

主論文の要約 (Summary)

Plants show diverse and complex sexual expression, and mixture of individuals bearing various combinations of female, male, and hermaphrodite flowers are observed within a population. The majority of flowering plants are hermaphroditic and empirical evidence indicates that production of only perfect flowers is the ancestral condition in angiosperms. Dioecy, which has female and male individuals, is found in 5-6% of angiosperms across a broad range of plant families, and thus dioecy is thought to have evolved repeatedly. Among five main pathways for the evolution of dioecy from hermaphroditism, many researchers have focused on ecological and genetic aspects of the evolutionary pathway towards dioecy via gynodioecy, however the complete picture of the gynodioecy–dioecy pathway remains unclear due to insufficient research on the latter stage of the pathway.

Subdioecy is a sexual system in which females, males and hermaphrodites coexist in a population, and is thought to occupy the latter position in the gynodioecy–dioecy pathway. Because reproductive success is thought to play an essential role in the evolution of individual's sex expression, studies on reproductive success in subdioecious plants are needed to elucidate the gynodioecy–dioecy pathway. Females contribute to the next generation via seeds only and males via pollen only, while hermaphrodites via both seeds and pollen. Therefore, to permit stable maintenance of females and males in a subdioecious population, females and males require more than a double reproductive success compared to hermaphrodites theoretically. Based on the theoretical model by Charlesworth & Charlesworth (1978), the evolutionary condition

that allow the transition to dioecy from gynodioecy is given the following formula;

$$\frac{1 + s - 2s\delta}{k + 2s\delta - s} < K$$

where s and δ are selfing rate of hermaphrodites and inbreeding depression, respectively. The reproductive success of females relative to hermaphrodites is described as $(k+1)$ and relative reproductive success of males against hermaphrodites is described as $(K+1)$. Another approach to explore the factors promoting the evolution to dioecy via gynodioecy is to examine the plasticity in sex allocation or sex expression (sex change) and to determine the conditions where females, males, or hermaphrodites are preferred. On the other hand, sex change may hinder subdioecious plants from moving to complete dioecy, because it may relax the intensity of the trade-off between female and male functions.

The aims of this study were to determine the reproductive successes through both female and male functions and to clarify the pattern of sex change in subdioecious *Eurya japonica* Thunb. (Pentaphylacaceae), in order to examine the gynodioecy–dioecy pathway. First, the female reproductive success was compared between female individuals and hermaphrodite individuals that produce only hermaphrodite flowers (H), using hand-pollinated individuals of similar size under similar light conditions (Chapter 3). Secondly, the siring success was assessed in hand-pollination treatments with single pollen and mixed pollen from males and hermaphrodites (H), using both females and hermaphrodites of similar size under similar light conditions as mother trees (Chapter 4). Thirdly, factors affecting the occurrence and the pattern of sex change were explored (Chapter 5). Finally, I

summarized my results of Chapter 3–5 and discussed the evolutionary implication of subdioecious *E. japonica* in the context of pathway from hermaphroditism to dioecy via gynodioecy (Chapter 6).

In Chapter 3, I found that *E. japonica* females had an advantage in female reproductive success; females had higher fruit set and produced heavier fruit and more seeds having higher germination rate than hermaphrodites. Based on the results of fruit set, the relative fertility of females and hermaphrodites was 2.5. These results were more pronounced for hand-pollinated than for natural-pollinated plants of both sexes, suggesting that pollinator-mediated pollen availability could relax the female advantage. In addition, no self-compatibility among hermaphrodites was observed. In Chapter 4, I found that *E. japonica* males had an advantage in male fertility; male pollen sired more fruits of larger size and more seeds with higher and more rapid germination than hermaphrodites. Based on the results of fruit set, the fertility ratio of males versus hermaphrodites ranged 0.67-1.76. The male advantage was prominent when females were hand-pollinated using pollen from single individual. These results show that males have an advantage in male fertility both quantitatively and qualitatively in *E. japonica*. In Chapter 5, frequent and repetitive sex change with various patterns was found in *E. japonica*. All sexual types of hermaphrodites seem to be more labile in sex expression than females and males, whereas there was no fluctuation in the sex ratio over five years and the sex ratio among F, M, and H-all (all sexual types of hermaphrodites) was almost 1 : 1 : 1. Sex change seems to be explained by the internal status of an individual as a result of

biotic and abiotic environments such as size and light conditions.

The results in Chapter 5 indicate that the *E. japonica* population in this study is stable subdioecy and that it is unlikely to transit complete dioecy. What maintains the hermaphrodites in this *E. japonica* population? First, I examined the relative fertility among females, males, and hermaphrodites. The relative fertility of hermaphrodites is the sum of the relative fertility through female and male functions (hereafter, H_{total}). Summarizing the results of fruit set and seed number per fruit in Chapter 3 and 4, H_{total} was less than the relative fertility of females and males under hand-pollination treatments (no pollen limitation; 0.89 vs 1.0). On the contrary, H_{total} outnumbered the relative fertility of females and males under natural condition (with pollen limitation; 1.12 vs 1.0), indicating that although the *E. japonica* population could be potentially dioecious, pollen limitation plays a role for diminishing the female or male advantage and it seems to allow the maintenance of hermaphrodites. The evaluations of the evolutionary condition to dioecy via gynodioecy, using k and K of the above formula, also supported my hypothesis. Therefore, *E. japonica* might be in the transition toward dioecy, but pollen limitation and frequent sex change deter this *E. japonica* population from moving to complete dioecy. Using the theoretical models, which were constructed in the context of hermaphroditism–gynodioecy–dioecy pathway by Ehlers & Bataillon (2007) and Crossman & Charlesworth (2013), my results also indicate the possibility of breakdown of dioecy in *E. japonica*.