The joint evolution and maintenance of self-incompatibility with gynodioecy or androdioecy

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H I G H L I G H T S

- Androdioecy and self-incompatibility (SI) helps the maintenance of each other.
- SI makes the maintenance of gynodioecy more difficult.
- Androdioecious species should show a lower SI diversity than hermaphroditic ones.
- Gynodioecious and hermaphroditic species should show similar SI diversities.

A R T I C L E   I N F O

A B S T R A C T

Mating systems show two kinds of frequent transitions: from hermaphroditism to dioecy, gynodioecy or androdioecy, or from self-incompatibility (SI) to self-compatibility (SC). While models have mostly investigated these two kinds of transitions as independent, empirical observations suggest that, to some extent, they can evolve jointly. Here, we study the joint evolution and maintenance of SI and androdioecy or SI and gynodioecy by the means of phenotypic models. Our models focus on three parameters: the unisexuals' advantage relative to that of the hermaphrodites due to resource reallocation, inbreeding depression and the selfing rate. We assume no pollen limitation or discounting. We show that SI helps the maintenance of androdioecy, but favors the loss of gynodioecy, and also that androdioecy facilitates the maintenance of SI, whereas gynodioecy does not affect it. We finally investigate how gynodioecy and androdioecy may affect the diversification of SI groups, especially considering an evolutionary pathway through SC intermediates. We show that while androdioecy prevents the increase of the number of SI groups, under certain conditions of inbreeding depression and selfing rates, gynodioecy allows it.

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1. Introduction

In plants, the lability of mating systems is striking and two types of transitions are frequent: first, from hermaphroditism to dioecy and their intermediates (gynodioecy and androdioecy, *i.e.* the co-occurrence in a single population of hermaphrodites and females or males, respectively) and second, from self-incompatibility, where individuals are unable to self-fertilize (either because of a molecular recognition systems that reject male gametes or because of morphological differences), to self-compatibility, where individuals are able to self-fertilize. Dioecy has indeed evolved independently many times from hermaphroditic species (Renner and Ricklefs, 1995) and the transition from self-incompatibility (SI) to self-compatibility (SC) is considered as one of the most frequent transitions in flowering plants (Stebbins, 1974; Igic et al., 2008; Goldberg et al., 2010). These transitions are governed by various evolutionary and ecological processes which affect gene transmission through the male (sperm or pollen) or the female function (ovules). The most important identified processes involved in the evolution and transition of mating systems are (i) self-fertilization, since individuals that are capable of self-fertilizing and fertilizing other individuals have a genetic transmission advantage through the male function (Fisher, 1941), (ii) inbreeding depression which decreases the fitness of selfed offspring (Lloyd, 1975), and (iii) differential resource allocation between male and female functions (Lloyd, 1975).

Gynodioecy and androdioecy can evolve from hermaphroditism if enough resources are reallocated to the female or the male functions in unisexual individuals (Lewis, 1941; Lloyd, 1975; Charlesworth and Ganders, 1979) and if inbreeding depression is high because it decreases the fitness of selfed progenies produced by hermaphrodites. A high selfing-rate facilitates the maintenance of gynodioecy

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because it increases the inbreeding depression cost for hermaphrodites (Lloyd, 1975; Charlesworth and Ganders, 1979; Dornier and Dufay, 2013) while it makes the maintenance of androdioecy more difficult because it decreases the fraction of ovules that can be sired by males (Lloyd, 1975). In the case of the transition from self-incompatibility to self-compatibility, there is a complex interplay between selfing and inbreeding depression but globally, high inbreeding depression and selfing rates are necessary to maintain SI (Charlesworth and Charlesworth, 1979; Porcher and Lande, 2005b).

Empirical observations suggest that both types of mating systems can affect each other's evolution. For instance, few plant species show a co-occurrence of gynodioecy and SI (reviewed in Dufay and Billard, 2012), but many species are either gynodioecious or SI. There are also documented cases suggesting a recent loss of SI in gynodioecious species while SI is maintained in closely related hermaphroditic species, or SI is lost in some populations of a gynodioecious species (reviewed in Ehlers and Schierup, 2008). This suggests that gynodioecy and SI tend to prevent each other's maintenance. On the other hand, there is a documented case where androdioecy is maintained in an Oleaceae species because of SI despite low resource reallocation to male functions (Saumitou-Laprade et al., 2010). Vassiliadis et al. (2000), Pannell and Korbecka (2010) and Husse et al. (2013) showed that, if males can sire all SI hermaphrodites, SI may help the maintenance of androdioecy, because pollen produced by males competes only with the pollen produced by compatible hermaphrodites and not all of the hermaphroditic pollen. Ehlers and Schierup (2008) showed that SI is lost more easily in gynodioecious than in hermaphroditic species as females do not suffer from inbreeding depression (they cannot self-fertilize) and can therefore facilitate the spread of a mutation allowing for SC. There is however a lack of general work on the joint evolution and maintenance of SI with gynodioecy or androdioecy.

The number of SI groups is another important, yet mostly neglected, feature regarding the joint evolution of SI, gynodioecy and androdioecy. SI generally involves a recognition system, either molecular (homomorphic SI), or morphological (heteromorphic SI), or both (most heterostylous species). Whatever the mechanism underlying SI, individuals belonging to the same SI group share the same recognition cues, recognize each other and cannot mate. The number of SI groups affects both the maintenance of SI and androdioecy. The higher the number of SI groups, the easier SI is maintained, because the fraction of individuals that can be sired by a given SI group tends to 1, *i.e.* tends to be equal to the mate availability of SC phenotypes (e.g. Porcher and Lande, 2005b). The lower the number of SI groups the easier the maintenance of androdioecy (Vassiliadis et al., 2000). However, we do not know if and how the number of SI groups affects the joint evolution of SI and gynodioecy or androdioecy. For example, the number of SI groups is expected to increase because of negative frequency dependent-selection (Wright, 1939) but we do not know if gynodioecy and androdioecy can affect this process. Finally, the emergence of new SI groups is certainly not trivial and involves at least two mutational steps, successively affecting the male and female functions involved in SI (Uyenoyama et al., 2001). It has been shown that a possibility for the evolution of new SI groups could occur by the evolution of a SC intermediate: a first mutation breaks SI down in the male function and a second mutation in the female function restores SI. Uyenoyama et al. (2001) and Gervais et al. (2011) showed that the emergence of new SI groups is possible if a SC intermediate phenotype can invade a population and be maintained jointly with SI phenotypes. How gynodioecy and androdioecy affect the possibility of the appearance of a new SI group is another open question.

In this paper, we will address different questions in a general and common framework based on phenotypic models: do androdioecy and gynodioecy help the maintenance of SI? Does SI help the maintenance of androdioecy and gynodioecy? Do gynodioecy and androdioecy affect the evolution of the number of hermaphrodite SI groups? Throughout the paper we assume that males and females are compatible with all groups of hermaphrodites and we only consider nuclear gynodioecy and androdioecy, *i.e.* the mutations causing male-sterility or female-sterility are transmitted identically through the paternal and maternal genome. We also assume no pollen limitation or discounting and we do not investigate the impact of partial SI.

2. The models

A full list of the models presented in this paper and the corresponding questions addressed are given in Table 1. These models are derived from Lloyd (1975) and are based on phenotypic models of fitness, which is sufficient for addressing general questions about mating system evolution when genetic determination is not important (Lloyd, 1977). Our models thus cannot be used to investigate the evolution of cytoplasmic gynodioecy since it would require that male-sterility mutations on cytoplasmic genes be explicitly modeled. The principle is to compute the fitness of each phenotype present in a population as the sum of the rate of gene transmission through the male and female functions. An example is detailed below for illustration, but the reader can find a more detailed derivation of how such fitness functions are computed and used in Charlesworth and Charlesworth (2010). It is expected that a phenotype increases in frequency if it has a higher total fitness than the other phenotypes. The fitness is generally frequency-dependent and evolution can lead to two situations: either a monomorphic situation when a given phenotype always has a higher fitness than the other possible phenotypes, in which case it invades the population and the other phenotypes are lost, or some phenotypes can have the same fitness for given frequencies and a polymorphic state can be reached at equilibrium. In order to determine the outcome of evolution, especially under which conditions polymorphism is a stable equilibrium, we searched for solutions where the fitness of a given set of phenotypes are equal.

2.1. General hypotheses and notations

We assume four possible phenotypes: males, females, self-incompatible hermaphrodites (SI) and self-compatible hermaphrodites (SC), whose frequencies in the population are denoted by m, f, h and s, and total fitness W_m, W_f, W_h, W_s, respectively. We suppose n different self-incompatible groups of hermaphrodites in the population. Note that h is the total frequency of SI hermaphrodites in the population, and we suppose that all SI hermaphrodites have the same frequency, *i.e.* the frequency of a single SI group is h/n. We also note $\hat{h}$, $\hat{m}$, $\hat{f}$ and $\hat{s}$ as the frequencies at equilibrium where all phenotypes have the same fitness. We assume that SC hermaphrodites produce a proportion γ of self-fertilized offspring, and that selfed offspring have a lower fitness than outcrossed offspring because of inbreeding depression, denoted δ. The hermaphrodites of a given SI group are assumed to be able to sire only $n-1$ of the total SI groups. Based on empirical observations in the Oleaceae family (Saumitou-Laprade et al., 2010), we make the assumption that males can fertilize all SI hermaphrodites and that females can be fertilized by any SI hermaphrodite: in other words self-incompatibility does not affect mating between unisexual individuals (males or females) and SI hermaphrodites. Note that SI is explicitly and genetically modeled in Ehlers and Schierup (2008), which implies that, contrary to the present models, females cannot be fertilized by the SI hermaphrodites that share the same genotype at the locus underlying SI (but we will see evolutionary outcomes are not changed qualitatively). We further assume that there is no pollen limitation nor pollen discounting: selection only acts through male fitness. Finally, we consider that males and females can reallocate reproductive resources to their reproductive function, and we denote K the unisexual advantage