

Desiccation-tolerance of *Fagus crenata* Blume Seeds from Localities of Different Snowfall Regime in Central Japan

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In beech (*Fagus crenata* Blume) forests on the Pacific Ocean side in Central Japan, snowpack depth is little and xeric conditions may prevail in winter, in contrast to heavy snow in beech forests on the Japan Sea side. The effects of such conditions during winter on the viability of beech seeds were studied at a beech forest on the Pacific Ocean side. Thickness and weight ratio of pericarp of beech seeds were significantly greater in populations on the Pacific Ocean side compared to the Japan Sea side, this apparently being related to snowpack depth in winter. During the initial stage of seed drying, the drying rate of seeds from the Fuji population (the Pacific Ocean side) was less than that from the Sumon population (the Japan Sea side), possibly due to the thicker pericarp. Germination percentage of seeds which dried to a water content as low as 7% d.w. did not decrease for either population, indicating desiccation tolerance of beech seeds. In the beech forest (University Forest at Yamanaka) on the Pacific Ocean side, water content of seeds sown below litter from both populations remained sufficient for viability during winter. Germinating seeds from the populations on the Japan Sea side were more desiccation-sensitive in early spring, compared to those from the Fuji population, partially due possibly to differences in pericarp thickness.

Key words: desiccation-tolerance, ecotypic variation, *Fagus crenata* Blume, overwintering of seeds, seed character

Regeneration mechanism of climax Japanese beech (*Fagus crenata* Blume) forests, particularly on the Japan Sea side, has been studied based on their structure, tree age structure and the growth of seedlings and juveniles (Hara, 1983, 1985; Nakashizuka, 1983, 1987; Maruyama *et al.*, 1989; Yamamoto, 1989). Such studies have indicated that constant seedling recruitment at a mast year once in several years is necessary for successful regeneration, and that rapid growth of seedlings and juveniles should follow after gap formation due to death or falling of one or several canopy trees. This gap formation and following partial regeneration are considered essential for maintaining dynamic equilibrium in a climax beech forest on the Japan Sea side. Structure and species composition of beech forests on the Pacific Ocean side differ from those on the Japan Sea side (Fujita, 1986; Fukushima *et al.*, 1995). The mode of regeneration pattern also differs for the two forest types (Shimano and Okitsu, 1993, 1994). Shimano and Okitsu (1994) notes that beech possesses only a few juveniles in beech forests on the Pacific Ocean side, whereas other deciduous broad-leaved tree species regenerate constantly with many juveniles. They suggest that beech is incapable of regenerating under the climate available and that other tree species may replace beech in the future.

One cause for differences in the abundance of beech seedlings of the two forest types may be that the amount of snowfall in these forests is not the same. Snowpack depth is much more (1m <) and snow coverage continues during longer winters (December to May) in beech forests on the Japan Sea side than the Pacific Ocean side, suggesting that snow coverage may possibly protect beech seeds from winter stress. About 70–80% of seeds overwinter and remain at the

time of germination in a beech forest on the Japan Sea side, whereas few seeds remain on the Pacific side, indicating a less amount of snow cover to result in greater seed consumption by rodents (Shimano and Masuzawa, 1995). A lesser amount of snow cover may lead to inadequate protections of *Fagus* seeds, owing to desiccation during a winter dry season on the Pacific Ocean side (Kaji *et al.*, 1992; Shimano and Masuzawa, 1995). The effects of winter dry conditions on beech seed survival have yet to be experimentally confirmed.

Nearly all seeds of *Quercus serrata* Murray, predominant tree species in warm temperate forests in Japan, germinate hycopotyl immediately after seed fall and seedlings easily incur desiccation and physical stress by soil freezing on the Pacific Ocean areas (Hiroki and Matsubara, 1982). *F. crenata* does not germinate until winter on either sides. Thus on the Pacific Ocean side, seeds are exposed to severe xeric conditions during the dry period from late autumn to early winter. Germinating seeds of beech may be exposed to such conditions in early spring. That the times of germination for *Q. serrata* and *F. crenata* are not the same may lead to differences in stress-sensitivity during winter.

The purposes of this study were (1) to determine the extent of desiccation of beech seeds and germinating seeds in a beech forest on the Pacific Ocean side, and (2) to compare seeds from both sides for capacity to adapt to xeric conditions.

Materials and Methods

Seeds of *F. crenata* from six wild populations at different sites with different winter snow depth in Central Japan were used (Fig. 1). Measured averages of maximum snow depth are 350 cm (Iide), 233 cm (Sumon, 1990–94), 200–300 cm (Tanbara), 20–30 cm (Chichibu) and 57 cm (Fuji, 1988–92). Based on the maximum snow depth, beech forests in Iide,

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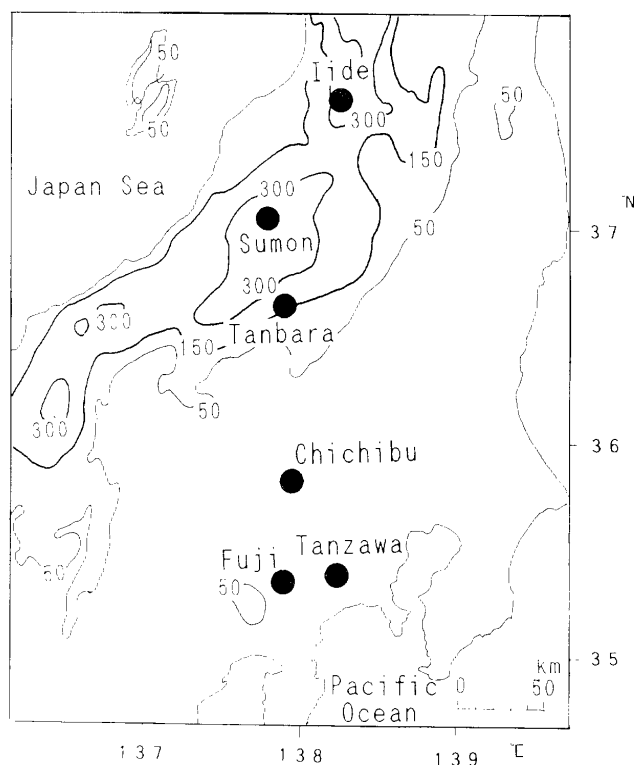


Fig. 1 Locations from which *Fagus crenata* seeds were collected. Lines, isogram of 50, 150, and 300 cm mean annual maximum snow depth from Forest environment map of Japan (Society of Forest Environment, 1972).

Sumon and Tanbara may be classed as the Japan Sea type, and those in Chichibu, Tanzawa and Fuji as the Pacific Ocean type. Seeds were collected from a natural beech forest at each site in late October 1993. Immatured and insect-damaged seeds were excluded. The seeds were soaked in water and those that remained at the bottom of the water were selected. After these seeds were confirmed to be full matured, they were used in subsequent experiments. These seeds were stored in plastic bags at 3–5°C until use.

1 Morphological characteristics of seeds from six populations

Fresh weight of selected full matured seeds exceeded 150 mg for each population. Fresh weight was determined and the pericarp was then removed and weighed. Pericarp thickness was measured with a micrometer (Mitutoyo Co. Ltd., Tokyo, Japan).

2 Desiccation experiment

On January 2–3, 1994, a desiccation experiment was carried out for beech seeds from the Fuji and Sumon populations. The seeds were left for different periods of time in a room at $12 \pm 2^\circ\text{C}$ and 40–50% relative humidity, in order to be dried to six levels of water content within the range of 7.1–56.3% d.w. At the end of each period, ten seeds from each population were examined for water content, and twenty seeds for germination test. Water content per dry weight (WC , % d.w.) of the seeds was determined based on fresh weight (FW) and dry weight (DW , oven drying for 48 h at 80°C) as follows,

$$WC = (FW - DW) / DW \times 100 \quad (1)$$

Sample seeds were sown in planters filled with a mixture of leaf mold and clods of red clay (1:1 of volume), which was

then allowed to stand in a room at 15°C . On March 16, 1994, the germination rate was assessed visually. Seeds were considered to have germinated if radicles could be seen.

3 Seed water content on the beech forest floor during the winter

Water content of seeds from Fuji and Sumon populations was monitored during the winter of 1993–1994 on the beech forest floor in University Forest at Yamanaka of University of Tokyo (996 m a.s.l., $35^\circ24'\text{N}$, $138^\circ52'\text{E}$), located at the north-western foot of Mt. Fuji. The area of the beech forest is 0.08 ha. The beech saplings were planted in 1959 and tree density was 2,138/ha in 1993. Microclimate of forest floor during the winter was observed to be equal to that of surrounding natural beech forests. The climate is typical of the Pacific Ocean side, with 74% annual precipitation from April to October (University Forest at Yamanaka; 1985–1994) and light snow covering in winter.

Twenty seeds were numbered with a felt pen, weighed and placed in a 15 cm \times 15 cm of plastic net bag (mesh size, 1 mm). Three bags for each population were placed below litter in the beech forest on November 24, 1993. The seeds were reweighed on December 2, 1993 and then returned to the bags. On March 18, 1994, the seeds were taken out of the bags, and fresh and dry weights were measured to determine water content according to Eq. (1). Water content on November 24 and December 2, 1993 was also calculated in the same way. It was assumed that respiratory loss of DW during the 4 months of winter was negligible. Surface soil temperature below the litter was measured with thermister probe (Kadec-U, Kona System Co. Ltd., Tokyo, Japan).

4 Seed and seedling conditions following snowmelt

In the beech forest of University Forest at Yamanaka on November 18, 1993, 50 seeds from each of the population of Fuji, Tanbara and Sumon were sown in a 50 cm \times 50 cm quadrat and covered with litter. Five sets were made for each population. The quadrats were protected from rodents by being enclosed in wooden frame structures covered with wire net (mesh size, 1 cm).

On April 8, 1994, litter in the quadrats was removed and the seeds and germinated seedlings were visually checked and classed as follows: stage 2, germinated and radicles developed to the soil surface; stage 1, germinated and undeveloped radicles still in the litter layer; stage 0, ungerminated but appearing in good condition; fungi-damaged, ungerminated and infected with fungi; desiccated, desiccated radicles in stage 1.

Data from all experiments were analyzed with the aid of SPSS (Base System and Exact Tests, 1993) computer program packages.

Results

1 Morphological characteristics of seeds from six populations

Average percentage of pericarp weight to total seed weight ranged from 35% for the Sumon seeds to 46% for the Tanzawa and Fuji seeds (Fig. 2A). The percentage of pericarp

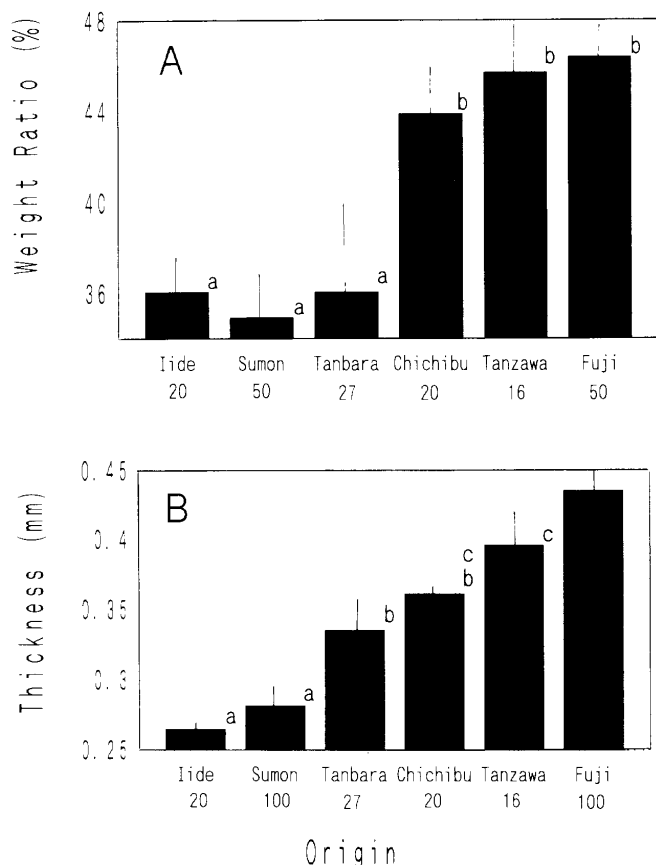


Fig. 2 Variation of pericarp characteristics among localities. (A) The average percentage of pericarp weight to total seed weight; (B) the average thickness of the pericarp for seeds from six populations along a winter snow depth. Vertical bars represent 1 SD. Values with common superscripts are not statistically different ($p > 0.05$). Sample sizes are shown below the names of localities.

weight was significantly (Scheffe test 1-way ANOVA, $p < 0.05$) greater for seeds from populations of the Pacific Ocean side (Fig. 2A). It was basically the same ($p > 0.05$) among the populations from each side (Fig. 2A).

Pericarp thickness ranged from 0.27 mm for the Iide seeds to 0.44 mm for the Fuji seeds (Fig. 2B). Pericarp thickness differed significantly (Kruskal-Wallis 1-way ANOVA, $p < 0.05$) among the populations. It was significantly (Scheffe test 1-way ANOVA, $p < 0.05$) greater for seeds from populations of the Pacific Ocean side (Fig. 2B).

2 Desiccation experiment

At the start of this experiment, average water content (WC) was 56.3% d.w. and 53.2% d.w. for the Fuji and Sumon seeds, respectively. At the initial stage of seed drying, WC declined more rapidly for the Sumon than Fuji seeds (Fig. 3A). Initial drying rates was 0.72% d.w./h (0 to 9.8 h) and 3.3% d.w./h (0 to 5.8 h) for the Fuji and Sumon seeds, respectively, corresponding to thickness of the pericarp (Fig. 2B). Then, WC of seeds from the Sumon declined more slowly, whereas it declined almost constantly for the Fuji seeds. At 79 h, it was 7% d.w. for either population.

The germination of dried seeds was nearly the same or somewhat more than that of fresh seeds for both populations (Fig. 3B). Seeds dried for 79 h had high germination ability for both populations. Namely, seeds dried to 7.1% d.w. showed

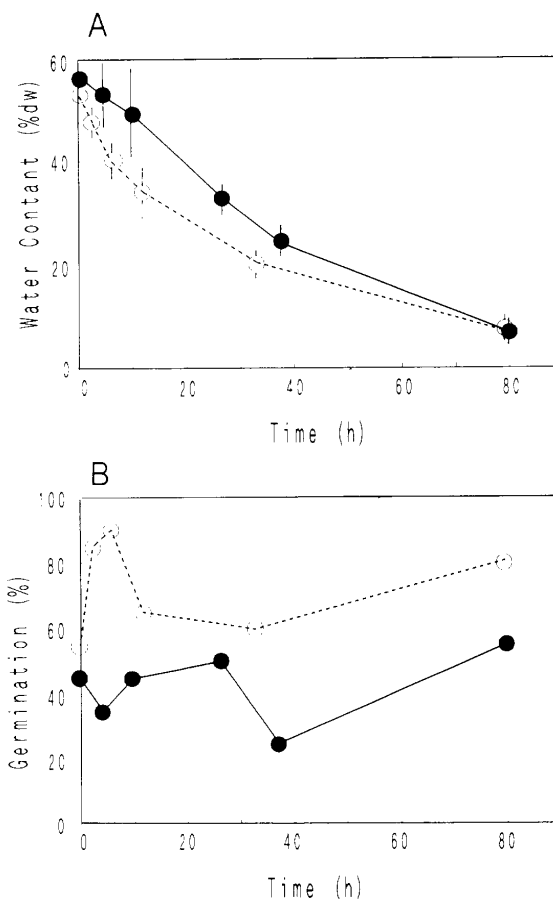


Fig. 3 Water content and germination ability of *Fagus crenata* seeds after drying procedure. (A) Drying curves for seeds from two populations dried at $12 \pm 2^\circ\text{C}$ air temperature and 40–50% relative humidity. Vertical bars represent 1 SE, (B) germination (%; criterion radicle emergence) of seeds after drying procedure. ●, Fuji; ○, Sumon.

55% germination for the Fuji population, while those dried to 7.3% d.w. gave 80% germination for the Sumon population (Fig. 3A, B). The germinations were not significantly ($p > 0.05$) correlated to WC for the Sumon seeds ($r^2 = -0.0603$) and the Fuji seeds ($r^2 = -0.1310$). Kendall correlation coefficient was -0.0667 and 0.1380 for the Sumon and Fuji seeds, respectively.

3 Seed water content on the beech forest floor during the winter at the beech forest floor

Soil temperature under the litter layer ranged from 0 to 10°C until late December 1993 (Fig. 4). From late December to early April, the forest floor was covered with snow at a depth of 10–20 cm. During this period, soil temperature remained near 0°C (Fig. 4). After snowmelt in early April, it increased rapidly and the range of daily change was as much as near 20 K.

Water content (WC) was averaged for each set of bags. At the start (November 24, 1993), average WC (70.5–72.9% d.w.) of the Fuji seeds was greater ($p < 0.05$) than that (55.4–60.5% d.w.) of the Sumon seeds (Fig. 5). Difference in the initial WC may have been due to greater water loss from the Sumon seeds during the treatment, as would be expected from the faster drying rate (Fig. 3A). By December 2, 1993, average WC declined to 60.1–61.9% d.w. for the Fuji seeds. For the Sumon seeds, it decreased to 36.9% d.w. and 47.1%

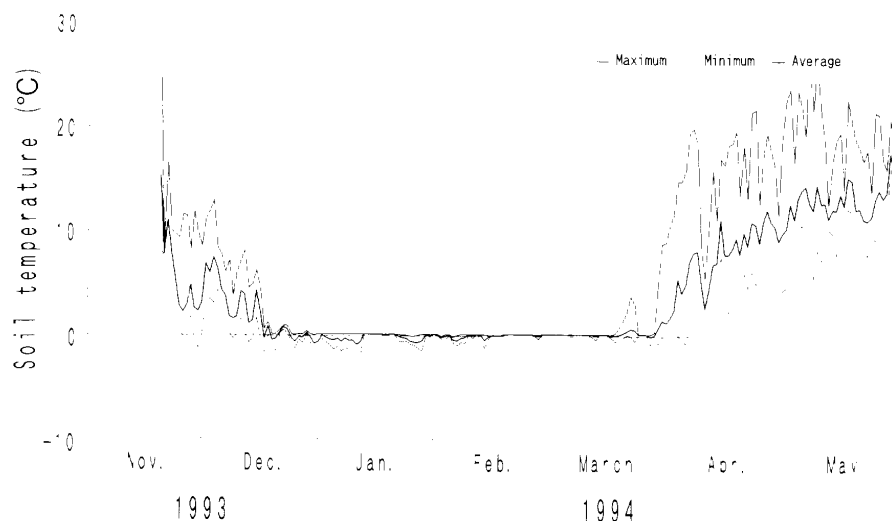


Fig. 4 Soil surface temperature under litter layer at the beech forest floor of University Forest at Yamanaka during the winter of 1993-94.

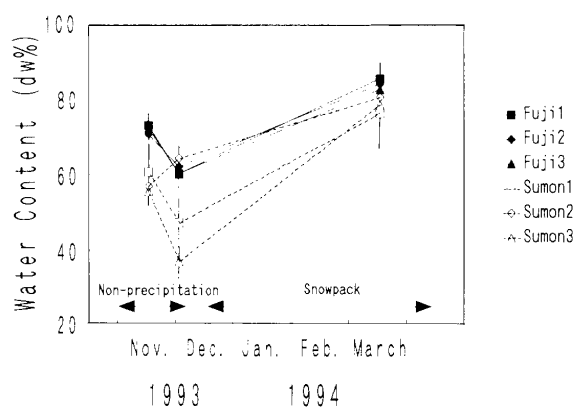


Fig. 5 Changes in seed water content for *Fagus crenata* at the beech forest floor of University Forest at Yamanaka during the winter of 1993-1994. Averages of twenty seeds in each three sets of the bag for Fuji (closed symbols) and Sumon (open symbols). Vertical bars represent 1 SD.

d.w. for two bags, whereas slight increase was noted for one bag.

There was no precipitation from November 22 to December 2, 1993, this being the longest non-precipitation period in the winter of 1993-1994 at University Forest at Yamanaka. From late December, seeds were protected from desiccation with snow cover. Water content (WC) of 36.9% d.w. for the Sumon seeds may thus have been a minimum value for that winter. By March 18, 1994, WC of seeds increased to 82.5-85.4% d.w. for the Fuji seeds and 76.0-80.4% d.w. for the Sumon seeds (Fig. 5). Seeds may have absorbed water under snow cover at a temperature near 0°C.

4 Seed and seedling conditions following snowmelt

Soil temperature indicates that snowpack may have melted completely by April 4, 1994, since temperature fluctuation increased after April 4 (Fig. 4).

On April 8, 1994, total number of remaining seeds in the five quadrats was 109, 79 and 113 for the Fuji, Tanbara and Sumon populations, respectively. Despite protection, 55-69% of sown seeds may have been carried away. The mesh size of wire net was 1 cm and small enough for protection

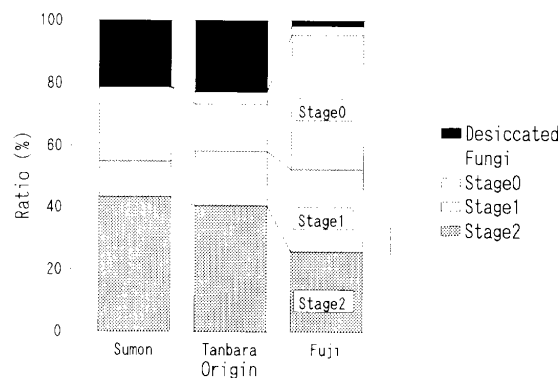


Fig. 6 Conditions of *Fagus crenata* seeds on April 8, 1994 at the beech forest floor of University Forest at Yamanaka. Seeds from Fuji, Tanbara and Sumon populations were sown in late autumn 1993. Developmental stages of Stage 0, 1 and 2 and sample sizes are explained in the text.

from consumers such as birds and hares. Thus, they were thought to be consumed by small mammals such as rodents during the winter. Ninety-four percent, 72% and 93% of seeds from Fuji, Tanbara and Sumon, respectively, remaining on April 8 has germinated by June 5, indicating also that seed viability was maintained during the winter. By April 8, 1994, seeds developed more for the Sumon and Tanbara populations than the Fuji population, nearly 40% of seeds from the Sumon and Tanbara populations reaching to stage 2, whereas 43% from the Fuji population remaining in stage 0 (Fig. 6).

Seedling death occurred in stage 1 due to radicle-desiccation in the litter layer. Thus, germinating seeds were susceptible to drought, preventing short radicles from extending to the soil surface to absorb soil water. Nearly 20% of the Sumon and Tanbara seeds died due to radicle-desiccation in stage 1, whereas only 2% of the Fuji seeds (Fig. 6). Radicle-desiccation accounted for 65% and 56% of germinating seeds mortality in stage 1 for the Sumon and Tanbara populations, respectively, and 6.5% for the Fuji population.

Discussion

European beech (*Fagus sylvatica* L.) shows geographical variation in its genetic, morphological and phenological characteristics (Borghetti *et al.*, 1993). In the xeric population from Sicily, there is delayed seedling water stress response of physiological characteristics such as predawn leaf water potential, net photosynthesis and leaf conductance, in contrast to Abetone where the climate is more mesic (Tognetti *et al.*, 1995), thus indicating physiological adaptation or acclimation to climate. Japanese beech apparently not exposed to extremely xeric conditions during the growing season anywhere in Japan. However, moisture conditions during winter on the Pacific Ocean side and the Japan Sea side differ considerably, there being much heavier snowfall on the latter. Geographical variation in leaf size (Hagiwara, 1977) and phenology (Hashizume *et al.*, 1996; Kaji and Nishitani, 1996) were also noted in Japanese beech, apparently corresponding to the maximum snow depth in winter. This suggests genetic variation and potential for physiological adaptation in Japanese beech populations along the moisture gradient during winter. Allocation of resource material to the pericarp was significantly greater (46%) for the seeds from populations on Pacific Ocean side than that (35%) on the Japan Sea side. This may be adaptation or acclimation of seeds to winter xeric conditions on the Pacific Ocean side. Beech seeds are covered with snow throughout the winter on the Japan Sea side and may thus not require thick pericarp for avoiding desiccation. Resource allocation may thus be less to pericarp (Fig. 2A).

Alternatively, greater amount of resource material are allocated to seed embryos on the Japan Sea side. This may be adaptation to the shorter growing season due to late thawing of snowpack until April or May. Large-seeded species are more capable of seedling growth and survival particularly under stressful conditions (Salisbury, 1942; Grime and Jeffrey, 1965; Harper *et al.*, 1970). Current-year seedlings of large-seeded deciduous tree species complete height growth and leaf expansion earlier than small-seeded species (Seiwa and Kikuzawa, 1989), indicating that large-seeded character may be adequate for shorter growing season. This also may be the case since the greater amount of allocation to embryos in beech seeds may correspond to large-seeded character.

Further studies (*e.g.* reciprocal transplanting) must be done to determine whether geographical differences noted in pericarp characteristics of *Fagus crenata* may have a genetic basis.

Geographical variation in pericarp thickness was the cause in this study for difference in the drying rate of seeds (Fig. 3A). During the initial stage, the drying rate of the Fuji seeds with thicker pericarp was less than that of the Sumon seeds, suggesting potential for adaptation or acclimation to more xeric conditions in winter. If seeds died due to desiccation below relatively high moisture content as is commonly the case for desiccation-sensitive species (Robert and Ellis, 1989), pericarp thickness and consequent drying rate may be major factors for geographic distribution. However, the germination of beech seeds dried at WC as low as 7% d.w.

remained sufficiently high in both populations (Fig. 3A, B).

Species differ considerably in ability of their seeds to survive desiccation (Robert and Ellis, 1989). Even within the same genus, critical water content for survival differs greatly according to species. For example, mature seeds of *Acer platanoides* L. tolerate desiccation up to 10% f.w., whereas those of *Acer pseudoplatanus* L. cannot survive at less than 40% f.w. (Hong and Ellis, 1990). The major types of species with desiccation-sensitive seeds appear to be those from aquatic habitats and some large-seeded trees (Hong and Ellis, 1990). The viability of *Quercus robur* L., large-seeded species, starts to decrease at 45% f.w., decreasing as little as and 1–30% viability at 25% f.w., demonstrating desiccation-sensitivity of this species (Hong and Ellis, 1990). Although *F. crenata* is a large-seeded species, its seeds were observed to be desiccation-tolerant (Fig. 3A, B).

From the time of their shedding to their germination, beech seeds may possibly be exposed to conditions of desiccation, particularly so on two occasions in the montane zone on the Pacific Ocean side. One occasion would be from late autumn to early winter, when the forest floor is not covered with snow and there is little precipitation. The other occasion would be early spring after the snowmelt. Despite greater precipitation at that time, the forest floor may be dry since it exposed to sun before flush of canopy leaves and solar radiation becomes higher. Even during the dry season from late autumn to early winter in 1993, minimal WC of seeds below litter layer at University Forest at Yamanaka appeared to be about 60% d.w. for the Fuji population and 37–47% d.w. for the Sumon population (Fig. 5). These values are sufficient for maintaining germination ability (Fig. 3A, B). Since beech seeds had shed before leaf-fall, native seeds were also present under the litter layer in the winter. Thus, desiccation of beech seeds would not likely occur during the dry season before mid winter in the montane zone on the Pacific Ocean side. Seeds of *Q. serrata* are desiccation-sensitive immediately after germination during late autumn (Hiroki and Matsubara, 1982). In this study, beech seeds from the Sumon and Tanbara populations were quite susceptible to desiccation at initial emergence in early April. Sixty-five percent and 56% of newly emerged seedlings (stage 1) from Sumon and Tanbara populations, respectively, died due to radicle-desiccation in the litter layer (Fig. 6). Thus, early spring may be the critical time for beech seed germination and survival in the montane zone on the Pacific Ocean side.

The mortality of seedlings in stage 1 was much lower (6.5%) for Fuji population. Thus, germinating seeds of beech from the Pacific Ocean side appear well adapted to xeric conditions in early spring at their native habitat, compared to those from the Japan Sea side. The thicker pericarp of the former and consequent slower drying rate would not appear advantageous in the winter, since seeds yet germinated were noted to be considerably desiccation-tolerant. Fully-imbibed beech seeds prior to germination may be desiccation-sensitive. This being case, a thicker pericarp would enhance chance of survival and germination successfully on the Pacific Ocean

side. In addition, thicker pericarp may protect embryos from desiccation immediately after radicle emergence and have resulted in much lower mortality of germinating seeds (stage 1) from Fuji population.

In conclusion, beech seeds from populations on both sides possessed sufficient desiccation-tolerance forward xeric conditions during winter in beech forests on the Pacific Ocean side. Germinating seeds in early spring were desiccation-sensitive and those from the Pacific Ocean side appeared more capable of adapting to xeric conditions.

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