Sexual dimorphism in reproductive traits in dioecious plants

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論　文　内　容　の　要　旨

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論文題目（外国語の場合は，その和訳を併記すること。）

Sexual dimorphism in reproductive traits in dioecious plants
（雌雄異株植物における繁殖形質の性的二型）

論文要旨

Sexual dimorphism is differences in primary and secondary sex characters between the sexes. Sexual dimorphism is widespread and recognizable phenotype variations in sexual organisms and may facilitate an increase in biological diversity.

Dioecy is a plant sexual system having female and male individuals like most animals. In dioecious flowering plants producing unisexual flowers, females and males have been known to differ in morphological, physiological and life-history traits. However, sexual dimorphism and the selection pressures facilitating the evolution of trait differences between sexes have not been sufficiently clarified in dioecious plants. Despite the little attention, to study sexual dimorphism and the evolutionary processes in dioecious plants will give important insights for understanding mechanisms of diversification in flowering plants.

Because plants are sessile and depend on abiotic and biotic vectors for pollen transfer, sexual dimorphism in reproductive traits can be shaped by the vector-mediated selection. In insect-pollinated plants, many examples of sexual dimorphism in reproductive traits have been reported. However, the underlying evolutionary process driven by vector-mediated selection have not been sufficiently examined. As for wind-pollinated dioecious plants, a little is known about sexual dimorphism in reproductive traits and the sex-specific selection pressures driving intersexual differences.

The different type and/or degree of sexual dimorphism in reproductive traits will have evolved depending on the vectors, but few studies have focused on this topic. In insect pollinated plants, the sexually dimorphic floral traits have been suggested to maximize both male and female success in relation to display size–pollinator attraction association. Meanwhile, in wind-pollinated plants, intersexual differences in floral traits are hypothesized to maximize pollen transfer by wind. To understand how the vector-mediated selection can shape the sexual dimorphism in reproductive traits in dioecious plants, further studies not only in insect-pollinated plants but also in wind-pollinated plants have been required.

In this thesis, I examined sexual dimorphisms in reproductive traits and the selection pressures in both insect- and wind-pollinated dioecious plants (flowering phenology traits of three insect-pollinated plant species in Chapter 2, flowering phenology traits of a wind-pollinated species in Chapter 3, inflorescence architectures in the wind-pollinated species, Chapter 4). Then, I compared the differences of sexual dimorphism in flowering phenology traits and the evolutionary process between insect- and wind-pollinated dioecious plants according to the results of Chapters 2 and 3. Based on the findings of Chapters 3 and 4, I examined how wind-mediated selection might shape sexual dimorphism in different reproductive traits (flowering phenology and inflorescence architecture traits). The goal of this thesis was to test the hypothesis that sexual dimorphism in reproductive traits in dioecious plants have evolved under vector-mediated selection and that the evolutionary output can differ depending on the vectors (Chapter 2–4). In Chapter 5, I also reported sexual dimorphism in vegetative traits in an insect-pollinated species to discuss how sexual dimorphism in reproductive traits is associated with that in vegetative traits.

In Chapter 2, I examined sexual dimorphism in flowering phenology traits in the three insect-pollinated *Ilex pedunculosa, I. serrata*, and *I. crenata*, whose female flowers are not smaller than male flowers. Their females produced significantly less flowers than males. Females opened flowers more synchronously on a given date, lasted flowers longer and maintained higher proportion of open flowers within shoots than males likely to compensate for disadvantage of smaller display size and achieve higher reproductive success. In contrast, when males open their flowers simultaneously, diminishing returns would increase with display size. These results suggest that sexual dimorphism in floral longevity and flowering synchrony might enhance both female and male success in relation to the display size–mating success (pollinator attraction) association irrespective of flower size dimorphism.

In chapter 3, I examined sexual dimorphism in flowering phenology traits in wind-pollinated dioecious *Rumex acetosa*. The synchrony of newly opening flowers on a given date did not significantly differ between the sexes (or even higher in males), although the longer floral longevity and higher proportion of open flowers within each inflorescence branch in females were found as in insect-pollinated plants. The index of flowering overlap with the opposite sex significantly increased with the synchrony of newly opening flowers on a given day in both sexes. This could explain no sexual dimorphism in this trait.

In chapter 4, I examined sexual dimorphism in inflorescence architecture in *R. acetosa* whose seeds are also wind-dispersed. Males had inflorescence branches compactly and arranged flowers at the upper positions. This male inflorescence architecture might enhance the pollen dispersal distance. Meanwhile, females arranged inflorescence branches diffusely likely to reduce the boundary-layer thickness around flowers. At seed maturation stage, infructescence architecture changed from diffuse to compact ones to elevate the seeds in females. Female flowers on experimentally widened branches set more seeds compared to those on intact branches, indicating that females may have a trade-off between pollen receipt and seed dispersal. These results suggest that sexual dimorphism in inflorescence architecture of anemophilous, anemochorous dioecious plants evolved under wind-mediated selection.

In chapter 5, I described sexual dimorphism in vegetative traits in insect-pollinated dioecious shrub *Ilex crenata*. Female individuals had a greater total basal stem area and more stems per individual than did males, which did not support theoretical predictions that sexual dimorphism in vegetative traits are associated with that in the trade-off between vegetative growth and reproduction, and that the cost of reproduction is usually greater in females than in males. I discuss the causes of the differences between the sexes based on the hypothesis of the sexual differences of size at first flowering.

This thesis provides the new insights how sexual dimorphism in reproductive traits evolve under vector-mediated selection in dioecious plants. The studies examining both insect- and wind-pollinated dioecious plant species (Chapter 2–4) clearly showed the optimal reproductive traits for each sex and clarified the reproductive conflicts between the sexes in angiosperms. Especially, I demonstrated that wind-mediated selection has also evolved sexual dimorphism in reproductive traits and similarities and differences of sexual dimorphism and the selection pressures between insect- and wind-pollinated plants (Chapter 2, 3). Because I examined only a single wind-pollinated species, further studies should examine more wind-pollinated species to generalize my findings. Moreover, I showed that the importance of focusing on not only pollination system but also seed dispersal system for understanding the evolutional process of sexual dimorphism in dioecious plants (Chapter 4). Thus, further studies of the evolution of sexual dimorphism in angiosperms will contribute to generalization of the existing theories concerning sexual dimorphism in organism and enhancing understanding the evolutional mechanisms of biological diversity.