Herbivory differentially alters plant litter dynamics of evergreen and deciduous trees

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Here we propose that herbivore-induced changes in leaf litter quality can modify aboveground litterfall dynamics differentially in evergreen and deciduous trees. Because aboveground plant litterfall is an important source of nutrients in terrestrial ecosystems, any factor that alters plant litter quality can have large "afterlife" effects on the decomposition rate of that litter and the subsequent rate of nutrient release. Two contrasting patterns emerge from the literature and are corroborated by our two experimental case studies. First, in evergreens, herbivory commonly results in premature leaf abscission, improved litter "quality" and an acceleration of litter decomposition. Second, in deciduous trees, herbivory commonly results in the induction of secondary compounds that decelerates decomposition. We argue that these broad patterns reflect predictable differential responses to herbivores that can have important consequences for terrestrial nutrient cycling and productivity and that warrant more attention in the literature.

In addition to consuming 10–20% of aboveground net primary productivity (ANPP) in any given, non-outbreak year (Cyr and Pace 1993), arthropod herbivores can exert inordinate effects on ecosystem-level properties (Schowalter 2000, Bardgett and Wardle 2003, Cebrian and Lartigue 2004, Hartley and Jones 2004). Hunter (2001) listed six ways that arthropod herbivory could impact soil nutrient dynamics and ecosystem-level properties: 1) additions of frass; 2) additions of insect cadavers; 3) altered throughfall chemistry (i.e. canopy leachates); 4) changes in leaf litter quantity or quality by herbivory; 5) changes in plant communities due to herbivore choice; and 6)

changes in canopy cover that alter soil temperature and moisture. Of these, the effects of herbivory on leaf litter quality or quantity, such as altered phenology, nutrient resorption, and induced secondary compounds, have received disproportionately little attention in the literature. We believe herbivore-induced changes in litter quality are common and are specific to tree life forms, thereby allowing predictability in herbivore effects on nutrient cycling.

Leaf litter inputs represent 50 to 80% of the recycled input of nutrients in many forest ecosystems (Vitousek 1982, Attiwell and Adams 1993). Herbivore modifications of litter phenology and quality could contribute to long-term regulation of ecosystem processes by providing a reliable source of nutrients. These nutrients may be utilized differently by microbes, both temporally and quantitatively, and these plant-soil continuum effects demonstrate important linkages between above- and belowground processes (Bardgett et al. 1998, Bardgett and Wardle 2003, Hartley and Jones 2004). We examined the incidences of aboveground herbivore modification of plant leaf litter and the mechanisms by which tree responses to herbivory may vary predictably depending on tree life form. We further illustrate how these differential responses alter leaf litter decomposition and nutrient cycling with two case studies that specifically demonstrate these patterns.

Differential responses to herbivores by evergreen and deciduous trees

Evidence of differential responses to herbivores by evergreen and deciduous broadleaf trees is common in the literature. Evergreens are more likely to employ premature leaf abscission than deciduous trees, whereas deciduous trees are more likely to induce secondary compounds (Haukioja and Niemela 1979, Raupp and Denno 1984, Wratten et al. 1984, Auerbach and Simberloff 1989, Clausen et al. 1991, Schowalter et al. 1991, Werner and Illman 1994). Two comprehensive reviews of this topic have been published and therefore preclude extensive coverage here. Karban and Baldwin (1997) found that 37% of evergreen species examined induced premature abscission in response to herbivory but seldom induced foliar secondary compounds, while 55% of deciduous trees exhibited induction of secondary compounds in response to herbivory and only a handful of examples of induced abscission. More recently, a review by Nykänen and Koricheva (2004) supported these findings by examining damage-induced changes in woody plants. They found that evergreen plants tended to increase nutrient content following herbivory (with no change or a decrease in deciduous plants). They also found that deciduous plants significantly increased the concentrations of phenolic compounds while there were few differences in phenolic concentrations in evergreen plants. This collective evidence supports the premise that abscission may be the most common form of leaf-level herbivore resistance for evergreens and deciduous trees most often induce recalcitrant secondary compounds in live leaves that may be retained with senescence. In turn, these two responses may commonly lead to differences in litter decomposition and other nutrient processes (Choudhury 1988, Findlay et al. 1996, Cobb and Orwig 2002, Chapman et al. 2003, Schweitzer et al. 2005).

Biochemical and evolutionary foundations

A biochemical and evolutionary framework for examining differences in tree responses to herbivory may be provided in part by the protein competition model of phenolic allocation (PCM). Jones and Hartley (1999) proposed this alternative to the carbon-nutrient balance hypothesis and the growth-differentiation hypothesis (Bryant et al. 1983, Herms and Mattson 1992) for plant defense. According to the PCM, plants produce high levels of phenolic compounds at the expense of high protein production due to tradeoffs in allocation of the nitrogen (N) rich amino acid phenylalanine. Nitrogen-limited conifers often have a high baseline concentration of constitutive phenolic compounds, likely to protect their more permanent photosynthetic machinery and acquired nutrients. However, because conifers have highly compartmentalized leaf area, they can selectively induce abscission of small units of herbivore-infested tissue, thus minimizing energetic losses. Therefore, the "first line of defense" for conifers may be high, constitutive defense levels whereby the "second line of defense" is induced abscission (sensu van den Berg and van den Bosch 2004). Conversely, the PCM would predict that broadleaf deciduous trees require high levels of protein to support relatively faster growth and the short season of photosynthetic activity and may do so at the expense of maintaining high levels of constitutive phenolic defenses. However, because deciduous trees are relatively plastic in their allocation to phenolic compounds deciduous species may be better able to induce these chemical defenses in response to herbivory (Gatehouse 2002).

Likewise, the phylogenetic constraints involved in carbon storage may provide further support for the mechanisms we have invoked in distinguishing between strategies of conifers and deciduous broadleaf trees (Nykänen and Koricheva 2004). Deciduous trees often store carbon in their roots and perennial tissues, thus allowing them flexibility in allocation to defensive phenolic synthesis (Karban and Baldwin 1997). Conversely, conifers and other evergreens store carbon in their leaves, usually in structural tissues, rendering it less mobile for phenolic synthesis (Bryant et al. 1998). These different patterns of carbon storage and movement are consistent with the differential patterns of allocation of phenylalanine seen in conifers and broadleaf trees and may reflect phylogenetic constraints of these two growth forms.

Responses to herbivory may modify litter decomposition in opposite directions

We propose that the documented ways in which evergreen and deciduous species commonly respond to herbivory should modify decomposition rates and nutrient flux patterns in opposite directions. Building upon the terminology of Ritchie et al. (1998), we suggest that in evergreen species, nutrient resorption is commonly altered by herbivory, and the resultant increased levels of soluble nutrients (specifically foliar N) in litter has an "accelerating effect" on litter decomposition and, potentially, nutrient cycling (Fig. 1). In contrast, the frequent production of secondary compounds (such as phenolics) by deciduous trees in response to herbivory in susceptible individuals may have a "decelerating effect" on litter decomposition and nutrient cycling due to the recalcitrant nature of these compounds retained in leaf tissue (Fig. 1; Hättenschwiler and Vitousek 2000). The divergent responses these tree types have in herbivore-altered litterfall dynamics may
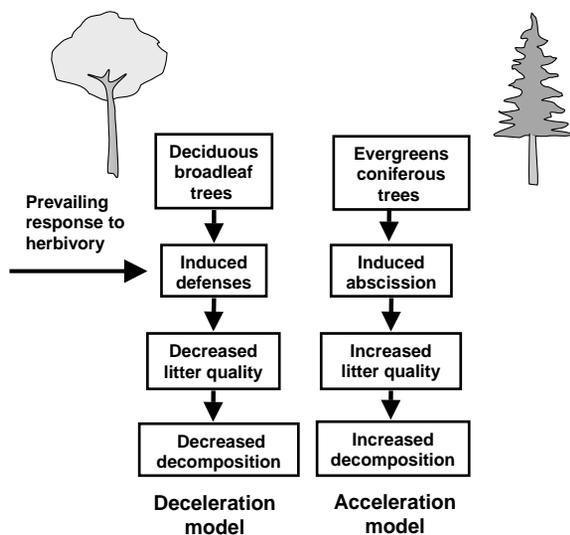
Fig. 1. Model of the differential responses to herbivory in evergreen and deciduous trees. Evergreens are more likely to induce abscission in response to herbivory, thus causing increases in litter quality due to reduced nutrient resorption. Deciduous trees will more often induce the production of secondary compounds in response to herbivory leading to decreases in litter quality.

impart predictable effects on litter decomposition and nutrient cycling at either the local or landscape scales.

Mechanisms

Litter phenology

Herbivores may alter litter decomposition and nutrient release rates by changing the timing of litter inputs. It is well established that litter quality, climate and the decomposer community control litter decomposition rates (Meentemeyer 1978, Couteaux et al. 1995, Aerts 1997). The seasonality of microclimate parameters (i.e. temperature and moisture) and the interaction of the decomposer community with climate indicate the importance of this interaction to the timing of litter inputs. Alteration of tree phenology can decouple litter inputs from their normal, climatic regulation (Guillame 2001). For example, ultraviolet radiation augments microbial litter decomposition (MacKay et al. 1994), and altered exposure due to altered timing of litterfall may modify normal decomposition regimes. Moreover, leaching of nutrients during the early stages of litter decomposition may represent an important and available nutrient flux for plants and/or soil microbes (Ibrahima et al. 1995). If litter phenology is changed, and thus decoupled from normal precipitation regimes, the rate of leaching of soluble nutrients may change both quantitatively and temporally. Such a decoupling will be especially important in systems that have high levels

of N in litterfall, and in which N loss and immobilization are predominant ecosystem fluxes (i.e. temperate and boreal forests). While it is difficult to predict the effects of altered phenology on total nutrient flux rates, the timing of nutrient pulses may be important in determining how nutrients are taken up or lost from the system (Jonasson and Chapin 1991, Lodge et al. 1994, Hartley and Jones 2004).

Nutrient resorption

In addition to changing the microclimate that leaf litter experiences (Classen et al. 2005), altered litterfall timing or phenology can result in modifications of litter nutrient status by altering nutrient resorption patterns. Nutrient resorption, the process by which plants remove nutrients from senescing tissues and transport them to perennial tissues in order to conserve nutrients, is a nutrient recycling mechanism which can be as important as soil uptake in determining plant nutrient balance in nutrient-poor environments (Pugnaire and Chapin 1993, Killingbeck 1996). Trees commonly limit herbivore attack by inducing abscission of herbivore-infested tissue (Faeth et al. 1981, Pritchard and James 1984, Williams and Whitham 1986, Blundell and Peart 2000). Premature abscission of leaf tissue can prohibit completion of senescence thereby reducing nutrient resorption (Risley 1986, Hunter 2001) and resulting in increased N concentration of litter (Risley 1986, Cobb and Orwig 2002, Chapman et al. 2003). Such increased litter quality due to decreased nutrient resorption may have large effects on litter decomposition and nitrogen inputs, and thus nutrient cycling (Fig. 1).

Induced secondary compounds

Herbivory commonly results in changes to plant tissue chemical content and subsequently alters the quality of remaining or new leaf tissue to future herbivores (Tallamy and Raupp 1991, Karban and Baldwin 1997, Nykänen and Koricheva 2004). Herbivore-induced secondary compounds such as polyphenols, alkaloids, or terpenes act on herbivores at many spatial and temporal scales within the plant (Schultz and Baldwin 1982, Berenbaum 1995, Agrawal et al. 1999) and may represent up to 30% of leaf dry weight (Haukioja 1990). These changes in tissue chemical composition induced by herbivores may be retained after leaf senescence in leaf litter and have "afterlife" effects on rates of litter decomposition and subsequent nutrient cycling (Findlay et al. 1996, Schweitzer et al. 2005).

Either due to premature leaf abscission leading to complexation of N, or simple retention of compounds due to their large molecular sizes, (e.g. polyphenols such as bound phenolics or condensed tannins),

induced secondary compounds retard leaf litter decomposition (Findlay et al. 1996). While there is a considerable literature documenting the relationship between leaf litter quality and rate of litter decomposition (Meentemeyer 1978, Melillo et al. 1982, Horner et al. 1988, Hättenschwiler and Vitousek 2000, Hättenschwiler et al. 2005), few studies have linked herbivore-induced variation in leaf quality and leaf litter decomposition. Only a handful of experimental studies have shown that the "non-obvious or non-apparent" (sensu Choudhury 1988) induced effects of insect herbivory can be translated into differences in the rates of decomposition and nutrient release. In general, these studies indicated that herbivore alterations of litter quality resulted in slower microbial colonization and activity and slower overall rate of litter breakdown (30–50% slower) and nutrient release (Choudhury 1988, Findlay et al. 1996, Cobb and Orwig 2002, Schweitzer et al. 2005).

Case studies

Comparisons based on plant life form, have often been used to illustrate patterns in nature and to provide a basis on which to design future experiments (Karban and Baldwin 1997, Haukioja and Koricheva 2000, Millard et al. 2001, Silver and Miya 2001, Nykänen and Koricheva 2004). Here we show specific examples of the mechanisms described above in a representative evergreen, *Pinus edulis* and a representative deciduous tree, *Populus* spp. These two distinct tree species provide a model for the evolutionary history of the two tree types (evergreens and deciduous broadleaf trees) in their responses to herbivores, which may be common to other species with similar growth forms. Because these two systems are both geographically widespread and abundant in North America, they represent appropriate models for understanding the afterlife effects of herbivores on litter decomposition and nutrient dynamics. We predicted that the case studies would follow the patterns found in the literature, specifically that: 1) tree life form will dictate how plants modify litterfall in response to herbivory; 2) herbivore alterations of plant litterfall will have large impacts on nutrient inputs and litter decomposition.

Litter phenology

Long-term research at Sunset Crater National Monument (near Flagstaff, Arizona, USA) in an arid pinyon-juniper woodland has documented important effects of chronic herbivory (by two insect herbivores, a scale insect, *Matsucoccus acalyptus* and a moth, *Dioryctria albovittella*, with contrasting feeding mechanisms) on population, community and ecosystem level processes.

Pinyon pines resistant and susceptible to both herbivores occur throughout the field site, and have been coupled with experimental trees from which the herbivores have been removed for over 15 years (n = 20). Scale insect feeding on susceptible pinyon pines, *P. edulis*, alters litter phenology by inducing premature abscission of foliage and causes a large pulse of litterfall to occur in the early spring and summer (Chapman et al. 2003). In contrast, trees resistant to the scale insect (as well as those from which the insect has been removed) drop most of their litter in late summer (Fig. 2). This herbivore-induced early pulse of litterfall, coupled with the higher N concentration in scale susceptible litter (discussed in next section), may allow fresh litter from herbivore infested trees to start decomposing earlier in the season. Further, the soil may be wetter in the spring and early summer than it is in June and July before the late summer monsoonal rains begin (August–September; Classen and Chapman, unpubl.), thus increasing decomposition rates at this time in this highly water limited system.

Similar to the herbivores on pinyon pine, the presence of the galling herbivores on cottonwoods also caused altered litter phenology (Williams and Whitham 1986, Schweitzer, unpubl.). In cottonwood hybrid zones throughout the western United States, narrowleaf cottonwood, *Populus angustifolia*, and backcross hybrid, *P. fremontii × P. angustifolia*, genotypes commonly demonstrate susceptibility to the gall-forming aphid, *Pemphigus betae* (Whitham 1989). Long-term studies of this herbivore with cottonwood have found that the presence of this gall-forming species can impact diverse communities ranging from microbes to birds (Dickson and Whitham 1996), and also have ecosystem-level impacts (Schweitzer et al. 2005). Experimental prevention of
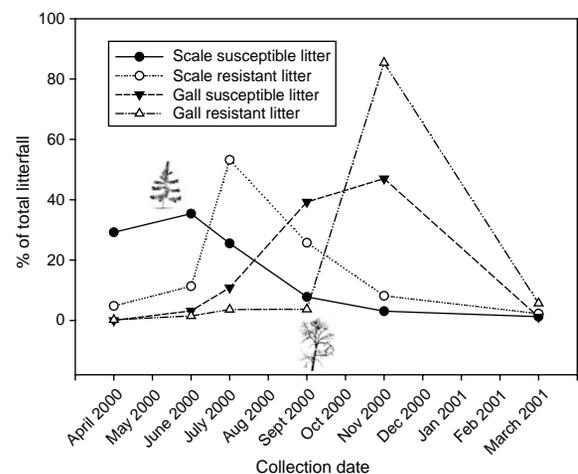

Fig. 2. Patterns in litter phenology for herbivore-susceptible and herbivore-resistant pinyon pines and cottonwood tree litter. (Figure modified from Chapman et al. 2003 and Schweitzer et al. 2005).

gall-formation on susceptible trees indicates that the gall is the causative agent for many chemical and ecosystem effects. Aphid-galled leaf litter begins falling in June whereas the majority of un-galled leaf litter falls in a large pulse in October. We find that up to 55% of galled litter falls before the majority of non-galled litter (Fig. 2). However soil moisture between the months of June and October differs by less than 1% (J. A. Schweitzer, unpubl.) due to winter and spring patterns of precipitation. Therefore, in contrast to pinyon pine, altered phenology in cottonwoods may not have a substantial effect on rates of litter decomposition due to the dry summer conditions that may prevent the earlier microbial colonization and decomposition. The magnitude of altered litter phenology influence on litter decomposition and N leaching is highly dependent upon annual climatic regimes and thus can be highly variable. However, coupling herbivore infestation data with microclimate data can allow predictability of these processes within a forest ecosystem.

Nutrient resorption

Herbivore-altered nutrient resorption is demonstrated in pinyon-juniper woodlands where herbivory by scale insects and moths significantly increased the N in litterfall and scale insects increased the P concentration in litterfall (Chapman et al. 2003), both of which changes we ascribe to decreased nutrient resorption. The scale insect, *Matsucoccus acalyptus*, causes premature abscission of needles and the moth, *Dioryctria albovittella*, severs terminal shoot vasculature, resulting in premature shoot death, which prevents resorption. This results in a 47% increase in litter N from scale susceptible trees and a 16% increase in litter N from moth susceptible trees (Fig. 3). Experimental removal of the two herbivores from susceptible trees resulted in litter N that is statistically indistinguishable from that of herbivore (moth and scale) resistant trees, isolating the herbivores as the direct cause for the increased litter N. As predicted from early litterfall and increases in nutrient concentrations, needle litter from trees susceptible to the herbivores decomposed 20% faster than uninfested litter (Fig. 4). As pine needles can take as long as up to 20 years to decompose, the cumulative effects of altered litterfall may have a profound influence on nutrient cycling in these woodlands.

Early abscission of galled litter in cottonwood also affects nutrient resorption in galled litterfall. Galled litterfall has 20–25% higher N (and P) than does un-galled litter (Fig. 3). However, it is unknown whether high concentrations of phenolics (next section) results in N complexation that prevents N resorption before senescence or if higher N is induced by herbivory. In contrast to pinyon pine, in which altered pheno-
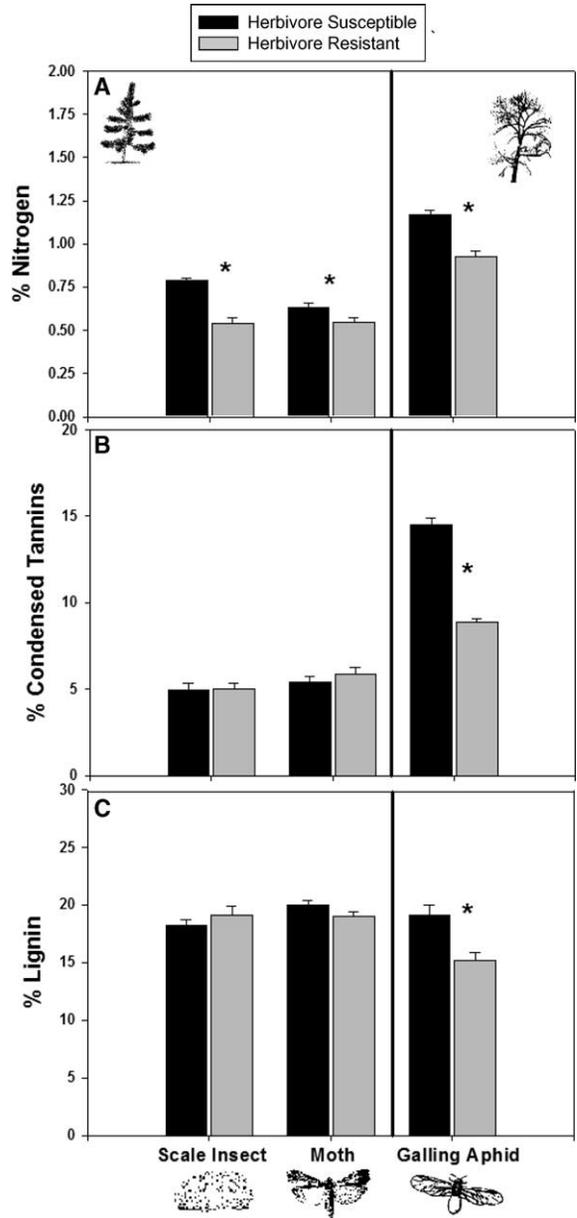

Fig. 3. Litterfall concentration of nitrogen (A), condensed tannin (B) and lignin (C) for herbivore-susceptible and herbivore-resistant pinyon and cottonwood trees; bars represent standard error. Each chemical constituent represents the concentration based on dry mass. Black bars represent litter from trees that are herbivore-susceptible while gray bars are litter from trees that are herbivore-resistant. (Figure modified from Chapman et al. 2003 and Schweitzer et al. 2005). Asterisks indicate significant differences between bars at the $\alpha = 0.05$ level.

logy and nutrient resorption results in substantial increases in rates of decomposition in susceptible litter, alterations of litter timing and nutrient content in galled cottonwood litter may not be as important as induced chemical resistance in determining the decomposition rates. Herbivore-induced alterations of litter timing and
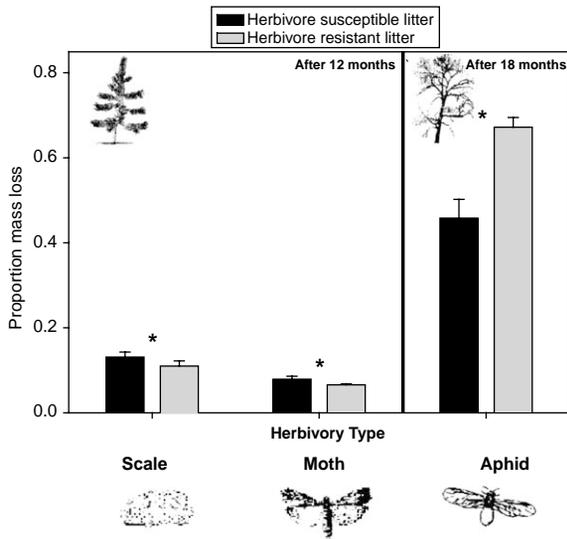
Fig. 4. Mass loss of leaf litter from herbivore-susceptible and herbivore-resistant pinyon pine and cottonwood trees; bars represent standard error. Black bars represent leaf litter from herbivore-susceptible trees; gray bars are leaf litter from herbivore-resistant trees. Proportion lost based on ash-free dry mass. (Figure modified from Chapman et al. 2003 and Schweitzer et al. 2005). Asterisks indicate significant differences between bars at the $\alpha = 0.05$ level.

nutrient status appear to be the primary mechanism in the pine response to herbivory which significantly increases leaf litter decomposition. However, induced resistance of polyphenols in aphid-susceptible cottonwoods may be the predominant herbivore defense mechanism that alters litter decomposition rates for galling aphid-infested cottonwood trees.

Induced secondary compounds

Although herbivory by both the scale and moth in pinyon pine modifies litter nutrient content, herbivory has little effect on leaf secondary compounds, such as lignin or condensed tannins (Fig. 3). There is less than 2% difference between insect resistant or susceptible pinyon pine litters in lignin or condensed tannins. As predicted by the literature, this argues that induced chemical resistance is not an important mechanism for pinyon pine (an evergreen) in response to herbivory (Chapman et al. 2003).

In contrast, induction of secondary compounds in live leaves may be an important response to herbivory in cottonwood that has "afterlife" effects after senescence (Schweitzer et al. 2005). The galling aphid induces up to a 40% increase in condensed tannins in susceptible leaves (Fig. 3) as well as a 20% increase in lignin content. This response has been shown observationally and experimentally (with prevention of gall formation from susceptible trees), which argues that the galling aphid

has a major effect on leaf and litter quality (Schweitzer et al. 2005). Moreover, the concentration of induced secondary compounds in cottonwood litter has been shown to be the best predictor of litter decomposition rate. The early abscission of galled leaves with higher litter N appears to be trumped by the effects of induction of recalcitrant polyphenols as galled litter decomposes up to 40% slower than un-galled litter despite higher concentrations of litter N (Fig. 4).

Discussion

Our two case studies illustrated that trees (based on their life form) respond to herbivory in the manner suggested by the literature and further suggests that differential alteration of litter may predictably alter ecosystem-level processes such as litter decomposition (Karban and Baldwin 1997, Nykänen and Koricheva 2004). Early abscision of litter from herbivore-susceptible pinyon pines, which has up to 50% higher N, accelerates decomposition and likely nutrient cycling (sensu Ritchie 1998). Conversely, cottonwoods susceptible to galling herbivores respond primarily through induction of secondary compounds (up to 40% higher condensed tannins) which decelerates decomposition and potentially nutrient cycling (sensu Ritchie 1998).

The increase in N cycling due to chronic herbivory that we have predicted for evergreen forests could have two contrasting effects on productivity in these forests. Increased N release from decomposing litter could either provide additional available N for plant uptake or generate increased N that can be leached and lost from these otherwise tight nitrogen cycling ecosystems (Johnson 1992). However, because we have predicted that herbivore-induced early abscission will result in stunted N resorption, this N is likely to be in the form of soluble amino acids and proteins. Though these compounds could be converted to nitrate, a highly leachable N compound, in its organic form this N is less likely to be leached than nitrate and thus, we predict it will be available for plant and mycorrhizal uptake and for mineralization by micro-organisms. This prediction is partially supported by a recent study by Cobb et al. (in press), the only study other than Chapman et al. (2003) we are aware of which investigated the direct impacts of herbivores on evergreen litter decomposition. Cobb et al. (in press) found that litter from hemlock wooly adelgid infested trees had higher nitrogen concentrations and lower C:N ratios after three months of decomposition. However, initial N concentration was not different between infested and uninfested litter, probably due to a lack of direct feeding damage by this herbivore. Because evergreen forests are frequently N limited, we predict that an increase in N availability and inputs, though perhaps slight, will help alleviate

N limitations and thus contribute to the persistence of evergreens in this environment.

In contrast, studies in deciduous forests have found that herbivores have a decelerating effect on nitrogen cycling via slowed leaf litter decomposition. While there is much anecdotal evidence for reduced leaf and litter quality following herbivory (Schultz and Baldwin 1982, Grime et al. 1996), to our knowledge there are only two other examples demonstrating the consequences of herbivore induced reductions in litter quality for litter decomposition rates and nutrient release. Choudhury (1988) found that leaf litters from aphid-infested trees have higher concentrations of phenolic compounds, which resulted in decomposition at slower rates than un-infested leaf litter. Likewise, Findlay et al. (1996) found that leaf litter with mite damage had $\sim 50\%$ higher composition of bound phenolics and decomposed 50% slower than undamaged litter despite higher concentrations of N. All of these examples occur in broadleaf, deciduous tree species. These examples demonstrate that independent of the herbivore's feeding mechanism, induced secondary compounds (especially phenolic compounds) following herbivory have the effect of slowing leaf litter decomposition and nutrient release, potentially decelerating nutrient cycling in these systems. Deceleration of litter decomposition and nutrient cycling is likely to conserve nutrients in stocks and may buffer these systems against nutrient losses.

The herbivore-induced delay in nutrient release in deciduous forests suggested by the above studies (due to decreased litter decomposition rates) should generate increased stocks of nutrients in organic layers and conserve nutrients. Due to their slower rates of decay, induced secondary compounds inhibit nutrient release and thus may prevent nutrients from being leached and lost from the system (Krause et al. 2003, Schweitzer et al. 2005). Though the mechanisms are different in evergreen forests, herbivore-induced accumulation of organic N may buffer deciduous forests against N loss from leaching. Although delay of nutrient release might be detrimental to overall NPP (net primary productivity) in the short-term, this conservative strategy may ultimately contribute to forest productivity by preventing N loss from these ecosystems (Northup et al. 1998, Schimel et al. 1998).

An important caveat to these patterns is that the alteration of nutrient cycling rates by herbivory may not actually alter the net amounts of ecosystem nutrients but rather their distribution in different compartments of the internal nutrient cycle. As was suggested by Hartley and Jones in a recent book chapter (2004), herbivores may change nutrient cycling without altering total ecosystem nutrient stocks. Altering the timing of nutrient re-circulation may cause a tight coupling or asynchronization with plant or microbial uptake creating a more or less leaky nutrient microenvironment for individual trees (Jonasson and Chapin 1991, Lodge et al. 1994, Guillaume et al. 2001). We also predict that the landscape mosaic created by the presence of both herbivore resistant and susceptible trees, and their associated differences in litter decomposition rates, could potentially further buffer forest ecosystems against outside changes in nutrient inputs and losses. Spatial variation in litter decomposition allows various rates of nutrients release across the landscape, thus allowing, in total, a more sustained nutrient release through time and varying climatic conditions.

Since trees and forests evolved in the presence of a constant but variable rate of herbivory, they may in fact function optimally in the presence of herbivory (Mattson and Addy 1975). For example, the few studies that have measured the contribution of non-outbreak (chronic), herbivore-altered litterfall to total N inputs have found that herbivore-induced changes in litterfall quality can account for a large proportion of the total N inputs in these systems (Chapman et al. 2003). Altered litter inputs in pinyon pine due to the scale insect can contribute up to 51% of total aboveground N inputs (i.e. the sum of all forms of N entering or recycling in the ecosystem) in pinyon woodlands (data not shown). If herbivore-increased litter quality accelerates nutrient cycling as predicted, then half of the aboveground N in pinyon woodlands may be available at earlier times under insect susceptible trees than N under insect resistant trees. Likewise, aphid-galled litter in cottonwood, though only representing 17% of the total litter biomass, contributes 22% of the total N inputs to these cottonwood forests (J. A. Schweitzer, unpubl.). A deceleration of litter decomposition and nutrient release due to gall-induced decreased litter quality might mean that a fifth of all aboveground available N in these forests may not be as available as litter N present in non-galled litter.

Conclusions

We believe that the differential contribution of herbivore-altered leaf litterfall to total N inputs, demonstrated both in the scientific literature and in these case studies, underscores the importance that this response may have for ecosystem-level properties such as litter decomposition and nutrient release and further elucidates the links between above- and below-ground processes (Bardgett and Wardle 2003). Because herbivore-altered litterfall can make such a large contribution to total N inputs, and because leaf litter has a mean residence time of 7–20 years in riparian gallery forests and arid pine woodlands, respectively, the altered litterfall pathway may better represent a predictable and continuous influence on nutrient cycling than other herbivore byproducts. Considering that plant life form

and the afterlife effects of herbivory can have important and measurable effects on ecosystem nutrient cycling, we suggest that incorporating the predicable effects of herbivory on litter fall dynamics is worthy of further investigation and incorporation in future research designs and models.

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