desiccation or freezing, (2) foraging on beechnuts by rodents, (3) deer browsing on seedlings, (4) different light conditions under dwarf bamboo, (5) water stress, (6) forest fires, and (7) the Little Ice Age. Two additional factors, (8) seed fertility and (9) predator satiation, will restrict *F. crenata* regeneration more when its density has already decreased due to one or more of the above factors. Here, I attempt a more detailed discussion.

Seed desiccation and freezing

In PO-type beech forests, snowfall begins later than in the JS-type, and some forests do not have a lasting snow cover during the winter. In this case, beechnuts easily dry out or are directly affected by cold temperatures, although they may be covered with leaf litter. It is known that beechnuts do not tolerate desiccation (YAMANAKA 1975, TAKEUCHI 1975, NAITO 1985), and HASHIZUME & FUKUTOMI (1978) reported that immature beechnuts under drought conditions tended to die within a few days. SHIMANO & MASUZAWA (1995, 1998) and SHIMANO et al. (1995) conducted anti-desiccation tests on beechnuts from snowy JS-type forests and from less snowy PO-type forests. They covered fallen JS-type *F. crenata* nuts with steel nets to minimize foraging by animals, and found that 70% germinated in the following spring in snowy areas, but that none germinated in a less snowy PO-type forest plot, where the dead beechnuts had dried and withered radicles. Unfortunately, SHIMANO & MASUZAWA (1995, 1998) and SHIMANO et al. (1995) collected the seeds during a mast year only in JS-type forests. SHIMANO & MASUZAWA (1998) suggested that if they had used native nuts produced in the sample plot on the PO side, some of the seeds might have germinated, because it is possible to find *F. crenata* seedlings in PO-type beech forests that are free of dwarf bamboo (SHIMANO & OKITSU 1993). In another PO-type forest, MARUTA & KAMITANI (1996) and MARUTA et al. (1997) reported that the native *F. crenata* seeds in the PO-type forests were able to germinate, even though the maximum snow depth exceeded 50 cm at that site.

Freezing as a result of reduced snow cover is also a considerable factor in seed mortality. Snow cover > 50 cm maintains a ground surface temperature above 0 °C (TAKAHASHI 1960, SAKAI 1982, HARA 1996). In less snowy PO-type beech forests, however, shallow snow cover and late snowfall may promote the freezing of seeds. Although SHIMANO & MASUZAWA (1995, 1998) and SHIMANO et al. (1995) reported that dead beechnuts in the PO-type beech forests were dried and withered because of reduced snow cover, it was not

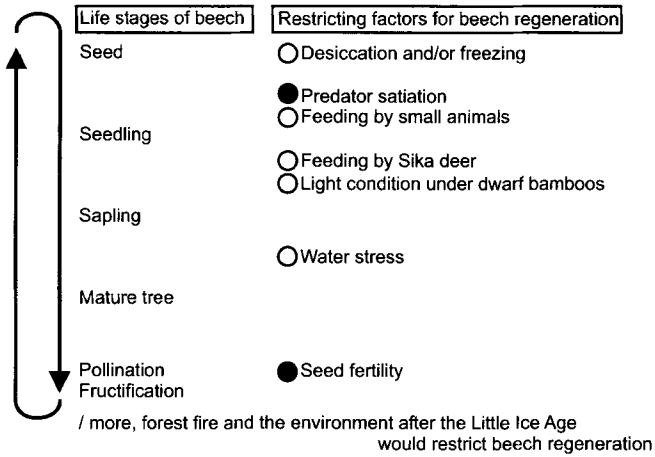


Fig. 2. Restricting factors of *F. crenata* regeneration in Pacific Ocean (PO)-type beech forests. Factors with opened circles will be affected by the condition of less snow, and those with solid ones by the lower dominance of *F. crenata*. Other two factors, forest fire and a Little Ice Age, would restrict the *F. crenata* regeneration connected with less snowy condition.

only drought, but also freezing that affected seed mortality. MARUTA et al. (1997) reported that over 50% of *F. crenata* nuts germinated after having been experimentally dried. The coldest ground surface temperatures during SHIMANO & MASUZAWA's tests (1995, 1998) were below -10 °C, so desiccation or freezing caused by the reduced snow cover would have affected the survival of the beech seeds (SHIMANO & MASUZAWA 1998).

Differences in foraging pressure by small animals between seeds and seedlings

It is well documented that rodents, such as mice, forage on beechnuts, and consequently affect the regeneration of trees (SHAW 1968, JENSEN 1985, WADA 1993, ABE et al. 2001). The feeding activity of rodents below snow cover is restricted (KIMURA 1979, IGARASHI 1980, KONDO 1980, KIMURA & SAWADA 1983, OHTA 1984, MIYAKI & KIKUZAWA 1986). SUZUKI (1989) suggested the possibility that shallow snow may promote foraging by rodents on the PO side, whereas snowy conditions eliminate foraging on the JS side. SHIMANO & MASUZAWA (1995, 1998) and SHIMANO et al. (1995) tested SUZUKI's (1989) hypothesis in both types of forest. They showed that about 70% of beechnuts placed in snowy JS-type forests during winter were intact (i.e., not removed by rodents), and that 70% of these seeds germinated, whereas rodents (mainly *Apodemus speciosus* and *A. argenteus*) removed all seeds placed in the PO-type forests. IMAI (1996) reported that rodents removed 90% of *F. crenata* and *F. japonica* nuts. IRIE et al. (1998) and HOMMA et al. (1999) also stated that seed predation by rodents promoted the mortality of beech seeds during the winter, while predation was lowered by thick snow cover.

MASUZAWA & SHIMANO (1995) tested the feeding activity of rodents between snowy and non-snowy periods in a PO-type beech forest. They found that feeding activity during the period of snow cover was low compared to that recorded during the period of no snow cover. SHIMANO & MASUZAWA (1998) discussed the importance of visual (VANDER WALL 1994)

and olfactory senses (CAHALANCE 1942, HOWARD et al. 1968, JENNINGS 1976, OTSU 1979, THOMPSON & THOMPSON 1980), and confirmed experimentally that snow interferes with the visual and olfactory senses of rodents. Since beechnuts are highly nutritious, rodents prefer them to the seeds of other species (JENSEN 1985); thus, feeding pressure on beechnuts is very high, although rodents also feed on other seeds in less snowy conditions.

Rodents affect beech regeneration not only at the seed stage but also at the seedling stage (TANIMOTO 1994, IDA & NAKAGOSHI 1996). MARUTA & KAMITANI (1996) reported that the frequency of feeding on *F. crenata* seedlings that had germinated in that year was higher on the PO side, and suggested that this was because these seedlings had not been protected by snow cover after germination.

Damage by insects also differs between the two types of beech forest. SUZUKI (1989) reported high rates of insect damage to beechnuts in the PO-type forests. KAJI & OHKUBO (1995) suggested that the reduced snow cover was insufficient to lower the density of harmful insects in the less snowy PO-type forests.

Feeding pressure by Sika deer

Feeding on beech seedlings by Sika deer (*Cervus nippon*), which inhabit the less snowy areas, is a significant problem for beech regeneration. TAKATSUKI & GORAI (1994) reported the feeding effect of deer on Kinkazan Island. They reported that the overpopulation (60 km⁻²) of deer disturbed beech regeneration, because only large *F. crenata* trees (30–60 cm DBH), and no small, younger individuals were found. Moreover, they found many juvenile beech in an area from which deer were excluded. AKASHI (1997) reported that about 80% of *F. crenata* seedlings that had germinated in the spring (2.94 m⁻²) died by the fall of that year, and that the main cause was the removal of the epicotyl by rodents and Sika deer. TOHYAMA & SAKAI (1993) reported that in the Tanzawa Mountains phytosociological associations of natural beech, *Corno-Fagetum crenatae* and *Miricacalio-Fagetum crenatae*, changed into *Veronico-Fagetum crenatae* associations. OHNO & OZEKI (1997) suggested that the original natural vegetation, *Miricacalio-Fagetum crenatae*, was converted into the degenerate phase because of intense feeding pressure by deer. Thus, browsing by deer is so severe that original natural communities have been altered.

The distribution of deer is higher in less snowy areas and differs from that of Japanese Serow (*Capricornis crispus*), which never reach very high densities. MARUYAMA (1981) suggested that snow accumulations of > 25 cm in depth cover dwarf bamboo (*Sasa nipponica*), the main food for deer, and therefore restrict foraging. TAKATSUKI (1992) suggested that snow deeper than 50 cm restricts deer behavior, because their legs are only about 50 cm long. As mentioned above, too much snow disturbs the behavior and feeding activity of deer and therefore restricts their distribution. In fact, deer are not found on the much snowier JS side. Although deer feed on other trees besides juvenile beech, their influence on beech is likely severe, because beech seedling density is lower than that of other trees on the PO side (SHIMANO & OKITSU 1993, SHIMANO 1999a). Japanese Serow, on the other hand, are distributed also in snowy areas. Their influence is less significant, because they have fixed territories and do not congregate, unlike deer, which often form crowded herds. Thus, foraging pressure by Japanese Serow should be less intense because of their low densities, although they also prefer tree buds.

Light conditions under dwarf bamboo cover during the spring

SHIMANO (1996, 2000b) suggested that snow-cover suppresses the growth of dwarf bamboo, thereby creating sunny openings on the forest floor in which beech seedlings are able to regenerate. Such conditions would not exist in the less snowy PO-type beech forests. Ordinarily, beech seedlings in the JS-type forests would die within a few years after germination in the dark conditions under dwarf bamboo cover (HASHIZUME & YAMAMOTO 1975, HASHIZUME 1982, 1991, KATAOKA 1989). However, when well-lit sites are available in the spring because of bamboo suppression, beech regeneration is favoured in snowy areas. SHIMANO (2000b) suggested that *F. crenata* seedlings survive for several years in such situations, while awaiting the next mast year, even if they ultimately die.

FUJITA (1986) discussed the difference in dwarf bamboo cover between the two types of beech forest. He suggested that beech could regenerate under dwarf bamboo cover in the JS-type beech forests because of the differences in dwarf bamboo characteristics, although beech in the PO-type forests never regenerate without the synchronous death of dwarf bamboo. HIROKI & MATSUBARA (1995) made the same suggestion. Although many studies have indicated the importance of simultaneous dwarf bamboo death for beech regeneration, the above hypotheses (FUJITA 1986, HIROKI & MATSUBARA, 1995, SHIMANO 2000b) suggest preferable conditions for beech regeneration in the JS-type forests regardless of dwarf bamboo cover.

There is a marked difference in the dwarf bamboo species in the two types of beech forest. The culm density of *Sasa kurilensis*, the most common dwarf bamboo in the JS-type forests, is high in canopy gaps, but low under canopy trees (SHIMANO 1999b). The culm density of *Sasamorpha borealis*, the major dwarf bamboo in the PO-type beech forests, does not vary (SHIMANO 1999b). The lower culm density of *Sasa kurilensis* under the canopy makes the forest floor brighter than in canopy gaps. In the JS-type beech forests, such bright conditions under the canopy are advantageous to beech seedlings, even where dwarf bamboo dominates the forest floor. More studies of this relationship should be made.

Water stress

In addition to snow, some researchers have indicated the importance of water stress. MARUTA & KAMITANI (1996) and MARUTA et al. (1997) reported that germinating beech seedlings, which are unable to use soil water in the litter layer, tended to die due to desiccation during the spring on the PO side. KAWAMATA & MARUYAMA (1972) found that beech opened their leaves within about 10 days after germination, and that the water content of leaves was at its highest during this period.

The intolerance of *F. crenata* to drought has been confirmed by ecophysiological studies. MARUYAMA & TOYAMA (1987) tested the influence of water stress on photosynthesis and evaporation of *F. crenata*, *Quercus serrata*, and *Q. mongolica* var. *grosseserrata*. They suggested that *F. crenata* was the weakest of these species, which may affect its habitat selection. TSUKADA (1982) suggested that beech could not enlarge its distribution area in the Kulomatunai Lowlands, at the northern limits of the *F. crenata* distribution, because during the postglacial age precipitation in the growing season was < 800 mm, even though air temperatures were high enough. KOIKE (1988) and KOIKE & MARUYAMA (1998) noted that

F. crenata in the PO-type forests have a leaf structure that is adapted against desiccation. Thus, water stress might affect *F. crenata* on the PO side.

PETERS (1992) suggested that the distribution of *Fagus* was limited not only by cold winter temperatures and spring frosts, but also by a shortage of rain in the summer. It is said that *Fagus* is sensitive to desiccation globally (PETERS 1997), e.g., *F. grandifolia* (GLEASON 1924, BORCHERT 1950, HAMILTON 1955, FOWELLS 1965), *F. sylvatica* (PETERKEN 1996, MAKITA 1981), and some *Fagus* spp. in China (HOU 1983, HONG & AN 1993), although *F. orientalis* can tolerate dry conditions (MAYER 1984, AKBARINIA et al. 1995).

Forest fires

NAKASHIZUKA (1994) and NAKASHIZUKA & IIDA (1995) suggested that PO-type beech forests have a high diversity because of disturbances like forest fires. Deciduous *Quercus* spp. regenerate through forest fires in northeastern North America, although *Fagus grandifolia* regenerates in small gaps caused by stem breakage (RUNKLE 1990). NAKASHIZUKA & IIDA (1995) suggested that the same phenomenon occurred in Japan, a hypothesis that was also proposed by TANAKA (1887) and HONDA (1912). They indicated that deciduous broad-leaved forests with fewer *F. crenata* in the intermediate temperate zone, such as the lower extent of the PO-type beech forests, were favoured by forest fires and human disturbance. As NAKASHIZUKA & IIDA (1995) pointed out, however, such forest fires are caused by human activities. The TOKYO REGIONAL FOREST OFFICE (1977) reported that over 70% of forest fires were caused by careless smoking or fire making. NAITO & IIZUMI (1987) also suggested that forest fires are more abundant in the lower distributions of beech forests than in the higher ones as a result of human activity. Forest fires primarily occur in less snowy areas during the spring, although snow cover would protect forests from fires during the winter.

Little Ice Age

As discussed above, there are many beech canopy trees, but little regeneration in the PO-type beech forests. KOIZUMI et al. (1988) advanced the hypothesis that this phenomenon is a relic of the Little Ice Age that occurred about 200–300 years ago, during which Japan experienced a cold and rainy climate (YAMAMOTO 1980, YOSHINO 1982, MAEJIMA 1984, GATES 1993). KOIZUMI et al. (1988) suggested that large present-day *F. crenata* trees were juveniles that regenerated during this cold and rainy (and probably also snowy) period, but that regeneration ended once this period ended, because beech preferred wet and snowy conditions. Therefore, it follows that *F. crenata* successors are found at lower densities compared to parent trees under present-day less snowy conditions (KOIZUMI et al. 1988, SHIMANO & OKITSU 1993, 1994, SHIMANO 1996). Unfortunately, the precipitation during that period has not been estimated quantitatively, although the mean temperature at that time has been estimated to have been about 3 °C lower than it is now on Yakushima Island, southern Japan (KITAGAWA 1995). Perpetual snow was reported on Mt. Hiuchi (ANONYMOUS 1809) where there is no perpetual snow now. SAKAGUCHI (1994) said that a pollen analysis of the area (Oze Moor) showed the influence of the Little Ice Age. Prolongation of the snow period would be preferable for the protection of beech seeds from feeding pressure and other factors.

In order to understand what effect the Little Ice Age had on beech regeneration, we must use dendrochronological methods to verify that large *F. crenata* truly regenerated during this period. This may prove difficult, because large beeches older than 200–300 years are now dying, and much older *F. crenata* would already be dead. However, the idea that environmental conditions for *F. crenata* have not always been stable deserves attention.

Seed fertility

Several studies have considered the possibility of low seed fertility in beech on the PO side. OHBA (1985) and SUZUKI (1989) noted a high occurrence of empty *F. crenata* seeds on the PO side, and HIROKI & MATSUBARA (1995) showed that the proportion of sound nuts in the Suzuka Mountains, near the Pacific Ocean, was 1/10 to 1/2 of that in the other JS-type beech forests. This may be due to unsuccessful pollination, which could result from poor-quality *F. crenata* pollen or low densities of *F. crenata* canopy trees. Although *F. crenata* is wind-pollinated, the pollen of *F. crenata* is exceptionally large, and falls to the ground rather than drifting with air currents (HASHIZUME 1975, TANAKA 1989). Most of the pollen falls within 10 m of the parental trunk (HASHIZUME & SUGAWARA 1985). Therefore, the decreased fertility of *F. crenata* nuts could be caused by the low density of *F. crenata* pollen because of the comparatively small number of canopy beeches and the many other trees that block the path of the pollen. HASHIZUME & YAMAMOTO (1974b) reported that in the JS-type beech forests where *F. crenata* was less dominant and the density of fruiting *F. crenata* was low, fewer nuts were fertile; they suggested that this may have been due to poor pollination and self-incompatibility. Beeches require pollination to produce fertile nuts. However, HASHIZUME & YAMAMOTO (1974b) showed insufficient pollination of *F. crenata* where other trees co-dominated, even in a JS-type beech forest. This implies more severe conditions for *F. crenata* pollination in the PO-type forests, where many tree species co-dominate with *F. crenata*. SHIMANO (1996) showed that the canopy tree density of *F. crenata* in PO-types was about half of that in JS-types, and that this density was the same as that of other tree species. NILSSON & WASTLJUNG (1987) confirmed that *Fagus silvatica* in large beech stands and in high-density beech stands had higher incidences of sound seeds. The AOMORI REGIONAL FOREST OFFICE (1973) suggested that the same phenomenon occurs in Japan.

Predator satiation

Predator satiation is not likely to be an efficient strategy on the PO side. It is difficult for *F. crenata* to produce many nuts each year, and predator satiation is thought to be another reason for masting (SILVERTOWN 1982), which occurs every five to eight years in *F. crenata* (MAEDA 1988). If beech were able to produce many nuts every year, these nuts would be eaten by predators that would occur at high densities due to the abundant supply of food provided every year. However, if beech produce only a few nuts every year, predators can only survive at relatively low densities; thus, these few predators are unable to consume the abundance of nuts produced during a mast year. Many beechnuts are therefore able to germinate in the next year. This strategy has been called “escape” (VOUTE 1946) or “predator satiation” (JANZEN 1971) and has also been discussed for *F. crenata* in Japan (MIGUCHI & MARUYAMA 1984, IGARASHI 1991, KAMATA 1996). However, it is assumed that beechnut

production is low on the PO side because of the low density of canopy beeches, which may lead to insufficient predator satiation. Furthermore, SHIMANO & MASUZAWA (1995, 1998), SHIMANO et al. (1995) and HOMMA et al. (1999) suggested that *F. crenata* nuts on the PO side would be intensively foraged on, compared to the JS side, because the few sound seeds found on the PO side were eaten by rodents more aggressively than empty ones (SHIMANO & MASUZAWA 1995, SHIMANO et al. 1995). In addition, KAJI & OHKUBO (1995) pointed out that there was significant insect damage to beechnuts because insect density was not kept low; this was a result of two beech species, *F. crenata* and *F. japonica*, not always having synchronous mast years.

These two factors (seed fertility and predator satiation) depend on *F. crenata* density. Therefore, if the effects of reduced snow cover decrease the density of *F. crenata*, the low density of *F. crenata* would exacerbate problems with poor beech regeneration.

Deciduous broad-leaved forests without *Fagus crenata*

We need to know which species make up a forest under the less snowy conditions to which *F. crenata* is not suited. Moreover, it is necessary to confirm whether tree composition is similar to tree communities in the less snowy PO-type forests.

If *F. crenata* is not suited to the PO-type climates, then which species are adapted to these less snowy areas? UEMURA (1989) showed that *Quercus mongolica* var. *grosseserrata* occurred not only in the snowy areas, but also in the less snowy areas, and that *F. japonica* and *Tilia japonica* occurred only in the less snowy areas. UEMURA et al. (1986) found that *Acer palmatum* var. *amoenum*, *Carpinus cordata* and *Ostrya japonica* occurred only in the less snowy areas. TAKAHASHI (1962) suggested that *F. japonica*, *Abies homolepis*, *Tsuga sieboldii* and *Carpinus tschonoskii* are distributed in the less snowy regions. FUJITA (1987) suggested that *Acer sieboldianum*, *Stewartia monadelphica*, *Abies homolepis*, and *C. tschonoskii*, which are typical species and major components of PO-type beech forests, were maldistributed on the PO side. NOZAKI & OKUTOMI (1990) studied the intermediate temperate natural forests of eastern Japan and suggested that too much snow accumulation impedes the distribution of such forests. They stated that intermediate temperate forests occurred naturally in the less snowy areas in the lower parts of the cool temperate zone on the PO side.

Other tree species, excluding *F. crenata*, are restricted in snowy areas, because many of them are unable to withstand snow pressure: their trunks are easily bent or broken (KAMITANI 1984, MAEDA et al. 1985, ONODERA et al. 1995, HOMMA 1997, SHIMANO 1999b). *F. crenata* is almost the only species that can grow straight trunks in areas of heavy snow. In other words, pure beech forests of the JS-type are special features of cool temperate broad-leaved forests.

Characteristic of PO-type beech forests

It is well known that beech species dominate in the cool temperate zone of the oceanic climate in Europe and North America. However, deciduous broad-leaved forests with fewer or no *F. crenata* would be distributed naturally both in the present and the past in Japan even if under oceanic climate. *F. crenata* dominates in snowy areas of the cool temperate zone, especially on the JS side, whereas mixed deciduous broad-leaved forests with few *F. crenata*

occur in the less snowy areas on the PO side. Based on the above discussion, we newly recognize the position of the PO-type beech forests. Until now it was considered that *F. crenata* is the climax species and dominates cool temperate deciduous broad-leaved forests, and that PO-type beech forests are mainly occupied by *F. crenata* with co-dominant deciduous broad-leaved trees. From the above discussion, however, PO-type beech forests are potentially deciduous broad-leaved forests with several co-dominant trees. In these forests, *F. crenata* often dominates because of its large size and long life span, although its regeneration traits are not necessarily optimal under less snowy conditions. This idea agrees with the regeneration pattern of *F. crenata* in PO-type forests reported by SHIMANO & OKITSU (1993, 1994) and SHIMANO (1996). Excluding Europe, where beech forests have low species richness as a consequence of the last glacial age, the occurrence of pure beech forests is also rare in the USA and China (OHSAWA & TAKIGUCHI 1987, PETERS 1992, 1997, CAO 1995, HARA 1996). Such forests are only likely to occur in environments unsuitable to the regeneration or distribution of other species. Therefore, we should consider the regeneration of *F. crenata* in Japan in this context, especially the differences between the two types of beech forest. We should reconsider the characteristic of beech forests especially in Japan, though which forests are under oceanic and summer-rainfall climate.

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