Trends in Plant Science

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Opinion

Integrating Studies on Plant–Pollinator and Plant–Herbivore Interactions

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Research on herbivore-induced plant defence and research on pollination ecology have had a long history of separation. Plant reproduction of most angiosperm species is mediated by pollinators, and the effects of herbivore-induced plant defences on pollinator behaviour have been largely neglected. Moreover, there is expected to be a trade-off between plant reproductive strategies and defence mechanisms. To investigate this trade-off, it is essential to study herbivore-induced plant resistance and allocation of resources by plants, within the same system, and to test if indirect plant resistance can conflict with pollinator attraction. Here, I review the key literature highlighting connection between plant defence and reproduction, and propose to exploit natural variation among plant species to assess the ecological costs of plant responses to herbivores and pollinators.

Trends

It is crucial to study herbivore-induced resistance and resource allocation by plants within the same study system.

There is a need to link the study of herbivore-induced responses with that of plant–pollinator associations, and ultimately to plant fitness.

Focussing on the underlying mechanisms of plant responses to herbivory and pollination will help to understand if and how the attraction of carnivores can conflict with the attraction of pollinators.

The use of natural variation in plant species will allow the assessment of the ecological costs associated with plant responses to herbivores and pollinators.

Plant Defence and Reproduction

Plants and insects are among the most abundant groups of organisms on Earth [1]. Within plants, biodiversity is highest among angiosperms [2,3]. For flowering plants, interactions with insects involve mutualistic associations with pollinators that mediate reproduction, as well as antagonistic interactions with a speciose group of herbivores [1,3]. To maximise fitness, flowering plants in nature are challenged to optimise relative investments in reproduction and defence against herbivores. Reproduction is mediated by the activities of pollinators for two out of every three angiosperm plant species [1,4,5]. Plant reproductive strategies and defence mechanisms are intrinsically linked and investments in defence and reproduction by plants have long been predicted to be involved in a trade-off [6]. This trade-off is hypothesised to occur in two main ways: first, when resources allocated to reproduction cannot be allocated to defence and vice versa; second, when the attraction of carnivorous insects – so-called indirect plant defence – conflicts with the attraction of pollinators that mediate reproduction. To test these hypotheses, it is essential (i) to investigate herbivore-induced plant resistance and allocation of resources by plants, within the same system, and (ii) to test if herbivore-induced resistance, including indirect plant resistance, can negatively affect the behaviour of pollinators that mediate plant reproduction. Most studies that have investigated plant defensive strategies have focused on plants in the vegetative stage [7,8]; therefore, the link with plant fitness is often missing [9–12] and, of course, natural selection on defensive traits can only be expected when this results in a net plant fitness benefit. It is timely to integrate research on plant defence and research on plant–pollinator interactions, and here I focus on the key literature that can enlighten the link between these two research fields. I use these studies to then discuss the ecological significance of plant responses to herbivores and pollinators, and propose a framework outlining research questions that can guide the research field to integrate studies of plant defence and reproduction.

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Herbivore-Induced Responses by Plants in the Flowering Stage

In the context of the defence–reproduction trade-off it has been questioned whether plants in the flowering stage can mount defences against herbivores or whether herbivore-induced defences are restricted to early developmental stages [6,13]. Plant defence is indeed influenced by ontogeny [14], and it has recently become clear that plants in the flowering stage do respond to herbivore attack [15–21]. Herbivory can influence plant chemistry, plant morphology, reproduction, and phenology, and these changes allow for a number of plant-mediated interactions with organisms at different trophic levels [16,18]. Insect herbivores can affect plant development by altering speed of reproduction and allocation of resources [19,22]. Herbivory can affect flower traits such as volatile emission and floral rewards [15,19–21,23,24], and can influence the behaviour of the plant-associated insect community including that of pollinators [19,21], and carnivores [15,20,21,25]. As a result, responses of flowering plants to herbivory can positively or negatively affect plant fitness [19,26–29]. Tables 1 and 2 highlight studies on brassicaceous and solanaceous plants, respectively – two of the best-studied plant families with regard to herbivore-induced responses. Plant life history traits, including plant life style and mating system (Tables 1 and 2), may have influenced how defensive mechanisms and reproductive strategies evolved within a plant family [30–32], and this is an open field for future research.

Herbivore-Induced Chemical and Physiological Responses: Direct Effects on Pollinator Behaviour and Plant Reproduction

Herbivore attack can induce resistance and tolerance traits in plants that can influence pollinator behaviour and plant reproduction, and there is considerable variability in herbivore-induced responses among plant genotypes or among plant populations [32–34]. Plant direct resistance traits can deter, repel, or ultimately kill the plant attacker [1,35]. Resistance traits induced in response to herbivory can be quantified in roots, leaves, and flowers, but also in floral rewards [36,37]. Presence of defensive metabolites in nectar and pollen might intuitively suggest a conflict between defence and reproduction [7,37]. Although the duration of flower visitation by pollinators can be negatively correlated with defensive compounds present in the floral reward, this does not necessarily lead to negative effects on pollination success [37]. In fact, when pollinators spend less time per flower, plant reproduction can in theory be maximised as long as pollination efficiency is not reduced [37]. Furthermore, secondary metabolites in floral rewards can serve as antibiotics for pollinators [38]. These studies suggest that herbivore-induced resistance or the simple presence of plant secondary metabolites in floral rewards can be beneficial for pollinators and, at the same time, optimise plant reproduction.

Induced plant resistance to herbivory is generally associated with changes at the level of plant secondary metabolism [39,40]. However, changes in primary plant metabolites can also confer resistance [40,41], or promote physiological changes that may eventually protect plants against their attackers [19,40,42]. Mechanisms that allow plants to compensate for direct effects of herbivory, that is, compensation for the loss of tissues or damage caused by herbivores, have repeatedly evolved in various plant species [1,33,35,43]. Herbivore attack can reconfigure plant primary metabolism and alter source–sink relationships [40]. Plants can store resources in roots and invest in regrowth of vegetative tissues when herbivore pressure aboveground is low, or reallocate resources to aboveground parts when roots are attacked [40,42,44–47]. The allocation of resources into different tissues can render plants more tolerant to herbivory [40,47–49], but also influences interactions with pollinators and plant reproduction. Upon herbivory, *Brassica nigra* plants reallocate resources into reproduction [19,49], while maintaining interactions with day-active pollinating insects and sustaining seed set [19]. Investing in reproduction upon herbivory seems to allow plants to maintain plant–pollinator interactions and sustain reproductive output [19,49]. However, when plants invest in roots upon herbivory this may lead to delayed flowering and fewer or smaller flowers, which can lead to reduced rate of visitation by pollinators, and also to shifts in the diversity of pollinator species that are exposed to the plant. I hypothesise