The pattern of pollen dispersal and its adaptive significance at the seed and seedling stages in *Fagus crenata*

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Summary

Gene dispersal via seeds and pollen strongly influences the genetic diversity and structure of plant populations. In general, pollen dispersal in wind-pollinated forest tree species often occurs over long distances and effectively limits genetic differentiation among populations. However, this pattern of pollen dispersal is based on a range-wide view. At local scales, the patterns may be different, involving significant contributions from both distance-dependent pollen dispersal (i.e. highly-frequent pollination at short distances and its decrease as distance increases) and long-distance transport. The aggregation of related individuals (SGS, spatial genetic structure) has been generally found in plant populations. The combination of SGS and distance-dependent pollen dispersal may lead to frequent mating between related individuals located close to each other (biparental inbreeding), and SGS may be strengthened by the biparental inbreeding.

Conversely, long-distance pollen dispersal and post-pollination mechanisms including self-incompatibility and inbreeding depression may promote outbreeding and weaken SGS by permitting mating with genetically and spatially distant individuals.

In addition to these mechanisms, the variation of genetic components (genetic variation) in populations is largely determined by reproductive processes (including pollen dispersal, mating, seed production and seed dispersal) as they determine the composition of effective parents of offspring. The genetic effects of seed and pollen parents on their offspring's performance (survival and growth rates) can be estimated from field observations. The genetic variation is the source of variations in responses among individuals to external influences, which are also likely to affect individuals' survival and growth. Although pollen dispersal patterns related to biparental inbreeding may strongly affect survival and growth at the seedling stage, few studies have detected such effects. Thus, the objectives of the studies this thesis is based upon were to estimate realized patterns of pollen dispersal and the mating system, and to address the adaptive significance of pollen dispersal patterns at the seed and seedling stages, in populations of the wind-pollinated tree species *Fagus crenata*.

In the study described in Chapter II, I estimated the pattern of pollen dispersal and mating system in a continuous large population of *F. crenata*. Leaves of 326 adult trees and 484 seeds were collected in a 4-ha plot (200×200 m) in the Mt. Daisen Forest Reserve. I analyzed the paternity of the seeds using seven microsatellite loci. The population showed weak but significant SGS. The pollen dispersal pattern in the population involved a

combination of distance-dependent (largely short-range) dispersion at the local scale and long-distance transport. Although SGS and distance-dependent pollen dispersal co-occurred, individual inbreeding coefficients for both adults and seeds were close to zero, suggesting that mating generating sound seeds may be genetically random, probably because of the weak SGS, long-distance pollen dispersal and post-pollination mechanisms including self-incompatibility and inbreeding depression.

In the study described in Chapter III, the potential of long-distance pollen dispersal in *F. crenata* was investigated in an isolated small population located at Gofuku-ji temple (designated the Gofuku-ji population) and two other populations, located within 7 km of this population (including 88 adult trees in total). These populations were surrounded by secondary forests, planted forests, farm lands and residential areas. Leaves were collected from 100 seedlings derived from seeds collected from the Gofuku-ji population. The results of parentage analysis of the 100 seedlings using 13 microsatellite loci indicated that pollen parents of six seedlings may have been outside the populations and four of these six seedlings had two alleles that were not detected in the 88 adult trees. These two alleles were probably derived from outside the populations through long-distance pollen dispersal. Therefore, this study demonstrated that pollen dispersal occurs from outside the populations at distances exceeding 7 km.

In the study reported in Chapter IV, I investigated the genetic effects of seed and pollen parents on seedling survival and growth rates in the

continuous large population. In 2011, a 0.25-ha subplot (50×50 m) was established within the 4-ha plot. Five hundred and ninety-eight *F. crenata* seedlings were censused from 2011 to 2013 within the subplot. Nine microsatellite loci were used for seed and pollen parent assignments of the seedlings. Finally, 290 seedlings were used for survival and growth analyses using generalized linear mixed models and linear mixed models, respectively. The results showed that having a pollen parent inside the 4-ha plot had negative effects, while the size of seedlings and canopy openness had positive effects, on seedling survival. Their size also had a significant positive effect on seedling growth. The seed parents, as random effects, significantly affected both the seedling survival and growth rates, possibly because of the environmental variation among locations of seed parents. The negative effect of having a pollen parent inside the plot may be due to the associated short pollen dispersal distances and SGS, with consequent mating between related trees, biparental inbreeding and inbreeding depression.

Overall, the results indicate that pollen dispersal patterns in *F. crenata* involve a combination of distance-dependent and long-distance pollen dispersal. The mating generating sound seeds may be genetically random, probably because of the weak SGS, long-distance pollen dispersal, and post-pollination mechanisms including self-incompatibility and inbreeding depression. However, the seedlings with pollen parents inside the 4-ha plot, which may have been generated by short-distance pollen dispersal, appeared to have lower survival ability than seedlings with pollen parents outside the plot. These results suggest that long-distance pollen dispersal

could improve the fitness of and survival rates of *F. crenata* individuals by mitigating inbreeding depression. The positive effect of long-distance pollen dispersal may contribute to not only seed production but also growth in early seedling stages.