REVIEW AND SYNTHESIS

Florivory: the intersection of pollination and herbivory

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Abstract

Plants interact with many visitors who consume a variety of plant tissues. While the consequences of herbivory to leaves and shoots are well known, the implications of florivory, the consumption of flowers prior to seed coat formation, have received less attention. Herbivory and florivory can yield different plant, population and community outcomes; thus, it is critical to distinguish between these two types of consumption. Here, we consider the ecological and evolutionary consequences of florivory. A growing number of studies recognize that florivory is common in natural systems and in some cases surpasses leaf herbivory in magnitude and impact. Florivores can affect male and female plant fitness via direct trophic effects and through altered pathways of species interactions. In particular, florivory can affect pollination and have consequences for plant mating and floral sexual system evolution. Plants are not defenceless against florivore damage. Concepts of resistance and tolerance can be applied to plant–florivore interactions. Moreover, extant theories of plant chemical defence, including optimal defence theory, growth rate hypothesis and growth differentiation–balance hypothesis, can be used to make testable predictions about when and how plants should defend flowers against florivores. The majority of the predictions remain untested, but they provide a theoretical foundation on which to base future experiments. The approaches to studying florivory that we outline may yield novel insights into floral and defence traits not illuminated by studies of pollination or herbivory alone.

INTRODUCTION

As much as 18% of terrestrial plant biomass and 51% of aquatic plant biomass is consumed by herbivores, making herbivory an important biotic interaction (Cyr & Pace 1993). While significant effects of leaf herbivory on plant biomass and fitness are well documented (e.g. Marquis 1984), the effects of florivory have been less studied. This is surprising considering that the evolution and radiation of flowering plants and insects is intertwined with opportunistic and obligatory feeding on flowers and reproductive structures (Ehrlich & Raven 1964). Thus, floral feeders may be important enough to drive adaptations in plant and floral traits (Frame 2003). Florivory combines the forces of herbivory and pollination, as damage to flowers or other reproductive tissues can have direct consumptive effects on gamete production or maturation (Krupnick & Weis 1999) as well as non-consumptive effects through changes in pollination service (Krupnick et al. 1999). These direct and indirect effects may affect individual plant fitness, populations, and communities. Nonetheless, many studies have failed to distinguish among damage to leaves and seeds vs. floral tissues. Despite the recognition that floral damage can decrease plant fitness to degrees comparable with or surpassing leaf damage (Strauss et al. 2004), few predictions exist concerning the effects of florivores on floral trait evolution and in current theories of plant defence (but see Euler & Baldwin 1996; Ashman 2002).

In this review, we outline patterns of florivory and then consider how different types of floral damage can affect plant fitness. Second, given that florivores damage flowers and can influence pollination, we explain how the causes and consequences of florivory are linked to plant mating system and floral gender. Third, because florivores can decrease plant fitness, we consider the mechanisms by which plants defend against florivores, including both resistance and tolerance, and we apply theories of chemical defence against herbivores and pathogens to make predictions about how plants may defend flowers against florivores. Finally, we suggest future areas of research in this field and ways in which emerging technologies can help determine the origin and expression of defence in reproductive tissues. Throughout this review, rather than formulating new theory, we extend ideas from established models to make testable predictions about the causes and consequences of florivory. Our findings suggest that the study of florivory may yield novel insights regarding not only ecological interactions but also may help explain the evolution and persistence of floral traits not explained by pollination pressure alone and floral defences not explained by herbivory alone.

DEFINITIONS AND PATTERNS OF FLORAL DAMAGE

Florivory is any type of consumer-caused damage to developing floral buds or mature flowers before the development of the seed coat and includes damage to bracts, sepals, petals, stamens, and pistils, as well as pollen and ovules (Burgess 1991). We limit our review of damage patterns to those that do not break apical dominance, and we do not include nectar robbers, low-efficiency pollinators, bees that primarily consume pollen or obligate seed-eating pollination mutualists; some of these other types of plant–animal interactions have been recently reviewed (e.g. Maloof & Inouye 2000; Irwin et al. 2001). Within insects, florivores are found in many orders with organisms displaying a variety of life-history strategies and food preferences, ranging from pollenivores (Kirk et al. 1995), to gall-makers (A. C. McCall, personal observation), to generalist herbivores that eat many other plant tissues in addition to flowers (McCall & Karban 2006).

The distinguishing characteristics of florivory vs. other types of plant damage are subtle, but important. First, florivory is associated with damage to structures related to potential reproductive output. In contrast, seed predation, both pre- and post-dispersal, is associated with the consumption of already-fertilized ovules at later life-history stages. Damage to seeds that have already developed can result in different plant reproductive outcomes than damage to pre-seed reproductive structures. For example,

damage to seeds is often not visible externally, while damage to petals or sepals may affect a plant's overall reproductive display, and may be evident to pollinators (Krupnick et al. 1999) that are essential to the reproduction of many flowering species (Buchmann & Nabhan 1996). Conversely, damage to seeds may be more costly for plant fitness than florivory, as fertilized ovules are presumably more valuable than the unfertilized ovules found in a new flower. Second, florivory is generally associated with the removal of resource sinks, but leaf herbivory is often associated with the removal of plant biomass important for photosynthate production (but see Aschan & Pfanz 2003). Thus, while florivory may alter source–sink resource relationships within a plant and may increase resource availability per surviving flower (Krupnick & Weis 1999), leaf herbivory generally changes resource acquisition and overall plant resource status and may decrease resource availability per surviving flower. Third, florivory and herbivory can sometimes have different effects on plant population dynamics as population growth rates can be differentially sensitive to changes at different life-history stages. For example, in annual or monocarpic species that rely on successful seed production, damage to floral or seed tissues often is more strongly linked to changes in demographic rates than damage to vegetative structures (Rose et al. 2005). In some perennial plant species, similar trends are observed; for example, flower removal decreased population growth rate by 20% in Primula veris whereas the effects of leaf tissue removal were weaker (Garcia & Ehrlen 2002). One caveat is that any interaction that effects fecundity (i.e. florivory, herbivory or seed predation) may similarly affect population growth, and the demographic consequences of florivory vs. other species interactions will ultimately depend on plant life history, spatial and temporal variation in attack, and the current demographic state of the population.

Quantifying florivory is not as straightforward as measuring leaf herbivory. First, because flowers are often ephemeral structures that are produced throughout the blooming season and do not persist over the lifetime of the plant, florivory in the field can be difficult to assess unless sampling occurs at frequent intervals throughout the flowering season (Breadmore & Kirk 1998) or on long-lived flowers. Even though other structures like leaves and roots are also ephemeral over the lifetime of a plant, flowers often are only open for a few days, and often no clear record of damage is visible for flowers when the corolla senesces. Second, separating the effects of florivores vs. other antagonists, such as seed predators, in the field and in the literature can be challenging. Researchers usually do not distinguish between consumption of developing seeds vs. other reproductive tissue, or are unable to manipulate either seed damage or petal/bract damage individually (e.g. Louda

& Potvin 1995; Calvo-Irabién & Islas-Luna 1999), as many consumers damage these structures sequentially (Maron 1998; Kelly & Dyer 2002). Similarly, the consumption of accessory structures, such as flowers or sepals, vs. gametes or gamete-bearing structures, such as ovules or pollen, is difficult to disentangle because these structures also get damaged sequentially or simultaneously (Heithaus *et al.* 1982; Riba-Hernández & Stoner 2005). Distinguishing when and what structures are damaged is essential to understanding the effects of florivores on plant reproduction. For example, some florivores concentrate their feeding on anthers and pollen (Kirk *et al.* 1995), which can affect the allocation of resources to sexual structures later in the flowering season and differentially affect male vs. female plant reproductive success. Moreover, Andersson (2003) found that artificial removal of stamens in *Nigella sativa* produced a higher rate of new flower initiation and production of heavier seeds than in unmanipulated controls. In both cases, direct damage to male structures changed reproductive patterns in plants, regardless of damage to ovule numbers.

Despite the challenges associated with assessing florivory, a growing number of studies have measured population- or community-wide amounts of floral damage (e.g. Heithaus *et al.* 1982; Washitani *et al.* 1996; Malo *et al.* 2001; Asikainen & Mutikainen 2005). Some studies suggest that florivory can be as widespread and extensive as leaf herbivory, and florivory can affect similar proportions of individuals or occur at similar or higher rates of consumption per day as leaf herbivory (but see McCall & Karban 2006. For example, florivory by a rove beetle, *Eusphalerum bosatsu*, nearly destroyed the reproductive output of a population of *Primula sieboldii* in Japan (Washitani *et al.* 1996), and 15% of all *Silene latifolia* individuals across 50 populations in Europe suffered from floral damage (Wolfe 2002). Approximately 30% of censused flowers of the tropical understory herb *Aphelandra aurantiaca* were damaged by a diversity of florivores, including adult Coleoptera, Hemiptera and Orthoptera, larval Lepidoptera, and ants (Calvo-Irabién & Islas-Luna 1999). Weiss (1996) found that at least 71% of flowers of *Centropogon solanifolius* in a Costa Rican cloud forest were infested with a pollen-consuming fly larva. In *Lupinus amplus*, 50–79% of flowers were damaged by a Lepidopteran larva (Breedlove & Ehrlich 1968). Wild parsnip populations (*Pastinaca sativa*) suffer severe damage to reproductive parts more frequently than damage to leaves or roots (Zangerl & Rutledge 1996), and a survey of 41 herbaceous species found that florivory rates could reach as high as 50% of all petal area removed in selected 0.16-m^2 quadrats (Breadmore & Kirk 1998). Thus, florivory can reach high levels at both small quadrat scales as well as across continents.

DIRECT AND INDIRECT EFFECTS OF FLORIVORY ON PLANTS

The effects of florivores on plant reproductive success can vary from negative effects (Mothershead & Marquis 2000) to neutral effects (Malo *et al.* 2001), depending on a variety of factors, including the type and amount of floral damage, plant mating system and life-history traits, changes in floral sexual expression, and the community context of other interacting antagonists and mutualists. Despite the context dependency of the reproductive outcomes of floral damage, the mechanisms by which florivores affect plants can be broadly classified into two common pathways: direct trophic effects and indirect non-trophic effects. It is important to note that these direct and indirect pathways are pervasive throughout webs of complex species interactions (e.g. Wootton 2002; Preisser *et al.* 2005) and may be similar to the pathways by which foliar herbivores affect plant reproduction (Strauss 1997).

Florivores directly affect male and female plant fitness estimates by consuming all or parts of gametes (pollen and ovules) as well as pistils and stamens (Muenchow & Delesalle 1992; Krupnick & Weis 1999; Leege & Wolfe 2002; Canela & Sazima 2003). Florivores also have direct costs to plants by consuming resource sinks (i.e. flowers) in resource-limited environments, especially in cases where plants reabsorb nitrogen and phosphorous from petals once fertilization has occurred (Ashman 1994) or when floral parts and ovaries are consumed late in the flowering season once resources have been committed to developing reproductive structures and embryos (Lowenberg 1994). Although not as common, flowers and associated reproductive structures, including petals, sepals, anthers and carpels, can be photosynthetically active and produce a substantial amount of photosynthate in some plant species (Werk & Ehleringer 1983; Galen *et al.* 1993; Antlfinger & Wendel 1997; Hogan *et al.* 1998; Aschan & Pfanz 2003; Aschan *et al.* 2005). In some cases, the photosynthetic contributions from the corolla can reach 60% of carbon contributed by leaves (Clement *et al.* 1997). Destruction or reduction of flower area in these species may reduce the amount of carbon available for assimilation into maturation of fruits and seeds. Finally, damaged petals may lose water through increased transpirational loss or simply through leakage. Florivory could thus increase water stress in damaged flowers, regardless of photosynthesis in the corolla, especially in dry or windy environments (Galen *et al.* 1999). An alternative scenario is that the loss of petal area following florivory could reduce transpirational loss if petal surface area is greatly reduced through damage. To our knowledge, the direct consequences of florivory that lead to diminished reuptake of nutrients, reduced photosynthesis or changes in transpirational loss have not been extensively examined in field experiments.

Florivores indirectly affect male and female plant fitness estimates by altering the quality and quantity of floral characters important for other species interactions. For example, florivory can affect a diversity of floral characters, including petal size (Mothershead & Marquis 2000), nectar production (Krupnick *et al.* 1999), and flower, floret or inflorescence production (Lohman *et al.* 1996), which can alter plant attractiveness to pollinators (Karban & Strauss 1993; Cunningham 1995; Lohman *et al.* 1996; Krupnick *et al.* 1999) and subsequent male and female plant reproduction in pollen-limited and pollinator-limited plant species (Krupnick & Weis 1999; Mothershead & Marquis 2000). Florivory can affect the quantity and quality of damaged flowers or subsequently produced flowers (Mothershead & Marquis 2000; McCall 2006) as well as the quantity and quality of pollinator visits, both of which may interact in an additive or non-additive manner to affect plant fitness. Florivores can also alter pollination through interference competition with pollinators (Canela & Sazima 2003) or by affecting population-wide pollen supply in wind-pollinated species (Bertness & Shumway 1992).

Even in cases where pollinators do not differentiate among damaged and undamaged plants and flowers or in cases where plants are not pollen limited or pollinator limited for reproduction, florivory can have indirect effects on plants by altering the likelihood and intensity of other species interactions important for plant fitness. For instance, if damaged flowers are less attractive to other antagonists, then florivory could benefit plants by deterring these other detrimental species. Florivory could also benefit plants if the same organism acts both as a pollinator as well as a florivore (Adler & Bronstein 2004), assuming the benefits of pollination outweigh any potential costs associated with damage to floral or reproductive parts. These interactions are akin to pollinating seed–predator interactions in which organisms pollinate and oviposit in the same flowers (Thompson & Pellmyr 1992; Holland & Fleming 2002; Cook & Rasplus 2003; Pellmyr 2003), and the same cost–benefit scenarios to predict plant reproduction may be applied (Bronstein *et al.* 2006). Moreover, florivory may alter the abundance and diversity of arthropods that live in and on flowers (Horvitz & Schemske 1984; Geddes & Mopper 2006) with potential plant-fitness consequences.

Although the direct and indirect mechanisms by which florivores affect plants are widely recognized, factorial experiments that manipulate florivory and other species interactions to compare the relative importance of direct vs. indirect effects are still largely lacking (but see Table 1), as are path analyses that tease apart direct and indirect pathways of florivory on plants (Cunningham 1995; Adler *et al.* 2001). Path analysis has been used effectively in showing how florivores, pollinators, ants and other plant antagonists interact (Schemske & Horvitz 1988). In this

Table 1 Examples of studies using factorial experiments to measure the direct consumptive effects of florivores on plant reproduction vs. the indirect effects mediated through changes in pollination

Plant species (family)	Florivore	Pollinator	Plant fitness component	Damage × pollination interaction	Reference
Spartina patens (Poaceae)	Grasshopper (*Conocephalus spartinae*)	Wind	% Undamaged ovules	No*	Bertness & Shumway (1992)
Spartina alterniflora (Poaceae)	Grasshopper (*C. spartinae*) and leafhopper (*Prokelisia marginata*)	Wind	% Undamaged ovules	Yes*	Bertness & Shumway (1992)
Distichlis spicata (Poaceae)	Grasshopper (*C. spartinae*)	Wind	% Undamaged ovules	Yes	Bertness & Shumway (1992)
Hibiscus moscheutos (Malvaceae)	Simulated petal removal	Bees (*Bombus pennsylvanicus* and *Ptilothrix bombiformis*)	Fruit set	Yes	Kudoh & Whigham (1998)
Isomeris arborea (Capparaceae)	Pollen beetle (*Meligethese rufimanus*)	Bees, hummingbirds	Fruit set, seed set	No, yes†	Krupnick & Weis (1999)
Helleborus foetidus (Ranunculaceae)	Mainly Lepidopteran larvae (*Trigonophora flammea*)	Insects	Number of seedlings	Yes‡	Herrera *et al.* (2002)

We report whether studies found a significant damage × pollination treatment interaction for estimates of female plant fitness. A significant interaction term suggests that pollination alters the degree to which florivory affects female plant reproduction. Studies were not included that did not clearly differentiate among the effects of florivory vs. other plant consumption.

*Results approximated from figure and/or text.

†Results variable depending on year, timing or amount of damage or some other factor.

‡Damage may represent a combination of consumption of flowers and developing fruits.

example, ants had a net positive impact on flower production as well as a positive association with florivores. Generality in the study of florivory, and other plant–animal interactions, will come from the identification of the relative importance of different mechanisms (in this case direct vs. indirect effects) driving variation in plant outcomes (see Werner 1998). Factorial experiments and path analyses provide two, albeit not the only, tools for understanding the mechanisms driving how and under what conditions florivores affect plant fitness and plant populations. The studies that have used factorial designs to assess direct and indirect effects of florivores on plants suggest that the indirect effects of florivores through changes in pollination are common, occurring in five of six plant species, depending on the response variable measured (Table 1). Moreover, interpretation of the effects of florivory via direct and indirect pathways will be strongly dependent on whether changes in floral characters, pollinator visitation, male and female reproduction, gene dispersal, and/or plant demography are measured. For example, florivory in the shrub *Isomeris arborea* decreases female fitness directly through ovary consumption, but alters male reproductive success indirectly through changes in pollen removal rates and donation (Krupnick *et al.* 1999). The strongest studies will incorporate multiple fitness and demographic responses and the mechanisms driving those responses to understand why and how florivory affects plant individuals, populations and communities (Strauss 1997; Irwin *et al.* 2001; Strauss & Irwin 2004). How these patterns and mechanisms quantitatively compare with other plant–animal interactions is still largely unexplored.

FLORIVORY, PLANT MATING SYSTEM AND GENDER

Because florivory can influence plant interactions with pollinators and pollinators affect patterns of pollen and gene movement, the causes and consequences of florivory are intimately intertwined with plant mating system. Moreover, because florivory is non-random with respect to floral sexual expression, florivory may play a central role in maintaining variation in plant sexual systems and in promoting gender specialization (Ashman 2002).

Plant mating system

The relationship between florivory and plant mating system is complex. Plants that can autogamously self-pollinate may suffer little or no fitness consequences of florivory, assuming that florivores do not directly damage floral reproductive structures and plants suffer little to no inbreeding depression. Alternatively, for obligately outcrossing species, changes in floral characters following florivory

(or interference competition between florivores and pollinators) can reduce both the total number of pollinator visits to plants as well as the time pollinators spend per flower and the per cent of flowers probed per visit (Krupnick *et al.* 1999; Adler *et al.* 2001). Reductions in the total number of pollinator visits and time spent per flower can reduce per flower and per plant pollen export and receipt (Mitchell & Waser 1992; Jones & Reithel 2001). However, a reduction in the per cent of flowers probed per plant visit can benefit damaged plants by reducing within-plant (geitonogamous) pollen transfer (de Jong *et al.* 1993; Juenger & Bergelson 2000; Irwin 2003). Depending on the degree to which male and female plant reproduction are limited by the total number of pollinator visits, the costs of reduced pollinator visitation may outweigh, balance or trail the benefits of reduced geitonogamy. If pollinators use area-restricted foraging tactics to move out of unrewarding damaged floral patches (Heinrich 1983), florivory may also affect outcrossing distance, assuming pollinator flight distance, pollen flow and gene flow are positively correlated. Finally, in plants with mixed mating systems, florivory may affect a plant's genetic neighbourhood due to a reduction in the proportion of outcrossed- to self-pollen receipt. The effects of florivory on pollen movement within and among plants, levels of inbreeding, and pollen and gene dispersal will interact to affect the spatial genetic structure of natural plant populations.

Surprisingly, few studies have tested the effects of florivory on patterns of pollen and gene movement within and among plants. In one of the most complete studies to date, florivory in a self-compatible shrub, *I. arborea*, by a pollen beetle, *Meligethes rufimanus*, reduced pollen export, an estimate of male reproduction, by one-half and decreased pollen receipt, due to reductions in pollinator service. Florivory, however, had no effects on pollen limitation for seed set or on levels of autogamy (Krupnick *et al.* 1999; Krupnick & Weis 1999). To date, few studies are available to evaluate the generality of these results.

Floral sexual expression and susceptibility to florivory

The sexual expression of plants and flowers affects plant susceptibility to florivores, which could have consequences for plant mating patterns, plant fitness and sexual-system evolution. For example, in dioecious and andromonoecious species, male flowers are often more attractive to florivores than hermaphrodite or female flowers (Cox 1982; Wolfe 1997), a pattern also observed for leaves of male plants (reviewed in Ågren *et al.* 1999). And in gynodioecious species, hermaphroditic flowers are often more attractive to florivores than female flowers (Ashman *et al.* 2004; Asikainen & Mutikainen 2005). Male or hermaphrodite flowers may be more apparent (*sensu* Feeny 1976) with larger, more

attractive flowers, provide more nutrition via pollen to florivores than female flowers or may be less defended (reviewed in Willson 1991; Ågren *et al.* 1999; Ashman 2002). In cases where florivores affect plant fitness, male- and hermaphrodite-biased florivory may contribute to the evolutionary transition of separate sexes (Ashman 2002). For example, the male structures of male and monoecious *Sagittaria latifolia* attract more oviposition attempts by the florivorous weevil *Listronotus appendiculatus* relative to female inflorescences; damage to monoecious plants interferes with female reproductive success on those damaged inflorescences (Muenchow & Delesalle 1992). Cox (1982) and Muenchow & Delesalle (1992) hypothesize that damage to female-bearing reproductive parts by florivores attracted to male flowers should select for male over co-sexual plants and flowers and may contribute to the evolutionary maintenance of unisexual plants.

Plant sexual expression not only alters plant susceptibility to florivory, but floral damage can induce changes in floral sexual expression in sexually labile species (e.g. Hendrix & Trapp 1981; Krupnick & Weis 1998). For example, damage to the primary umbel of andromonoecious *Pastinaca sativa* by the parsnip webworm (*Depressaria pastinacella*) increases the proportion of hermaphroditic flowers in late-developing umbels (Hendrix 1984). The change in sexual expression by *Pastinaca sativa* is likely driven by the reallocation of limited resources. Plants without floral damage mature large numbers of seeds on primary umbels, and secondary umbels produce a higher proportion of male flowers, whereas plants with damaged primary umbels divert resources into the production of hermaphroditic flowers and seeds in the secondary umbels (Hendrix 1984). In this case, changes in floral sexual expression can mitigate the negative effects of florivory on plant reproduction, although the result is also dependent on whether plant species are semelparous or iteroparous (Hendrix 1984). Finally, if florivores induce a shift towards female or male functional gender (Leege & Wolfe 2002), then florivory may constrain or promote the evolution of dioecy (Ashman 2002).

Taken together, the relationships among florivory, plant mating system and floral sexual expression suggest that a broader understanding of plant population genetic structure and sexual system evolution requires consideration of plant–florivore interactions. Given that florivory combines the forces of herbivory and pollination, the most promising studies will unite techniques of plant–animal interactions with plant reproductive ecology to evaluate the hypotheses presented.

FLORIVORY AND PLANT DEFENCE STRATEGIES

While on the one hand, florivory is linked to studies of pollination biology, florivory is also related to studies of plant–herbivore interactions. Because damage to gamete-bearing structures can limit plant reproduction, plants may be under selection to decrease florivore feeding and/or mitigate the fitness costs associated with floral damage. The concepts of resistance (the ability of plants to reduce the frequency of damage) and tolerance (the ability to maintain fitness after damage) have been used to understand how plants cope with damage by herbivores and pathogens (reviewed in Painter 1958; Karban & Baldwin 1997; Strauss & Agrawal 1999; Irwin *et al.* 2004) and to understand more broadly how prey cope with attack by predators (e.g. Tollrian & Harvell 1999). Here, we show that these same concepts of resistance and tolerance can be extended to understand how plants and flowers cope with damage by florivores. It is important to note that many of the characters that promote resistance and tolerance to florivores may have evolved from structures or pathways that were originally used for other purposes, such as pollinator attraction or leaf herbivore deterrence (Armbruster 1997; Irwin *et al.* 2004) or are pleiotropic consequences of plant–herbivore or plant–pollinator interactions (Adler 2000).

Resistance

The same mechanisms associated with plant resistance to herbivores can be used to understand how plants resist florivores. Petals and sepals, consistent with their evolutionary development from leaves (Gutierrez-Cortines & Davies 2000), share many resistance characteristics with leaves, including: (i) chemical deterrents or toxins; (ii) escape in space and time; (iii) physical barriers; and (iv) indirect resistance characters. First, plant compounds associated with herbivore resistance are common in petal tissue (e.g. Hartmann & Zimmer 1986; Euler & Baldwin 1996; Fordyce 2000; Gronquist *et al.* 2001; Strauss *et al.* 2004; Irwin & Adler 2006). Plants with higher levels of secondary compounds in reproductive structures can be more resistant to florivores than those with lower levels of chemical defence. For example, *Castilleja indivisa* with higher levels of inflorescence alkaloids suffered less florivory than plants with lower levels of alkaloids (Adler *et al.* 2001). Second, just as plants can escape herbivore damage by leafing out at locations or during times when herbivory is rare (Feeny 1970), plants may avoid florivore damage by varying the location or timing of bud and flower production. For example, Breedlove & Ehrlich (1968) hypothesized that the flowers of *Lupinus amplus* may be able to avoid the damaging effects of Lycaenid larvae by maturing buds early in the flowering season before adult butterflies emerge. Third, physical barriers, such as trichomes, are also found on or inside flowers (De Craene & Miller 2004; Leitao *et al.* 2005) and could limit florivore access to reproductive tissues.

Moreover, many flowers close their corollas or bracts at night (nyctinasty), which may help protect primary reproductive organs against florivory, although such a hypothesis requires experimental investigation. Fourth, predators of florivores may also serve to protect plants from florivory. For example, ants tending the extrafloral nectar of the neotropical perennial herb *Calathea ovandensis* reduce damage to inflorescences from florivorous *Eurybia elvina* (Horvitz & Schemske 1984). Floral volatiles may also serve to attract natural enemies of florivores. For instance methyl salicylate is a component of floral odour in some species (Knudsen *et al*. 2006). Methyl salicylate can be used by plants to attract natural enemies of herbivores, to facilitate communication between damaged and undamaged tissues within and among plants (Dicke & Bruin 2001), can directly affect the survival of some insects (Ollerstam & Larsson 2003), and is an important signalling molecule in plant defensive reactions to pathogen infection (Shuvalev *et al*. 1997). The indirect and direct effects of methyl salicylate, and other floral volatiles, on florivores and plants merit further experiments. Finally, any floral characters that reduce floral apparency or nutritional quality, such as small corollas or inserted anthers, may also confer resistance to florivores (Ashman *et al*. 2004).

For any of these resistance traits to provide defence against florivores, the traits must not only reduce florivory but must also increase plant fitness in the presence of florivores (Karban & Myers 1989). Defending flowers against florivores, however, presents plants with a quandary often not experienced in plant resistance to foliar herbivores. Traits that deter florivores may also deter pollinators (Strauss *et al*. 2002), and plants may experience opposing selection on floral traits through pollination vs. floral consumption (Ashman *et al*. 2004). These tradeoffs are similar to the contrasting selection pressures flowers experience in deterring nectar robbers vs. attracting pollinators (Adler & Irwin 2005). While studies have identified putative resistant traits against florivores, surprisingly few studies have tested whether these traits reduce the likelihood or intensity of florivory and increase plant fitness in the presence of florivores (but see Adler *et al*. 2001; Ashman *et al*. 2004; Romero & Vasconcellos-Neto 2004). The degree to which florivore-resistance traits benefit plants in the field warrants further attention.

Tolerance

Just as plants have multiple strategies to cope with leaf damage, plants may also have multiple strategies to cope with floral damage. For example, plants may also be able to tolerate appreciable amounts of florivory. In leaves, tolerance can result from the production of new leaf primordia or the ability to boost photochemical processes in undamaged leaves (Strauss & Agrawal 1999). Plants may be able to tolerate the effects of florivores through at least three non-mutually exclusive mechanisms (Louda 1982). First, plants may tolerate florivory by making more flowers after damage or by aborting damaged flowers in order to shunt resources to future flowers (Olesen 1992), especially when floral damage occurs early in the flowering season (Lowenberg 1994). In a similar fashion, through resource reallocation, 'reserve' flowers, ovules or fruit may be selectively matured when other ovules are damaged or removed (Stephenson 1981; Melser & Klinkhamer 2001; Wise & Cummins 2002; Ashman *et al*. 2004). For example, *Lathyrus vernus* compensated for the removal of individual flowers through increased fruit set in the remaining flowers of the same raceme (Ehrlen 1993). Holtsford (1985) found that removal of the first flower in an effort to simulate florivory in *Calochortus lechtlinii* resulted in an increased seed set in second flowers on the same plant, whereas second flowers rarely set fruit when first flowers were left intact. Moreover, although florivores reach high densities on buds and flowers of *Yucca filamentosa*, the effects of florivores on plant fitness can be masked by high floral abscission rates (Althoff *et al*. 2005). Thus, florivores may be feeding on flowers that will be lost anyway as the season progresses. Finally, plants may increase the per capita attractiveness or potential fecundity of individual flowers, for example, by increasing flower size or the number of pollen grains per flower following damage.

As florivores are generally consuming resource sinks and herbivores are consuming resource sources (but see *Direct and indirect effects of florivory on plants*), plants may be able to compensate more fully for florivory than for leaf herbivory, depending on the timing and intensity of damage and whether plants are annual vs. perennial. Moreover, tolerance to florivory vs. foliar herbivory may not be expressed equally through male vs. female plant fitness, as male function is often more sensitive to changes in pollinator visitation whereas female function is often more sensitive to changes in plant resource status (Young & Stanton 1990). Testing such hypotheses requires comparing male and female plant fitness in the damaged and undamaged state for florivory vs. foliar herbivory and controlling for total amount or proportion of tissue removed. Moreover, particular attention should be paid to the physiological aspects of how plants alter resource levels and transportation of secondary compounds after damage occurs.

THEORIES OF CHEMICAL DEFENCE AGAINST FLORIVORY

Although we have identified resistance and tolerance traits against florivores, it is not clear when and under what conditions plants should express such traits. Here we

Table 2 Plant defence theories modified to predict levels of defence in plant reproductive tissues

Theory and factor	Prediction
Optimal defence theory	
Tissue value	Flowers will be more heavily defended and less inducible than leaves
Tissue value	Flowers early in the season that are more likely to be fertilized will be more defended than later flowers
Floral apparency	Conspicuous floral parts will be more heavily defended than inconspicuous leaves or flowers
Costs of defence	Costs of deterring mutualist pollinators will favor reduced, or induced, floral defences
Mating system	Flowers of selfing plants will be more defended than those of outcrossers when damage is to reproductive parts. However, flowers of selfing plants will be less defended than outcrossers when damage is to floral parts used for pollinator attraction
Sexual system	The floral sex with the higher fitness value will be more defended. Costs of attracting vs. deterring pollinators may modify floral defence in pollinator-limited sexes
Floral longevity	Longer-lived flowers will be more defended than shorter-lived flowers
Growth rate hypothesis	
Growth rate	Flowers that develop slower will be more heavily defended than flowers that develop faster
Flower number	Plants will defend few large flowers more than many small flowers, assuming flower number is correlated with, and flower size inversely correlated with, growth rate
Tissue growth rate	Faster growing floral tissues will be more heavily defended than slower growing leaf tissues
Growth differentiation–balance hypothesis	
Carbon	Damage to carbon sinks will reduce growth more than photosynthesis, causing an accumulation of carbon available for defence in extant flowers or fruit

modify theories of chemical defence against herbivores to make predictions about how plants should defend against florivores. We focus on three main theories: optimal defence theory (ODT), growth rate hypothesis (GRH) and growth differentiation–balance hypothesis (GDBH), to understand and predict how plants should invest in defence against florivores (Table 2). Additionally, we discuss how plant mating system, floral sexual expression and plant life-history traits alter defence predictions. These are not the only theories of plant defence that can be applied to florivory. Rather, we modify these theories as a starting point to facilitate the development of further research.

Optimal defence theory

Optimal defence theory addresses intraspecific patterns of defence against herbivores (McKey 1974; Rhoades 1979; Stamp 2003). Of particular use in florivory studies are subhypotheses of ODT that assess variation in defence levels within plants, and when inducible defences should be employed. ODT predicts levels of defence in different plant tissues by considering the: (i) fitness value of an organ to a plant; (ii) probability of attack to that organ; and (iii) costs of defence or resistance to attack (McKey 1974; Rhoades 1979).

Optimal defence theory predicts that greater levels of defence or more constitutive levels of defence (vs. induced defence), should be associated with plant tissues that are more valuable to plant fitness. On a per-mass basis, the removal of petal tissue may have greater ties to plant fitness than the removal of leaf tissue; thus, floral parts may be more heavily defended than leaves. Moreover, the early flowers that plants produce often contribute disproportionately more to seasonal plant fecundity than flowers produced later in the flowering season, since later flowers often do not set fruit in some species (Holtsford 1985). Thus, first flowers should be more defended than later ones (Baldwin & Karb 1995). ODT also predicts that defence

levels should be high and constitutive when plant tissues are attacked with greater frequency than other tissue types. When flowers are apparent and showy, they may be more easily discovered by consumers than leaf parts; thus, we predict that when flowers are conspicuous, they should be heavily defended. Alternatively, when flowers are more ephemeral or inconspicuous, they may be less easily discovered by consumers; in these cases, ODT predicts lower defence levels than in more persistent flowers. Furthermore, florivores often consume multiple floral parts and damage to buds early in development or flowers early in the flowering season may be reliable indicators that damage will occur later in the flowering season (A. C. McCall, unpublished data). In such cases, ODT would predict high, consistent levels of defence.

Levels of floral defence, however, may be modified by both ecological and allocation costs (Strauss *et al.* 2002). For instance, regardless of intrinsic costs, chemical defences in flowers may deter mutualist pollinators as well as florivores. For example, in *Gelsemium sempervirens*, the addition of the alkaloid gelsemine to nectar deterred nectar-robber visitation as well as pollinator visitation and significantly reduced pollen analogue export from anthers (Adler & Irwin 2005). If the ecological and allocation costs of floral defences outweigh their fitness benefits associated with reduced florivory, then reduced or induced defences in flowers may be favoured over high and constitutive defence (Strauss 1997; Irwin *et al.* 2004; Strauss *et al.* 2004).

Finally, an important assumption of ODT is that plants are able to regulate levels of defence in different tissues independently. Some ecological studies suggest that independent regulation may occur. For example, different levels of constitutive and induced expression of furanocoumarins were found in roots, leaves and reproductive structures in wild parsnip (Zangerl & Rutledge 1996), and levels of glucosinolate induction varied widely across plant tissues in wild radish (Strauss *et al.* 2004). Moreover, molecular studies have identified high levels of gene and protein expression in floral tissues that are not found in other tissues (Hause *et al.* 2000; Damle *et al.* 2005). Some of these studies pinpoint gene expression to specific parts of flowers (Lantin *et al.* 1999), thus allowing the potential to apply ODTs predictions to individual flower organs, such as the stigma, ovules or anthers. Finally, some of these protein products are associated with defence against microbes or insects or may be involved in plant communication to herbivore enemies (Shuvalev *et al.* 1997; Ollerstam & Larsson 2003).

Do patterns of defences in flowers follow the general predictions of ODT? For the most part, the few studies that have tested the presence or strength of chemical defence among plant tissues have found that flowers and fruit had higher levels of constitutive defence than leaves, and flowers were less inducible than leaves. For example, Zangerl &

Rutledge (1996) found that flowers and fruit of *Pastinaca sativa* had higher levels of constitutive chemical defence than leaves and roots; they also found that flowers and fruit were more extensively attacked than the other tissues. Also consistent with ODT, *Pastinaca sativa* had the highest induced defences in leaves and lowest in flowers and fruit. Strauss *et al.* (2004) also found that overall glucosinolate concentrations were higher in flowers than in leaves of *Raphanus sativus*, and leaf defensive chemicals were more inducible than floral defences, consistent with ODT. Moreover, Wackers & Bonifay (2004) found that increased nectar production could be stimulated in foliar, but not subfloral, nectaries in cotton, suggesting that these indirect defences were more plastic when associated with leaves vs. flowers.

Similar patterns supporting predictions of ODT have been found in cultivated species and their wild relatives. For example, some proteinase inhibitors are expressed at 400–700 times the levels in tomato (*Lycopersicon esculentum*) flowers compared with leaves or fruits (Damle *et al.* 2005). When fed to specialist herbivores (*Helicoverpa armigera*) of tomato, these chemicals inhibited larval growth rate, adult formation and fecundity. Also in tomato, allene oxide cyclase (AOC) mRNA and its protein, an enzyme that facilitates the production of jasmonic acid, is found at much higher concentrations in flowers than in leaves (Hause *et al.* 2000). Because jasmonic acid and its methyl ester, methyl jasmonate, are important signalling molecules in the induced defence cascade against herbivores between and within plants (Karban *et al.* 2003; McCall & Karban 2006), AOC accumulated in flowers could facilitate effective defence in these organs.

The differential expression of proteinase inhibitors, jasmonic acid and defensive genes regulated by jasmonic acid in floral tissue vs. leaves and fruits is not confined to tomato. Dioxygenase mRNAs are expressed in potato (*Solanum chacoense*) pistils during development, which may lead to increased biosynthesis of deterrent alkaloids. Interestingly, jasmonic acid, damage to the style, and pollination all increased the levels of this transcript, suggesting that induced defence may operate in potato flowers and may not be independent of pollination (Lantin *et al.* 1999). High levels of mRNA transcript encoding for proteinase inhibitors are also found in *Nicotiana alata* stigmas and have high inhibitory activity towards trypsin and other proteases (Atkinson *et al.* 1993). One caveat is that jasmonic acid also plays a role in male organ development, and the genes affecting its production and regulation may act pleiotropically in floral tissues (Hause *et al.* 2000).

There is some evidence that floral tissues are at least as inducible as foliar tissue. For example, damage to leaves in wild tobacco, *Nicotiana attenuata*, can result in increased levels of nicotine in flowers (Euler & Baldwin 1996). Moreover, application of methyl jasmonate, an elicitor of

secondary compound production, to leaves of *Nicotiana attenuata* resulted in a 70% reduction in foliar damage compared with a 100% reduction in floral damage, suggesting that induction in floral tissue was more effective at deterring consumers than induction in leaf tissue (McCall & Karban 2006). Finally, both artificial and natural damage to early *Nemophila menziesii* flowers induces resistance to florivores in later flowers (McCall 2006).

Optimal defence theory can also be extended to include the value of flowers in species with different mating systems. Many plants produce flowers but attract few pollinators (Lavergne *et al.* 2005), and some plants self-pollinate through autogamy prior to anthesis. If florivores are consuming gametes, in selfing species we expect that defences in flowers and reproductive parts should be high, because ecological costs associated with floral defences deterring pollinators should be low. Alternatively, if florivores are simply consuming petals in selfing species, we predict that defence levels in flowers should be low, assuming that defences have allocation costs and that petals are not beneficial to selfers for pollinator attraction or actively photosynthesize. We know of no studies that have explicitly compared floral defence levels in selfing vs. outcrossing species or the ecological costs vs. benefits of floral defence in species with different mating systems. The best tests of such a hypothesis would compare floral defence levels as a function of plant mating system while controlling for phylogeny and other plant life-history traits. Moreover, other factors may counter high floral defences in selfing plants. For example, if selfing plants produce large numbers of short-lived flowers, any particular flower may be relatively less valuable than those of outcrossing species that produce only a few longer-lived flowers. In this case, ODT would predict that the few, more valuable, long-lived flowers may be more heavily defended.

Similarly, monoecious vs. dioecious plant species and hermaphrodites vs. single-sex flowers may allocate floral chemical defences differentially based on ODT. For example, female plants may assign a higher fitness value to their flowers than male plants because female flowers rely on both pollination and successful seed production to ensure reproduction, whereas male flowers only need to disperse their gametes. Alternatively, if floral damage has stronger indirect effects on plant reproduction through changes in pollinator behaviour than direct trophic effects, male plants, which are often more pollinator limited than females, may be under selection for increased production of floral defences. In addition, if male flowers are more attractive or nutritious for florivores compared with female flowers, ODT would predict higher levels of defence in the more apparent floral sex. In any of these scenarios, the magnitude of the ecological and allocation costs of floral defence will affect the ultimate expression of floral defences.

Finally, ODT can be used to make predictions about plants with flowers that persist for different amounts of time. Flower longevity is often variable among and within species (Ashman & Schoen 1994) and can depend on the timing of pollination (Ashman & Schoen 1997). Variability in floral longevity may affect the type and quantity of defence in flowers. Based on ODT, we predict that plants with more long-lived flowers would be more apparent and susceptible to florivores compared to plants with short-lived flowers, resulting in selection for greater amounts of constitutive, quantitative defences than shorter-lived counterparts. We are aware of no studies that have compared levels of floral defence among plants with long-lived vs. short-lived flowers, although one study found that longer-lived flowers received less damage per day than short-lived flowers (Breadmore & Kirk 1998), suggesting that longer-lived flowers may benefit more from floral defence than more ephemeral flowers. In any experimental analysis of this hypothesis, controlling for phylogeny, flower number and other life-history traits will be key to obtaining conclusive results.

Growth rate hypothesis

Within the context of plant–herbivore interactions, the GRH predicts that plants that sustain rapid growth will dedicate less total resources to defence than plants that grow more slowly, in part because slow growers may not be able to tolerate damage (Coley *et al.* 1985; Stamp 2003). As with ODT, the GRH assumes that plants have limited resource availability and that defences will have costs. Applying the GRH to floral structures suggests that among plant species, as the development time of a flower decreases, levels of constitutive defence should decrease. Thus, plants with many ephemeral flowers are predicted to have mobile secondary metabolites with high turnover and low resource commitment to defence relative to plants with less ephemeral flowers, a prediction similar to that of ODT applied to short-lived unapparent vs. long-lived apparent flowers. In testing the GRH within the context of floral defences, it is important to note that floral growth rate may be correlated with plant growth rate. Thus, assessing whether floral defence levels match the GRH will require controlling for overall plant growth rate and assessing whether different plant parts can independently regulate secondary compound production.

The GRH can also be applied to specific plant tissues. For example, tissues that grow rapidly or have high rates of cell division (e.g. shoot apical meristems) should have less defences than slower growing tissues. In cultivated tobacco, *Nicotiana tabacum*, floral growth rate is higher and is sustained for a longer period of time than leaf growth (Hill & Malmberg 1991). Thus, according to the GRH, tobacco

flowers should have lower defence levels than leaves, a prediction opposite to that of ODT. In wild tobacco, *Nicotiana attenuata*, corolla tissue contains *c.* 60 µg of nicotine per gram of tissue vs. *c.* 150 µg of nicotine per gram of tissue for leaves (data computed from Baldwin & Karb 1995; Euler & Baldwin 1996; Lou & Baldwin 2004), a result predicted by the GRH for tissue growth rate and relative defence level. More studies are needed testing the predictions of the GRH for flowers, especially among different plant species and with the appropriate phylogenetic controls.

Turning to the molecular level, can the GRH explain patterns of defence gene expression or protein accumulation? Because cultivated species, such as tomato and potato, have been selected for increased rates of fruit growth or production, these species may yield novel insights into how florivore deterrents accumulate or are expressed in flowers and reproductive structures vs. other tissues. For example, cultivated tomato has much larger and more productive fruit than its ancestor. Based on the GRH, we might expect that defence compounds will have lower expression in cultivated tomato flowers compared with its ancestor's reproductive organs. Proteinase inhibitors can make up to 50% of the total soluble protein in the unripe fruits of the wild tomato, *Lycopersicon peruvianum*, although little is known about the accumulation of these inhibitors in flowers (Schauer *et al.* 2005). Because proteinase inhibitors and their expression are well characterized, it may be insightful to clone similar genes in the wild progenitor of tomato to explore defence gene expression patterns in flowers and fruit that have not been subject to artificial selection.

Growth differentiation–balance hypothesis

A more general form of the GRH is the GDBH, which posits that processes that retard growth to a greater degree than they retard photosynthesis (e.g. cold temperatures) can result in excess carbon, leading to increased differentiation and, potentially, an accumulation of carbon-based defences (Loomis 1932, 1953; Herms & Mattson 1992). Thus, nutrient-limited plants should accumulate carbon-based defences. If florivory affects sink strength, then there may be significant consequences for carbon-based secondary compound concentrations in leaves or flowers. For example, in resource-poor environments, a reduction in the number of flowers (sinks) by florivores may result in increased differentiation and potentially increased concentrations of secondary metabolites in remaining leaves, flowers or fruits. Alternatively, in resource-rich environments, a reduction in the number of flowers (sinks) may favour growth at the expense of differentiation-related products. To our knowledge, no studies have specifically addressed florivory within the context of GDBH.

CONCLUSIONS AND AVENUES FOR FUTURE RESEARCH

On a bite-for-bite basis, the removal of floral tissue may have effects on plant reproduction and plant populations comparable with and surpassing the removal of leaf tissue. Understanding the causes and consequences of florivory, however, requires linking studies and techniques from pollination biology with studies of herbivory. A growing number of studies recognize that florivory is common in natural systems and is influenced by and can subsequently affect floral gender expression, patterns of plant mating and sexual system evolution. The mechanisms by which florivores affect plant reproduction are multifaceted and can include both direct consumptive effects as well as indirect effects mediated through changes in species interactions, especially with pollinators. Factorial experiments and path analyses that isolate the mechanisms by which florivores affect plant fitness, populations and communities are key. Plants are not defenceless against florivore attack; the concepts of resistance and tolerance to herbivores can be used to understand the strategies plants use to defend against florivores. Similarly, theories of plant chemical defence, typically associated with plant–herbivore and plant–pathogen interactions, can be extended to predict when and how plants should defend against florivores, although the majority of these predictions remain untested.

Exciting challenges remain in the study of florivory. Throughout our discourse, we have highlighted gaps in current knowledge of florivory as well as untested assumptions and hypotheses, and throughout we have provided testable predictions that warrant further investigation. Here we list three questions that we think are particularly relevant to address within the study of florivory.

Can plants independently control the expression of secondary compounds in different tissue types?

Theories of plant defence applied to florivory and floral parts rely on the notion that plants can independently control the expression of secondary compounds in different tissue types. Evidence suggests that leaf damage or chemical elicitors related to damage can differentially affect levels of induction in different tissue types (Zangerl & Rutledge 1996; Strauss *et al.* 2004). However, the concentrations of secondary compounds are correlated across tissue types in some species (Irwin & Adler 2006). Understanding whether the expression of secondary compounds in different tissue types is independent is critical in theories of plant defence as well as for understanding the degree to which plants can coevolve independently with florivores vs. herbivores. Data from molecular biology will provide some information to

answer this question, albeit in cultivated species or in model systems.

To what degree do theories of plant defence serve as frameworks for understanding patterns of defence against florivores?

A central goal in the study of plant–herbivore interactions has been to understand and predict patterns of plant defence (Stamp 2003). We contend that the array of theories developed to understand patterns of plant defence against herbivores and pathogens can be extended to understand patterns of plant defence against florivores. Here we provide predictions from three commonly cited plant defence theories (ODT, GRH and GDBH) with respect to florivores. The majority of the predictions that we propose remain untested. Integrating florivores into the study of plant–animal interactions is essential because florivores have the potential to influence the evolution of defensive traits and floral characteristics.

Do theories of herbivore diet breadth predict how and why florivores feed on flowers and different floral parts?

Our synthesis has been solely focused on florivory from the plant's perspective (i.e. effects of florivores on plant reproduction, plant mating systems, etc.). However, to understand the evolutionary ecology of plant–florivore interactions, a similar analysis, but from the florivore's perspective, is needed. Why do florivores feed on flowers? To what degree does floral density and composition influence florivore reproduction and population dynamics? Can theories of herbivore diet breadth be extended to understand how and why florivores consume flowers? Are there patterns in the type, magnitude, and predictability of damage produced by specialist florivores vs. more opportunistic generalists? Some of these questions are currently being addressed in a variety of systems (e.g. Matter *et al.* 1999; Held & Potter 2004). The results of these studies, in combination with the work reviewed here, will provide novel insights into the potential for coupled population dynamics and coevolutionary relationships between plants and florivores.

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