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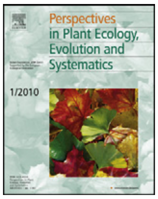

Review

Sex-specific patterns of antagonistic and mutualistic biotic interactions in dioecious and gynodioecious plants

Rocío Vega-Frutis[a,*], Miguel A. Munguía-Rosas[b], Sandra Varga[a], Minna-Maarit Kytöviita[a]

[a] *Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40014 Jyväskylä, Finland*
[b] *Departamento de Ecología Humana, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV-IPN), AP 37 Mérida, Yucatán 97310, Mexico*

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ABSTRACT

A major transition in flowering plants has been the evolution of separate sexes from hermaphroditism via gynodioecy which is considered to be the most important route. Biotic interactions, both antagonist and mutualistic, have been proposed to influence this transition which is generally accompanied by the evolution of sexual dimorphism in secondary sexual traits. While some researchers have studied sex-specific patterns in herbivory and pollination, less attention has been paid to pathogens/parasites and a limited number of studies have revised sex-specific patterns in mycorrhizal symbiosis. In this article, we explore sex-specific interactions in dioecious and gynodioecious plants, examining the interrelationships among the incidence and/or frequency of herbivory, pathogen/parasite infestation, pollination and mycorrhizal symbioses. We review how multiple interactions (both above and belowground) act synergistically or antagonistically to shape the ecological and evolutionary results of pairwise interactions. Finally, we identify gaps in the knowledge of sex-specific patterns in multiple interactions in dioecious and gynodioecious plants, as well as future and promising lines of research.

Contents

Introduction 46
Antagonistic interactions 47
  Herbivores 47
  Pathogens and parasites 47
Mutualistic interactions 48
  Pollinators 48
  Mycorrhizas 48
Multiple interactions 49
  Plant–herbivore–pathogen/parasite interactions 49
  Plant–pollinator–mycorrhiza interactions 50
  Plant–herbivore–pollinator interactions 51
  Plant–pathogen/parasite–pollinator interactions 51
  Plant–mycorrhiza–herbivore interactions 51
  Plant–mycorrhiza–pathogen/parasite interactions 52
  Plant interactions between mycorrhizas, herbivores, pathogens/parasites and pollinators 52
Future directions 52
Acknowledgments 53
References 53

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* Corresponding author. Tel.: +358 040 8 053 914.
E-mail addresses: rociovegaf@yahoo.com.mx, rocio.vega-frutis@jyu.fi (R. Vega-Frutis).

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Introduction

In natural ecosystems, plants live in complex environments in which they interact with other organisms above and belowground. In terms of fitness, some of these interactions, e.g., pollination, are evidently beneficial to the plants (Ayasse and Arroyo, 2011) others, such as herbivory or interactions with pathogens, are clearly detrimental (van Dam, 2009). However, certain biotic interactions may vary along a continuum from mutualism to parasitism (e.g., mycorrhizas; Johnson et al., 1997), while other interactions lead to neither positive nor negative effects (e.g., commensalism; van Dam, 2009). Belowground interactions between plants and other organisms can influence, and can be influenced by interactions that take place aboveground (Heil, 2011; van Dam and Heil, 2011). Normally, plant responses to a diversity of stresses and environmental cues have an effect on other species that depends directly or indirectly upon the plant as a source of nutrients and/or energy (Kiers et al., 2010). In this way, plants mediate interactions between above and belowground organisms. Therefore, understanding how multiple biotic interactions can act synergistically or antagonistically is a major goal in ecology and evolutionary biology that is reflected in the recent increase in investigations on this topic (Strauss and Irwin, 2004; Larimer et al., 2010; Heil, 2011; van Dam and Heil, 2011; Eisenhauer, 2012).

Most flowering plants are hermaphroditic, i.e., produce female and male sexual organs in the same flower, but unisexuality where the female and the male sexual functions are placed on separate individuals (dioecy) has evolved several times during the course of evolution in different plant lineages (Renner and Ricklefs, 1995; Charlesworth, 2002). Dioecy is relatively uncommon in flowering plants; only ca. 6% of flowering plants have dioecious populations, although it is represented in over 38% of all angiosperm families (Renner and Ricklefs, 1995). On the other hand, few flowering plants (∼7%) feature other breeding systems, where combinations of female, male or hermaphrodite flowers at the plant and population levels are involved (e.g., gynodioecy; populations composed of female and hermaphroditic plants), which may represent intermediate steps toward the evolution of full unisexuality, or stable terminal breeding systems (Ainsworth, 2000). Several pathways for the transition from hermaphroditism to dioecy have been proposed (see Barrett, 2002), but current evidence suggests that the gynodioecy pathway is particularly common (Charlesworth and Charlesworth, 1978; Weiblen et al., 2000; Barrett, 2002; Spigler and Ashman, 2012). Male-sterility genes (caused by mutations in nuclear genes or in mitochondrial loci) spread within hermaphrodite populations, leading to an intermediate stage involving females and hermaphrodites. Genetic modifiers of female fertility subsequently convert hermaphrodites to males, gradually resulting in dioecy. In gynodioecious plants, the hermaphrodites are generally “less female” relative to the females, i.e., the hermaphrodites could be functionally more male if high frequencies of females exist in the population (Spigler and Ashman, 2012). The type of mutation (nuclear or cytoplasmic) and the ecological environment may affect the transition to dioecy (Ashman, 2006; Spigler and Ashman, 2012). Dioecy can be considered the most extreme mechanism for avoiding the effects of fixation of deleterious genes and inbreeding depression, although self-pollination (autogamy) has evolved in some angiosperm species (20%) as a mechanism of reproductive assurance (Schoen et al., 1996; Eckert et al., 2006). Regardless of the pathway, evolution of separate sexes in plants seems to have been (and is being) influenced by above and belowground interactions (see e.g., Ashman, 2002, 2006). The biotic interactions along with life-history trade-offs are pivotal elements of the theory of the evolution of dioecy (Geber et al., 1999; Ashman, 2000, 2002) and thus, understanding the evolutionary consequences of sex-specific preferences in these interactions and how sexual morphs deal with such biotic interactions is of primary importance.

Life-history trade-offs (Gleeson and Tilman, 1992; Seger and Eckhart, 1996) can be used to predict sex-specific resource allocation patterns between sexual morphs. Plant resources are limited, and therefore resource allocation trade-offs between plant functions normally exist. These trade-offs manifest themselves so that allocation to one function reduces allocation to other functions. Classically, plant functions such as growth, reproduction, maintenance and defense are considered to be constrained by shared resource pool. In dioecious and gynodioecious plants, females generally allocate more resources to reproduction and defense than to growth, while males or hermaphrodites allocate more to growth than reproduction (Delph, 1999; Obeso, 2002). As a result, secondary sexual dimorphism (of traits not related directly to gamete production, Sakai and Weller, 1999) between sexual morphs has been documented (Geber et al., 1999), including those observed in the incidence and strength of above and belowground biotic interactions such as herbivory (e.g., Cornelissen and Stiling, 2005), parasitism (e.g., Williams et al., 2011), pollination (e.g., Munguía-Rosas et al., 2011) and, more recently, the interaction with arbuscular mycorrhizal fungi (e.g., Varga and Kytöviita, 2008; Vega-Frutis et al., 2012). Only if there are no sexual differences in resource allocation or if resources are not compromised (trade-offs), we would expect a lack of differences in biotic interactions between sexes.

Given that the gynodioecy–dioecy pathway has been proposed as the principal route of evolution from hermaphroditism to dioecy, understanding how below and aboveground biotic interactions may impact the evolution of dioecy is a central topic in evolutionary biology (e.g., Barrett, 2002; Ashman, 2006). Our objective is to review and highlight the main research themes concerned with plant sex and multiple interactions. First, we summarize effects of antagonistic and mutualistic biotic interactions on some traits relevant to dioecious and gynodioecious species. Second, we review studies dealing with multiple biotic interactions. Third, we present a comprehensive list of studies of multiple interactions in both dioecious and gynodioecious plants, owing to the currently limited understanding of this topic, and the fact that below and aboveground interactions have traditionally been studied in isolation from one another. Some previous revisions have been conducted partially on this issue, especially regarding interactions with herbivores and pollinators (Ågren et al., 1999; Ashman, 2000, 2002; Cornelissen and Stiling, 2005) and these have been extremely valuable for understanding the role of biotic interactions in the evolutionary and ecological context between sexual morphs of dioecious and gynodioecious species. However, most studies were focused specifically on single interaction (e.g., herbivory) and on one plant host, and thus do not provide the full insight in an ecological context. Our review focuses mostly in dioecious and gynodieocious systems since information from other breeding systems is almost absent. Studies considering other breeding systems such as androdioecy (populations with male and hermaphrodite flowers in different individuals), trioecy (populations with female, male and hermaphrodite flowers in different individuals) and subdioecy (populations with female and male flowers in different individuals, but with males that usually produce hermaphrodite or female flowers) will expand our understanding of the role of mutualists and antagonists in the evolution of breeding systems, but these sexual systems are beyond the scope of our revision.