CHAPTER EIGHT

Influence of plant defenses and nutrients on trophic control of ecosystems

KARIN T. BURGHARDT and OSWALD J. SCHMITZ
Yale University, New Haven, CT, USA

Introduction

Ecological systems are extraordinarily complex. Thus classical approaches to resolve ecosystem functioning have simplified analyses by conceptualizing ecosystems as being organized into trophic level compartments that contain organisms with similar feeding dependencies (e.g., producers, herbivores, carnivores) (Elton, 1927; Lindeman, 1942). Two competing worldviews on the regulation of ecosystem productivity emanated from such a conceptualization of ecosystem structure. The bottom-up view posits that the productivity of each trophic level is essentially limited by the one immediately below it (Lindeman, 1942; Feeny, 1968), while the top-down view recognizes that resource levels influence production, but contends that herbivore populations are mostly limited by predators rather than producer biomass (Hairston et al., 1960). Accordingly, predators can indirectly increase the productivity of a given system by reducing the negative effects of herbivores on plant biomass, resulting in a world that is green with plant material, rather than denuded by herbivory (Paine, 1969; Oksanen et al., 1981). Bottom-up theory countered that the world is green not because of predators, but instead due to variation in plant quality as a result of anti-herbivore defenses or weather patterns (Murdoch, 1966; Ehrlich and Birch, 1967; Scriber and Feeny, 1975; White, 1978; Feeny, 1991; Polis and Strong, 1996). This variation causes much of the "green" world to be inedible to herbivores; thus herbivores are still resource-limited.

The recognition of context-dependence in the degree of top-down or bottom-up control of ecosystems has resulted in gradual changes in how ecosystem functioning is envisioned. For instance, the "exploitation ecosystems" hypothesis (EEH) addresses context-dependence by combining elements of top-down and bottom-up concepts (Oksanen et al., 1981; Oksanen and Oksanen, 2000). At low levels of soil resource availability, plants are not productive enough to support herbivore populations and are thus bottom-up controlled (see Fig. 5.3).

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At medium levels of soil resources, an ecosystem can support herbivore populations, which in turn control plant productivity, while carnivores enter the ecosystem and control the herbivore population at the highest resource availability, thus releasing plant productivity from herbivore control. As a result, there is now a general consensus that both top-down and bottom-up control can occur within the same ecosystem, but that their relative magnitude is context specific (Hunter and Price, 1992; Power, 1992; Chase et al., 2000b). Understanding of the basis for this context-dependence in strength remains incomplete: while explanations for cross-ecosystem differences have been offered (Shurin et al., 2002), explanations for spatial differences within ecosystems remain elusive. This chapter aims to begin resolving the basis for within ecosystem context-dependency in the strength of trophic control by focusing on one of the important mediating factors identified in early debates about top-down and bottom-up forcing within ecosystems: the expression of plant defensive traits. This focus is a natural extension of classic theory because the expression of plant defensive traits is also intimately tied to resource availability. We review here the interplay between resources, plant defenses, and top-down and bottom-up control strength in an effort to offer generalizable principles that extend to explain differences across terrestrial and aquatic ecosystems.

Strong (1992) suggested that aquatic and terrestrial ecosystems are controlled in fundamentally different ways, with top-down control more prevalent in aquatic ecosystems, due in part to differences in primary productivity. However, a recent meta-analysis of experimental evidence concludes that net primary productivity does not differ between aquatic and terrestrial habitats, and instead producer nutritional quality is a consistently better indicator of the importance of consumers for top-down control (Cebrian and Lartigue, 2004). This makes sense in light of the fact that plant defensive strategies directly interact with nutritional quality to determine plant palatability (Raubenheimer, 1992). Subsequent theory (Vos et al., 2004) and experimental work (Verschoor et al., 2004b) have demonstrated that defensive traits that limit the efficacy of consumers to impact plants can be an important determinant of the relative strength of top-down and bottom-up effects, ultimately mediating the presence of trophic cascades in ecosystems. That is, this integrative view of trophic control of ecosystems is beginning to be one of "control from the middle out" (*sensu* Trussell and Schmitz, 2012), rather than from the top-down or bottom-up.

We introduce and elaborate on why defensive traits may play a key role in moderating trophic control of ecosystems from the middle out. We begin by clarifying the terminology used throughout the chapter to refer to defensive traits and then introduce a trait-based framework for thinking about how plant defenses may impact trophic control. Next, we highlight the dominant defensive traits found within aquatic versus terrestrial systems and review how nutrient availability may impact the strength of individual plant defenses within a species through phenotypic plasticity (Cipollini et al., 2003) or through average community trait defense levels via filtering of species that perform well in particular nutrient environments (Uriarte, 2000) across terrestrial, freshwater, and marine ecosystems. We propose here that a trait-based approach offers greater opportunity for understanding context-dependency in the way defenses mediate trophic control than approaches that focus merely at the species level or lump all species into trophic groups. We then end with an exploration of the link between the expressed plant defense traits and ensuing food web interactions and ecosystem functioning.

Primary producer anti-herbivore defenses

Most plants lack the capability to actively move away from potential herbivores. Vascular plants in terrestrial or littoral systems are rooted in place and floating phytoplankton species in marine and pelagic systems lack directional escape from their consumers. However, none of these organisms are passive in their interactions with consumers. Thousands of plant species reduce herbivory by producing an arsenal of anti-herbivore defenses (Karban and Baldwin, 1997). These include structural defenses, such as thorns, spines, or tough tissues that are difficult to chew, as well as chemical defenses, such as toxic compounds. Chemical defenses can be qualitative, where the mode of action is to poison a herbivore, or quantitative, such as leaf toughness or digestion inhibitors that force a herbivore to consume a larger quantity of food in order to extract the same nutrients, thereby prolonging their exposure to potential predation or parasitism (Feeny, 1976). Defensive traits that decrease plant damage from herbivores or lower herbivore performance are collectively known as *resistance* traits.

A second general defensive strategy, known as *tolerance*, minimizes the negative impact of herbivory by enabling a plant to regrow quickly and thus regain lost photosynthetic capacity (Strauss and Agrawal, 1999). This strategy may include an increase in growth rate, utilization of stored reserves, activation of dormant meristems, or a decrease in allocation to structural tissue, which lowers leaf toughness and leaf mass per area (LMA) (Tiffin, 2000). These traits would seem to increase the palatability of plant tissue, thereby rendering them ineffective as a defense. But, if a plant is able to produce tissue faster than the herbivore can remove it, or if the herbivore completes its life cycle and leaves the plant, then tolerance can overcome herbivore impacts.

In addition, these defenses can be described as being either *constitutive* or *induced*. If the defenses are always produced within a plant regardless of the presence of a herbivore, they are constitutive. Defenses are considered induced if they are expressed after a herbivore begins to inflict damage (Agrawal and Karban, 1998). Inducible tolerance or resistance responses are a form of phenotypic (trait) plasticity that may be adaptive (Agrawal, 2001) and could impact community dynamics through increasing trait variation within populations

(Schmitz et al., 2003). The focus of this chapter will be on direct defenses, such as those described above; however, many plants also utilize indirect defenses, such as the release of plant volatiles that attract parasitoids and predators of the herbivore to the attacked plant (Arimura et al., 2005; Pohnert et al., 2007). Indirect defenses merit independent treatment and are described in more detail in Chapter 13 of this volume. Moreover, the efficacy of a plant defense is inherently tied to the environmental context in which it is expressed. A putative defense may not decrease a herbivore attack when it is expressed within a milieu of plants all expressing defense, but may work quite well if better quality, less defended plants are in the surrounding environment (Belovsky and Schmitz, 1994).

Historically plant defenses have been measured in isolation. However, terrestrial and aquatic plants may respond to herbivores through the simultaneous expression of several commonly co-occurring traits or “plant defense syndromes” (Agrawal and Fishbein, 2006; Ruehl and Trexler, 2013). Structural and chemical defense expression and tissue allocation are individual traits that cumulatively determine the overall tolerance or resistance of a particular plant. As such, we consider tolerance and resistance strategies (albeit not mutually exclusive; Mauricio et al., 1997) to represent two common “plant defense syndromes” with distinct trait expression levels that are nonetheless useful for exploring potentially different effects of plant defense on trophic cascades.

Conceptual framework

Mechanism Switching Hypothesis

The impact of a herbivore on plants will depend on the nature of herbivore resource limitation. Herbivores could be limited by *relative* resource supply if their per capita uptake rate of edible plant biomass is limited by the amount of time available to feed (Schmitz, 2008). In this case, there may be a surfeit of plants that herbivores cannot eat due to daily limitations on feeding imposed by the abiotic environment. Alternatively, herbivores could be limited by *absolute* resource supply if their per capita uptake of plant biomass is limited by the availability of total edible plant biomass (Schmitz, 2008). In this case, herbivores increase their per capita intake rate of edible plant biomass in direct proportion to the abundance of edible plant biomass. The nature of herbivore resource limitation also determines the extent to which predators can indirectly alleviate plant damage via direct interactions with herbivore prey. These ideas are encapsulated in the *Mechanism Switching Hypothesis* (MSH) of trophic control of ecosystems (Schmitz, 2008).

For example, consider a simple system of three trophic levels comprised of plants, herbivores, and predators. In the absence of predators, plant abundance is limited by consumption from herbivores. Predators can reduce herbivore

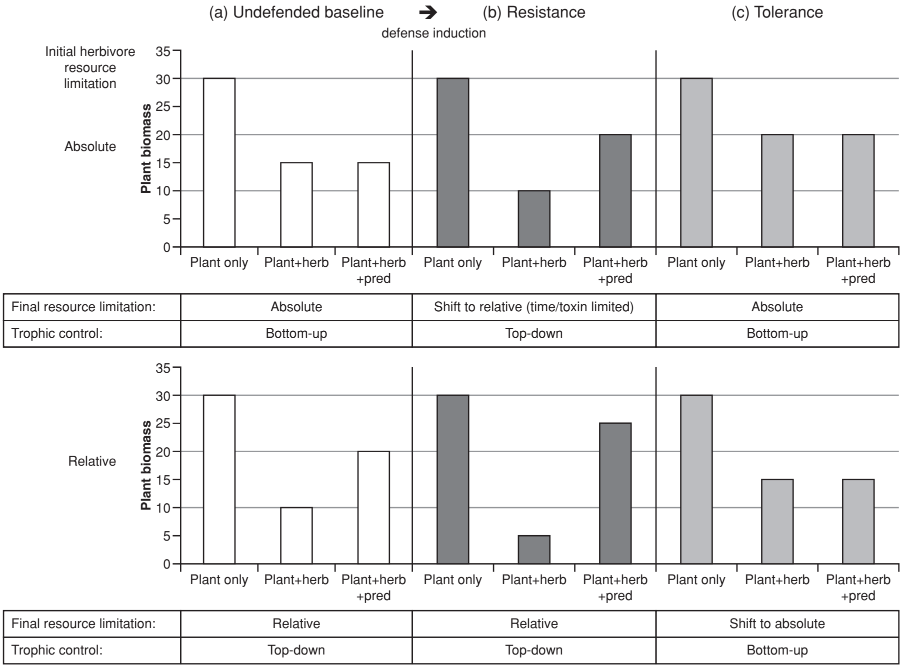

Figure 8.1 A conceptual framework for extending the Mechanism Switching Hypothesis of trophic control (Schmitz, 2008) to include plant defenses and their impact on herbivore resource limitation. Bars represent predicted outcomes of herbivore resource limitation and plant defense on plant biomass. (a) Undefended leaf tissue can be eaten by herbivores experiencing either absolute resource limitation leading to bottom-up control or relative resource limitation (e.g., temperature limitations on feeding time) leading to top-down control of plant biomass. (b) If plants induce a resistance response to herbivory (toxin or structural), the defenses impose relative resource limitation on herbivores because herbivores cannot increase feeding rate when a predator removes a herbivore (time or toxin limited feeding). (c) In contrast, induced tolerance traits impose absolute resource limitation on herbivores due to high-quality regrowth tissue. If a predator removes a herbivore, other herbivores will consume more, preventing a trophic cascade.

abundances, and thereby have an indirect effect on plants through cascading effects that alleviate plant damage – called a trophic cascade (Fig. 8.1a). However, this response will only occur if the herbivores that remain do not compensate and consume a larger per capita share of the plant biomass (i.e., herbivores experience relative resource limitation). If instead, herbivores experience absolute resource limitation, any remaining herbivores are able to increase their per capita uptake of plants, such that predators have no net indirect effect on plant damage. In this conceptualization, the interaction between resource limitation and predators determines whether top-down control emerges.

We suggest that the MSH offers the means to extend the consideration of trophic control of ecosystems to include plant defenses. In essence, plant defenses can determine whether herbivores become relative or absolute resource limited. For example, the presence of a structural “resistance” defensive trait may increase the amount of foraging time a herbivore requires to gain the same nutritional pay-off (Moran and Hamilton, 1980; Raubenheimer, 1992). This strategy also has the advantage of increasing the amount of time that a herbivore is exposed to predation. In addition, when a predator consumes a herbivore, the remaining herbivores on the plant cannot increase their per capita feeding rate because spines and structural defenses inhibit feeding rate. These herbivores are foraging time limited and experience relative resource limitation that leads to a trophic cascade and top-down control (Fig. 8.1b). If the resistance defense is a toxin rather than structural the same qualitative outcome occurs, but the mechanism differs. The herbivores experience toxin-limitation upon feeding. Despite perhaps having ample time to feed, herbivores can nonetheless only process a limited quantity of any toxin-containing tissue per unit time. Therefore, when a predator removes a herbivore from the plant, other herbivores cannot increase their per capita feeding rate, resulting again in a trophic cascade. This case of a herbivore experiencing relative resource limitation created by a toxin, rather than by time, is not a scenario included in the undefended world originally assumed by MSH.

If the herbivores were originally absolute resource limited before plant induction, the presence of resistance causes a switch in the nature of trophic control, relative to undefended plants, leading to a trophic cascade. If the herbivores were originally relative resource limited, then there is no switch in trophic control; however, through inducing a defense (bottom-up effect), a plant is able to exacerbate the positive direct effects of the defense through the help of predators (top-down effect) that prey on herbivores.

In contrast, the induction of tolerance traits (increased growth rate, thinner leaves) may lead to an overall increase in herbivory through absolute resource limitation of herbivores (Fig. 8.1c). If a predator removes a herbivore from a plant with tolerance traits, all other herbivores will increase their per capita feeding rate due to a lack of defended tissue. This will result in bottom-up control of primary production. If herbivores were relative resource limited in the presence of undefended tissue, the induction of tolerance traits would then shift them to absolute resource limitation, removing top-down control.

Because plant defensive traits or herbivore behaviors mediate the strength of trophic control over productivity, trophic control is from the middle out, rather than from the top-down or bottom-up. Moreover, the framework leads to an interesting new insight. While plants with resistance traits certainly derive a direct benefit by reducing herbivore feeding, plants expressing such traits gain a greater indirect benefit from predators through trophic cascades than would similar plant species that did not express such traits. While predators have been invoked before to explain low nutritive defenses that cause more damage to the plant through increased feeding requirements of the herbivore (Moran and Hamilton, 1980), the result here is more general and applies to toxin-based qualitative defenses as well as structural ones. In addition, while the quantity of primary production shifts in response to herbivores and plant defensive syndrome response (resistance versus tolerance), the traits of uneaten plant material are also impacted by these same factors. For example, plant litter in the absence of herbivores will be qualitatively different due to the lack of expressed defensive traits. Accordingly, the MSH can be extended to consider how these shifts in quality have the potential to impact community dynamics through nutrient cycling (see *Nutrient cycling links top-down and bottom-up effects* section below).

Functional trait-based approach

The MSH does not attempt to predict which plants will express which defensive traits in what environment (as do the plant defense or tolerance theories). Instead, given a defensive plant syndrome (resistance or tolerance), it predicts qualitatively whether bottom-up and top-down effects will prevail to impact community processes. Because it does not assume all individuals within a trophic level (or even species) have identical responses and traits, the MSH has the components of a trait-mediated approach for determining what regulates community processes (Schmitz et al., 2003; 2004; Duffy, 2009). This functional trait approach of resistance versus tolerance can be applied within communities, species, or genotypes. We propose this framework as a way to predict when plant defensive traits will impact top-down and bottom-up control in ecosystems. This approach may also be useful for better understanding the basis for the purported contingency in trophic control observed between and within ecosystem types, such as between aquatic and terrestrial ecosystems.

Dominant defense strategies in aquatic and terrestrial systems

Much previous work elucidating the differences between terrestrial and aquatic systems focused on the differences between the dominant primary producers in each system (Strong, 1992; Chase, 2000). Below, we summarize the known defenses of the primary producers within pelagic (open water), terrestrial, and littoral (nearshore) ecosystems to explore whether there are systematic differences among ecosystem types in defense expression. We do not provide an exhaustive treatment here, as recent reviews have already been completed for most systems (Pohnert, 2004; Hanley et al., 2007; Toth and Pavia, 2007; Van Donk et al., 2011).

Pelagic autotrophs

The dominant players in aquatic pelagic systems are unicellular and multicellular phytoplankton that allocate little to structural tissue, resulting in highly edible tissues due to low C:N ratios (Sardans et al., 2012). Phytoplankton must be small enough to remain suspended in the water column, yet can escape predation if they exceed an herbivore's gape limitation (Fogg, 1991). As a result, one common defense strategy is for groups of unicellular phytoplankton to join into colonies called coenobia, at the cost of an increased risk of sinking out of resource-rich surface waters and potential decreases in nutrient uptake due to lower surface area (Lürling and Beekman, 1999; Verschoor et al., 2004a). In contrast to terrestrial systems, phytoplankton are small relative to the zooplankton and other herbivores that eat them; an encounter with a herbivore often means a complete loss of fitness. Thus traditional tolerance strategies are not likely to be effective; instead, some phytoplankton and diatoms exude activated chemical defenses (secondary metabolites) into the water to deter herbivores from attacking or produce morphological structures, such as spines (Leibold, 1989; Leibold, 1999; Van Donk et al., 2011), in the presence of herbivores. Another strategy expressed at low resource availability in green algae is a tough morphology that allows some individuals to pass through the zooplankton digestive system unharmed (Van Donk, 1997).

Often plant defenses are induced, not by direct contact with the herbivore, but by the detection of chemical cues in the water column (kairomones) released by the herbivore (Pohnert et al., 2007). At high resource availability and in the presence of herbivores, some species are also able to induce changes in life history traits to speed up growth rates and generation times to outgrow herbivore species (Agrawal, 1998). While not referred to as such in the literature, we argue that changing life history traits in the presence of herbivores can be thought of as belonging to a "tolerance" defensive strategy, because the effect is that different induced plant traits are expressed within the system. Defense induction is a more ubiquitous response within freshwater pelagic systems than in marine systems (Lass and Spaak, 2003). In marine systems, induction is rare, but a few species of algal phytoplankton produce constitutive chemical resistance traits that can lead to toxic algal blooms and corresponding consumer die-offs (Pohnert, 2004).

Terrestrial autotrophs

Terrestrial plants tend to be vascular, relatively long-lived, and allocate more resources to plant structure than most aquatic plants. Overall, plant tissue quality is lower than in aquatic systems due to the increased presence of lignin and cellulose (Sardans et al., 2012). In addition, terrestrial plants produce a cornucopia of chemical defenses (Harborne et al., 1999; Kaplan et al., 2008; Arnason and Bernards, 2010). Some of these defenses, such as digestion inhibitors and structural defenses, force herbivores to consume more tissue to attain the same nutrition. These defenses are common in terrestrial plants, in part, because herbivores do not consume an entire plant at one time and can choose to move to a more palatable plant before causing plant mortality (Moran and Hamilton, 1980; Hanley et al., 2007). In contrast to pelagic systems, one encounter with a herbivore does not usually cause vascular plant mortality. Direct contact with a herbivore's salivary chemicals or characteristic damage patterns are usually required for induction in vascular plants, although recent evidence also points to neighbor induction by leaf volatiles through airborne plant/plant communication (Karban et al., 1999; 2000). The ability of terrestrial plants to avoid mortality when attacked enables tolerance to be a more viable strategy for them to deal with herbivores (Rosenthal and Kotanen, 1994). Some of the best examples of tolerance come from terrestrial systems with grazing herbivores; for instance, grasslands can be more productive in the presence of herbivory than without due to compensatory growth strategies (McNaughton, 1985).

Resistance traits also vary by plant functional group. The resistance traits of the closely related grasses are dominated by phenolics, nitrogen-containing defenses, toughness, and silica deposits in leaf tissue. While herbaceous and woody plants are derived from across the vascular plant phylogeny and express a wide range of resistance traits, there is a general pattern of greater inducibility and N-based defensive chemistry in herbaceous plants compared to woody species (Massad et al., 2011). Differences in functional group defense expression are manifest through succession, as perennial plants and then woody plants replace annual, herbaceous colonizers. As a result, resource-rich early successional systems are often dominated by tolerance responses and N-based defenses that shift toward toxic C-based defenses in late-successional, slow-growing species (Davidson, 1993).

Littoral and benthic autotrophs

Littoral and benthic autotrophs possess size, life history traits, and stoichiometric properties that are often intermediate between pelagic and terrestrial systems (Shurin et al., 2006). Communities consist of periphyton and macrophytes, including macroalgal species as well as vascular macrophytes (derived from terrestrial lineages), which root and access light in the photic zone. Often these systems are characterized by resource subsidy inputs from the terrestrial community (Nowlin et al., 2008).

Marine systems contain a diverse array of non-vascular macroalgae that are both free-living and part of benthic periphyton communities. Their tissue can become calcified which confers both structural and chemical defense (Hay et al., 1994). Many toxic resistance compounds (primarily phlorotannins in brown algae) are expressed as well (Hay and Fenical, 1988). However, few of these putative resistance compounds have been shown to provide effective defense against herbivores (*sensu* Karban and Baldwin, 1997). In addition, the lack of a vascular system in these plants would suggest a limited capacity for induction; however, recent work has demonstrated widespread induced resistance in response to small crustaceans and gastropods within this plant group, particularly in brown and green algae (Toth and Pavia, 2007). There is also within-plant variation in chemical defense expression (Cronin and Hay, 1996).

Historically, herbivores were considered unimportant to freshwater macroalgae, as herbivory rates were thought to be very low (Hutchinson, 1975). However, meta-analysis has shown that herbivory rates are higher on macrophytes than terrestrial plants (Cyr and Pace, 1993), suggesting that selection should favor defense expression in these plants. Although there is evidence of chemical resistance in macroalgae (Prusak et al., 2005), evidence of induction is rare (Camacho, 2008). While unusual in marine systems, vascular macrophytes dominate littoral zones in freshwater communities. They produce chemical defenses, such as alkaloids, that are also common in terrestrial plants due to derived ancestry from many terrestrial vascular plant lineages (Ostrofsky and Zettler, 1986; Chambers et al., 2008). In addition they produce structural defenses that lower plant palatability (Cronin and Lodge, 2003; Lamberti-Raverot and Puijalon, 2012). Tolerance traits are not very well studied in either freshwater littoral or marine benthic systems, but they have the potential to be quite important, particularly in systems dominated by large grazers (Burkepile and Hay, 2006; 2013; Nolet, 2004).

Grouping plant defense response by habitat or relatedness?

Most syntheses of trophic control in terrestrial and aquatic systems look for broad-brush similarities and differences and thus treat all species within a shared habitat type (e.g., pelagic) as though they are selected for and capable of expressing the same convergent, adaptive traits. This may not be appropriate to do. For example, macrophytes are found within seven plant divisions, resulting in Chlorophyta (green algae) macrophytes that are more closely related to green algal phytoplankton species than to any vascular macrophyte (only found within Pteridophyta and Spermatophyta divisions; Chambers et al., 2008). A result of macrophytes being spread across most of the plant phylogeny is that their trait expression may be constrained by the evolutionary history of the group from which they are derived.

For example, the molecular machinery necessary to produce many polyphenolic chemical defenses in terrestrial plants, such as tannins, flavonoids, and lignins, is thought to be a relic of evolutionary history, originally deployed to protect aquatic plants from damaging UV light as they gradually evolved to live on land (Rozema et al., 2002). These UV-activated defenses are therefore less prevalent in algal species that remained in aquatic environments, because water is much more effective at filtering UV rays. Therefore, chemical defenses (at least

UV-activated ones) are predicted to be of greater importance in terrestrial than aquatic systems. However, closely related vascular macrophytes that reinvaded aquatic environments from many terrestrial vascular lineages (at least 211 independent re-colonization events; Cook, 1999) should have molecular machinery more similar to terrestrial plants and thus produce these defenses (Rozema et al., 2002). Therefore, we argue for more finely resolved comparisons when exploring contingency among ecosystems, such as considering vascular land plants and littoral zone vascular macrophytes as equivalent and pelagic phytoplankton as being different. While rarely implemented in the aquatic literature, this approach would respect phylogenetic constraints on trait evolution in response to herbivores that may determine which potential plant defense strategies are available to an organism and perhaps explain some of the contingency in the outcomes across distantly related species.

Influence of nutrient availability on expressed defense strategies

MSH is incomplete in that it excludes a factor known to be important to plant defense expression: resource availability to plants. A shift in nutrient availability can change the absolute and relative costs of constitutive and induced defenses and potentially the outcome of plant competitive interactions (Cipollini et al., 2003). Thus the efficacy and selection for the plant defensive traits outlined above are influenced by the environmental context in which they are expressed (Belovsky and Schmitz, 1994). Classical ways of thinking about the interaction of resource availability and trophic control depict a static pool of resources (Oksanen et al., 1981). Another approach is to take a dynamic perspective of nutrient pools in ecosystems that allows for consideration of feedbacks between the abiotic nutrient pool and biotic responses such as plant defense traits and trophic interactions (Loreau, 2010; DeAngelis et al., 2012). In this section, we review a number of ways to approach how plant defense expression interacts with nutrient availability and then propose a more dynamic way of viewing interactions between primary producers and their environment.

Interspecific variation and community shifts

Environments with particular resource conditions may favor communities comprised of species with particular plant traits. Within the MSH framework previously outlined, at an interspecific level, defensive response can be thought of as an aggregate expression of functional traits of all members of a community – a so-called interspecific defense perspective. The growth/defense tradeoff hypothesis posits that at high nutrient levels, adapted plants grow so rapidly as to preclude investment in defense. At low nutrient levels, however, species are favored that grow slowly and have time to invest in defenses for their longer-lived more valuable leaves (Coley et al., 1985). In theory, therefore, if low nutrient availability filters out species that express tolerance traits and over-represents species with resistance traits, then we may expect to see trophic cascades in those systems.

While there are many evaluations of this interspecific defense theory for terrestrial systems (Fine et al., 2006), few tests have been performed in aquatic systems particularly within littoral habitats or between macroalgal species (Pavia and Toth, 2008). Because the goal of this chapter is to compare ecosystems on an equal footing, we will not focus on interspecific plant defense theory. Nevertheless, it is noteworthy that in planktonic algal systems, an interspecific growth/defense tradeoff is often invoked to explain community shifts due to herbivory or nutrients (Grover, 1995). Here edible phytoplankton with high growth rates are replaced by defended, but slow-growing species at low nutrient levels or high herbivory rates. The existence of such a growth–defense tradeoff was supported by meta-analysis, but size-selective grazing by zooplankton species complicates the effect on trophic cascades, with edible species still able to bloom in the presence of herbivores (Agrawal, 1998).

Intra-specific variation and phenotypic plasticity

While interspecific species turnover is more often invoked in aquatic systems, possibly due to the short lifespans of phytoplankton, plants can also exhibit genotypic and phenotypic variation in defense allocation to resistance or tolerance within a species or over a single individual's lifespan (Glynn et al., 2007). A recent meta-analysis of ontogenetic changes in plant defense allocation in terrestrial plants showed little influence of ontogeny on tolerance. However, herbaceous plants shifted from relying on induced chemical defenses when young to constitutive chemical defenses when old. Woody plants also exhibited an increase in constitutive defenses over time, with an initial reliance on chemical defenses in the seedling stage shifting to physical defenses during the juvenile stage, and then an overall decrease in defense allocation when mature (Barton and Koricheva, 2010). While untested, according to the MSH hypothesis extended in this chapter, these life-cycle stage shifts in defense expression in response to ontogenetically staged herbivory may result in different likelihoods of trophic cascades occurring throughout a growing season or plant's lifetime.

Resistance models

Plants show the bottom-up effect of nutrient gradients even in the absence of herbivores through variation in quality (nutrient content) and the level of constitutive defense allocation. For resistance traits, these relationships have been extensively investigated and formalized as plant defense theories, particularly for terrestrial systems (Herms and Mattson, 1992; Stamp, 2003; Wise and Abrahamson, 2007). There are competing views about how plant defense allocation is related to nutrient and other abiotic resource levels. According to these different views, peak defense allocation could happen at high (for nitrogenous-based defenses) (Bryant et al., 1987), low (Coley et al., 1985), or intermediate (Herms and Mattson, 1992) nutrient levels. Detailed treatment of resistance-based defense theory lies outside of the scope of this chapter and has been reviewed recently elsewhere (Koricheva, 2002; Stamp, 2003; Pavia and Toth, 2008). However, a review of recent studies that manipulated nutrients and measured constitutive defensive traits found increasing, decreasing, and no effect of nutrient supply on resistance trait expression across ecosystems (Table 8.1). This supports the view that no clear theory has yet emerged as a leading contender to explain resistance defense expression in terrestrial or aquatic systems (Stamp, 2003; Toth and Pavia, 2007).

Tolerance models

While many intra-specific theories of tolerance have been proposed and tested (e.g., the compensatory continuum hypothesis or the growth rate model), one recent approach integrates previous models to explain tolerance across resource conditions and may help predict where we might expect to see either tolerance or resistance traits dominating in ecosystems. The limiting resource model of tolerance (LRM), developed in terrestrial systems for vascular plants, uses a multistep dichotomous key to predict how changing the availability of a focal resource will impact tolerance by accounting for: (1) whether the focal abiotic resource is limiting plant fitness in the low-focal resource environment; (2) if the herbivore damage affects the use/acquisition of the focal resource or of an alternative resource; and (3) whether the herbivore damage causes the alternative resource to limit plant fitness (Wise and Abrahamson, 2005).

While complex, these three factors offer the flexibility needed to explain whether tolerance would be higher, lower, or equal at different nutrient levels. For example, imagine that nitrogen is the focal limiting resource for a plant species and a foliar herbivore primarily impacts carbon acquisition. If the addition of nitrogen does not cause carbon to become limiting, then the model predicts that the plant should exhibit equal tolerance in both high and low nitrogen environments (Wise and Abrahamson, 2005). When tested, the model accurately predicted the level of tolerance in 22 out of 24 cases of varying nutrient availability in terrestrial plants; 17 of these showed higher tolerance at lower nutrient availability (Wise and Abrahamson, 2007). This result may be generalizable to most terrestrial species. We know of only one study to apply the LRM to aquatic plants – which measured brown seaweed response to herbivory across different N environments (Hay et al., 2011) – and the prediction of the LRM of equal tolerance between high and low nitrogen environments in this system was supported. Clearly, further examination of this idea (and possible expansion to include herbivore-mediated linkages between resources; Bagchi and Ritchie, 2011), especially in non-terrestrial ecosystems, is needed.

Table 8.1 *Studies that manipulated a focal nutrient and measured the effect on constitutive plant defense expression*

Reference	Ecosystem	Zone	Primary producer	Species	Focal nutrient (FN)	Type of defense	Trait measured	Effect of ↑ in FN on trait
(Lundgren, 2010)	Marine	Pelagic	Phytoplankton	*Phaeocystis globosa*	N, P, N&P	Structural	Colony formation	↑
(O'Donnell et al., 2013)	Freshwater	Pelagic	Phytoplankton	*Scenedesmus acutus*	P	Structural	Colony formation	↑
(Gavis et al., 1979)	Freshwater	Pelagic	Phytoplankton	*Scenedesmus quadricauda*	Nitrate (N)	Structural	Colony formation	↑
(Trainor and Siver, 1983)	Freshwater	Pelagic	Phytoplankton	*Scenedesmus quadricauda*	Ammonium (N)	Structural	Colony formation	↑
(Lampert et al., 1994)	Freshwater	Pelagic	Phytoplankton	*Scenedesmus acutus*	Urea (N)	Structural	Colony formation	=
–	–	–	–	–	Ammonium (N)	Structural	Colony formation	=
(Wiltshire and Lampert, 1999)	Freshwater	Pelagic	Phytoplankton	*Scenedesmus obliquus*	Urea (N)	Structural	Colony formation	↑
(Van Donk, 1997)	Freshwater	Pelagic	Phytoplankton	*Scenedesmus* spp.	Mult. nutrients	Structural	Cell wall thickness	↓
–	–	–	–	–	–	Structural	Size	↓
(Cronin and Lodge, 2003)	Freshwater	Littoral	Vascular macrophyte	*Potamogeton amplifolius; Nuphar advena*	Mult. nutrients	Chemical	Phenols	↑
–	–	–	–	–	–	Growth	Growth rate	↑

(Lamberti-Raverot and Puijalon, 2012)	Freshwater	Littoral	Vascular macrophyte	*Myosotis scorpioides; Mentha aquatica*	Mult. nutrients	Structural	Breaking force	↓
–	–	–	–	–	–	Structural	Density	↓
(Cronin and Hay, 1996)	Marine		Macroalgae	*Dictyota ciliolata; Sargassum filipendula*	Mult. nutrients	Chemical	Terpenoids	=
–	–	–	–	–	–	Growth	Growth rate	↑
(Van Alstyne, 2000)	Marine		Macroalgae	*Fucus gardneri*	P	Chemical	Phlorotannin	↓
–	–	–	–	–	–	Growth	Growth rate	↓
(Arnold, 1995)	Marine		Macroalgae	*Lobophora variegata*	N	Chemical	Phlorotannin	↓
(Ilvessalo et al., 1989)	Marine	Littoral	Macroalgae	*Fucus vesiculosus*	N	Chemical	Phlorotannin	↓
(Hemmi and Jormalainen, 2002)	Marine	Littoral	Macroalgae	*Fucus vesiculosus*	Mult. nutrients	Chemical	Phlorotannin	=
–	–	–	–	–	–	Structural	Toughness	↓
(Gowda et al., 2003)	Terrestrial	Forest	Woody	*Acacia tortilis*	Mult. nutrients	Structural	Spine mass	↑
(Cash and Fulbright, 2005)	Terrestrial	Forest	Woody	*Acacia* spp.	Mult. nutrients	Structural	Spine mass	=
(Bazely et al., 1991)	Terrestrial	Grassland	Herb	*Rubus fruticosus*	Mult. nutrients	Structural	Spine density	↓

(cont.)

Table 8.1 *(cont.)*

Reference	Ecosystem	Zone	Primary producer	Species	Focal nutrient (FN)	Type of defense	Trait measured	Effect of ↑ in FN on trait
(Hoffland et al., 2000)	Terrestrial	Grassland	Herb	*Lycopersicon esculentum*	Mult. nutrients	Structural	Trichome density	↓
(Richardson et al., 1999)	Terrestrial	Fen	Herb	*Cladium jamaicense*	P	Chemical	Phenols	↓
(Forkner and Hunter, 2000)	Terrestrial	Forest	Woody	*Quercus* spp.	Mult. nutrients	Chemical	Tannins, phenols	↓
(Osier and Lindroth, 2001)	Terrestrial	Forest	Woody	*Populus* spp.	Mult. nutrients	Chemical	Tannins	↓
(Cornelissen and Stiling, 2006)	Terrestrial	Forest	Woody	*Quercus* spp.	Mult. nutrients	Chemical	Tannin	=
–	–	–	–	–	–	Structural	Toughness	=
–	–	–	–	–	–	Growth	N content	↑
(Wallace, 1989)	Terrestrial	Grassland	Herb	Var. Monocots	N	Structural	Silica	↓
(Osier and Lindroth, 2004)	Terrestrial	Forest	Woody	*Populus* spp.	Mult. nutrients	Chemical	Phenolic glycosides, condensed tannins	=
(Cipollini and Bergelson, 2001)	Terrestrial	Greenhouse	Herb	*Brassica napus*	Mult. nutrients	Chemical	Protein-based trypsin inhibitors	↑

While tolerance is rarely investigated under that terminology in aquatic systems, aquatic ecologists have thoroughly tested the Growth Rate Hypothesis (GRH), which links N and P usage within an individual via protein synthesis. Fast growth strategies require high P-allocation to synthesize ribosomal RNA (Sterner and Elser, 2002), thus environments with low N:P ratios favor species with fast growth rates. There is considerable empirical support for GRH from aquatic pelagic environments, but the model is rarely tested in terrestrial systems, where support is weak (Sardans et al., 2012). While not explicitly presented as an intra-specific tolerance model, the GRH meets the criteria for tolerance if a mitigation of fitness impact is produced within a species in response to herbivory and available resources, and is therefore complementary to the LRM, outlined above. The GRH and LRM represent an example where terrestrial and aquatic ecologists are wrestling with similar concepts, but with different jargon, leading to the incorrect perception that aquatic and terrestrial systems operate differently.

Induced defenses

Studies rarely explicitly investigate whether resource availability influences whether plants induce or continuously express anti-herbivore defenses. An intriguing recent study that quantified this with the phytoplankton *Scenedesmus acutus* showed that low P availability resulted in the induction of colony formation in the presence of herbivores, whereas under high P colony formation was constitutive (O'Donnell et al., 2013). In terrestrial systems, a similar kind of experiment found that the constitutive expression of protein-based trypsin inhibitors and the ability to induce them increased with nutrient availability (Cipollini and Bergelson, 2001). Future studies that manipulate both nutrient availability and herbivore presence are needed to resolve the general patterns among herbivory, nutrient availability, and defense induction across aquatic and terrestrial ecosystems.

Nutrient cycling links top-down and bottom-up effects

All classical plant defense theories (including EEH) view soil nutrient conditions as static and homogeneous. However, this may not be an accurate representation of nutrient dynamics. There is increasing recognition that species, especially consumers in higher trophic levels, play an important role in structuring nutrient environments through resource consumption, nutrient cycling, and translocation (Kitchell et al., 1979; Vanni, 2002; Pringle et al., 2010; Schmitz et al., 2010). Moreover, phenotypic variation in species traits may determine spatial heterogeneity in the nutrient environment as well (Norberg et al., 2001; Cornwell et al., 2008). Thus, while the nutrient environment certainly impacts the degree to which plant resources express tolerance and resistance traits, their expression may also feedback to influence nutrient cycling and hence change

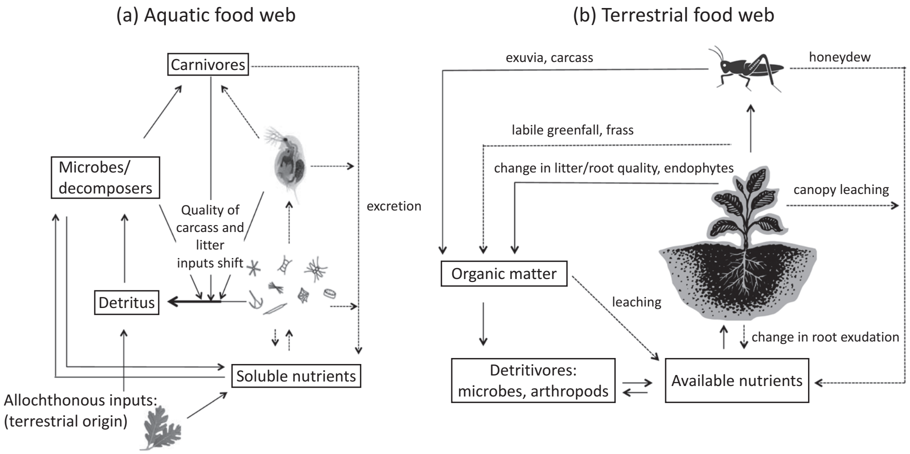

Figure 8.2 Potential pathways through which herbivores can influence nutrient cycling in (a) a generalized aquatic food web (adapted from Moore et al., 2004) and (b) a generalized terrestrial food web. Dashed lines indicate a fast-cycle pathway that has within season/generation effects on nutrient cycling. Solid lines represent slow-cycle pathways with primarily between season or generation effects. Induced plant defensive trait responses to herbivory have the potential to alter the relative magnitude of these pathways resulting in differential cycling rates. Clip art from Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

nutrient conditions. Whether a plant species utilizes a resistance or tolerance strategy against herbivores may thus have implications at both the community (Chase et al., 2000a) and ecosystem level by mediating bottom-up and top-down effects on nutrient cycling.

How defensive phenotypes (resistance versus tolerance) may alter ecosystem processes can be examined by expanding the linear trophic interaction chain perspective to include both above- and belowground linkages through nutrient cycling (Fig. 8.2). Nutrient cycling broadly encompasses several ecosystem processes, including production following nutrient uptake and decomposition leading to nutrient release (Deangelis, 1980; Deangelis et al., 1989; Moore et al., 2004; see Chapter 9 of this volume for more on nutrient cycling). Nutrients create a common currency for all trophic levels (Andersen et al., 2004). Moreover, linking above- and belowground processes reveals interesting reciprocal feedbacks between herbivores and the nutrient base through direct and indirect interactions (Van der Putten et al., 2001; Bardgett and Wardle, 2003; Schmitz, 2010).

This conception facilitates consideration of a dynamic nature of plant–herbivore interactions. For instance, herbivores not only influence productivity through direct consumption of plants, but also indirectly by influencing the way nutrient availability becomes altered via induced plant responses that can decrease or increase plant palatability (nutrient content) and thereby alter decomposition of organic matter by microbes or the release of inorganic waste by animals (Schmitz, 2010). Herbivore-induced responses by plants may impact slow-cycle inputs from uneaten organic plant litter (termed “after-life” effects), as well as fast-cycle inputs, such as inorganic materials from herbivore fecal output and canopy leaching (Hunter, 2001). These indirect effects on cycling (Fig. 8.2) are rarely quantified, particularly in terrestrial systems (Choudhury, 1988; Bardgett and Wardle, 2003; but see Frost and Hunter, 2008), but point to the potential importance of a plastic plant trait (defense allocation) for mediating the relative magnitudes of nutrients entering the slow- and fast-cycle pathways of ecosystems.

Can plant defenses affect how nutrients move through aquatic and terrestrial systems?

A classic idea of herbivore-mediated nutrient cycling is the acceleration hypothesis (McNaughton et al., 1989; Belovsky and Slade, 2000; Chapman et al., 2003), which proposes a positive feedback between herbivory and nutrient cycling. Herbivores consume a dominant species with highly nutritious leaf litter. These plants tolerate herbivory and by producing highly nutritious leaf regrowth cause herbivores to release large quantities of high quantity egesta, as well as facilitating plant canopy leaching and greenfall inputs. These factors collectively act to increase decomposition rates and ultimately increase the rate of nutrient supply to plants. In subsequent years, high resource supply favors the same dominant, nutritious plant species. In contrast, the deceleration hypothesis (Ritchie et al., 1998) posits that herbivores consume palatable plants selectively, thus shifting community composition toward less palatable species (Fig. 8.3). Litter from a community of unpalatable species decomposes more slowly than that from a palatable community because of a positive relationship between palatability and decomposability (Grime et al., 1996; but see Palkova and Leps, 2008; Ohgushi, 2008).

The acceleration hypothesis uses intra-specific changes in plant tolerance traits to predict an increase in nutrient cycling through herbivory, while the deceleration hypothesis relies on interspecific trait changes within a community. We propose that both deceleration and acceleration of nutrient cycling are viable outcomes at both the inter- or intra-specific levels depending on (1) the degree of intra-specific variation in plant traits (genotypic and phenotypic plasticity) and (2) the degree to which the plant community is dominated by a single plant defense syndrome. For example, uneaten litter from a plant (or plant community) that expresses structural or quantitative resistance defenses may be broken down more slowly by the microbial community than plants expressing tolerance traits, thereby impacting available nitrogen in the system (Schweitzer et al., 2008). Qualitative resistance defenses that persist in the environment may have a similar effect (Fig. 8.3). In contrast, plants that express tolerance traits

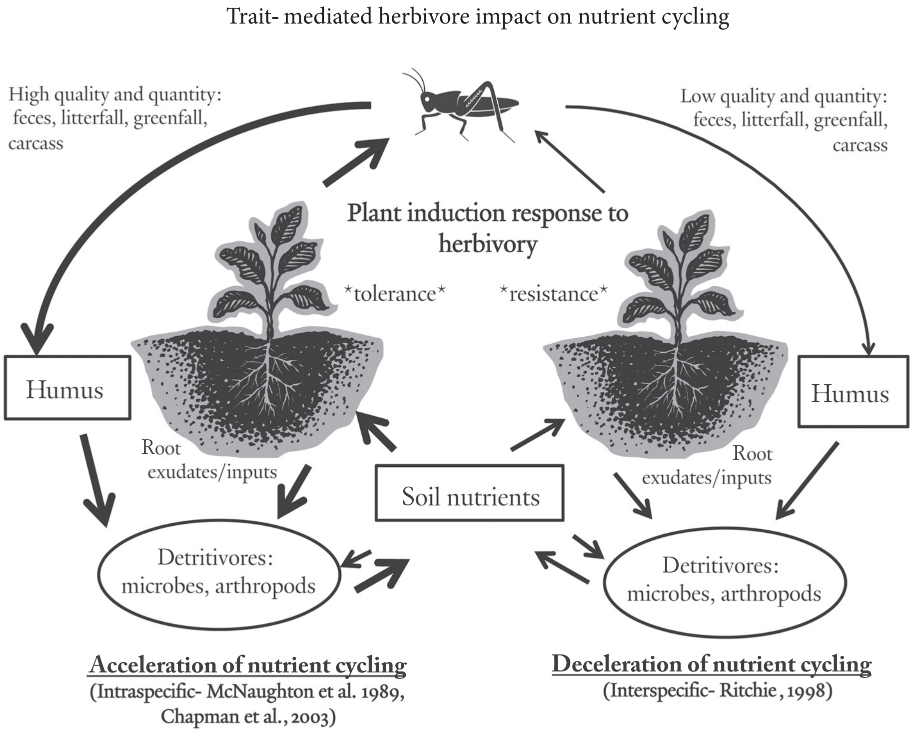

Figure 8.3 The defensive response trait (resistance versus tolerance) a plant produces in the face of herbivory may change the rate of nutrient cycling in a given system. Arrow line width represents the magnitude of nutrients moving through the pathway. Tolerance traits may result in an increase in herbivore egestion and high-quality litter entering the detrital food web. Resistance responses may decrease nutrient return to the soil through herbivory, as well as providing low-quality recalcitrant leaf tissue that is slowly broken down by the detrital food web, thus decreasing cycling rates.

produce high-quality litter that may be broken down rapidly by the microbial community, resulting in a larger available nitrogen pool (Fig. 8.3).

Few studies have looked for evidence of the impact of plant defense traits on nutrient cycling. However, it is clear that herbivores do have the potential to affect cycling rates across all systems. For example, in benthic kelp beds or pelagic lakes, consumers can increase net primary productivity (NPP) through increased nutrient cycling (Sterner et al., 1992; Steinberg, 1995; Vanni, 2002). Experiments also demonstrate that herbivores and plant traits can influence nutrient cycling in terrestrial systems. For example, pulses of cicada cadavers in northern temperate forests increase plant growth rates the following year (Yang, 2004). In addition, intra-specific variation in oak leaf phenotype influences fast- and slow-cycle litter decomposition (Madritch and Hunter, 2005), and recent meta-analyses indicated plant traits (e.g., LMA, lignin, and nutrient content) are the most important drivers of litter decomposition across global ecosystems (Cornelissen, 1996; Cornwell et al., 2008). Moreover, there is evidence that resource pulses move more quickly through aquatic than terrestrial systems (Nowlin et al., 2008). Whether this is due in part to differential expression of defensive traits, while plausible given our synthesis above, remains unknown.

Differences in herbivore feeding guilds

Aquatic algae (phytoplankton and reef periphyton) experience greater herbivory than vascular macrophytes, which experience greater herbivory than terrestrial plants, with median annual primary productivity removed of 79%, 30%, and 18%, respectively (Cyr and Pace, 1993). These differences in herbivory rates have often been cited as reasons for differences between top-down and bottom-up effects among ecosystems (Strong, 1992). However, plant responses may also be impacted by the functional group of the herbivores that consume them (Gruner and Mooney, 2013). Plant responses to herbivory in the grazing systems of the Serengeti may be more similar to marine kelp forests with extensive grazing by marine mammals than to other terrestrial ecosystem types (Burkepile, 2013). It is often assumed that herbivores are more specialized on land (insects) than in pelagic or littoral ecosystems (Newman and Rotjan, 2013). Specialized herbivores are likely to induce different plant defense responses than generalists (Feeny, 1976; Bernays, 2001; see also Chapter 13, this volume). Herbivore feeding guild and specialization is not currently explicitly incorporated into the MSH, but it is another trait-based approach that may be worthwhile to pursue in an examination of contingency in the interplay between plant defense and nutrients on trophic control of ecosystems.

Conclusions

Plants can produce both tolerance and resistance responses to herbivory and we see examples of each of these strategies across terrestrial and aquatic ecosystems. Chemical and structural resistance defenses tend to dominate terrestrial ecosystems, but play a smaller role in aquatic systems. The exception to this is terrestrial grazing ecosystems that are clearly dominated by plant tolerance responses to herbivory. In terrestrial systems, there is evidence that defense allocation is constrained to some degree by phylogenetic relationships (Armbruster, 1997; Ronsted et al., 2012; but see Haak et al., 2013), however this subject remains ripe for investigation within aquatic ecosystems. In particular, we suggest that a phylogenetic approach would be useful for understanding patterns within the phylogenetically diverse functional group of macrophytes. While tolerance responses are not often studied in aquatic systems under that terminology, we argue that induced changes in life history attributes that increase fitness in the presence of herbivory should be considered a tolerance trait and that tolerance traits may be very common yet overlooked in pelagic, benthic, and littoral communities. Plant defense theories are more refined and well tested in terrestrial systems than in aquatic systems. In aquatic systems the stoichiometrically based GRH accurately predicts higher growth rates in low N:P ratio environments. Which plant defense strategy (tolerance or resistance) a plant induces in response to herbivory has different ramifications for nutrient cycling, the coevolution of herbivores and plants, and community dynamics (Chase et al., 2000a).

Plant defense theory could advance through empirical tests among a broader range of ecosystem types, as well as benefiting from contextualizing a system not in terms merely of a plant–herbivore linkage, but instead in terms of a trophic chain with direct and indirect effects among soil nutrients, plants, herbivores, and predators. Tests could also benefit from more emphasis on the role of tolerance as a defensive trait, because it helps to unify thinking across ecosystem types once a common conceptual jargon is used. In general tolerance has been overlooked as an explanatory plant functional trait. For example, in Korcheiva's extensive meta-analysis on the cost of defensive traits, chemical, mechanical, and induced defenses were examined, but not tolerance traits (Koricheva, 2002). A recently proposed terrestrial-based model, LRM (Wise and Abrahamson, 2005), holds great promise for predicting tolerance traits across resource environments. We suggest that this model be tested broadly across ecosystems to determine whether it is generalizable.

The unresolved basis for wide variation in expression of resistance traits may stem from an incomplete conceptualization of the "system" and the context-dependent feedbacks that determine their expression. We suggest that taking a trait-based approach in the context of a food chain may help to resolve when and where these traits are expressed and how they impact trophic control of ecosystems. The MSH of trophic control may provide the basis for including plant defense traits (Schmitz, 2008). We predict that "resistance" traits (both structural and qualitative) will result in a trophic cascade through relative resource limitation of herbivores, while "tolerance" traits will invoke absolute resource limitation of herbivores, resulting in herbivore control of primary productivity. We realize that this framework does not yet consider important additional factors, such as plant volatiles, herbivore feeding guild, and ontological shifts in plant defense, but nonetheless view it as a useful starting point.

This conception may also help offer a complementary explanation for variation in the strength of top-down control across nutrient supply or productivity gradients implicit in the classic EEH of trophic control of ecosystems. This theory predicts that top-down control should be strongest at intermediate levels of productivity, which is attributed to predator satiation (Oksanen and Oksanen, 2000). This result, as well as the finding that herbivore and predator efficiency are important explanatory factors, was supported by meta-analysis (Borer et al., 2005). The MSH framework developed here suggests that plant defense traits may also account for the weakening of top-down control. The expression of tolerance regrowth traits at high nutrient levels could cause herbivores that were relative resource limited at lower nutrient levels to become absolute resource limited. In turn, predators would no longer have an indirect positive effect on productivity. At high nutrient levels, these tolerance traits may allow plants to escape their herbivores by outgrowing them. This outcome is not formalized within the EEH, but is consistent with the outcomes presented there.

The induction of resistance and tolerance traits in plant communities may also have important effects on nutrient cycling and future resource availability through "after-life" effects of plant defense or tolerance traits that remain in uneaten plant litter entering the detrital food web. While different rates of nutrient cycling have been predicted and recorded within aquatic and terrestrial systems (Nowlin et al., 2008), it remains to be seen whether taking this functional trait approach may explain some of the contingency found within and between aquatic and terrestrial ecosystems.

The lack of empirical investigation into these topics makes generalization difficult. However, as anthropogenic nitrogen inputs increase (Vitousek et al., 1997) and climate change increases herbivory and the potential induction of plant defenses (Ayres, 1993), it is increasingly important to understand how herbivory and nutrient context influence plant and herbivore populations across ecosystems. Tackling this question of whether and when plant defensive traits and nutrient availability modify trophic cascades within many ecosystem types is the first step. Only then will we be able to adequately address the question of whether defensive traits map to similar community responses in both aquatic and terrestrial ecosystems. This knowledge of how soil nutrient environment changes the expression of plant defensive traits and productivity may also be useful to agriculturists interested in lowering pesticide use while maximizing yield.

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