

RESEARCH COMMENTARY

Sexual conflict in plants

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What is sexual conflict?

In dioecious species, the two sexes often make different investments in reproduction, or have different reproductive strategies, leading to divergent selection pressures across sexes. This, combined with a shared genome, can potentially result in an intragenomic conflict called sexual conflict (Chapman *et al.* 2003). Sexual conflict can further be divided into two components: interlocus and intralocus conflict.

Interlocus conflict designates the form of conflict in which the expression of a sex-limited locus results in a net fitness benefit to the sex expressing it and a fitness cost to the other sex, usually through direct reproductive interactions. This leads to strong selection for a counteracting mechanism, usually governed by a different locus, in the other sex. The result is rapid evolution of the loci involved and open-ended cycles of antagonistic coevolution between the sexes (Holand and Rice 1998).

Intralocus conflict involves traits (and hence alleles) that are expressed in both sexes, but have different optima in each sex (Rice and Chippindale 2001), thereby creating divergent selection pressures across sexes. However, because males and females of the same species share the same genome, genetic correlations for the same trait between sexes impede the independent evolution of the trait within each sex, leading to a conflict between the sexes. A part of the conflict can potentially be resolved by evolution of sex-limited gene expression leading to sexual dimorphism. The unresolved part of the conflict maintains each sex away from its optimum, creating a gender load.

Sexual conflict has mainly been investigated in animals and the interlocus component has been the principal focus of past studies. However, among the very large diversity of reproductive systems of plants, dioecy gathers all the

conditions to give rise to sexual conflict: separate sexes, different fitness optima for males and females, and a common genome. In the present paper, we review different studies that give cues into the existence and evolutionary importance of the two forms of sexual conflict in dioecious plants.

Looking for interlocus conflict in plants

The existence of interlocus conflict is not obvious in plants. This is not surprising given that there is almost no direct interaction between males and females. Most of the interaction is through pollen transfer, often mediated through an agent. Though several studies have demonstrated prezygotic selection in plants through effects on pollen number, pollen tube competition and siring ability (reviewed in Murphy 1998), there is no evidence for negative effects of these factors on female fitness. On the contrary, studies indicate that multiple pollination and greater pollen loads increase female fitness through greater fruit set (e.g. Bañuelos and Obeso 2003). Factors that can potentially reduce female fitness — such as nonrandom ovule abortion and variation in seed provisioning — have largely been attributed to female effects and sibling rivalry among the developing seeds within a fruit (reviewed in Uma Shaanker and Ganeshaiah 1997). Thus, although there are ample opportunities for interlocus conflict to operate in plants (Haig and Wilczek 2006), there is paucity of empirical results showing such conflict.

Looking for intralocus conflict in plants: direct evidence

Intralocus sexual conflict, though never formally stated, is implicitly invoked as a possible constraint in plant studies that focus on the evolution of sexual dimorphism. The presence of positive between-sex correlation for fitness-related traits, coupled with opposing patterns of selection across sexes, essentially constitutes strong evidence for intralocus

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Keywords. sexual conflict; dioecious plants; genetic correlation; sexual dimorphism; *Silene latifolia*.

conflict as a major factor constraining evolution of sexual dimorphism. This pattern of results has been repeatedly seen in multiple studies ranging from surveys at the intrapopulation level (Kohorn 1994) and interpopulation level (Delph *et al.* 2002) to artificial-selection approaches (Meagher 1994; Delph *et al.* 2004, 2005). In one of the first such studies, using vegetative morphology, Kohorn (1994) classified individuals of the dioecious plant *Simmondsia chinensis* (jojoba) into four classes ranging from extreme male-like to extreme female-like and measured several fitness-related traits. Male plants with more male-like morphology produced more inflorescences and had a higher chance of flowering than males with more female-like morphology. Female plants with more female-like morphology had more flower buds and greater seed mass than females with more male-like morphology. This study clearly shows that the optimum vegetative morphology for males and females is different and consequently, intersexes have lower fitness; a scenario completely compatible with the idea of intralocus conflict, provided that at least part of the observed variation had a genetic basis.

The genetic basis and evolution of sexual dimorphism in flower number have been carefully studied in *Silene latifolia* by Delph and coworkers and reported in a series of papers. Flower number is often one of the most sexually dimorphic traits and seems to be at the heart of sexual conflict in plants. Many studies have reported a higher number of flowers and inflorescences on male plants compared to females (e.g. Kohorn 1994; Bond and Maze 1999; Delph *et al.* 2002). This is argued to be due to competition among males for access to females through an increase in pollinator visitations and/or pollen production (Bond and Midgley 1988; Kohorn 1994; Bond and Maze 1999). On the other hand, the females are selected to produce larger flowers in order to increase the number of ovules, since it is less costly to produce a larger flower with more ovules than producing another flower.

In a common garden experiment, using nine geographically isolated populations, Delph *et al.* (2002) showed a consistent pattern of high sexual dimorphism in flower number and flower size (males produced a large number of small flowers compared to the females), thus establishing a genetic basis for the observed variation across populations. Additionally, they found that both flower size and flower number showed positive phenotypic correlation between sexes, whereas the phenotypic correlation between flower size and number was negative within each sex. The underlying genetic basis for the observed phenotypic correlations was confirmed by additional artificial-selection experiments on flower size on replicate lines of *S. latifolia*. Delph *et al.* (2004) initiated two sex-specific selection regimes, one favouring males with large flowers (or more female-like males) and the other favouring females with small flowers (or more male-like females). Within four generations of selection, they observed huge direct responses to selection, with flower size on females decreasing in the small lines and flower size on males increasing in the large lines. An ex-

amination of three correlated responses to selection yields a clearer insight into the nature of conflict in *S. latifolia*. First, there was a positive genetic correlation between sexes for flower size, with the unselected sex responding in the same direction as the selected sex. Second, a flower size and number tradeoff was evident with males and females from the small-flowered lines producing significantly more flowers than the large-flowered lines and controls. Third, the selection experiments revealed a positive correlation between flower size and ovule number, but pollen number did not change with flower size.

Thus the observed pattern of dimorphism in *S. latifolia* can be expressed in terms of disruptive selection across sexes for flower number. For the sake of simplicity, let us assume that the flower size and number in *S. latifolia* are determined by a single locus with pleiotropic effects. In males, since pollen number does not increase with flower size, alleles that increase flower number (and hence pollen number) at the cost of flower size (and hence reduced ovule number) are strongly favoured by selection. When the same alleles are expressed in females, as evidenced by the strong between-sex correlation for floral traits, they are selected against, preventing the independent evolution of each sex towards its own optimum, thereby setting up a strong intralocus conflict.

The consequences of such a conflict are many. First, it poses a severe constraint on evolution of dimorphism. This is consistent with the observation that sexual dimorphism showed relatively little variation across isolated geographical populations even when trait values varied considerably (Delph *et al.* 2002). Second, it maintains additive variation in traits that are closely linked to fitness, otherwise not expected to have high levels of variation. In this regard, it is interesting to note that Delph *et al.* (2004) observed a strong response to selection within four generations. Finally, intralocus conflict reduces the average fitness of both the sexes and hence that of the population, thereby creating a gender load. For example, in the study of Delph *et al.* (2004), within four generations of selection the males in the small-flowered lines produced about 30% more flowers (and hence were more fit, all else being equal) than the control males. The failure of the control males to increase flower production (and hence their fitness) is probably due to counterselection on small-flowered females. The same is true for control females compared to females of the large-flowered lines.

An additional source of gender load is the correlation between a trait under disruptive sexual selection and other life-history traits. Delph *et al.* (2005) measured a number of traits related to morphology, physiology and allocation in replicate lines of *S. latifolia* selected for increased or decreased flower size (Delph *et al.* 2004) and found a strong correlated response to selection. Their results indicate that both sexes in lines that had small but numerous flowers had an increased cost of reproduction owing to genetic correlation between the trait disruptively selected between the sexes (flower number) and life-history-related traits, with negative

consequences on growth and maintenance. This result is also a potential explanation for the sexual dimorphism observed in a suite of floral, vegetative, life-history and physiological traits in plants. It is interesting to note that the traits that did not show a correlated response to selection on flower size were those that were expressed before flowering (Delph *et al.* 2005). This is in agreement with the idea that sexual conflict is likely to be less pronounced in the prereproductive phase, as shown by the absence of sexual conflict in juvenile stages in *Drosophila melanogaster* (Chippindale *et al.* 2001).

Looking for intralocus conflict in plants: indirect evidence

Parental imprinting, where the level of expression of a locus depends on the parent of origin, is a possible mechanism of resolving intralocus conflict. Imprinting is predicted to be an evolutionary outcome of intralocus conflict (Day and Bonduriansky 2004). For this reason, imprinting can be considered as a signature of intralocus sexual conflict and it has been repeatedly observed in flowering plants (Haig and Westoby 1991; Scott *et al.* 1998; Adams *et al.* 2000; Brandvain and Haig 2005), indicating the extent of intralocus conflict in plants. In *Arabidopsis thaliana*, the imprinted loci are involved in seed provisioning (Scott *et al.* 1998; Adams *et al.* 2000), with paternally imprinted genes increasing seed size and maternally imprinted genes decreasing seed size, clearly indicating parental conflict over offspring provisioning. Brandvain and Haig (2005) report similar results from a survey of crosses between outbreeding and selfing plants.

Future directions

Several aspects of sexual conflict remain unexplored in plants and constitute important evolutionary questions. For example, both theory and experimental evidence suggest that the X chromosome in animals is especially enriched with sexually antagonistic variation that mediates intralocus conflict (Rice 1984; Gibson *et al.* 2002). A vast majority of dioecious plants show male heterogamety, similar to the XX–XY system of animals (Charlesworth 2002). This makes dioecious plants an interesting material to analyse distribution of sexually antagonistic alleles across the genome and test the role of the X chromosome in maintenance of sexually antagonistic variation. Another interesting aspect is the potential for adaptive female choice. It has been predicted that intralocus conflict causes reversed inheritance of fitness across sexes (Chippindale *et al.* 2001) and experiments show that female lizards can exert an adaptive sperm choice to reduce the fitness consequences of such reversed inheritance (Calsbeek and Sinervo 2004). Given that female plants are known to discriminate between pollen from different males and are known to induce nonrandom embryo abortion and seed provisioning, it would be interesting to investigate if females are able to bias sex ratios or seed provisioning based on the fitness of the pollen donor. Artificial controlled pollinations

make experimental investigation of this phenomenon possible.

To conclude, little of the plant literature addresses the question of sexual conflict in dioecious plants directly. However, presence of intralocus sexual conflict is strongly suggested by both direct and indirect evidence and, hence, dioecious plants constitute an interesting group for study of intralocus conflict.

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