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.

（注）3,000～6,000字（1,000～2,000語）でまとめること。

［課程博士用］

論文審査の結果の要旨

氏　　名	松久聖子		
論文題目	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）		
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要　　旨

本博士論文では，これまで研究例が非常に限られてきた被子植物の性的二型に着目して研究を行っている．性的二型とは雌雄間で様々な形質が異なる事象で，主に動物を中心に研究がなされてきた．陸上で優占する被子植物では70%以上が両性花植物であり，動物と同様にメス個体とオス個体の見られる雌雄異株植物は全体の6-7%を占めるにすぎず，被子植物における性的二型については知見が非常に限られている．本博士論文は，花粉媒介様式の異なる雌雄異株植物種の繁殖形質の性的二型を同時に研究し，その差異について議論することを目的としている．本論文は，6章構成で，序論である第1章と虫媒種の開花スケジュールにおける性的二型を研究した第2章，風媒種の開花スケジュールおよび花序構造における性的二型を研究した第3～4章，虫媒種の栄養成長形質における性的二型を明らかにした第5章，以上の個別研究で得た結果の総括を行う第6章，謝辞，引用文献から構成されている．

1章の序論では，被子植物における性的二型の先行研究について総括し，虫媒種の繁殖形質の性的二型に関しては現象記載や性的二型をもたらす選択圧に関する仮説の提案は増えつつあるものの，提案された仮説の検証が十分にはなされてないこと，風媒種については繁殖形質における性的二型の記載自体も少なく，その進化の選択圧については仮説の提案はほとんどされてないことが説明されている．2章では，虫媒の雌雄異株であるモチノキ属3種を対象に、開花スケジュール（特に開花同調性と個花寿命）における二型について研究している．その結果，メス株では，オス株より生産花数が少ないことに起因する送粉者誘因における不利を補うために，オス株よりも高い開花同調性と長い個花寿命を進化させていることを明らかにした．3章では、ギシギシ属の風媒雌雄異株であるスイバを対象に，虫媒植物とは異なり開花スケジュールにおける性的二型が顕著でなくなることを発見し，これが雌雄に同様の選択圧が働いているためにみられた現象であることを示唆している．4章では，3章と同様に風媒種スイバを対象として，虫媒種では報告されてない花序形態の性的二型（メス花序は水平方向に花序枝を伸ばす形態，オス花序は垂直方向に花序枝を伸ばす形態）がみられることを発見し，この性的二型が風による送受粉成功を高めるために進化してきたことを議論している．5章では、モチノキ属のイヌツゲを対象に繁殖投資量の雌雄の差に起因して栄養生長形質にも性的二型がみられることを記述している．6章では，以上の研究結果を受けて，植物の繁殖形質における性的二型の進化が花粉媒体の特性に依存して引き起こされていること，花粉媒体間の比較を行うにはもっと多くの風媒種を対象とした研究が必要となることを議論している．

本博士論文は上記の通り被子植物における繁殖形質の多様化をもたらす性的二型の進化について，虫媒種におけるこれまでの知見を補完・一般化する研究を行い，これまで研究がなかった風媒種の繁殖形質における性的二型の記載とその進化の選択圧について研究を行っている．また，虫媒種と風媒種の比較から植物の繁殖形質でみられる性的二型の進化における花粉媒体の役割について考察を行っているなど，世界的にみても新規性の高い内容を含む論文となっている．以上，本論文は性的二型の進化の観点から被子植物の形質多様性の進化・維持機構について新しい視点を与えたという点において非常に高く評価できる。

なお，本論文を構成する各章（第2～5章）は個別の投稿論文としてまとめており，第2章は American Journal of Botany誌（査読あり）にて公表されている．第5章は岐阜県植物研究会誌（査読あり）にて投稿論文が受理され，公表予定である．第3章と第4章は投稿論文を書き上げ投稿直前である．下記に投稿論文の詳細を示す．

Matsuhisa, S. and Ushimaru, A. (2015) Sexual dimorphism in floral longevity and flowering synchrony in relation to pollination and mating success in three dioecious *Ilex* species. *American Journal of Botany* 102: 1187-1197.

松久聖子・柳沢直・丑丸敦史（受理）雌雄異株樹木イヌツゲにおける栄養生長形質の性的二型．*岐阜県植物研究会誌*

以上より，学位申請者の松久聖子は，博士（理学）の学位を得る資格があると認める．

レフェリー付きの論文の発表について，記載すること。