

REVIEW

Plant damage from and defenses against ‘cryptic’ herbivory: A guild perspective

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Abstract

Despite considerable interest in the factors affecting trophic cascades in terrestrial systems, there has been relatively little attention paid to the importance of the herbivore-plant link in explaining why some systems “cascade” (have strong top-down effects on plant survival and population growth) and others “trickle” (have top-down effects on plant damage, but little effect on plant fitness). This is despite the fact that herbivore guild identity has long been recognized as a major force affecting herbivore-plant interactions. We address the potential importance of herbivore guild identity in determining the strength of tritrophic interactions by reviewing literature concerning plant damage from and induced defenses against two “cryptic” herbivore guilds, predispersal seed predators and root/stem borers. Although both guilds are capable of strongly affecting plant fitness, the impact of root/stem borers on plants in natural systems seems far greater than that of predispersal seed predators. The large impact of root/stem borers occurs via their disruption of plant vascular systems, while a variety of factors (safe-site-limited plant populations, long-lived seed banks, temporal plant escape, etc.) each seem important in explaining the smaller effect of predispersal seed predators. While the lack of attention to herbivore guilds is understandable, given the (by necessity) single-species focus of much trophic cascade research, we suggest that predator suppression of root/stem borers and predispersal seed predators will, respectively, yield strong versus weak top-down effects on plant fitness. The potential tritrophic consequences of herbivore feeding mode highlight the importance of research on varied predator-herbivore chains that share a common basal resource.

Keywords: *Trophic cascade, seed predator, stem-borer, root-borer, induced defense, herbivory*

Introduction

Does herbivory necessarily affect plant fitness and community dynamics? Some researchers have argued that trophic cascades, where predators indirectly benefit plants by suppressing herbivores, can be statistically significant (e.g., reducing leaf damage to 2% from 4%) without affecting community dynamics (e.g., producing large changes in plant biomass, productivity, or species composition) (Polis et al. 2000). If plant fitness is not always affected by plant damage, the question of “do cascades exist?” may be overshadowed by “does it matter?” The relationship between plant damage and fitness seems particularly unclear in terrestrial systems, where several meta-analyses (Schmitz et al. 2000, Halaj & Wise 2001, Shurin et al. 2002) have found stronger indirect effects of predator presence on plant damage than on population growth/standing biomass. There have been a variety of suggested explanations for this pattern, which is in sharp contrast to the strong top-down effects on producer growth and biomass found

in aquatic systems (Carpenter & Kitchell 1996, Shurin et al. 2006). Competition for light in terrestrial systems means that land plants invest heavily in structural compounds, while the size of their aquatic counterparts is constrained by the need to remain buoyant (Shurin et al. 2006). Terrestrial plants are thus often larger than their herbivores, which may reduce the strength of herbivore control of plant biomass (Shurin & Seabloom 2005). Terrestrial plants may also possess a wider array of chemical and structural defenses than is found in aquatic producers (Strong 1992); these defenses may further reduce herbivores’ impacts on plant fitness. Further explanations for this pattern include food web complexity, ecological stoichiometry, and the time scale of terrestrial population dynamics (Holt 2000, Power 2000); however, there is as yet no generally accepted single reason for why some terrestrial trophic interactions “cascade” (have strong, population-level effects on plants) and others “trickle” (have weak effects, consisting mostly of small amounts of plant damage).

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In many cases, the term “terrestrial herbivore” encompasses organisms with varied feeding strategies and diverse effects on plants (Root 1996). Studies comparing the effects of different herbivore guilds on a common host generally find that each guild affects the plants differently: examples include leaf-chewing vs. stem-boring beetles on *Rhus glabra* (Strauss 1991), folivores versus root-feeders on *Lupinus arboreus* (Maron 1998), rhizome galls vs. folivores on *Solidago missouriensis* (Preus & Morrow 1999), and sap feeders vs. folivores on *Solidago altissima* (Meyer 1993). Differing effects of herbivory on a shared host plant seem to be the rule rather than the exception. Plants also respond differently to herbivory on different structures (Meyer 1993, Trumble et al. 1993); for instance, experiments involving a range of plant species have shown that removal of belowground biomass has larger effects on plant fitness than removal of an equivalent percentage of aboveground biomass (Reichman & Smith 1991, Moron-Rios et al. 1997); but see (Houle & Simard 1996).

Although the term herbivory is often nearly synonymous with defoliation in terrestrial systems (Karban & Baldwin 1997), other herbivore guilds can strongly affect plant fitness. Specifically, plant biomass removed by “cryptic” herbivore guilds such as root/stem borers and predispersal seed predators has a potentially disproportionate impact on plant fitness and population dynamics. Damage inflicted on connective tissues by stem and root borers can disrupt nutrient and water transport while increasing the plant’s vulnerability to pathogens; the net effects of this damage can be so great that even small (~ 10) numbers of root borers can kill mature woody plants (Preisser & Strong 2004). By specifically attacking reproductive tissues, predispersal seed predators can drastically affect plant population dynamics in cases where plant populations are seed-limited. The consequences of this feeding mode can be seen in the fact that seed-feeding weevils introduced to control invasive thistle species now threaten the existence of native species (Louda & Potvin 1995). The internal feeding modes of both root/stem borers and predispersal seed predators makes them difficult to census, and the consequences of internal plant damage are often hard to assess.

This review contrasts two understudied herbivore guilds, root/stem borers and predispersal seed predators, in order to illustrate the range of population- and community-level effects of herbivory. We begin by summarizing literature concerning the type and magnitude of damage inflicted by these two guilds, while examining when these impacts influence plant populations. We then review literature addressing induced plant defenses against each of these guilds, which could minimize their community-level effects. We conclude by considering root/stem borers and predispersal seed predators in the context of tri-

trophic interactions. Although both guilds can impact plant fitness, the effect of root/stem borers on plant population fitness appears greater than that of predispersal seed predators. We conclude by discussing why the population- and community-level effects might differ between these two guilds.

Root and stem borers

Although the direct consumption of plant tissue by root and stem borers (hereafter “RSBs”) is harmful, it is the corresponding disruption of vascular and support tissues that seems most devastating. Strauss (1991) found that adult *Oberea ocellata* beetles repeatedly girdle selected sumac (*Rhus glabra*) stems before laying a single egg. The biomass of stems above the girdled section rarely survive the damage, causing a loss of 6–13 cm of stem growth even before the wood-boring larvae begin to feed. Such ‘indirect’ effects are often magnified by the length of time that borers spend within the plant; it can take a year or more before pupation occurs and adults emerge (Strauss 1991, Shibata 2000). The effect of RSBs is similar to that of sea urchins in the strongly cascading otter-urchin-kelp system (Estes & Palmisano 1974, Estes & Duggins 1995): urchins kill large amounts of kelp by eating the connective tissue at the base of the algal blades, severing the holdfast and allowing the floating biomass above it to drift away. As a result, even low herbivore densities can have significant effects on plant growth and survival: Densities of <1 root-boring weevils (*Cleonidus trivittatus*)/plant reduced purple locoweed (*Astragalus mollissimus*) from 2–30 plants/m² to less than 0.04 plants/m² in two years (Pomerinke et al. 1995).

The damage caused by aboveground borers ranges from cosmetic to catastrophic, with bark and stem borers appearing to have a greater effect than terminal shoot borers. Plants affected by terminal shoot borers can often compensate via the regrowth of new terminal shoots or the production of side shoots (Howard & Meerow 1993, de Groot & Schnekenburger 1999); but see (Tschardtke 1999). However, even low densities of stem borers can produce significant damage. An average density of 1.7 pyralid moth (*Melipotera dentate*) larvae/patch kills 92% of *Opuntia fragilis* stem fragments (Burger & Louda 1994), while cerambycid larvae damage trees at densities of 6–50 individuals/tree/year (Singh & Prasad 1985, Ito & Kobayashi 1993, Hanks et al. 1999). Higher herbivore densities occur in bark-boring beetles (Coleoptera: Scolytidae), which overwhelm plant defenses by mass attacks (Wallin & Raffa 2001). These beetles are extremely small relative to the trees that they kill; the average adult *Ips cembrae* is only 4.9–6.0 mm in length (Zhang et al. 1992).

In plants that experience boring both in the root crown/meristem and in vascular tissues, disruption of the vascular system causes the most damage. Even

when plants compensate by shifting additional resources to regrowth, root weight (Hopkins et al. 1993) and shoot growth may be reduced. This cost can also be seen in reduced fruit production (Gandolfo et al. 1997), lower seed weight (Saner & Muller-Scharer 1994), fewer seeds/plant (Muller-Scharer 1991, Preisser 2003), and in extreme cases, plant death (Mayer et al. 1995, Strong et al. 1999, Bebbler et al. 2002).

A striking aspect of literature pertaining to this guild is how few RSBs are required to produce high levels of plant damage (Table I). For example, two to three larvae of the syrphid fly *Cheilisia corydon* reduced total seedset of the common toadflax *Linaria vulgaris* by 45% (Sheppard et al. 1995). Similarly, one to two larvae of the weevil *Hylobius transversovittatus* reduced height, total biomass, inflorescence weight and flowering time in purple loosestrife (*Lythrum salicaria*) over two years (Notzold et al. 1998). Thousands of bush lupine (*Lupinus arboreus*) die off during outbreaks (15–20 larvae/plant) of the hepialid moth *Hepialus californicus* (Strong et al. 1996); in the same system, average densities of four larvae/plant reduced growth by 53% and seedset by 44% in two months (Preisser 2003). Given the large effects of many RSBs on plant survival and seed production, predators successfully suppressing this guild will likely produce cascading benefits to producers.

Induced plant defenses against root and stem borers

Plants respond to the presence of RSBs with a variety of direct (plant-mediated) and indirect (predator-mediated) induced defenses (van der Putten 2003, Bezemer & van Dam 2005). Direct plant defense against these herbivores often starts immediately upon their entry into plant tissue and involves physical defenses like increased resin flow. This form of defense is most commonly associated with conifers (Raffa & Berryman 1982; Schowalter & Filip 1993; Tisdale et al. 2003); herbivore attack on this taxa induces an increase in resin production as well as a shift in resin composition to include increased concentrations of chemicals such as monoterpenes (Cook & Hain 1985, Raffa & Smalley 1995, Miller et al. 2005) and decreased amounts of moisture and sugars (Cook & Hain 1985). Shifts in resin composition are often accompanied by necrotic lesions around the herbivore that “walls off” the damaged region (Raffa & Berryman 1987, Heath 1998). This phenomenon also occurs in response to cicada oviposition into plant stem tissue (reviewed in Karban & Baldwin 1997). The formation of such lesions and the subsequent abscission of damaged tissue can be particularly effective against sedentary insects like RSBs (Anderson et al. 1989; Fernandes 1990; Fernandes 1998) and has been found across a range of plant taxa (Fernandes & Negreiros 2001).

Induced defense against RSBs often also involves the increased synthesis and sequestration of various chemicals. Infection of tobacco (*Nicotiana tabacum*) by root-knot nematodes induces nicotine synthesis in root tissue (Zacheo et al. 1974, Hanounik & Osborne 1975); such increases in nicotine content decrease nematode motility and survival (Davis & Rich 1987). Increases in cucurbitacin-C affect egg phenology in southern corn rootworm (Brust & Barbercheck 1992), and roots of wild parsnip showed large increases in xanthotoxin concentrations following mechanical wounding (Zangerl & Rutledge 1996). Phytoecdysteroids, compounds that affect molting and development, are induced in spinach roots following nematode infection and increase mortality of root-knot nematodes (Soriano et al. 2004). Root-feeding wireworms induced cotton roots to increase their production of terpenoid aldehydes (Bezemer et al. 2004); interestingly, these belowground herbivores also stimulated the increased production of aboveground extrafloral nectaries that may serve to attract predators (Wackers & Bezemer 2003).

Herbivore-induced plant volatiles (HIPVs) that signal herbivore's natural enemies occur in a variety of systems (Thaler 1999, Kessler & Baldwin 2001, Hountondji et al. 2005), and there is increasing evidence that such indirect defenses also play a role in induced defense against RSBs (Van der Putten et al. 2001). Oviposition by the sawfly *Diprion pini*, whose stem-boring larvae can cause widespread damage, induces production of the HIPV (*E*)- β -farnesene in Scots pine (Hilker et al. 2002); this chemical is not induced by mechanical wounding (Mumm et al. 2003). Conifer roots damaged by vine weevil larvae have been shown to release HIPVs that attract entomopathogenic nematodes (van Tol et al. 2001), also see (Boff et al. 2002). Similar findings have been reported for maize, which produces (*E*)- β -caryophyllene after attack from the western corn rootworm *Diabrotica virgifera* (Rasmann et al. 2005). This HIPV strongly attracts entomopathogenic nematodes, which enter roots in pursuit of these herbivores. (*E*)- β -caryophyllene also diffuses readily through moist sand and resists degradation, making it ideal for 'long-distance' belowground signaling. While European maize varieties and the maize ancestor teosinte also produce this compound, North American varieties do not; this fact might help explain the equivocal results of rootworm control via predatory nematodes in North America (Rasmann et al. 2005). An intriguing example of belowground herbivory affecting aboveground processes (Bezemer & van Dam 2005) occurs in turnips, where root-feeding fly larvae induce the production of aboveground HIPVs used by parasitoids to locate their underground dipteran hosts (Neveu et al. 2002).

Table I. Root and stem borers.

Herbivore	Herbivore density	Plant	Herbivore impact	Experimental duration	Citation
Coleoptera: Cerambycidae, <i>Apagomeralla versicolor</i>	?	Cocklebur, <i>Xanthium strumarium</i>	1.5-month-old plants reduced fruit production by 66%. 2.5-month-old plants showed no significant decrease in fruit production.	?	Gandolfo et al. 1997
Coleoptera: Cerambycidae, <i>Apriona cinerea</i>	maximum of 6 larvae/tree	<i>Populus</i> , <i>Salix</i> , <i>Ficus</i> , <i>Morus</i> , etc.	Larvae girdle branches of 2–3 cm girth. Boring facilitates entrance of fungi and bacteria.	?	Singh and Prasad 1985
Coleoptera: Cerambycidae, <i>Moneilema semipunctatum</i>	?	Wright fishhook cactus, <i>Sclerocactus wrightiae</i>	Responsible for 23% of plant mortality, including >40% mortality of largest cactuses.	7 years	Kass 2001
Coleoptera: Cerambycidae, <i>Oberia ocellata</i>	?	Smooth sumac, <i>Rhus glabra</i>	Girdling by adult beetles of ramets in preparation for laying single egg reduces ramet growth by 6–13 cm.	3 years	Strauss 1991
Coleoptera: Cerambycidae, <i>Phorocantha semipunctata</i>	up to 40 eggs/tree	<i>Eucalyptus</i> species	In 6 years of drought conditions, 15–25% of trees died from herbivore damage.	6 years	Hanks et al. 1995
Coleoptera: Curculionidae, <i>Cleonidus triviattatus</i>	0.5 individuals/plant	Purple locoweed, <i>Astragalus mollisimus</i>	Densities decreased from 2–30 plants/m ² to less than 0.04 plants/m ²	2 years	Pomerinke et al. 1995
Coleoptera: Curculionidae, <i>Cyphocleonus acahates</i>	2.4 larvae/plant	Spotted knapweed, <i>Centaurea maculosa</i>	Reduced whole-plant growth by 25%.	11 months	Steinger and Muller-Scharer 1992
Coleoptera: Curculionidae, <i>Diaprepes abbreviatus</i>	?	<i>Citrus</i> spp.	Larvae kill plant by girdling trunk at root crown, causing 70 million US\$ of damage in Florida alone.	?	Mayer et al. 1995
Coleoptera: Curculionidae, <i>Hyllobius transversovittatus</i>	1 larvae/plant	Purple loosestrife, <i>Lythrum salicaria</i>	In second year, reduced height by 50%, total biomass, inflorescence weight, and delayed flowering.	2 years	Notzold et al. 1998
Coleoptera: Curculionidae, <i>Pissodes strobi</i>	?	Jack pine, <i>Pinus banksiana</i>	Damaged 14.5% of trees. Attacks terminal shoot, reducing growth.	3 years	de Groot and Schnekenburger 1999
Coleoptera: Curculionidae, <i>Trichosirocalus horridus</i>	?	Nodding thistle, <i>Carduus nutans</i>	12–96% reduction in thistle density	4–6 years	Sheppard et al. 1995
Diptera: Anthomyiidae, <i>Delia floralis</i>	?	Swede, <i>Brassic napus</i>	Entrance of root-borer allows entry of secondary pathogens. Egg densities of 5–20 eggs lowered root weight by 34–73%.	4 months	Hopkins et al. 1993
Diptera: Syrphidae, <i>Cheilosia corydon</i>	2–3 larvae/plant	Nodding thistle, <i>Carduus nutans</i>	45% reduction in seeds/plant	2 months	Sheppard et al. 1995
Lepidoptera: Cochyliidae, <i>Agapeta zoegana</i>	1–6 larvae/plant	Spotted knapweed, <i>Centaurea maculosa</i>	Low herbivore densities increased flowering plant survival. Herbivores reduced the shoot:root ratio, and intermediate rates of herbivory (1–4 larvae) reduced fecundity by 75%. Low (1–2 larvae) and high (2–6 larvae) herbivory had no effect. Root herbivory reduced seed output by 20%	15 months	Muller-Scharer 1991
Lepidoptera: Cochyliidae, <i>Agapeta zoegana</i>	5 larvae/plant	Spotted knapweed, <i>Centaurea maculosa</i>	No effect	11 months	Steinger and Muller-Scharer 1992
Lepidoptera: Hepialidae, <i>Hepialus californicus</i>	0–20 larvae/plant	Bush lupine, <i>Lupinus arboreus</i>	Increase in root-boring larvae lead to die-offs of 1000s of mature bushes.	6 months	Strong 1997
Lepidoptera: Noctuidae, <i>Archanara geminipunctata</i>	Mean 7.2 larvae m ⁻² , range 0–22	<i>Phragmites australis</i>	Reduced shoot growth by 80%	2 years	Tscharntke 1999
Lepidoptera: Noctuidae, <i>Busseola fusca</i> ; Pyralidae, <i>Chilo partellus</i>	?	Maize and grain sorghum	The most destructive pests of maize and grain sorghum in eastern/southern Africa.	?	Kfir 1997
Lepidoptera: Pyralidae, <i>Hypsipyla grandella</i>	?	Mahogany, <i>Swietenia mahogani</i>	5th-year mahogany trees exposed to borers grew 17% less than trees protected from borers.	5 months	Howard and Meerow 1993

Table I (Continued)

Herbivore	Herbivore density	Plant	Herbivore impact	Experimental duration	Citation
Lepidoptera: Pyralidae, <i>Melitara dentata</i>	1.7 larvae/patch	<i>Opuntia fragilis</i>	Larvae caused death of 92% of cladodes (chains of modified stem fragments).	3 months	Burger and Louda 1994
Lepidoptera: Tortricidae, <i>Euosma gloriola</i>	?	Jack pine, <i>Pinus banksiana</i>	Damaged 26.6% of trees. Attacks terminal shoot, reducing growth.	3 years	de Groot and Schnekenburger 1999
Lepidoptera; Cosmopterigidae, <i>Erebodea serratella</i>	3 larvae/plant	Common toadflax, <i>Linaria vulgaris</i>	Reduced shoot production >50%.	11 months	Saner and Muller-Scharer 1994
Coleoptera; Apionidae, <i>Apion onopordi</i>	1–2 larvae/plant	Canada thistle, <i>Cirsium arvense</i>	Larval infestation increases number of roots infected with rust fungus (<i>P. punctiformis</i>); after two years, significantly reduced aboveground biomass	2 years	Friedli and Bacher 2001
Coleoptera; Curculionidae, <i>Listronotus setosipennis</i>	>2 larvae per plant	Parthenium, <i>Parthenium hysterophorus</i>	In field cage trial, larvae introduced to plant at the rosette stage decreased height by 26% and flower production by 38%, but did not affect root or total plant biomass. Larvae introduced to plant at preflowering and flowering stages did not affect plant.	6 months	Dhileepan 2003
Coleoptera; Curculionidae, <i>Lixus cardui</i>	2–16 pairs per plant	Thistles, <i>Onopordum acanthium</i> , <i>O. illyricum</i> , and <i>O. acanthium-illyricum</i> hybrids	In field experiment, viable capitula reduced from 20% (2 weevil pairs/plant) to 80% (16 weevil pairs/plant); plant death occurs at higher weevil densities.	3 months	Briese et al. 2004
Coleoptera; Curculionidae, <i>Conotrachelus albocinctus</i>	?	Parthenium, <i>Parthenium hysterophorus</i>	Larvae induce stem gall that interferes with or prevents water and carbohydrate transport. Frass deposits within stem tissue poison surrounding cells and prevent plant from repairing damage.	1.5–2 months	Florentine et al. 2002

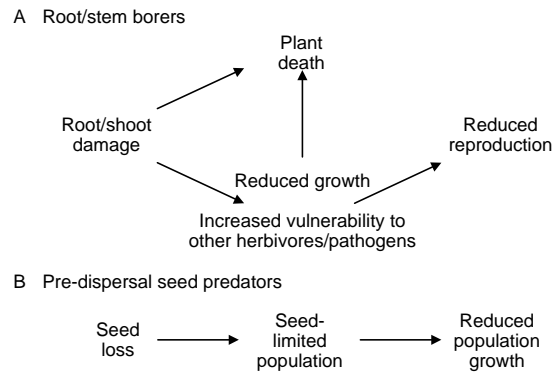


Figure 1. Schematic diagram summarizing the direct and indirect effects of root/stem borers (A) and pre-dispersal seed predators (B) on plant survival, reproduction, and population growth rate.

Plants may also benefit from the presence of entomopathogens such as bacteria or fungi (Brown et al. 1995, Elliot et al. 2000); the ability of such organisms to exploit fissures or tunnels in woody tissue in order to access otherwise protected herbivores can make them important predators of RSBs (Wagner 1985). Mite-infested cassava plants produced HIPVs that induced sporulation of the predatory fungus *Neozygites tanajoae*, while volatile cues from undamaged plants suppressed sporulation (Hountondji et al. 2005). Such an example illustrates the potential for finely-tuned induced indirect defenses via entomopathogens. While similar interactions have not yet been reported for RSBs, the fact that bacteria and fungi flourish in the tunnels formed by RSBs suggests that similar interactions may also affect this guild.

Seed predators

Predispersal seed predation (hereafter “PDSPs”) is a second form of cryptic herbivory. While seed predation is widely studied, several factors make it difficult to draw general conclusions about the impact of seed predators on plant populations. First, considerable variation is generally observed in the amount of seed predation. In addition, many studies do not measure the abundance or report the identities of PDSPs responsible for an observed reduction in seedset and/or survival. Finally, it is often unclear how reductions in the number of seeds in one season affect overall plant population growth rates.

Enormous variation in levels of seed loss to PDSPs (Crawley 2000) occurs both between systems and between years or patches in the same system (Jordano et al. 1990, Petersen 1990, Sheppard et al. 1994, Ehrlen 1996, Bishop 2002, Lau & Strauss 2005). Loss of over 90% of available seeds is not uncommon (Table II), suggesting that predispersal seed predation may have important consequences for plant population dynamics. Despite the potentially large impacts of PDSPs, the actual consequences of such herbivory may only marginally

Table II. Pre-dispersal seed predators.

Herbivore	Herbivore density	Plant	Herbivore impact	Experimental duration	Citation
?	?	Wild and slender oats, <i>Avena fatua</i> , <i>A. barbata</i>	0–65% seed loss	?	Yao et al. 1999
Coleoptera: Bruchidae sp; Hymenoptera: Pteromalidae, <i>Oedaule</i> sp.	?	<i>Acacia tortilis</i>	10–82% seed loss	per cohort	Ernst et al. 1990
Sunflower moths, sunflower “budworm”, seed weevils	?	Sunflower, <i>Helianthus annuus</i>	1.8–365% seed loss	per cohort	Cummings et al. 1999
Insects	?	Platte thistle, <i>Cirsium canescens</i>	67% seed loss, 83% reduction in seedlings, 83–97 reduction in next generation	per cohort	Louda et al. 1990
Coleoptera: Curculionidae, <i>Apion rostratum</i>	?	White wild indigo, <i>Baptisia leucantha</i>	0–45% seed loss	per cohort	Petersen 1990
Diptera: Tephritidae sp.; Lepidoptera, Cecophoridae sp.	?	<i>Aster ledophyllum</i>	No impact	per cohort	Wood and Andersen 1990
Coleoptera: Curculionidae, <i>Acanthoscelus obtectus</i>	?	Cultivated beans, <i>Phaseolus</i> sp.	92% reduction in germination	per cohort	Cipollini and Stiles 1991
Coleoptera; Bruchidae, <i>Callosobruchus maculatus</i>	?	<i>Ebenus armitagei</i>	94.4% seed loss	per cohort	Hegazy and Eesa 1991
Diptera: Tephritidae, <i>Orellia ruficauda</i>	?	Canada thistle, <i>Cirsium arvense</i>	1% seed loss	per cohort	Lalonde and Roitberg 1992
Hemiptera: Pentatomidae, <i>Sibaria englemanni</i> ; Hemiptera: Miridae, <i>Piasus cribricollis</i> ; Coleoptera; Curculionidae, <i>Cyrlonyx</i> sp.	0.000003–0.00005/seed, 0.008–0.14/fruit	<i>Piper sancti-felicis</i>	9% ($\pm 2\%$) seed loss	per cohort	Greig 1993
Insects	?	<i>Piper culebratum</i>	12% ($\pm 5\%$) seed loss	per cohort	Greig 1993
Insects	?	<i>Piper arieianum</i>	29% ($\pm 6\%$) seed loss	per cohort	Greig 1993
Hemiptera: Pentatomidae, <i>Sibaria englemanni</i> ; Hemiptera: Gelastocoridae, <i>Hyalymenus pulcher</i> ; Coleoptera; Curculionidae, <i>Cyrlonyx</i> sp.	0.00009–0.0006/seed, 0.01–0.08/fruit	<i>Piper urostachyum</i>	65% ($\pm 5\%$) seed loss	per cohort	Greig 1993
Hemiptera: Pentatomidae, <i>Sibaria englemanni</i> ; Hemiptera: Gelastocoridae, <i>Hyalymenus pulcher</i> ; Coleoptera; Curculionidae, <i>Ambates chaetopus</i>	0.0001–0.0004/seed, 0.01–0.025/fruit	<i>Piper phytolaccaefolium</i>	76–87% seed loss	per cohort	Greig 1993
Large insects and small vertebrates	?	<i>Calathea ovandensis</i>	6.2% seed loss	per cohort	Horvitz and Schemske 1994
Coleoptera: Curculionidae, <i>Rhinocyllus conicus</i>	?	Nodding thistle, <i>Carduus nutans</i>	9–57% seed loss	per cohort	Sheppard et al. 1994
Coleoptera: Curculionidae, <i>Larimus</i> sp.	?	Nodding thistle, <i>Carduus nutans</i>	6–48% seed loss	per cohort	Sheppard et al. 1994
Diptera: Tephritidae, <i>Urophora solstitialis</i>	?	Nodding thistle, <i>Carduus nutans</i>	4–63% seed loss	per cohort	Sheppard et al. 1994
Diptera: Tephritidae, <i>Tephritis hyoscyami</i>	?	Nodding thistle, <i>Carduus nutans</i>	14–18% seed loss	per cohort	Sheppard et al. 1994
Coleoptera: Phalacridae, <i>Olibrus bisignatus</i>	?	Nodding thistle, <i>Carduus nutans</i>	1–37% seed loss	per cohort	Sheppard et al. 1994
Lepidoptera: Geometridae, <i>Eupithecia immundata</i>	?	<i>Actaea spicata</i>	28–30% seed loss	?	Eriksson 1995

Table II (Continued)

Herbivore	Herbivore density	Plant	Herbivore impact	Experimental duration	Citation
Diptera: Tephritidae, <i>Orellia occidentalis</i> and <i>Pocacantha culta</i> ; Lepidoptera: Pyralidae, <i>Homeosoma stypetallum</i>	?	Platte thistle, <i>Cirsium canescens</i>	63–76% seed loss, 71–75% reduction in seedlings, 70–75% reduction in next generation	per cohort	Louda and Potvin 1995
Diptera: Cecidomyiidae sp.	?	Field mustard, <i>Brassica rapa</i>	36–44% seed loss	per cohort	Nakamura et al. 1995
Lepidoptera: Tortricidae, <i>Acrolita subsequana</i>	?	<i>Euphorbia dendroides</i>	40% inflorescence loss	per cohort	Traveset 1995
Hymenoptera: Eurytomidae, <i>Bruchophagus</i> sp.	?	<i>Euphorbia dendroides</i>	37–93% seed loss	per cohort	Traveset 1995
Lepidoptera: Noctuidae, <i>Hadena bicruris</i>	?	<i>Silene alba</i> and <i>S. dioica</i>	29.1–58.4% seed loss	per cohort	Biere and Honders 1996
Coleoptera; Bruchidae, <i>Bruchus atomarius</i>	?	<i>Iathyrus vernus</i>	0–83.7% seed loss, 0–7.6% reduction in population growth rate	per cohort	Ehrlen 1996
Hymenoptera: Formicidae, <i>Cataglyphis velox</i> and <i>Aphaenogaster iberica</i>	?	<i>Crataegus monogyna</i> , <i>Prunus mahaleb</i> , <i>Taxus baccata</i>	5–25% diaspores removal	3d	Hulme 1997
Diptera: Anthomyiidae, <i>Hylemya</i> sp.	?	<i>Ipomopsis aggregata</i>	26.1% fruit loss	per cohort	Brody and Mitchell 1997
Beetle larvae	?	<i>Julbernardia globiflora</i>	10% seed loss	per cohort	Chidumayo 1997
Beetle larvae	?	<i>Isobertinia angolensis</i>	65–85% seed loss	per cohort	Chidumayo 1997
Weevils, katydids and caterpillars	?	<i>Calypterogyne ghiesbreghtiana</i>	60% seed loss	11w	Cunningham 1997
Lepidoptera: Pyralidae, <i>Hypsipyla grandella</i>	1–5/capsule	<i>Svietemia mahagoni</i>	50–96% capsules loss	per cohort	Howard and Gibling-Davis 1997
Coleoptera: Curculionidae, <i>Conotrachelus fissunguis</i>	?	<i>Hibiscus moscheutos</i>	82–100% fruit infestation	28d	Kudoh and Whigham 1998
Coleoptera; Bruchidae, <i>Althaeus hibisci</i>	?	<i>Hibiscus moscheutos</i>	15–26% seed loss	28d	Kudoh and Whigham 1998
Insects	?	<i>Hakea sericea</i>	0–40% seed loss	per cohort	Brown and Whelan 1999
Insects	?	<i>Petrophile sessilis</i>	0–80% seed loss	per cohort	Brown and Whelan 1999
Coleoptera: Curculionidae sp.	?	<i>Palicourea salicifolia</i>	56% seed loss	per cohort	Wesselingh et al. 1999
Coleoptera: Curculionidae sp.	?	<i>Zanthoxylum melanostictus</i>	8.2% seed loss	per cohort	Wesselingh et al. 1999
Coleoptera: Curculionidae sp.	?	<i>Styrax argenteus</i>	44.1% seed loss	per cohort	Wesselingh et al. 1999
Coleoptera: Curculionidae sp.	?	<i>Symplocos</i> spp.	37.3% seed loss	per cohort	Wesselingh et al. 1999
Coleoptera: Curculionidae, <i>Larimus latus</i>	?	Thistle, <i>Onopordum acanthium</i>	25% ($\pm 6\%$) head infestation	per cohort	Briese 2000
Coleoptera: Curculionidae, <i>Larimus latus</i>	?	Thistle, <i>Onopordum argolicum</i>	8% ($\pm 5\%$) head infestation	per cohort	Briese 2000
Coleoptera: Curculionidae, <i>Larimus latus</i>	?	Thistle, <i>Onopordum bracteatum</i>	67% ($\pm 8\%$) head infestation	per cohort	Briese 2000
Coleoptera: Curculionidae, <i>Larimus latus</i>	?	Thistle, <i>Onopordum illyricum</i>	71% ($\pm 29\%$) head infestation	per cohort	Briese 2000
Coleoptera: Curculionidae, <i>Larimus latus</i>	?	Thistle, <i>Onopordum tauricum</i>	18% ($\pm 10\%$) head infestation	per cohort	Briese 2000
Coleoptera: Bruchidae sp. and Scolytidae sp.	?	<i>Bactris acanthocarpa</i>	28–54% seed loss	?	Silva and Tabarelli 2001

Table II (Continued)

Herbivore	Herbivore density	Plant	Herbivore impact	Experimental duration	Citation
Coleoptera: Curculionidae, <i>Cydmaea dorsalis</i> and <i>Cydmaea</i> sp.	?	<i>Grevillea buxifolia</i>	22–27% seed loss	per cohort	Auld and Denham 2001
Coleoptera: Curculionidae, <i>Cydmaea dorsalis</i> and <i>Cydmaea</i> sp.	?	<i>Grevillea caleyi</i>	12–26% seed loss (19.5% ave.)	per cohort	Auld and Denham 2001
Hymenoptera: Eurytomidae, <i>Eurytoma</i> sp.	?	<i>Grevillea caleyi</i>	0–1% loss (0.15% ave.)	per cohort	Auld and Denham 2001
Coleoptera: Curculionidae, <i>Cydmaea dorsalis</i> and <i>Cydmaea</i> sp.	?	<i>Grevillea linearifolia</i>	1–2.4% seed loss (1.5% ave.)	per cohort	Auld and Denham 2001
Hymenoptera: Eurytomidae, <i>Eurytoma</i> sp.	?	<i>Grevillea linearifolia</i>	1–22% seed loss (11.55% ave.)	per cohort	Auld and Denham 2001
Hymenoptera: Eurytomidae, <i>Eurytoma</i> sp.	?	<i>Grevillea shiressii</i>	46% seed loss	per cohort	Auld and Denham 2001
Coleoptera: Curculionidae, <i>Cydmaea dorsalis</i> and <i>Cydmaea</i> sp.	?	<i>Grevillea speciosa</i>	3.2–3.4% seed loss	per cohort	Auld and Denham 2001
Hymenoptera: Eurytomidae, <i>Eurytoma</i> sp.	?	<i>Grevillea speciosa</i>	1.1–13.4% seed loss	per cohort	Auld and Denham 2001
Diptera: Tephritidae, <i>Terellia ruficauda</i>	?	Marsh thistle, <i>Cirsium palustre</i>	25% seed loss	?	Masters et al. 2001
Hymenoptera: Formicidae sp.	?	River red gum, <i>Eucalyptus camaldulensis</i>	28–92% seed loss	4d	Meeson et al. 2002
Lepidoptera; Lycaenidae, <i>Plebejus icarioides</i> ; Diptera; Anthomyiidae, <i>Crinurina</i> sp.	?	<i>Lupinus lepidus</i> var. <i>lobbii</i>	4–92% seed loss (36% ave.)	up to five years	Bishop 2002
Insects	?	20 species of Asteraceae	0–46.5% seed loss (9.5% ave.)	per cohort	Fenner et al. 2002
Coleoptera; Bruchidae sp.	?	<i>Samanea saman</i>	20–30% seed loss	?	Cascante et al. 2002

impact plant population dynamics. The reasons for this are varied and include factors such as long-lived seed banks, microsite limitation, and density-dependent seedling mortality. The majority of studies looking for seed- versus safe-site limitation in plant populations have found safe-site limitation (Crawley 1992). Even high amounts of seed predation may not influence plant populations in such systems, although there are circumstances in which seed herbivory affects even safe-site limited populations (Maron & Gardner 2000). While introduced PDSPs have had some success in slowing population growth of *Centaurea solstitialis* (Gutierrez et al. 2005), simulation models of the closely-related *C. diffusa* indicate that improved seedling survival prevented even a 95% decrease in seedset from reversing population growth (Myers & Risley 2000). The restricted phenology of many PDSPs may also allow either early- or late-flowering plants to 'escape' and obviate any population-level effects of seed loss (Milbrath & Nechols 2004).

Studies following the impacts of PDSPs through seedling germination in the field vary widely in their findings. PDSPs had no impact on *Aster ledophyllum* seedset (Wood & Andersen 1990), while seed predation losses of 0–83.7% on a forest legume (*Lathyrus vernus*) by a bruchid beetle translated into only a 0–7.6% reduction in population growth (Ehrlen 1996). This suggests that *L. vernus*' population is not seed limited, and that even high amounts of seed predation have little consequence for its population dynamics. In a seed-limited population of the annual vetch *Vicia angustifolia*, low (~10%) amounts of seed loss had virtually no influence on the number of seedlings produced the following year (Szentesi & Jermy 2003). Seed predation on the Platte thistle *Cirsium canescens*, however, reduced the number of viable seeds by 40–68% and subsequent adult thistle density by 57–67% (Louda & Potvin 1995). A similarly large effect has been recorded in *Liatris cylindracea*, where PDSPs caused 50–80% seed loss and a subsequent 60–80% reduction in recruiting plants after two years (Kelly & Dyer 2002). These populations of *C. canescens* and *L. cylindracea* appear to be at least partially seed limited, such that seed loss leads to comparable reductions in population growth.

Another strategy for estimating the impact of PDSPs on plant population dynamics involves using matrix models to estimate plant population growth rates in their presence and absence. Modeling the effect of a specialist PDSP on the perennial herb *Actaea spicata* showed that 20–80% seed loss had little overall effect on plant population growth rates (Froberg & Eriksson 2003). In the case of the invasive musk thistle *Carduus nutans*, matrix modeling confirmed the results of field surveys suggesting that the 30–40% reduction in seedset inflicted by the PDSP weevil *Rhinocyllus conicus* was ineffective at

preventing population growth (Shea & Kelly 1998). Later work found that the impact of PDSPs was much greater on Australian populations of *C. nutans* characterized by low fecundity and high survival than on New Zealand populations with high fecundity but shorter life-spans (Shea et al. 2005).

Induced plant defenses against seed predation

Given the potential impact of PDSPs on plant fitness, it is not surprising that plants have evolved a variety of defenses against such herbivores. Constitutive defenses against seed predators are well known: Janzen (1969) compiled a list of 31 chemical, morphological and phenological defenses of legumes against bruchid seed predators. These defenses include poisonous compounds such as saponins and alkaloids that reduce the nutritive value of the seeds, physical barriers to prevent ovipositing or entry by larvae, rapid seed maturation followed by immediate dispersal, masting, and seed maturation during seasons unfavorable to the adult seed predators. He also argued that legumes are not unique in this regard, and that a similar diversity of defenses could be compiled for any diverse plant group (Janzen 1969).

Induced defense against PDSPs often involves physical responses such as abscission of damaged fruits. Abscission kills PDSPs and increases the amount of energy available for non-predated seeds (Holland & DeAngelis 2002), and has been documented in a variety of plant taxa (Fernandes & Whitham 1989, Huth & Pellmyr 1997). Another form of induced seed defense has been documented in bitter cress, *Cardamine scutata*, which uses bursting siliques to explosively disperse its seeds. Damage by PDSPs can prematurely trigger seed pod bursting, killing the insect while scattering the remaining immature but undamaged seeds (Yano 1997). Although the immature seeds germinate at a lower rate than do mature seeds, PDSPs can destroy all of the pod's seeds in the absence of this defense.

Evidence for induced chemical defenses against PDSPs is far more limited. Ding et al (2000) found that infestations of wheat midge larvae, *Sitodiplosis mosellana*, induced ferulic acid production in wheat seeds, and that high levels of ferulic acid were associated with increased midge mortality. In the short-lived perennial *Sesbania drummondii*, PSDP-damaged seeds increased both their accumulation and exudation of a range of allelochemicals (Ceballos et al. 2002). Karban and Baldwin (1997) provide several arguments for the relative rarity of induced defenses in reproductive structures, including that reproductive structures are so ephemeral that induced defenses are ineffective. This argument contends that induced defenses are most effective when plants can compensate for damage and the removed tissue does not dramatically affect fitness. These premises suggest that seeds are so small, easily-

destroyed, and critical to plant fitness that they should primarily feature constitutive rather than induced defenses. The paucity of information regarding induced defenses against PDSPs may thus reflect the true rarity of such processes rather than an absence of research.

Cryptic herbivores and trophic cascades

The cascading effects of predators, especially in terrestrial systems, can fail to substantially affect producers (Shurin et al. 2002). A trophic cascade requires that both predator-herbivore and herbivore-plant interactions exert top-down control. Stronger herbivore-plant links in aquatic versus terrestrial systems have recently been invoked to explain why community-level trophic cascades occur often in aquatic systems but only rarely in terrestrial environments (Shurin et al. 2006). While reduced damage may be interpreted as evidence of a cascading system, plants can often successfully compensate (Trumble et al. 1993) or overcompensate (Paige 1999) for moderate amounts of herbivory. Given this, it seems reasonable to ask whether most cascades 'matter'; that is, does a reduction in damage affect plant fitness? The answer to the above question may be largely dependent on the feeding guild of the individual herbivore; some types of herbivory are far more destructive to plants than others.

Root- and stem-boring insects seem to have a disproportionate impact on plant fitness. By disrupting water and nutrient transport and increasing the risk of pathogen presence, they affect plant biomass, seedset, and survival even when only a few individuals are present. The damage potential of these herbivores is suggested by both the array of direct and indirect induced defenses that their presence elicits, as well as by the number of RSBs that are biocontrol agents (Pomerinke et al. 1995, Notzold et al. 1998). Predators capable of suppressing this guild should thus strongly impact plant survival and fitness.

In contrast, the impact of predispersal seed predators in natural systems seems limited despite their potential for dramatically affecting seed-limited populations. The explanations for this apparent contradiction range from safe-site limitation to density-dependent seedling mortality, long-lived seedbanks, and temporal escape from seed predation. Individual PSDPs also often damage only a small number of seeds; as a result, low herbivore densities may only marginally reduce total seedset. Many plants seem capable of sustaining even high (>90%) rates of seed loss without substantially affecting their populations. PDSPs may also act as pollinators; in the tightly-linked yucca-yucca moth system, the PDSP is also an obligate mutualist required for plant reproduction. While the balance between costly herbivory and beneficial pollination varies dynamically (Huth

& Pellmyr 1997), plant-pollinator interactions may sometimes offset this guild's negative effect on plant populations. Taken together, the above arguments suggest that PDSPs may often be relatively inefficient at controlling plant populations (or acting as biocontrol agents for weedy or invasive plant species). As a result, predator suppression of PDSPs may often decrease seedset (trophic trickles) more than population growth (cascades).

It is intriguing to speculate as to whether herbivores that feed within plants are inherently less vulnerable to top-down predator control than their externally-feeding kin. Structural refuges reduce the range of potential predators in a range of systems: belowground borers are less affected by predators and parasitoids than similar aboveground species (Brown & Gange 1990). The difficulty of detecting and accessing endophytic herbivores may mean that they are primarily controlled by specialist (rather than generalist) predators and parasitoids. Because specialist consumers cannot shift to alternate prey when their preferred prey is temporarily reduced or absent, they are also thought to be less effective than generalist predators at controlling prey populations. There is some evidence that terrestrial foodwebs tend to be dominated by specialist predators, while the reverse is true in aquatic systems; if broadly applicable, this may provide one explanation for why top-down effects of predators are less apparent in terrestrial versus aquatic systems (Shurin et al. 2006). If this argument holds, the reduced vulnerability of both guilds should make both the trophic cascades expected for SRBs and the trophic trickles anticipated for PDSPs rare in nature. While predators capable of controlling root borers have been shown to increase plant fitness and survival in natural systems (Preisser & Strong 2004), the relative inability of specialist consumers to control endophytic herbivores may provide an additional explanation for why strong trophic cascades are uncommon in terrestrial systems.

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