

Review

Sex ratios in dioecious plants in the framework of global change



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ARTICLE INFO

Article history:

Received 27 June 2014

Received in revised form 5 August 2014

Accepted 6 August 2014

Available online 25 August 2014

Keywords:

Dioecy

Phytohormones

Reproductive effort

Sex ratios

Stress tolerance

Vegetative traits

ABSTRACT

Male- or female-biased sex ratios in natural populations of dioecious plants reveal that dioecy is an important trait determining stress tolerance in plants. However, to what extent sex ratios in dioecious plants can be explained by sex-related differences in stress tolerance? Will sex ratios in natural populations change within the framework of global warming? And finally, are these sex-related differences in stress tolerance under hormonal control? This review aims to answer these three basic questions related to the biology of dimorphic species, with special emphasis on developments in research in this area over the last decade. The causes of male- or female-biased sex ratios in natural populations are still poorly understood, but they may be related to the specific life-history traits and adaptation strategies of each species to its natural habitat. The expression of dioecy leads to sex-related differences in hormones at the level the whole plant, which can affect vegetative growth and stress tolerance differently in females and males. This, in turn, may influence the evolution of dioecy in a given species. Indeed, evidence obtained thus far suggests two-way influences between stress tolerance and hormones in dioecious plants. Studying mechanisms of stress adaptation in dioecious plants will be essential if we aim to understand the evolution of these species within the framework of global warming.

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1. Introduction

The sexuality of flowering plants is extremely diverse. The maturation of male and female parts of a flower at different times (dichogamy) or of male and female flowers in separate individuals (dioecy) has evolved to prevent self-pollination. Each individual of a dioecious plant species has only male or only female flowers. In monoecious plants, each individual has separate male and female flowers. In hermaphroditism, the most common type of plant sexuality, male and female parts are found in each individual flower. Sometimes a monoecious plant will occur in a population of a plant species that is normally considered dioecious. When this

is documented, the species is referred to as subdioecious. Although the incidence of dioecy in flowering plants globally is relatively uncommon (6–7%), it is reported in close to half of all angiosperm families and may have originated from hermaphroditic ancestors on at least 100 occasions; thus probably representing an ecological and evolutionary advantage (Renner and Ricklefs, 1995; Geber et al., 1999; Heilbuth, 2000; Charlesworth, 1999, 2002; Barrett and Hough, 2013).

Once dioecy has arisen, this does not bring natural selection of gender dimorphism to an end, but rather initiates the evolution of secondary sexual dimorphism (Charlesworth, 1999). Secondary sexual dimorphism is the separation of male and female characters that are not directly related to gamete production (i.e., the androecium and gynoecium in plants). Secondary, or somatic, sexual dimorphism can include differences in morphology (e.g., differences in leaf or plant size), physiology (e.g., differences in water

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use, photosynthesis or hormonal contents) or phenology (e.g., the timing or age of the onset of reproduction) (Delph, 1999). Indeed, secondary sexual dimorphism occurs not only in plants, but is also very common in animals and has consequently been a subject of intensive research in evolutionary biology, ecology and physiology; ever since pioneering studies by Darwin (1877).

Great effort has been dedicated to understanding the nature, ecology, evolution and genetics of sexual dimorphism in angiosperms, which has recently been reviewed (Barrett and Hough, 2013; Charlesworth, 2013). Similarly, physiological aspects associated with sexual dimorphism in plants have received significant consideration. Obeso (2002) elegantly reviewed the processes associated with the costs of reproduction, including reproductive costs in sexually dimorphic plants, and the underlying evidence indicating mechanisms that compensated for the costs. Here I focus on developments that have occurred over the last decade within our understanding of sex-related differences in the physiology of dioecious plants, focusing particularly on sex ratios and stress tolerance. Three fundamental questions will be considered in what follows. To what extent sex ratios in dioecious plants can be explained by sex-related differences in stress tolerance? Will sex ratios in natural populations change within the framework of global warming? And finally, are these sex-related differences in stress tolerance under hormonal control? These three basic questions related to the biology of sexually dimorphic species will be considered here, with special emphasis on developments in research in this area over the last decade.

2. Sex ratios within the framework of global warming

The origin of separate sexes (dioecy) from combined sexes (cosexuality) via the gynodioecy pathway has occurred repeatedly throughout the evolutionary history of flowering plants (Weiblen et al., 2000) and consists of two stages. The first involves the invasion of hermaphrodite populations by female plants, resulting in gynodioecy. The second step occurs as hermaphrodites in gynodioecious populations increasingly favour pollen over seed production, resulting in their replacement by pure males and the establishment of dioecy (Darwin, 1877; Lloyd, 1976). The genetic aspects of this evolutionary transition are now well understood as a result of considerable theoretical and empirical research (reviewed in Charlesworth, 1999). However, less is known about the ecological mechanisms that favour the evolution of separate sexes from combined sexes via the gynodioecy pathway. It is generally assumed that gender dimorphic species are often found in drier habitats than their sexually monomorphic relatives; and that gynodioecious populations appear closer to a dioecious state as resources, particularly water, become scarce (Case and Barrett, 2004). In dioecious plants, the classical theoretical arguments of Düsing (1884, see Edwards, 2000) and Fisher (1930) predict 1:1 primary sex ratios after the period of parental investment, when the costs of producing females and males are equal. However, departures from equality are commonly reported in the literature of dioecious angiosperms. Some estimates suggest that only 29% of species show populations with 1:1 sex ratios, while more than half (59%) display male-biased populations (Delph, 1999; but see also Rotenberg, 1998). A more recent survey of sex ratios among angiosperm families revealed that about half showed significant deviations from parity, with male bias almost twice as common as female bias (Barrett et al., 2010). In a recent comparative analysis of sex-ratio variation in 243 species of flowering plants, Field et al. (2012) found that sex-based differences in life-history traits and their influence on the costs of reproduction contribute to variation in sex ratios between different species. Furthermore, heterogeneity of sex ratios also occurs between different populations of a

given species, leading to questions regarding the processes that contribute to this variation.

Within dioecious species, three major aspects have been related to male-biased populations. First, the higher investment in reproduction by females, both due to repeated episodes of flowering and large maternal investment in costly fleshy fruits, so that male-biased populations are more frequent in long-lived dioecious species that produce large fleshy fruits (reviewed by Sinclair et al., 2012; Barrett and Hough, 2013). Second, a greater susceptibility to stress in females. Sex ratios in a given population have been shown to be strongly modulated by environmental conditions (reviewed in Korpelainen, 1998; Golenberg and West, 2013). In dioecious plants, environmental conditions that stress the plants or reduce their growth or productivity tend to bias plants away from developing seed-producing female flowers; although some exceptions exist (see i.e., Stehlik and Barrett, 2005; for a recent list of examples found in the literature, see Golenberg and West, 2013). Third, spatial segregation of the sexes, which has been reported in several dioecious species and in the vast majority of cases is linked to male-biased sex ratios at more stressful sites (Bierzychudek and Eckhart, 1988). It should be noted, however, that despite these general trends, it is not always possible to establish cause–effect relationships between stressful environments and male-biased ratios in dioecious plants.

Predicting the effects of global warming on dimorphic plants is a challenge for current research. The CO₂ and O₃ levels in the troposphere have increased significantly in recent times because of industrialization and emissions arising from the burning of fossil fuels. Furthermore, average global temperatures are likely to increase by up to 3.9°C by the end of this century and patterns of precipitation are changing significantly over the globe, leading to increased salinity problems in the more arid areas (IPCC, 2014). Increases in atmospheric CO₂ concentrations favour enhanced carbon gain because of the stimulation of photosynthesis, and they are likely to ameliorate O₃ damage due to reduced O₃ uptake and increased carbon assimilation. However, the beneficial effects of elevated CO₂ concentrations on photosynthesis and hence productivity, particularly in C₃ plants, may be offset by increases in global temperatures (Long et al., 2005). Furthermore, climate change factors such as predicted increases in temperature and the availability of CO₂ and O₃ will have a profound effect on oxidative signalling in plants, particularly in relation to photosynthetic metabolism and environmental stress responses (Munné-Bosch et al., 2013). Consequently, studying mechanisms of stress adaptation in male and female dioecious plants is essential if we aim to understand the evolution of these species within the framework of global warming. In this respect, Zhao et al. (2012) showed that an elevated temperature

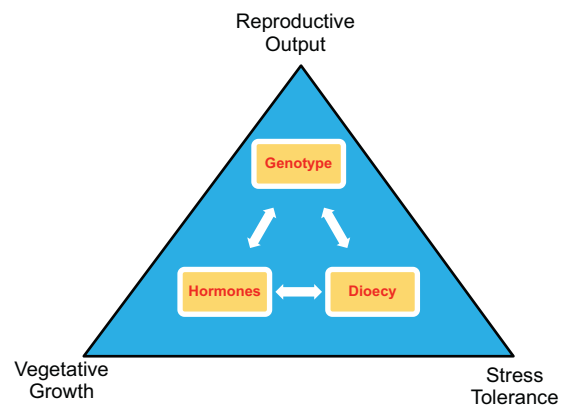


Fig. 1. Hormonal effects are key determinants of the vegetative growth, stress tolerance and reproductive fitness in dioecious plants. Note that dioecy can affect the hormonal balance of leaves and it can in turn be controlled by the hormones in plants.

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