Coexistence mechanism of two closely related Commelina species under reproductive interference

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論 文 内 容 の 要 約

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論文題目

Coexistence mechanism of two closely related *Commelina* species under reproductive interference
(繁殖干渉下における在来近縁ツユクサ属２品種の共存機構)

論文要約

To reveal the mechanisms explaining why so many plant species coexist in the field has been a most important theme in the ecology, because plants are a keystone group supporting biodiversity and ecosystem functions as primary producers. In the closely related flowering plant species, sharing the same pollination niche makes coexistence difficult due to pollinator mediated competition, which is often referred to as reproductive interference. Therefore, two or more closely related plant species have been thought to can coexist only with pollination niche partitioning, often with floral trait displacement such as color, shape and/or flowering phenology, otherwise they are mutually exclusively distributed.

It has been suggested that self-pollination can mitigate the negative effects of reproductive interference by sympatrically distributed relatives. Experimental studies using planted array of close relatives showed that selfing species (species predominantly producing seeds via autonomously self-pollination) did not suffer from reproductive interference by congeners. The recent studies have suggested that prior autonomous selfing rather than delayed selfing can mitigate a reduction in seed production via reproductive interference (the

pre-emptive selfing hypothesis).

Although the pre-emptive selfing hypothesis may enhance our knowledge on the coexistence mechanism of closely related species under reproductive interference and the mating system evolution in flowering plants, there are some issues that should be examined before generalizing the relationship between reproductive interference and selfing. First, previous studies that detected negative effects of reproductive interference were mainly based on experimental arrays where the relative densities and spatial distributions were arbitrarily determined although experimental approaches often over- and underestimated the effects of reproductive interference. Second, the reported selfing species has small and inconspicuous flowers with less frequent pollinator visits compared to outcrossing congeners. Clarifying the mechanisms how selfing mitigate reproductive interference is difficult in such cases, because these selfers rarely received heterospecific pollen grains due to very low pollinator visits. Finally, adding the viewpoint of eco-evolutionary dynamics including changing densities of coexisting species through successive generations and the cost of selfing will greatly improve our understanding for the relationship among reproductive interference, species coexistence and selfing. Relative population density compared to competing species is related with the strength of reproductive interference, and thus can strongly affect selection pressure for the evolution of self-pollination. Meanwhile, the costs of selfing, such as inbreeding depression and ovule discounting, should be taken into account when considering the evolution of autonomous self-pollination. Threfore, to examine the possibility of evolutionary rescue by self-pollination and resultant coexistence of competing species under reproductive interference, these factors and their interactions are desired to be together considered.

The aim of this thesis is to test my hypothesis, which is developed based on the pre-emptive selfing hypothesis: the evolution of prior autonomous self-pollination mitigates the negative effects of reproductive interference and consequently promotes coexistence of closely related species sharing the same pollination niche. For this purpose, I conducted empirical ecological and genetic studies on sympatrically distributed two native *Commelina* species, *Commelina communis* (Cc) and *C. c.* f. *ciliata* (Ccfc) and a theoretical study based on eco-evolutionary dynamics framework.

In chapter 2, I described the mutual reproductive interference between sympatrivally distributed two native *Commelina* species in detail under natural condition. Cc and Ccfc exhibit largely niche overlap, such as flowering phenology, habitat preference and pollinator composition. Based on field survey, I found that Cc population exhibit dominant distribution compared to Ccfc population in meso-scale spatial distribution and the negative effect of reproductive interference on seed production is stronger in Ccfc than in Cc although heterospecific pollen transfer via pollinator is evenly occur. By combining with field survey and glasshouse experiment, I also showed that prior self-pollination can assure seed production even with heterospecific pollen deposition and asymmetry of reproductive interference might be explained by the higher ability of prior self-pollination in Cc. These findings suggested that the prior autonomous selfing could mitigate the negative effect of reproductive interference from competitor and likely promote coexistence of these species.

In chapter 3, I investigated how reproductive interference affect selfing rate and genetic structure in Ccfc based on population genetics method using microsatellite markers. I firstly developed microsatellite marker for Ccfc using next generation sequencer. My results showed sympatric population (Ccfc distributes with Cc) tend to exhibit higher population inbreeding coefficient and selfing rate (close to 1.0) than allopatric population (only Ccfc distributes) although an increase of relative flower abundance of Cc does not affect seed's selfing rate of Ccfc flower in sympatric population. It might be interpreted that outcrossing individual of Ccfc in the sympatric population is already excluded out via selection due to reproductive interference. Besides, genetic diversity and genetic differentiation from other populations were not difference between sympatric and allopatric populations. It might be interpreted that study Ccfc individuals in sympatric populations produced seeds predominantly though selfing.

In chapter 4, to test my hypothesis in the context of eco-evolutionary dynamics, I developed individual based model in which two plant species that share the same pollination niche and can evolve prior autonomous selfing compete against each other in the form of mutual reproductive interference. Based on model simulations with various parameter condition, my model revealed that the evolution of prior selfing can promote the coexistence in the presence of mutual reproductive interference when pollinator availability and strength of inbreeding depression were intermediate levels. Meanwhile, the coexistence rarely occurred without the evolution of prior selfing. With the variable inbreeding depression (inbreeding depression decreases with increasing the population's selfing rate), coexistence was facilitated by the evolution of prior selfing in wider conditions than with the fixed inbreeding depression. Especially when the strength of inbreeding depression gently decreased and pollinator availability was intermediate level, the coexistence with evolutionary rescue often occurred and stably continued for very long-term. Totally, my simulation results showed the long-term coexistence with evolutionary rescue occurred with moderate pollinator limitation, variable and moderate levels of inbreeding depression, the relatively higher initial prior selfig rate and the presence of reproductive interference.

In the chapter 5, I discussed the contribution of my thesis for understanding of species coexistence mechanism and evolution of plant mating system as a general discussion. In the context of species coexistence, coexistence of closely related species is traditionary thought to be difficult due to sharing very similar ecological niche, such as habitat, resource demand and reproductive biology. although previous theoretical studies have shown stable coexistence under reproductive interference must require niche partitioning between and among competing species, my model results showed evolutionary rescue by prior selfing could occur and stably continued and cause long-term coexistence under reproductive interference even when two species is completely same in ecological features (chapter 4). Some studies have shown that spatial structure can enable the coexistence under reproductive interference because reproductive interference promotes spatial segregation among competing species and make interspecific competition relatively weaker than intraspecific competition. In my study plant system, Cc and Ccfc exhibited largely niche overlap, such as flowering phenology, habitat preference and pollinator composition (chapter 2). My results suggested Cc and Ccfc might exhibit conspecific aggregation in micro (individual) spatial scale distribution but not in meso (population) scale, so contribution of conspecific aggregation for coexistence of Cc and Ccfc is still unclear (chapter 2). Because I found strong mitigation effect of prior selfing against reproductive interference and relatively higher population's selfing rates in sympatric Ccfc populations, I believe the evolution of prior autonomous selfing play a more important role for the coexistence of Cc and Ccfc. It is thought to have large applicability for other systems because evolution of shift to higher selfing rate is often occur in many independent plant taxa. This coexistence supported by the evolution of prior selfing without any kinds of niche partitioning and specific spatial structure should improve our understanding especially on coexistence between closely related plant species.

In the context of evolution of plant mating system, I revealed the coexistence under reproductive interference can occur only with co-evolution of extremely high prior selfing rate in both competing species ($\geq$ 0.9; chapter 4). This result is consistent my empirical study in which selfing rate is estimated close to 1.0 in Ccfc population growing with Cc although selfing rate of Cc have been not estimated (chapter 3). That it should be noted, however, Cc and Ccfc have been visited frequently by pollinators such as bumble bee and syrphid fly (chapter 2). Flowers of Cc and Ccfc flowers with showy blue petals and yellow stamens were visited frequently by pollinators such as bumble bee and syrphid fly even in sympatric populations (Chapter 2). The features are inconsistent with typical predominately selfing flowers that evolve under pollinator limitation, strong inbreeding depression and transfer advantage of selfing gene. Recent studies, including my studies, pointed out that reproductive interference via interspecific pollen transfer can facilitate the evolution of selfing. My results suggest that the high selfing rate in showy flowers might be often found in the presence of competing species sharing the same pollinators.

Finally, I discuss a few suggestions of future studies. First, based on field survey of various populations, to examine the relation among inbreeding depression, selfing rate and population size must be important to test my model prediction, which is strength and dynamics of inbreeding depression are important determinants for coexistence possibility of competing species (chapter 4). Second, to clarify the floral traits related with prior selfing rate is thought to be also important although there are some candidates such as degree of herkogamy and dichogamy. Especially, the evolvability of these traits, such as heritability and genetic variation in the field, is quite important for deciding whether the evolutionary rescue can increase population size of minority species before competitive exclusion.