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The role of insect herbivores in the nutrient cycling dynamics of forest
ecosystems remains poorly understood. Although past research in herbivory has
focused primarily on the deleterious effects that insects can have on tree growth
and mortality, the overall effects of herbivory are more complex. Herbivores have
the potential to alter key ecosystem processes in a number of ways. One is by
altering the flow of nutrients from the canopy to the forest floor. The studies
presented here examine the effects that frass (insect excreta), greenfall (green leaf
fragments) and herbivore modified throughfall, have on decomposition processes
and soil nutrient dynamics. Both studies were carried out in a lower montane
tropical rain forest near the El Verde Field Station, Luquillo Long-Term Ecological
Research (LTER) site, Puerto Rico.

The first study presented here tested the hypotheses that green leaves are of
higher quality and decompose more rapidly than senesced leaves. Green and
senesced leaves of four common native tree species (*Dacryodes excelsa, Manilkara
bidentata, Guarea guidonia* and *Cecropia schreberiana*), were collected and
analyzed for C, N, and complex C compounds. Litterbags containing green and
senescent leaves of each species were placed in the field for up to 16 weeks in order
to compare rates of litter decomposition. Green leaves contained significantly
higher ($p < 0.05$) concentrations of N and lower lignin:N ratios than senescent
leaves for all four species. Decomposition rates were significantly higher

($p < 0.05$) for green leaves compared to senescent leaves for all four species. These results demonstrate that insect herbivores may influence key ecosystem processes via the production of greenfall. The relevance of this study extends to green leaf deposition resulting from multiple sources, including high wind and rain events, as well as disturbance by larger canopy organisms.

The second study tested a direct link between herbivory and soil processes. By altering levels of herbivory on a common understory plant (*Piper glabrescens*), using a prevalent folivore (*Lamponius portoricensis*), this study tested for effects of herbivory on nutrient inputs to the soil, as well as rates of litter decomposition. Enclosures were constructed around *P. glabrescens* individuals in the field and assigned to one of four treatments: herbivore exclusion, control, low herbivory and high herbivory. Total leaf area loss and greenfall production were measured for each plant using a sub-sample of randomly chosen leaves. Litterbags and ion exchange resin bags, placed under each plant, recorded rates of litter decomposition and the flow of NO_3, NH_4 and PO_4 to the forest floor during this 76-day experiment. The treatments were effective in establishing a wide range of herbivory. Both the total leaf area removed and greenfall deposition demonstrated significant positive correlations ($p < 0.05$) with NO_3 transfer to the forest floor, but not with NH_4 or PO_4. Although decomposition rates showed no significant correlation with total leaf area losses or the greenfall component, a significant correlation was found between decay rates and frass related inputs (defined as the total leaf area removed minus the portion removed as greenfall). This study clearly demonstrates the ability of insect herbivores to alter nutrient cycling in tropical forest ecosystems and is the first study to demonstrate a direct link between herbivory and decomposition processes.

These experiments provide clear evidence that insect herbivores can alter nutrient cycling and soil processes in forest systems. Such findings elucidate the need to more fully consider the effects of herbivores in both ecosystem models and management issues of tropical forest ecosystems.

The Influence of Herbivore Generated Inputs on Nutrient Cycling and Soil
Processes in a Lower Montane Tropical Rain Forest of Puerto Rico

by

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Chapter 1

Introduction

Herbivory exists as a fundamental process in terrestrial ecosystems and has understandably received a great deal of attention in the realm of ecology. Numerous studies have focused on the impacts that herbivory has on plant growth and survival. However, relatively little attention has been directed at understanding the role of herbivores in an ecosystem context. The potential consequences of herbivory are diverse and can resonate through out multiple levels of an ecosystem, influencing both its structure and function. These effects may involve changes in foliar chemistry (Schultz and Baldwin 1982, Finlay et al. 1996), modifications to plant-mycorrhizal relationships (Gehring and Whitham 1994) and altered flowering patterns (Zagt 1997). Or they may target a wider array of organisms and have more severe implications for ecosystem nutrient dynamics. Such broad based effects may include increased light penetration to the understory (Collins 1961), changes in litterfall dynamics (Grace 1986, Hollinger 1986, Risley and Crossley 1988), shifts in plant community composition (Pastor and Naiman 1992, Ritchie and Tilman 1995, Ritchie et al. 1998) or even the export of nutrients from an ecosystem (Swank et al. 1981, Eshleman et al. 1998). The impacts of herbivory are complex and can vary greatly in magnitude. The potential for cascading effects in the wake of herbivory necessitates consideration of these processes at multiple spatial and temporal scales. In light of the complexities surrounding herbivory and the potential for fundamental shifts in ecosystem nutrient flow, these processes must be taken into account if we wish to further our understanding of ecosystem nutrient dynamics.

Past Literature: Multiple Perspectives

A number of authors have discussed the effects of herbivory on ecosystem processes and nutrient cycling through both experimental and theoretical means. Crossley and Howden (1961) were among the first to look at the role of insect herbivores in ecosystem nutrient flow through the use of radioactive isotopes. Schultz (1964), in addressing lemming population cycles, recognized the potential for herbivores to influence soil processes and nutrient cycling. In the following decade this idea was expanded upon by several researchers suggesting that herbivores might act as ecosystem regulators, potentially accelerating nutrient cycling and increasing ecosystem productivity (Mattson and Addy 1975, Springett 1978, Kitchell et al. 1979, Owen 1980). This hypothesis asserts that herbivores maintain primary producers at optimal levels and in doing so increase the quality of inputs to the detrital food web. Others have proposed that such an effect is plausible in some systems, but only at moderate levels of herbivory or under a particular set of conditions (Seastedt and Crossley 1984, Lamb 1985, Dyer et al. 1993, de Mazancourt et al. 1998). At the same time, several authors suggest mechanisms to the contrary, arguing that the production of herbivore induced defense compounds in leaves may retard decay processes (Finlay et al. 1996, Grime et al. 1996) thus slowing rates of nutrient cycling. Other consequences of herbivory may be present at longer time scales. Herbivory may lead to slower rates of nutrient cycling via the selective foraging of nutrient rich plant species (Pastor and Naiman 1992, Ritchie and Tilman 1995, Pastor and Cohen 1997, Uriarte 2000). Over time nutrient poor species would increase in dominance and lead to slower overall rates of decomposition and nutrient return. However, Belovsky and Slade (2000) suggest that herbivores don't always select nutrient rich species, and increased soil fertility resulting from herbivore inputs may disproportionately benefit the nutrient rich plant species. In such cases low to moderate levels of herbivory can provide a positive feedback, increasing ecosystem productivity and rates of nutrient cycling (Belovsky and Slade 2000).

It becomes evident that the influence of herbivory on nutrient cycling is highly variable and may greatly depend on the ecosystem in question (Hobbie 1992, de Mazancourt and Loreau 2000). The intensity of herbivory, the organisms involved and time scale in question are important as well. The examples presented here are by no means a complete representation of the discussion surrounding the effect of herbivory on ecosystems, but they do serve to illustrate the diversity of ideas. Although broad generalizations about the effects of herbivory do not seem plausible, we can conclude that herbivores play a key role in shaping ecosystem processes.

The particular focus of this discussion is on forest systems and how inputs generated by canopy herbivores influence soil processes and nutrient cycling. Although forests can possess a diverse assemblage of herbivores, ranging from mammals to mollusks, insects are by far the most ubiquitous and have the potential to impart the greatest influence on forest ecosystems. Thus, insects are of primary interest here, folivorous (foliage feeding) insects in particular. Other insect herbivores are important as well, but the effects of folivores are more conspicuous and the most easily quantified in forest systems.

Herbivore Modifications to Canopy Inputs

Folivorous insects can alter canopy inputs by several principal mechanisms. The deposition of frass (insect excreta) and greenfall (green leaves or leaf fragments removed prior to senescence) represent alternative pathways for nutrients to reach the forest floor. They differ in chemical composition from senescent leaf litter and may have a distinct influence on soil processes. Greenfall may contain as much twice the N and P as senesced leaves (Lodge et al. 1991, Risley and Crossley 1993), due to the absence of nutrient remobilization from green leaves. Frass has been shown to have C:N ratios similar to soils, and much lower than those found in foliage (Christenson et al. 2002). Furthermore, the nutrients in frass exist in highly labile forms. For example, gypsy moth frass was shown to have N that is 110 times more extractable than N in forest soil (Lovett and Ruesink 1995). This contrasts

greatly with C and N found in leaves, that is largely bound in organic structures and released at a much slower rate (Christenson et al. 2002). Herbivores can also modify throughfall chemistry. By damaging leaves, herbivores have been shown to increase leaching losses of K, N, Ca and S (Kimmins 1972, Seastedt et al. 1983, Schowalter 1999, Reynolds et al. 2000).

Insect outbreaks and large-scale defoliation events provide some of the clearest evidence that herbivores can alter canopy inputs to the soil. Several studies have suggested substantial increases in N flow from the canopy following herbivore outbreaks in hardwood forests of North Carolina (Swank et al. 1981, Webb et al. 1995, Reynolds et al. 2000). During cyclic outbreaks in a California oak system by a native moth, Hollinger (1986) found frass and insect body parts to account for almost 70% of the annual N and P input to the soil. Frass inputs accounted for up to 46% of the total litterfall in a Scots pine plantation in eastern Canada, greatly augmenting the flow of N, K and P from the canopy to the forest floor (Fogal and Slansky 1985). Infestations of leaf feeders and aphids yielded increased levels of dissolved organic carbon (DOC) and dissolved organic nitrogen in leachates from spruce in forest systems in Germany (Stadler et al. 2001). Grace (1986) found frass and greenfall to make up nearly 60% of the litterfall inputs of N, P and K during a gypsy moth infestation of a Pennsylvania oak forest. Furthermore, in infested forest plots over half of the litter fell during the growing season, whereas in unaffected stands 90% of all fine litterfall occurred in autumn, as senescent leaves (Grace 1986). Hence in situations of intensive herbivory, we see that herbivore pathways may dominate the flow of canopy nutrients to the soil, not only affecting the composition of litterfall, but the quantity and seasonality as well. These dramatic shifts in nutrient return over large areas may produce substantial consequences for ecosystem nutrient flow

Even under non-outbreak conditions herbivore derived inputs may be important, especially when considered over longer time intervals. Estimates of herbivory average about 7% per year in temperate broad leaf forests and may be somewhat higher in the tropics (Coley and Barone 1996). In sub-tropical

Australian rain forests background rates of herbivory have been estimated as high as 27% (Lowman 1992). Ohmart et al. (1983) reported frass and insect bodies to constitute as much as 4% total N, P, and K inputs in an Australian eucalypt forest at relatively low rates of herbivory (less than 10%). Background herbivory rates in hardwood forests of North Carolina have shown greenfall to be as high as 5% of summer time inputs and 3-6.5% of the total annual foliar N inputs (Risley and Crossley 1988). Potassium and sulfur concentrations in throughfall were significantly enhanced by relatively low levels of herbivory in these same forests (Seastedt et al. 1983). Considering the wide range of background herbivory rates and the distinct chemical nature of herbivore-derived inputs, low levels of herbivory may very well have a significant impact on ecosystem processes (Hunter et al. 2003). This may hold especially true in areas with abnormally high rates of annual leaf loss to herbivores (Lowman 1992).

Effects on Soil Processes and Nutrient Cycling

Herbivores clearly alter the flow of canopy inputs to the forest floor, but the effect that these modified inputs have on soil processes and nutrient cycling remains uncertain. N and P are commonly considered limiting nutrients in terrestrial ecosystems (Schlesinger 1997). However, other nutrients may play critical roles as well (Marschner 1995). If indeed frass and greenfall decompose and mineralize N and other essential nutrients more rapidly than does senescent litter, then we might expect this component of litterfall to affect soil processes and ultimately accelerate rates of nutrient cycling for the limiting nutrients in question. Nutrients dissolved in throughfall may play a similar role, but could provide more immediate results since they generally exist in utilizable forms for plants and microbial uptake. Herbivore derived inputs could supply nutrients for plant growth directly or indirectly by facilitating decomposition and nutrient release processes. A number of studies have found increased decomposition rates following N additions (Hunt et al. 1988, Sanchez 2001), but the effects of added N on decay rates are inconsistent and depend on various litter quality factors and the time

interval considered (Fog 1988, Magill and Aber 1998, Vestgarden 2001). Other nutrients are likely to be important in decomposition processes as well (Bloomfield 1993), but have yet to receive the same attention as N.

Just as insect outbreaks provide the best evidence for herbivore alterations to litterfall inputs, they offer the clearest example of herbivore impacts on ecosystem processes. Several studies have documented increases in watershed nitrate exports following epidemic levels of herbivory (Swank et al. 1981, Webb et al. 1995, Reynolds et al. 2000). These findings suggest that herbivory can have substantial impacts on soil processes and that subsequent effects can extend well beyond the boundaries of the impacted region (Webb et al. 1995, Lovett et al. 2002).

Other studies have employed experimental means to test the effects of herbivore inputs on ecosystem processes. Lovett and Ruesink (1995) added gypsy moth frass to soil incubations and found increased microbial respiration resulting from the frass additions, but observed no net N mineralization in these treatments. Christenson et al. (2002) labeled gypsy moth frass and leaf litter with N^{15} and compared N dynamics in the soil. Although they found no significant differences in plant uptake or pools of available N, the frass-N was thoroughly distributed throughout the soil profile within days, while litter N was largely retained in the litter layer. In laboratory incubations using desert soils, frass from native snail species was found to rapidly release large quantities of mineral N upon wetting. However, this N was quickly immobilized by the microbial populations (Zaady et al. 1996). These experiments provide valuable insight to the dynamics of frass N, but do not consider all of the processes associated with herbivory and thus may not provide an accurate depiction of how natural systems behave.

Several field experiments have provided more realistic tests of the effects of herbivory on ecosystem processes. Seastedt et al. (1983) used insecticide to decrease herbivore populations present on young trees. Although they did find alterations to throughfall concentrations of K and S, they reported no differences in tree growth between treatments. By manipulating folivorous and sap-sucking

herbivores on Douglas fir saplings, Schowalter et al. (1991) found herbivory to increase the flow of K, N and Ca from the canopy, but found no effect on decomposition. However, herbivory did affect litter microarthropod communities (Schowalter and Sabin 1991). In grassland mesocosms, Belovsky and Slade (2000) manipulated grasshopper populations and found that increased levels of herbivory enhanced soil N availability. They attributed this effect to shifts in plant species composition and the addition of herbivore inputs. Reynolds and Hunter (2001) measured background inputs of frass, greenfall and herbivore modified throughfall and manipulated these inputs to look for effects on decomposition, nutrient availability or soil respiration. Although they found no effect of doubling background frass inputs on soil processes, they did find frass and throughfall additions to affect litter biota communities (Reynolds et al. 2003). They also found that the removal of greenfall and the doubling in N and P in throughfall resulted in decreased soil respiration, while throughfall additions had variable effects on soil P depending on the season (Reynolds and Hunter 2001).

Although not directly relevant to this discussion, several studies considering the effect of aphid honeydew on soil processes do provide useful insight about the effect of other herbivore guilds on soil processes. Michalzik and Stadler (2000) found honeydew inputs to temporarily increase soil respiration, while decreasing concentrations of dissolved organic N in the soil solution. Aphid honeydew may stimulate N fixation by free living soil bacteria (Owen and Weigert 1976, Owen 1980), thereby enhancing soil N status. Petelle (1980) tested this hypothesis and found the addition of sugars, such as those found in honeydew, to increase N fixation in soil. However, a field study in the Pacific Northwest found increased levels of aphid honeydew not only to decrease soil N availability, but to reduce N uptake by trees and aboveground net primary production (Grier and Vogt 1990). It appears that the effects of nutrient immobilization, resulting from the addition of simple organic C compounds, may overshadow any increases in N fixation by non-symbiotic bacteria. Such findings suggest the need for caution in generalizing the

effects of insect herbivores, since in some systems honeydew inputs may offset any effects generated by the inputs of folivorous insects.

Summary

As the dominant primary consumers in forest ecosystems, insect herbivores are a key element of these systems. They can exert considerable influence on ecosystem processes and nutrient cycling through a variety of means. Although their effects vary greatly in magnitude and can have long-lasting consequences for ecosystem function, the role of insect herbivores in forest ecosystems remains poorly understood.

Forests provide a multitude of essential functions globally. In addition to supplying building materials for humans, the forests of the world play a key role in C cycling, influence large scale precipitation patterns, provide clean water and provide habitat for most of the world's biodiversity. As the demands placed on forest ecosystems increase with the growing human population, the need to better understand these systems and their individual components becomes ever more vital. By studying the effect of herbivore inputs on soil processes, we gain valuable insight to how herbivory may influence ecosystem nutrient dynamics. Such knowledge will hopefully contribute to future forest management and conservation practices.

Chapter 2

**The Decomposition of Greenfall vs. Senescent Foliage as Related to
Herbivory and Disturbance in a Tropical Forest Ecosystem**

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Keywords: litterfall, greenfall, herbivory, decomposition, nutrient cycling, hurricanes

Abstract

In many forest ecosystems, canopy organisms and intense weather events facilitate the transfer of large quantities of green foliage to the forest floor. This green leaf input (greenfall) constitutes an enrichment over background levels of litterfall nutrients and therefore may influence key ecosystem processes. This study examined the nutrient content and decomposition rates of green leaves compared to senescent litterfall in four dominant tree species (*Dacryodes excelsa*, *Manilkara bidentata*, *Guarea guidonia* and *Cecropia schreberiana*) in a lower montane rain forest at El Verde Field Station, Luquillo Long Term Ecological Research site in Puerto Rico. Green leaves from the canopy and freshly senesced leaves from the forest floor were analyzed for C, N and complex C compounds and placed in litterbags in the field for up to sixteen weeks. Green leaves displayed significantly higher rates of decomposition than did senescent litter among all four species. Significantly higher N concentrations and lower lignin:N ratios were observed as well in the green foliage. These results suggest that the influence of greenfall in forest ecosystems may be significant, especially in forests that experience frequent high wind events, have high levels of herbivory or possess an active assemblage of large canopy organisms.

Introduction

The decomposition of organic matter exists as a principal mechanism for the supply of available nutrients in most terrestrial ecosystems. Therefore decomposition plays a critical role in regulating rates of nutrient cycling and productivity in these systems (Swift et al. 1979, Schlesinger 1997). Although climate has been shown to exert perhaps the greatest influence over decomposition on a global scale, (Meentemeyer 1978, Coûteaux et al. 1995, Aerts 1997) substrate quality is important as well (Fogel and Cromack 1977, Swift et al. 1979, Melillo et al. 1982, McClaugherty et al. 1985, McClaugherty and Berg 1987, Gallardo and Merino 1993). In humid tropical forests, with abundant moisture and warm annual temperatures, litter quality becomes the dominant control on decomposition rates and the release of nutrients to an ecosystem (Lavelle et al. 1993, Aerts 1997, Loranger et al. 2002). Thus, any phenomena altering the quality of litterfall inputs would be expected to influence rates of litter decay and have significant impacts on the flow of nutrients through these forests.

The addition of green leaf material to the forest floor represents a modification to the quality of litter inputs (Bloomfield 1993, Risley and Crossley 1993, Cuevas and Lugo 1998) and may influence rates of decomposition and nutrient release in forest systems (Constantinides and Fownes 1994). This modification can be attributed to essential nutrients that are retained in green leaves, since they are not subject to nutrient remobilization that occurs during senescence (Marschner 1995). Nitrogen (N) and phosphorus (P), in particular, are often limiting to decomposition and plant growth (Swift et al. 1979, Hunt et al. 1988, Enriquez et al. 1993). Thus, green leaves might be expected to decompose and release nutrients more rapidly than senescent litter, potentially ameliorating nutrient deficiencies in the surrounding litter-soil system and elevating decomposition rates as a whole. Studies in tropical agroforestry provide clear evidence in support of this idea. Green prunings, usually from high N tree species, are commonly applied in agroforestry systems as a means of enhancing soil fertility and supplying nitrogen for plant growth. Extensive research in these managed

systems has focused on the accelerated rates of decomposition and nutrient release from green leaves (Palm and Sanchez 1991, Handayanto et al. 1997, Mafongoya et al. 1998). Such findings demonstrate the potential for green leaf deposition to influence litter dynamics and soil processes in all forest ecosystems.

Although the decomposition of green leaves has undergone extensive study in managed forest systems, this process has received only minimal attention in unmanaged forest ecosystems. Under most circumstances the deposition of greenfall in natural systems does not exceed five percent of total foliar production (Risley and Crossley 1988), but under some circumstances green leaf inputs may be substantial. Hurricanes and other high wind or heavy rain events are the most obvious mechanism for the removal of green foliage from the canopy. Such events can completely defoliate trees, resulting in short term pulses of litterfall that may exceed average annual inputs. These inputs include large quantities of green leaves that contain up to twice as much N and P (on a per leaf basis) compared to senescent leaves (Lodge et al. 1991, Whigham et al. 1991, Herbert et al. 1999). However, canopy dwelling organisms can exert a significant influence as well. Insect herbivores have been shown to significantly increase levels of greenfall, through incomplete or inefficient herbivory (Grace 1986, Risley 1986, Risley and Crossley 1988). Larger organisms such as birds and primates can also remove considerable amounts of green foliage (personal observation). The addition of greenfall to the forest floor is an important process in natural systems and requires further evaluation.

This study compared the decomposition of green leaves with that of senescent leaves of four native tree species of contrasting litter quality within a tropical forest in Puerto Rico subject to relatively frequent high wind and heavy rainfall events. We hypothesized that green leaves would be of higher quality than senescent leaves within each species and that these differences would translate into faster rates of decay for green leaves.

Materials and Methods

Study Site: This study was conducted within an intact tabonuco (*Dacryodes excelsa*) dominated forest at roughly 400 m in elevation near El Verde Field Station, Luquillo LTER Site in Puerto Rico (18°10'N, 65°30'W). The site is classified as a subtropical wet forest, with average temperatures ranging between 21°C in January and 25°C in August (Waide and Reagan 1996). Annual precipitation averages 3700 mm and varies seasonally, with 200-250 mm per month January-April (dry season) and 350 mm per month the remainder of the year (McDowell and Estrada-Pinto 1988). Precipitation exceeds evapotranspiration in all months. Soils are Ultisols belonging to the Los Guineos series, which are well-drained, acidic clays and silty clay loams (Waide and Reagan 1996).

Litterbag Preparation: Although litterbags might not accurately depict true rates of litter decomposition due to the artificial drying of the leaves (Taylor 1998), exclusion of large soil fauna (Stewart and Davies 1989, González and Seastedt 2001) and microclimatic alterations imposed on the decaying material (Heal et al. 1997), the technique is useful tool for experimental comparison of litter decay (Swift et al. 1979, Heal et al. 1997). Green and senesced foliage of four prevalent tree species (*Dacryodes excelsa*, *Manilkara bidentata*, *Guarea guidonia* and *Cecropia schreberiana*) was collected near the site of the study within a tabonuco forest type. Green leaves and leaflets were collected from the mid canopy (10 m off the ground) by pruning small branches off a minimum of three different individuals for each tree species. Recently senesced litter was collected from the forest floor during the month of October 2001. Leaves were obtained from the same collection sites on a daily basis to ensure that the litter had not been on the ground for more than 24 hours. All leaves, green and senescent, were free of obvious deformations and undamaged by herbivory. Upon collection, leaves were air-dried for 48 hrs and stored until use. Litter of each type was thoroughly mixed and litterbags (10 cm x 10 cm, 1 mm fiberglass mesh) were then filled, so that each contained 2.5 ± 0.1 g of leaf litter from only one of each species and treatment (green or senesced). Leaves of all species except *G. guidonia* were cut into pieces

small enough to fit in the litterbags. Four sub-samples from each litter type were oven-dried for 7 days at 50°C in order to determine individual conversion factors from air-dried to oven-dried weights.

Bags were spread around on the forest floor in early November of 2001 and five replicates of each species and treatment combination were collected at each of four sampling dates: 14, 28, 56 and 112 days. Upon collection, litterbags were oven-dried for 7 days at 50°C. Bags were then dismantled, leaf litter was separated from soil, roots and other debris, and the remaining leaf material was weighed in order to determine the fraction of leaf mass remaining.

Nutrient Analysis: Sub-samples, four for each species and treatment, were collected from the bulk litter during litterbag construction and analyzed for total C, N, and C compounds using methods described by Madritch and Hunter (2002). Briefly, samples were dried at 65°C for 3 days, ground into a fine powder, and then stored at -80°C prior to analyses. Carbon and nitrogen were measured using a Carla Erba NA 1500 CHN Analyzer® (Carla Erba Instrumentazione, Milan Italy). Dry mass percentages of cellulose, hemicellulose and lignin were determined using sequential neutral detergent/acid digestion in an Ankom Fiber Analyzer® (ANKOM, Fairport, New York, USA).

Data Analysis: The decomposition of leaf litter is commonly described by a negative exponential function of the form: $X_t/X_0 = e^{-kt}$, where X_0 is the initial mass of litter, X_t is the mass of litter at time t, and k is the decay rate constant (Olson 1963, Swift et al. 1979). The decay rate constant, k, thus provides a single, functionally relevant parameter for describing decomposition. However, this simple model has been shown to poorly represent early stages of mass loss in some studies, thus prompting modifications to the model (Gallardo and Merino 1993, Sullivan et al. 1999). In this study, rapid initial mass losses of over 20 percent in the first two weeks resulted in a poor fit of this traditional decay model since the model requires the y-intercept to go through zero. To confront this problem we allowed an intercept term y_{int} in the model that serves as a measure of the initial mass loss or leaching losses (Sullivan et al. 1999). This resulted in a model of the

form: $\ln(X_t/X_0) = -k't + y_{int}$, where X_t is the mass remaining at time t, X_0 is the original mass of the substrate and k' is essentially a decay rate constant describing a secondary (post-leaching) phase of decomposition.

Multiple linear regression models, using indicator variables for treatment, were applied separately for each species to test for differences in slope, k', and y_{int} between green and senescent litters. N, C, complex C compounds and other litter quality indices were analyzed for differences between green and senescent leaves across species using ANOVA and within species using two-sample t-tests. These litter quality indices were also tested against the decay rates, k', using simple linear regression in order to determine which indices best correlated with decay rates across all species and treatments. All statistical analyses were conducted using S-Plus statistical software (MathSoft 2000).

Results

Mass loss: Differences between the slopes, k', of green and senescent litter were highly significant (Table 2.1) for all species (Figures 2.1, 2.2, 2.3, 2.4). These differences varied greatly between species and ranged from *G. guidonia*, that had a decay rate 2.5 times higher for green as compared to senescent leaves, to *C. schreberiana* where k' was only 1.26 times greater for green leaves. Despite the relatively small difference in slope for *C. schreberiana*, a large difference in y_{int} (Table 2.1) and clearly greater mass loss for the green litter (Figure 2.2) suggests that decomposition is substantially faster for green leaves than senescent litter. Initial leaching losses, $y_{int,}$ also were found to be significantly higher for greenfall in all species except for *M. bidentata* (Table 2.1). This may be due to *M. bidentata* having a particularly thick leaf with a waxy cuticle. Traditional k values (no y_{int}) were also calculated (Table 2.1) for comparison with previous studies. They suggest yet higher rates of decomposition and even larger differences between treatments than were indicated by k'. However, due to the notably poor fit of k for most litter types and the fact that y_{int} was significantly different from zero in all

Table 2.1. Decay rate constants (k') and y-intercept values (y_{int}) for green and senescent leaves of trees species with contrasting foliage quality during a 16-week litterbag experiment in a lower montane tropical rain forest in Puerto Rico starting in November of 2001.

Species	Treatment	k'	95% Confidence Interval for k'	y_{int}	95% Confidence Interval for y_{int}	R^2	k
Cecropia schreberiana	green	2.05	(2.34, 1.75)	- 0.23	(- 0.28, - 0.18)	0.86	3.11
	senescent	1.62	(1.91, 1.32)	- 0.07	(- 0.12, - 0.02)	0.96	1.93
Dacryodes Excelsa	green	2.63	(2.91, 2.34)	- 0.20	(- 0.25, - 0.15)	0.93	3.55
	senescent	1.55	(1.83, 1.26)	- 0.10	(- 0.16, - 0.05)	0.94	2.02
Guarea Guidonia	green	1.63	(1.92, 1.34)	- 0.23	(- 0.28, - 0.18)	0.80	2.70
	senescent	0.65	(0.94, 0.37)	- 0.11	(- 0.16, - 0.06)	0.93	1.16
Manilkara bidentata	green	1.67	(2.00, 1.34)	- 0.08	(- 0.14, - 0.03)	0.78	2.05
	senescent	0.89	(1.22, 0.56)	- 0.07	(- 0.12, - 0.01)	0.84	1.19

k' and y_{int} are included with corresponding 95% confidence intervals for each species and treatment.
R^2 values are based on simple linear regression models described by k' and y_{int} (n = 20).
k is the traditional decay rate constant, (Olson 1963) with no y-intercept.
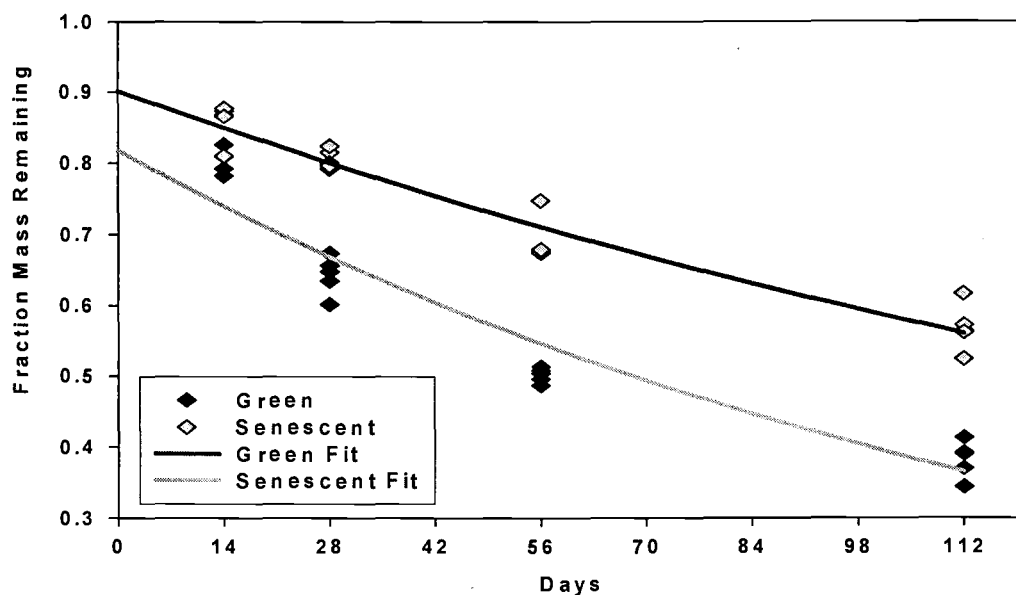
Figure 2.1. Comparison of mass loss between green and senescent litter for *Dacryodes excelsa* at 14, 28, 56, and 112 days in a lower montane tropical rain forest in Puerto Rico starting in November of 2001. Data points represent individual litterbags and are shown with lines fit from the regression model.
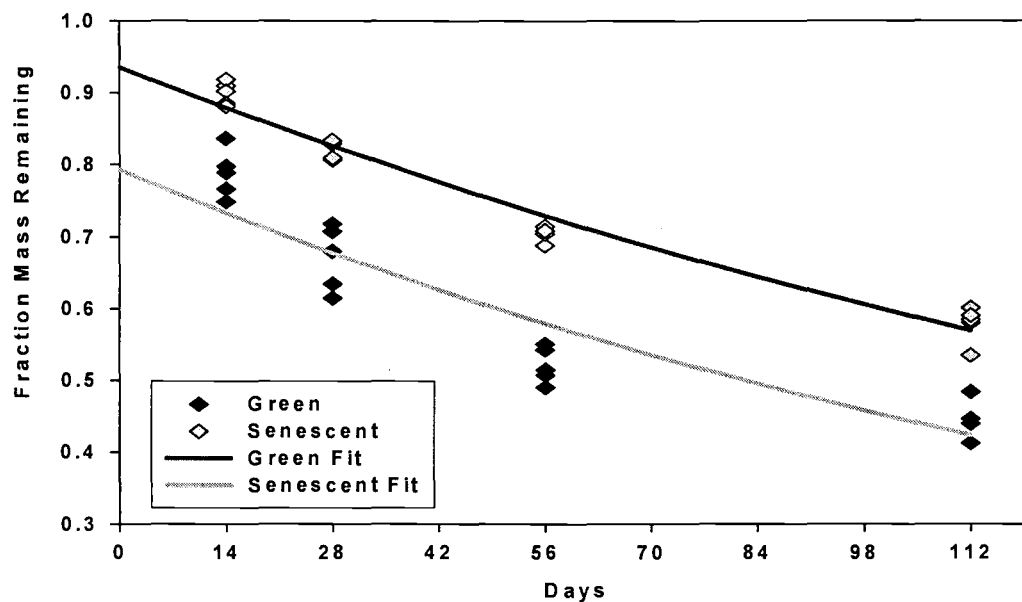
Figure 2.2. Comparison of mass loss between green and senescent litter for *Cecropia schreberiana* at 14, 28, 56, and 112 days in a lower montane tropical rain forest in Puerto Rico starting in November of 2001. Data points represent individual litterbags and are shown with lines fit from the regression model.
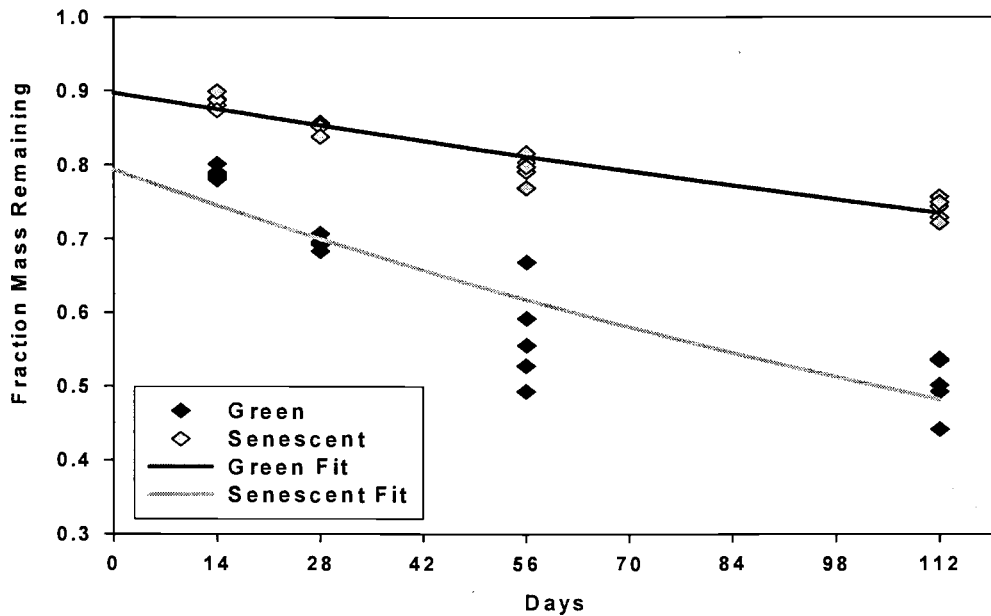
Figure 2.3. Comparison of mass loss between green and senescent litter for *Guarea guidonia* at 14, 28, 56, and 112 days in a lower montane tropical rain forest in Puerto Rico starting in November of 2001. Data points represent individual litterbags and are shown with lines fit from the regression model.
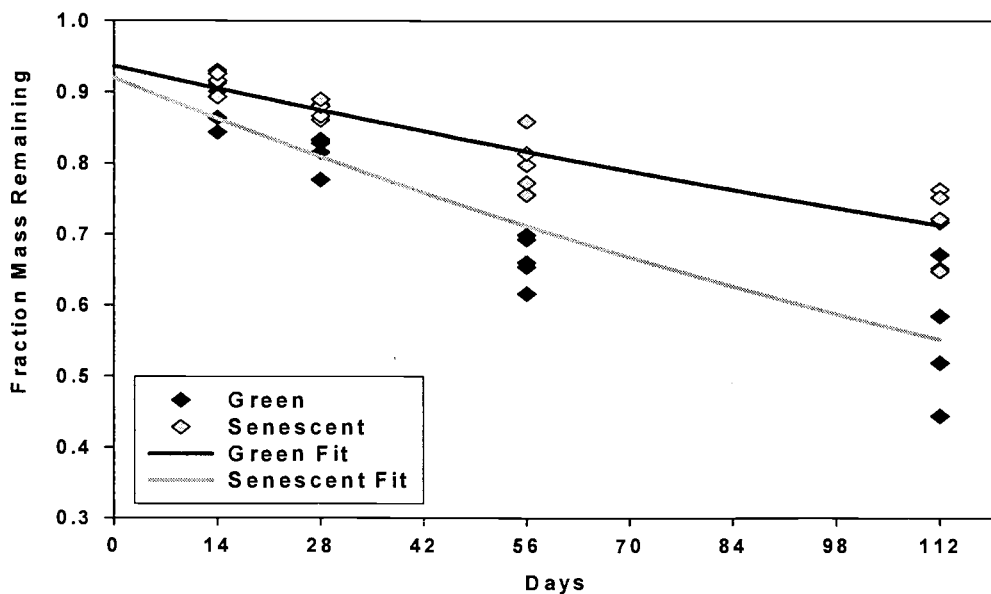
Figure 2.4. Comparison of mass loss between green and senescent litter for *Manilkara bidentata* at 14, 28, 56, and 112 days in a lower montane tropical rain forest in Puerto Rico starting in November of 2001. Data points represent individual litterbags and are shown with lines fit from the regression model.

litter types, the decay constant k' seems to hold greater ecological relevance in this study.

Litter Quality: Percent nitrogen and hemicellulose were found to be significantly higher for green leaves than for senesced litter in all four species (p < 0.001), although the magnitude of this difference varied between species (Table 2.2). Cellulose showed a similar trend except in the case of *C. schreberiana*, which exhibited higher cellulose content in senescent leaves. Lignin concentrations were significantly lower in green leaves for all species except *Dacryodes excelsa*, which showed slightly higher percentage (0.13%) of lignin in green leaves (p = 0.024). However, both lignin:N and C:N ratios were significantly lower (p < 0.001) for green leaves than senescent leaves, indicating higher litter quality. The lignocellulose index (LCI), defined as the ratio of lignin to combined lignin and cellulose (Melillo et al. 1989), was also lower for green leaves than for senescent leaves in all species except for *D. excelsa* (Table 2.2).

When green and senescent litter were compared across all four species no significant correlation was found between decay rates (k') and any of the leaf quality indices analyzed (N, C/N, cellulose, hemicelluloses, lignin, lignin:N and LCI). The two best determinants of decomposition across all species and treatments were cellulose content (positive correlation) and the LCI (negative correlation), with R^2 values of 0.336 and 0.248, respectively (Table 2.3). However, significant negative correlations (p-values < 0.05) were found for LCI and lignin content vs. k' (R^2, 0.936 and 0.974 respectively) when looking at only senescent litter of the four species. No such correlations were found when looking at green leaves alone, suggesting that other factors may control the decomposition of greenfall. Cellulose content was the best predictor (positive correlation and R^2, 0.418) of decay rates among green leaves (Table 2.3).

Table 2.2. Mean nutrient contents and leaf quality indices for green and senescent leaves of trees species with contrasting foliage quality in a lower montane tropical rain forest in Puerto Rico in November 2001. C, N, lignin, cellulose and hemicellulose are presented in dry mass percentages of leaf tissue, while other litter quality indices are expressed as ratios of various leaf tissue components.

Species	Treatment	N	C	Lignin	Cellulose	Hemicellulose	C:N	Lignin:N	LCI$_a$
Cecropia	green	2.20 ‡	43.47 †	6.58 ‡	21.99 *	22.24 †	19.76 ‡	2.99 ‡	0.23 ‡
		0.03	*0.19*	*0.39*	*1.47*	*2.38*	*0.21*	*0.19*	*0.02*
schreberiana	senescent	0.99 ‡	42.83 †	10.96 ‡	24.21 *	16.72 †	43.19 ‡	11.05 ‡	0.31 ‡
		0.03	*0.16*	*0.15*	*0.59*	*0.86*	*1.08*	*0.25*	*0.01*
Dacryodes	green	1.30 ‡	45.31 ‡	9.85 *	23.13 *	12.23 ‡	34.92 ‡	7.59 ‡	0.30
		0.02	*0.12*	*0.06*	*0.38*	*0.18*	*0.59*	*0.11*	*0.00*
excelsa	senescent	0.53 ‡	43.40 ‡	9.72 *	22.47 *	9.80 ‡	81.94 ‡	18.35 ‡	0.30
		0.05	*0.33*	*0.06*	*0.18*	*0.26*	*6.45*	*1.53*	*0.00*
Guarea	green	2.96 ‡	46.54 †	15.56 ‡	17.72 †	17.64 ‡	15.74 ‡	5.26 ‡	0.47 ‡
		0.05	*0.25*	*0.16*	*0.64*	*0.53*	*0.21*	*0.15*	*0.01*
guidonia	senescent	1.23 ‡	47.56 †	20.12 ‡	16.32 †	11.15 ‡	38.75 ‡	16.40 ‡	0.55 ‡
		0.03	*0.35*	*0.21*	*0.13*	*0.45*	*0.73*	*0.53*	*0.00*
Manilkara	green	0.93 ‡	45.15 ‡	7.27 ‡	20.14 ‡	9.72 †	48.39 ‡	7.79 ‡	0.27 ‡
		0.03	*0.59*	*0.27*	*0.27*	*0.15*	*1.36*	*0.18*	*0.01*
bidentata	senescent	0.48 ‡	48.95 ‡	9.30 ‡	17.83 ‡	8.74 †	103.85 ‡	19.77 ‡	0.34 ‡
		0.06	*0.32*	*0.22*	*0.19*	*0.45*	*10.74*	*2.53*	*0.01*

Within species differences were compared using two-sample t-tests (* $p < 0.05$, † $p < 0.01$, ‡ $p < 0.001$).
The standard deviation below each value (in italics) is based on 4 replicates.
a LCI = lignin/(lignin + cellulose) *from* Melillo et al. (1989)

Table 2.3. R^2 values and coefficients for the regression of the various leaf quality indices vs. decay rate (k') for green and senescent leaves of trees species with contrasting foliage quality in a lower montane tropical rain forest in Puerto Rico starting in November of 2001.

Indices	Combined Litters (n = 8)		Senescent Litter (n = 4)		Green Litter (n = 4)	
	R^2	Coefficient	R^2	Coefficient	R^2	Coefficient
Nitrogen	0.04	0.150	0.59	1.021	0.02	0.109
C:N ratio	0.15	- 0.019	0.38	0.010	0.15	- 0.019
Cellulose	0.34	0.123	0.41	0.083	0.42	0.200
Hemicellulose	0.13	0.047	0.01	0.011	0.10	0.041
Lignin	0.22	- 0.063	0.97*	- 0.093	0.00	0.011
Lignin:N ratio	0.13	- 0.035	0.00	0.001	0.04	- 0.061
LCI$_a$	0.25	- 2.830	0.94*	- 3.965	0.00	- 0.462

Negative coefficients imply a negative effect of that index on the decay rate (k').
* p value < 0.05
$_a$ LCI = lignin/(lignin + cellulose) *from* Melillo et al. (1989)

Discussion

Leaf litter quality is fundamental in determining rates of decomposition and nutrient release from forest litter (Fogel and Cromack 1977, Melillo et al. 1982, McClaugherty et al. 1985, Palm and Sanchez 1990, Scott and Binkley 1997, Loranger et al. 2002). This study supported this hypothesis and identified several factors influencing leaf decay in a tropical forest.

Decay Indices: Although none of the quality indexes measured in this study were highly correlated with decay rates across all species and treatments, green leaves generally had significantly higher quality (when considering total N, C:N and lignin:N) than did senescent leaves and decayed more rapidly. The lack of correlation between decay rates and leaf quality indices is not entirely surprising, given the relatively small number of litter types tested in this study. With such a small sample size general trends are easily masked by the presence of extreme values. The relatively short duration of this study (16 weeks) also may be a factor. Some researchers have suggested that lignin based indices such as the LCI and the lignin:N ratio might better predict later, as opposed to earlier stages of decomposition (Melillo et al. 1989, Heal et al. 1997). However, given that some of the green litters experienced as much as 60% mass loss, it seems that advanced stages of decomposition were observed even in the short time frame of this study. Loranger et al. (2002) demonstrated that indices involving lignin and phenolics exerted control on decay after only one month in the humid tropics. In addition, results from this study suggested that both lignin and LCI were correlated with decay rates in senescent leaves that had lost between 25% and 45% of initial mass. Hence, the lack of correlation between decay rates and litter quality indices across both treatments can be attributed to the small sample size and possibly some unmeasured fundamental difference between green and senescent leaves.

Constantinides and Fownes (1994) incubated green and senescent leaves with soil in order to look for trends in N mineralization. Although they found significant correlations between N release and ratios of lignin:N, (lignin + soluble

polyphenols):N as well as total initial N and P, the coefficients of these correlations seemed to vary between green and senescent litter. In addition, they found soluble polyphenolics alone to be correlated well with green litter, but not senesced leaves. This suggests that soluble polyphenolics may be leached or remobilized during senescence. Numerous researchers have linked decay rates or N mineralization rates involving green litter with polyphenols or polyphenolic based indices, such as the ratios polyphenols:N and (lignin + polyphenols):N (Palm and Sanchez 1990, 1991, Oglesby and J.H. 1992, Handayanto et al. 1995, Mafongoya et al. 1998). The inverse relationship between polyphenolics and decay may be explained by the ability of polyphenols to bind organic N and inhibit microbial growth (Mafongoya et al. 1998, Hättenschwiler and Vitousek 2000). Studies involving senescent litter have commonly related decomposition to indices involving N or lignin (Fogel and Cromack 1977, Melillo et al. 1982, McClaugherty and Berg 1987, Melillo et al. 1989, Taylor et al. 1989, Valachovic 1998). However, the inconsistencies between these findings may result from disparities in tropical versus temperate sites as much as it relates to green versus senescent leaf quality (Valachovic et al. 2003). Although not directly tested in this study, we suggest that polyphenols may play an important role in regulating green litter decomposition.

Effects at Ecosystem Scale: Our study indicates that, within a particular region of the tropics or ecosystem type, litter quality is the dominant control on decomposition rates (Meentemeyer 1978, Lavelle et al. 1993, Aerts 1997, Loranger et al. 2002). Both Bloomfield et al. (1993) and Sullivan et al. (1999) found no significant differences in decomposition rates of *D. excelsa* or other species between upslope and riparian areas or between differing watersheds within the Luquillo Experimental Forest (LEF). This suggests that patterns of decomposition observed in this study may be applicable across a greater area than covered in this experiment, since small scale climatic effects do not significantly influence rates of decay in this forest. Furthermore, the four species tested in this study represent a relatively wide spectrum of litter quality and all showed the same difference in decomposition rates of green versus senesced leaves, suggesting that these patterns

may be extrapolated across a greater range of species. However, such a conclusion must be observed with caution. Bloomfield (1993) found higher mass loss after six months for green leaves than for senesced litter of *C. schreberiana* and *Inga vera*, but differences for *I. vera* were not significant. This may be due to the relatively high initial N content in both green and senesced leaves of *I. vera* and that mass loss was only observed at one point in time, six months, beyond the time interval covered in this study. In addition, site differences in soil fertility or moisture can alter the retranslocation of nutrients from senescing leaves, and subsequently leaf quality and litter decay rates within litter of a single species (Vitousek et al. 1994, Vitousek 1998). This suggests that in extremely fertile sites, trees might gain little from retranslocating nutrients from senescing leaves, and differences in litter quality between green and senesced leaves might be negligible.

We note that the species included in this study represent over half of the total litterfall at El Verde (Lawrence 1996). Hence, we expect that greenfall is likely to have at least a short-term influence on litter decomposition in the LEF following storms or other events that transfer pulses of green litter to the forest floor.

Relevance to Multiple Situations: The most obvious application of the findings presented here might be to better understand how ecosystem nutrient cycles respond to hurricanes. In months immediately following a hurricane, the fate of green litter is not as clear, due to altered climatic conditions, large amounts of fine woody debris and a host of other factors associated with hurricane alterations to the forest system (Lodge and McDowell 1991, Herbert et al. 1999). Herbert et al. (1999) reported minor differences in decomposition of green versus senescent leaves of *Metrosideros polymorpha* following Hurricane Iniki in a Hawaiian forest. However, this result represents only one species and may be an artifact of the collection technique used for the senescent litter. Both green and senescent leaves were "hurricane-caused" litterfall and showed only minor differences in initial N and P contents. Sullivan et al. (1999) compared short-term litter decay before and after Hurricane Hugo. They found that senescent litter decayed faster in the

summer of 1989 (before the Hurricane) than in the summer of 1990, after the storm. They suggest that the difference in decomposition rates may have resulted from drier conditions in the year following the storm. Although the hurricane deposited large amounts foliage and produced a pulse of available soil nutrients (N in particular) immediately after the storm, soil nutrient status had returned to pre-hurricane conditions by the spring of 1990 (Lodge and McDowell 1991, Silver et al. 1996). Hence, any potential influence that the post-hurricane, nutrient rich environment might have had on decomposition processes disappeared before the placement the litterbags in the summer of 1990. Had decay been measured in the months immediately following the hurricane, the large surplus of soil nutrients might have accelerated the decay process, and provided different results. Due to the lack of experimental data on decomposition processes following such disturbances and the greatly altered environmental conditions associated with hurricanes, it is difficult to conclude what role green litter would play in forest floor nutrient dynamics or for how long such effects would persist.

The results from this study can be more easily extended to less intense storm events or leaf removal by canopy organisms, where significant amounts of organic matter are deposited without severely disturbing the ecosystem. Among the less severe disturbances, the effect of greenfall deposition is likely to be somewhat dependent on the mechanism of leaf removal. As demonstrated by this experiment and numerous other studies, decomposition rates and the associated release of nutrients are highly variable between plant species. Storms are more likely to remove leaves higher in the canopy and from species with leaves that are larger or have a physically weak attachment to the branch. By contrast, insect herbivores not only feed throughout various canopy levels, but also can be highly selective and have the potential (if feeding on species high in N, for example) to greatly modify nutrient cycling (Coley 1987, Schowalter and Lowman 1999). Greenfall generated by insect herbivores is generally in the form of leaf particles, in addition to whole leaves, and these may undergo yet higher decomposition rates due to the larger relative surface area available for microbial activity and leaching.

Larger arboreal organisms such as primates, may prefer certain species as well, but are less likely to be as selective in which leaves they remove, since much of this removal may be due to activities other than feeding. Generalizations regarding the effect of greenfall deposition need to consider both the mechanism of leaf removal and plant species involved.

In summary, the deposition of greenfall may have important consequences for ecosystem nutrient dynamics. Whether or not nutrient release is accelerated from greenfall was not directly addressed in this experiment. Only one study has addressed nutrient release from decomposing green versus senescent leaves (Constantinides and Fownes 1994). In their 16 week laboratory incubation experiment, they used tropical soil and leaves from 9 plantation species, spanning a large range of litter quality, and found that in all cases the decomposition of green leaves resulted in net release of N, but senescent leaves were still immobilizing N at the end of the experiment. Such an effect is further supported by numerous studies of N mineralization following the application of green leaves to agroforestry systems (Palm and Sanchez 1990, Handayanto et al. 1995, Mafongoya et al. 1998). Large flushes of nutrients following hurricane Hugo were thought to result from green leaf decay (Lodge and McDowell 1991). This hypothesis is supported by the results of our study. The ultimate fate of these nutrients is unclear and depends on the mechanism and scale of green leaf deposition, as well as the state of the ecosystem. Significant levels of green leaf deposition in the absence of major disturbance might provide an increase in nutrients available for plant and microbial growth and could ultimately enhance key ecosystem properties such as soil fertility and primary production.

Chapter 3

The Influence of a Neotropical Herbivore (*Lamponius portoricensis*) on Nutrient Cycling and Soil Processes

Steven J. Fonte and Timothy D. Schowalter

Abstract

The role of phytophagous insects in ecosystem nutrient cycling remains poorly understood. By altering the flow of litterfall nutrients from the canopy to the forest floor herbivores may influence key ecosystem processes. In this study, in a lower montane tropical rainforest of Puerto Rico, we manipulated levels of herbivory using the common herbivore, *Lamponius portoricensis* (Phasmatodea), on a prevalent understory plant, *Piper glabrescens* (Piperaceae), and measured effects on the input of nutrients to the forest floor and on rates of litter decomposition. Four treatment levels of herbivory generated a full range of leaf area removal, from plants experiencing no herbivory to plants that were completely defoliated (> 4000 cm^2 leaf area removed during the 76-day study duration). A positive correlation was found between all measures of herbivory (total leaf area removed, greenfall and frass related inputs) and the concentration of NO_3 in ion exchange resin bags located in the litter layer. No correlation was found between any of the herbivory components and resin bag concentrations of NH_4 or PO_4. Rates of litter decay showed significant correlations with frass related inputs (total leaf area removed minus greenfall). A marginally significant negative correlation was also found between the litter mass remaining at 47 days and total leaf area removed. This study is the first of its kind in a tropical system and the first to demonstrate a direct relationship between herbivory and litter decomposition. These results suggest that insect herbivores can play a significant role in regulating forest nutrient dynamics and merit further consideration in ecosystem modeling and management decisions.

Introduction

Insect herbivores are a prevalent component of forest ecosystems and a key factor in regulating canopy processes (Schowalter et al. 1986, Huntly 1991, Schowalter 2000, Rinker et al. 2001). Their high mobility and relatively rapid rates of growth and reproduction allow them to respond quickly to alterations in their environment and exploit emerging resources. The high diversity of insect herbivore species translates into an array of unique metabolic capabilities and adaptations, allowing them to utilize numerous plant resources. These characteristics provide insect herbivores with the ability to exert a strong influence on a number of forest ecosystem properties. In addition to the well documented and conspicuous effects that they can have on plant growth and survival, herbivores can substantially alter the flow of nutrients within forest systems (Swank et al. 1981, Hollinger 1986, Eshleman et al. 1998, Hunter 2001).

Phytophagous insects directly modify nutrient flows by altering the timing, quantity and quality of canopy inputs to the forest floor. Herbivore-derived inputs are commonly in the form of frass (insect feces), green leaf fragments (greenfall) and modified throughfall and all form a chemically distinct component of litterfall. Insect frass has been shown to contain large fractions of labile C and N (Lovett and Ruesink 1995), whereas greenfall can have as much as twice the N and P found in senescent leaves (Grace 1986, Lodge et al. 1991, Risley and Crossley 1993). The enrichment of canopy throughfall is the best-documented alteration of canopy inputs by insect herbivores, and perhaps the most important. By damaging leaves and exposing inner leaf tissues to leaching, herbivores have been shown to increase throughfall concentrations of K, N, S, Ca and dissolved organic C (Kimmins 1972, Seastedt et al. 1983, Schowalter et al. 1991, Reynolds et al. 2000, Stadler et al. 2001). These herbivore-induced alterations generally constitute an enhancement to the quality and sometimes the quantity of canopy inputs to the forest floor and could facilitate further modifications to nutrient flow by influencing the availability of nutrients in ecosystems.

The effects that herbivore-derived inputs have on soil processes and nutrient cycling are variable and poorly understood, yet are likely to depend on the nature of the inputs and the ecosystem in question. Although a number of studies have measured the modification of canopy inputs by insect herbivores (Kimmins 1972, Ohmart et al. 1983, Fogal and Slansky 1985, Grace 1986, Hollinger 1986, Risley and Crossley 1988, Stadler and Michalzik 2000), few have tested the effects of these modified inputs on the soil subsystem or plant growth (Seastedt et al. 1983, Schowalter et al. 1991, Lovett and Ruesink 1995, Reynolds and Hunter 2001). Some speculate that the addition of herbivore inputs may accelerate rates of nutrient cycling and even enhance primary productivity (Mattson and Addy 1975, Kitchell et al. 1979). Frass and greenfall may release nutrients rapidly and, along with herbivore-enriched throughfall, could supply essential nutrients to the soil subsystem. Most terrestrial ecosystems are nutrient limited and rely on decomposition for the supply of available nutrients (Swift et al. 1979, Schlesinger 1997). Therefore, fertilization in the form of herbivore inputs could increase soil nutrient availability by both the direct addition of mineral nutrient forms and by stimulating litter decomposition and nutrient release processes. This hypothesis, however, may oversimplify complex interactions between decomposer organisms, detritus and the soil subsystem (Lerdau 1996, Lovett et al. 2002). The variability surrounding such interactions forces us to consider ecosystems separately and at multiple spatial and temporal scales.

Research focusing on the impact of herbivore-generated inputs on soil processes and nutrient cycling has yielded rather inconclusive results. Lovett and Ruesink (1995) found gypsy moth frass to increase microbial activity when added to soil, but observed no net release of N during a 120-day laboratory incubation. In a desert system, inputs of mineral N from snail feces were found to greatly exceed that of atmospheric inputs, but this N was quickly immobilized and only temporarily available for plant uptake (Zaady et al. 1996). Christenson et al. (2002) showed N in frass to be rapidly distributed throughout all soil and plant N pools upon deposition, whereas leaf litter N was largely retained in the decaying

leaves and released slowly. Although they showed that frass-N was rapidly mobilized, this N was quickly incorporated into soil organic matter and largely unavailable (Christenson et al. 2002, Lovett et al. 2002). The distinct behavior of frass-N in this study suggests its potential to more actively influence nutrient dynamics in the soil subsystem.

Several studies have investigated direct links between canopy herbivory and ecosystem processes by using field experiments. Some researchers have tested the effects of herbivore modified nutrient fluxes on plant growth and litter decomposition by directly manipulating herbivores, but none have found significant effects on these processes (Seastedt et al. 1983, Schowalter et al. 1991). Schowalter and Sabin (1991) did, however, find changes in litter microarthropod communities under Douglas fir seedlings subject to elevated herbivory. Reynolds and Hunter (2001) manipulated the quantity of herbivore-derived inputs based on background levels of herbivory and looked for effects on soil respiration, decomposition and soil nutrient availability. Although there were no direct effects on litter decomposition, they found greenfall and throughfall manipulations to influence soil microbial activity. Enriched throughfall was also found to affect soil nutrient availability and nematode abundance. Both nematode and collembola populations were stimulated by frass additions (Reynolds et al. 2003).

Though none of these studies demonstrated a clear effect of herbivore-modified inputs on decomposition or plant growth, they do suggest the potential for such effects. Soil organisms are fundamental regulators of litter decomposition (Seastedt and Crossley 1984, Coleman and Crossley 1996) and changes to the structure of soil fauna communities could lead to perturbations in the turnover of organic matter. Likewise, alterations in soil microbial activity or soil nutrient availability could influence plant nutrient acquisition (Marschner 1995), rates of litter decomposition (Paul and Clark 1996) and ecosystem nutrient losses (Lovett et al. 2002). The effect of canopy herbivory on soil processes remains unclear, but might become more pronounced under more intensive levels of herbivory or in other forest ecosystem types.

In this study we manipulated levels of herbivory using walkingsticks (*Lamponius portoricensis*) and evaluated effects on leaf area loss, rates of litter decomposition and nutrient fluxes to the forest floor. This is the first study to address the effects of herbivory on soil processes in a tropical system. Furthermore, this study tested a broad range of herbivory, from plants that experienced no herbivory to plants that were completely defoliated during the course of the experiment. We hypothesized that elevated levels of herbivory would increase the flow of available nutrients (N and P) to the forest floor and accelerate rates of litter decomposition.

Materials and Methods

Study Site: This study was conducted at the El Verde Field Station, Luquillo LTER Site in Puerto Rico (18°10'N, 65°30'W). The site is classified as a subtropical wet forest, with average temperatures ranging between 21°C in January and 25°C in August (Waide and Reagan 1996). Annual precipitation averages 3700 mm and varies seasonally, with 200-250 mm per month January-April (dry season) and 350 mm per month the remainder of the year (McDowell and Estrada-Pinto 1988). Precipitation exceeds evapotranspiration in all months. Soils in this region are dominated by Ultisols belonging to the Los Guineos series, which are well-drained, acidic clays and silty clay loams (Waide and Reagan 1996). The study site was located at approximately 300 m in elevation in a tabonuco forest type dominated by *Guarea guidonia*, *Prestoea montana* and *Dacryodes excelsa* in the upper canopy. The site was selected due to the relatively high abundance of *Piper glabrescens* (Piperaceae), a common understory plant and food source of the common walkingstick, *Lamponius portoricensis* (Willig et al. 1993). These species of plant and herbivore were chosen for study because they are both prevalent components of the forest, easy to manipulate and relatively resilient to minor disturbances.

Treatments: Forty *P. glabrescens* individuals of similar size were selected within an area of roughly 0.5 hectare. Cubic enclosures (60 x 60 x 60 cm, 3.2 mm plastic

mesh) were placed around the foliage of each *P. glabrescens* and suspended above the ground using a single 2 m PVC pole. Each enclosure was carefully fitted, allowing room for plant growth, and sealed to restrict the passage of large herbivores (mainly *L. portoricensis* adults). The plants were randomly assigned to one of four treatments (10 replicates each): high and low levels of herbivory, herbivore exclusion, and control. The controls had large openings cut in the underside of the cage to allow free access to herbivores, while the upper side was left intact in order to maintain any shading effects imposed on the other treatments. The low herbivory treatment had one adult male *L. portoricensis* in each cage and the high herbivory treatment had one adult male and one adult female *L. portoricensis* in each cage. Females were used due to the difficulty in obtaining a sufficient number of adult specimens of the same sex. All enclosures were visited every 2-4 days in order to maintain the prescribed herbivore levels and to remove litter from the tops of the cages.

Herbivory measurements: The total leaf area and leaf area missing were measured three times during the experiment on five randomly chosen leaves for each plant. These measurements occurred prior to the start, one month into the experiment and after two months. A non-destructive point interception method was used to measure leaf area. Leaves were placed under a transparent sheet with a printed grid pattern (5 mm). The number of points covered by the leaf were then tallied, each point representing the center of a 5 mm x 5 mm square. The selected leaves were tagged and measured again at each sampling time, unless they were missing, in which case a new leaf was assigned. The five leaf areas and areas missing were averaged and then multiplied by the total number of leaves in order to obtain an estimate of the total leaf area and leaf area missing for each plant. A quick visual inspection confirmed that herbivory on these leaves was representative of the entire plant. Emerging leaves (including leaves with an area of less than 2 cm^2) were noted, but not included in the total leaf area estimates until they had expanded and matured.

Total herbivore inputs were expressed as cm^2 of leaf area removed. This was calculated by adding the area of leaves missing entirely, to the area lost from the remaining leaves. Total leaf area removed was also divided into two components, greenfall (consisting of all large green leaf fragments) and frass related inputs (calculated as the total leaf area removed minus leaf area removed as greenfall). The portion of the leaf area removed in the form of greenfall was calculated by collecting fallen leaf pieces at the bottom of the enclosures. Each green leaf fragment was estimated as a fraction of a whole leaf. These fractions were then multiplied by the average area of a leaf for each plant and summed in order to provide a per plant area estimate of greenfall losses. Although individual leaf areas differed greatly between plants, within plant leaf size was relatively uniform, thus allowing for a quick and reasonably accurate assessment of area. Greenfall was measured in this way every 2 to 4 days, then scattered beneath the corresponding plant. The greenfall component calculated in this manner is likely to underestimate true greenfall deposition, due to our inability to detect and measure the smallest fragments that fell through the mesh. In addition, greenfall estimates for the controls may have artificially low values due to the potential for some greenfall to escape measurement by falling through the openings at the bottom of the enclosures. Likewise, the deposition of frass related inputs (the non-greenfall component) may overestimate actual quantities, since this number includes small leaf fragments and plant material assimilated by the walkingsticks.

Litterbag preparation: Although litterbags may provide artificial estimates of leaf decomposition rates due to the partial exclusion of soil fauna (González and Seastedt 2001), pre-drying of leaves (Taylor 1998), and potential alteration of litter microclimates (Swift et al. 1979), they are a useful tool in comparing relative rates of decomposition between treatments. Recently senesced leaflets of *D. excelsa* were collected from the forest floor several weeks prior to the start of the experiment. This species was used due to its prevalence in the forest and the ease of collecting sufficient quantities of litter over a limited area within a minimal time frame. Leaflets were air-dried for 48 hrs in a room with a dehumidifier and

thoroughly mixed before weighing. Litterbags (10 cm x 10 cm, 1 mm nylon mesh) were filled with 2.5 g ± 0.1 g air-dried litter. Thirty leaf samples were collected at regular intervals during litterbag construction in order to obtain an oven-dry (50°C) weight conversion for the air-dried leaves.

At the start of the experiment, in early March 2002, four litterbags were placed beneath each *P. glabrescens* individual and picked up after 9, 18, 47 and 76 days in the field. All litterbags were oven-dried at 50°C for 7 days upon collection. The litter was carefully separated from roots, soil and other debris and weighed in order to determine mass loss.

Ion-Exchange Resin Bags: Ion-exchange (IE) resin bags provide a useful tool for measurement of available soil nutrients (Binkley and Matson 1983, Binkley 1984, Binkley et al. 1986). They function by adsorbing dissolved nutrient ions onto charged resin beads as solution passes through the bags (Skogley and Dobermann 1996). The resin bags used in this study were fabricated from nylon stockings, each containing two separate compartments. One compartment was filled with 10 g of positively charged resin beads and the other with 10 g of negatively charged beads. Each compartment covered an area of approximately 16 cm^2 on one side. Due to the high variability of substrate (litter, rock, roots, woody debris) below each *P. glabrescens*, the resin bags could not be uniformly buried in the traditional manner. Instead, each resin bag was placed on the forest floor surface, centered directly under each individual *P. glabrescens* canopy, in early March 2002. Although not providing a direct measure of soil nutrient availability, resin bags placed in this manner provided relative comparisons of nutrient inputs to the soil from above. They recorded nutrients dissolved in throughfall or released, via leaching or mineralization, from greenfall and frass deposited on top of the bags during the course of the experiment.

Resin bags were collected after 64 days. Debris and large roots were removed before placing the resin bags into individual plastic bags. The bags were placed on ice and shipped overnight to the laboratory for analysis. The contents of each bag were extracted in 100ml of 1 M KCl and analyzed for NO_3, NH_4 and PO_4

using automated cadmium reduction, phenate, and automated ascorbic acid reduction methods respectively (Greenberg et al. 1992) on an Alpkem Flow-Injection Analyzer® (ANKOM, Fairport, New York, USA).

Data Analysis: Litter decomposition is often described by a negative exponential function of the form: $X_t/X_0 = e^{-kt}$, where X_0 is the initial mass of litter, X_t is the mass of litter at time t, and k is the decay rate constant (Olson 1963). k thus provides a single, functionally relevant parameter for describing decay. Decay rate constants, k, were generated separately for each group of four litterbags beneath each plant. Decay rates and nutrient contents, NO_3, PO_4 and NH_4, in resin bags were analyzed for treatment differences using one-way ANOVA, and as a function of the various herbivore input components using simple linear regression. All analyses were performed using S-Plus statistical software (MathSoft 2000).

Results

Herbivory: Treatments successfully produced significantly different levels of leaf area removed ($F = 37.5$, df =3,36, $p < 0.001$). However, large variation within each treatment resulted in a continuum of herbivore inputs (leaf area removed) across all treatments rather than discrete levels (Figure 3.1). This was expected due to initial variability in plant and herbivore size and led to analyses relying primarily on simple linear regression.

Walkingsticks in the elevated herbivory treatments removed an average of 22.1 cm^2 per gram of live insect per day during the course of the study. The average leaf area loss was higher for the single herbivore treatment, than for the high herbivory treatment. Greenfall was predominantly in the form of nearly intact leaves that had been chewed off near the petiole. This accounted for 46% the total leaf area lost, yielding slightly higher proportions in the high herbivory treatment (Table 3.1). Due to large variability between study units these differences were not significant. However, differences between the high and low herbivory treatments were anticipated since walkingsticks in the high herbivory treatments experienced
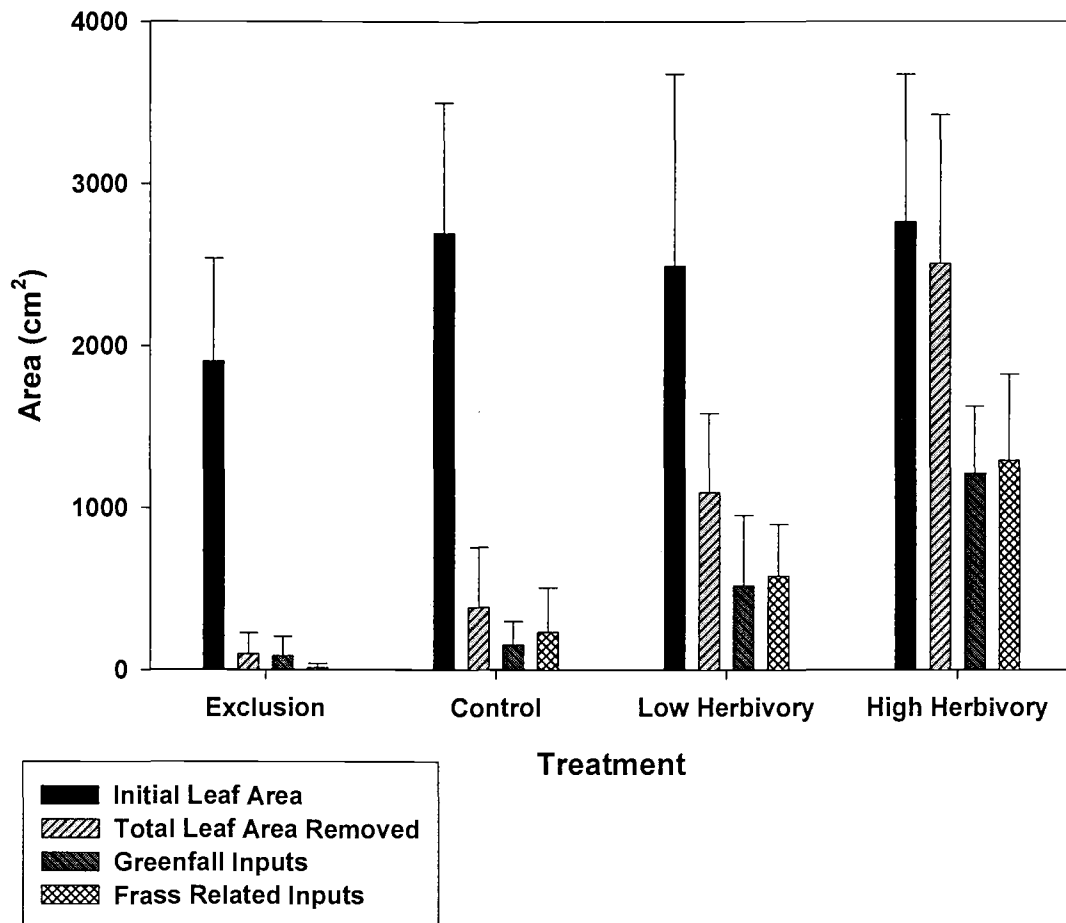
Figure 3.1. Comparison of herbivory measurements on *Piper glabrescens* among herbivore (*Lamponius portoricensis*) treatments in a lower montane tropical forest in Puerto Rico in 2002. Averages shown for initial leaf area, total leaf area removed, leaf area removed in the form of greenfall, and leaf area removed in the form of frass related inputs (total herbivore leaf area removed – greenfall). Inputs account for area losses during the entire experiment (up to 76 days). Error bars represent the standard deviation about the average of each treatment (n =10)

Table 3.1. Consumption rates and feeding behavior of the walkingstick, *Lamponius portoricensis* feeding on *Piper glabrescens*, during a 76-day experiment in a lower montane tropical rain forest in Puerto Rico during 2002. Herbivore inputs are separated into total leaf area removed, leaf area removed in the form of greenfall, and frass related inputs. These categories are further subdivided into low-level (1 adult male) and high-level (1 adult male and 1 adult female) herbivory treatments or averaged across both high and low herbivory treatments (combined). Rows divide herbivore behavior into the first and second half of the experiment or provide values averaged across the entire experiment.

Time Interval	Leaf Area Loss (cm^2)/ g of live insect / day			Greenfall loss (cm^2)/ g of live insect / day			Frass Related losses (cm^2)/ g of live insect / day		
	Low	High	Combined*	Low	High	Combined*	Low	High	Combined*
1st Half (0-39 days)	28.03	20.06	24.04	6.24	10.37	8.30	21.79	9.69	15.74
	24.47	*6.82*	*17.95*	*9.67*	*5.53*	*7.95*	*24.68*	*3.41*	*18.24*
2nd Half (39-76 days)	21.29	20.04	20.66	12.79	8.88	10.83	8.50	11.16	9.83
	11.70	*12.49*	*11.80*	*9.77*	*6.01*	*8.15*	*6.24*	*7.06*	*6.61*
Entire Experiment	23.95	20.32	22.13	10.53	9.99	10.26	13.42	10.32	11.87
	11.14	*8.33*	*9.76*	*7.67*	*4.31*	*6.06*	*9.98*	*4.31*	*7.65*

Standard Deviation in italics below each value (based on n =10)
* Values of column based on n = 20

varying degrees of resource limitation, territoriality and sexual behaviors that were absent from the low herbivory treatment.

Nutrient Flux: The resin bags revealed that the nutrient ions entered the soil in differing concentrations, with NH_4 greatly exceeding NO_3 or PO_4 (Figure 3.2). Of the three nutrient ions measured (NO_3, NH_4 and PO_4), nitrate was the only compound to show significant correlations with herbivore inputs. The total leaf area removed and frass related inputs estimated at 64 days displayed the strongest correlations with NO_3 levels ($p = 0.014$, df = 37, $R^2 = 0.15$ and $p = 0.017$, df = 1,37, $R^2 = 0.14$ respectively). The relationship between leaf area removed (cm^2) and nitrate flux (mg/L) was described by the equation:

$$NO_3 = 0.0002 * \text{total leaf area loss} + 0.798$$

suggesting that each 1000 cm^2 increase in leaf area loss is associated with a 0.2 mg/L increase in NO_3 concentration in resin bags (Figure 3.3). A significant correlation was also found between NO_3 inputs and greenfall ($p = 0.024$, df = 1,37, $R^2 = 0.13$). None of the herbivore input components correlated well with phosphate or ammonium ($p > 0.10$ in all cases). Although the high herbivory treatment yielded the highest average concentrations of both NO_3 and NH_4 in resin bags, comparisons in ANOVA revealed no significant differences among treatments for any of the nutrient ions.

Decomposition Rates: With an average mass loss of over 35 % after 76 days, decay in this experiment proceeded rapidly and was comparable to the decay of *D. excelsa* reported from other studies (see Chapter 2). The simple decay rate function generated according to Olson (1963) fit the data well in this experiment. Regression lines, used to determine k, were highly significant across all treatments ($p < 0.01$, n = 4), except for three cases where missing litterbag weights may have exaggerated k, prompting these study units to be dropped from the analysis.

A natural log transformation of the herbivory components (total leaf area removed, greenfall and frass) best met the assumptions for regression analysis
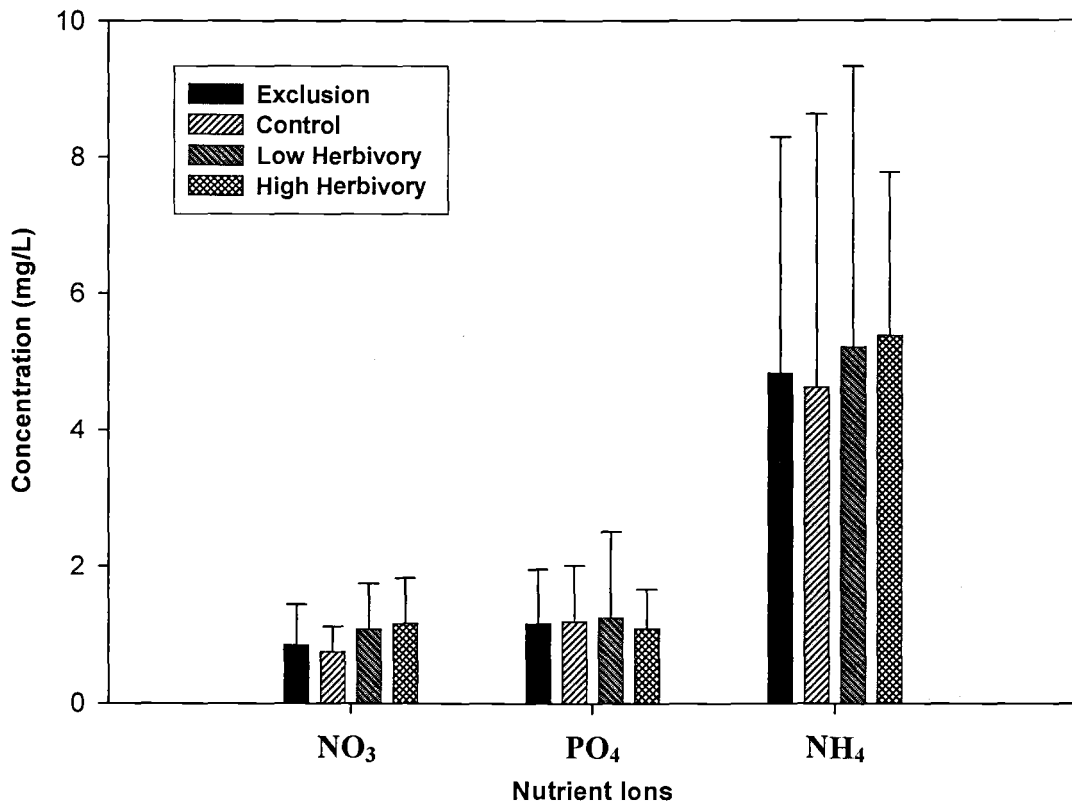
Figure 3.2. Mean nutrient ions concentrations in ion exchange resin bags placed on the forest floor under four treatments of varying herbivory after 64 days in a lower montane tropical rain forest in Puerto Rico. Error bars represent the standard deviation about the average concentration of each treatment (n =10).
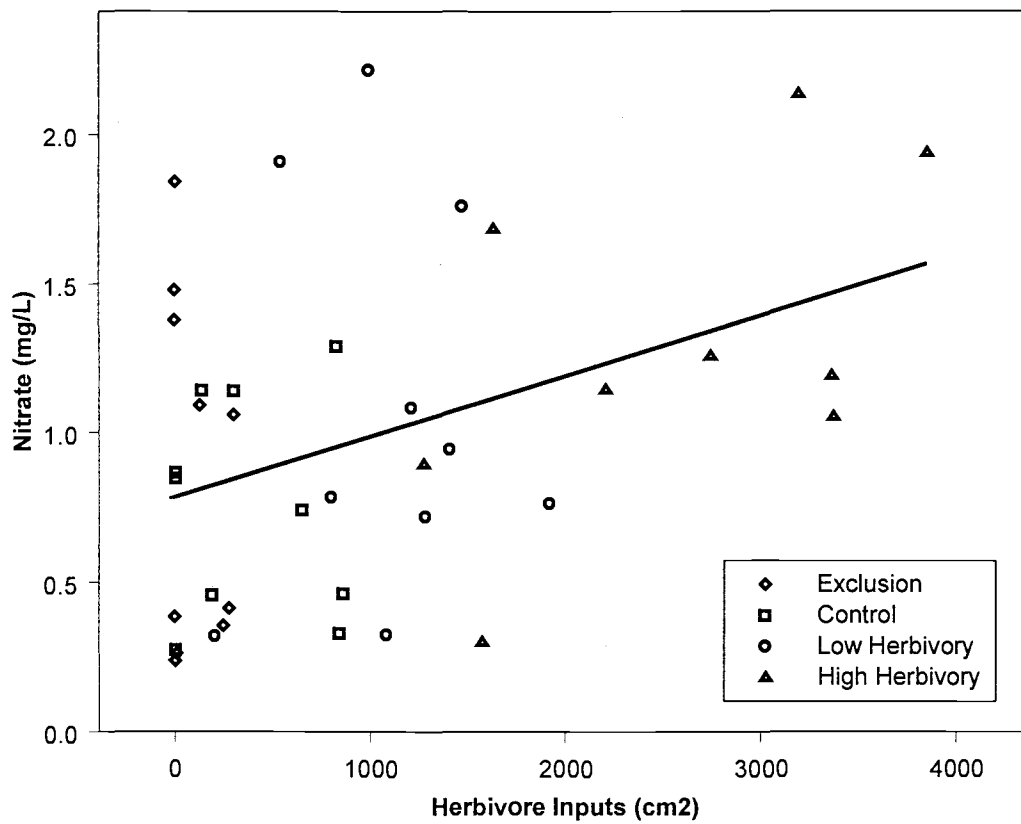
Figure 3.3. Concentration of nitrate (NO$_3$) in ion exchange resin bags vs. the total leaf area removed by *Lamponius portoricensis* feeding on *Piper glabrescens* after 64 days in a lower montane rainforest in Puerto Rico in 2002.

against k (Ramsey and Schafer 1997). Neither ln(total leaf area deposited) nor ln(greenfall deposited) adequately explained the rates of decay measured in the litterbags (p = 0.149, df = 1,35 and p = 0.252, df =1,35, respectively). However, the natural log of frass deposition, defined as the ln(total leaf area lost – greenfall), was significantly correlated with decay rates (p = 0.034, df = 1,35, R^2 = 0.12). This correlation is described by the equation:

$$k = 0.022 * \ln(\text{frass inputs}) + 2.048$$

implying that for every doubling of frass inputs the mean of the decay rate constant increases by 0.015, or 0.75 percent (Figure 3.4). Treatment comparisons using ANOVA (Figure 3.5) failed to explain variability in k (p = 0.17, df = 3,33).

Due to the complete defoliation of some plants before the end of the experiment, herbivore-generated inputs did not fall continuously throughout the entire study for all of the replicates in the high herbivory treatments. The retrieval of the third set of litterbags after 47 days coincided with the first plant becoming completely defoliated. Therefore, we examined the effects of herbivore inputs on mass loss at 47 days, before inputs from some of the higher herbivory treatments were discontinued. A significant correlation between ln(frass inputs) and the litter mass remaining at 47 days (p = 0.044, df = 1,38, R^2 = 0.10) is consistent with results reported above using a single k value generated from four litterbags under each plant. A marginally significant correlation was found between ln(total leaf area lost) and litter mass at 47 days (p = 0.069, df = 1,38, R^2 = 0.08), suggesting that total herbivore inputs may have some importance as well.

Since N and P are often limiting in litter decomposition (Schlesinger and Hasey 1981, Hunt et al. 1988, Enriquez et al. 1993), we also evaluated correlations between the decay rates and nutrient ions measured in the resin bags, but found no significant (p > 0.10) relationships.
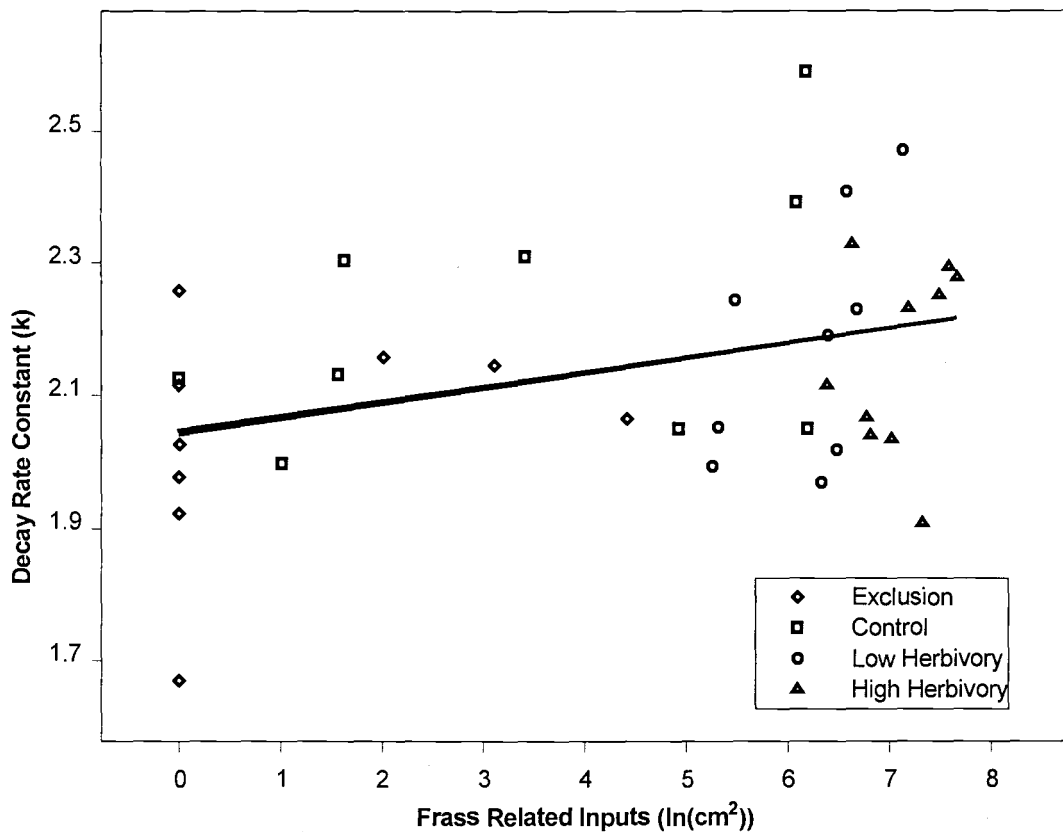
Figure 3.4 Decay rate constant (k) vs. the natural log of frass related inputs (total leaf area removed – leaf area removed in the form of greenfall) by *Lamponius portoricensis* feeding on *Piper glabrescens* after 64 days in a lower montane rainforest in Puerto Rico in 2002.
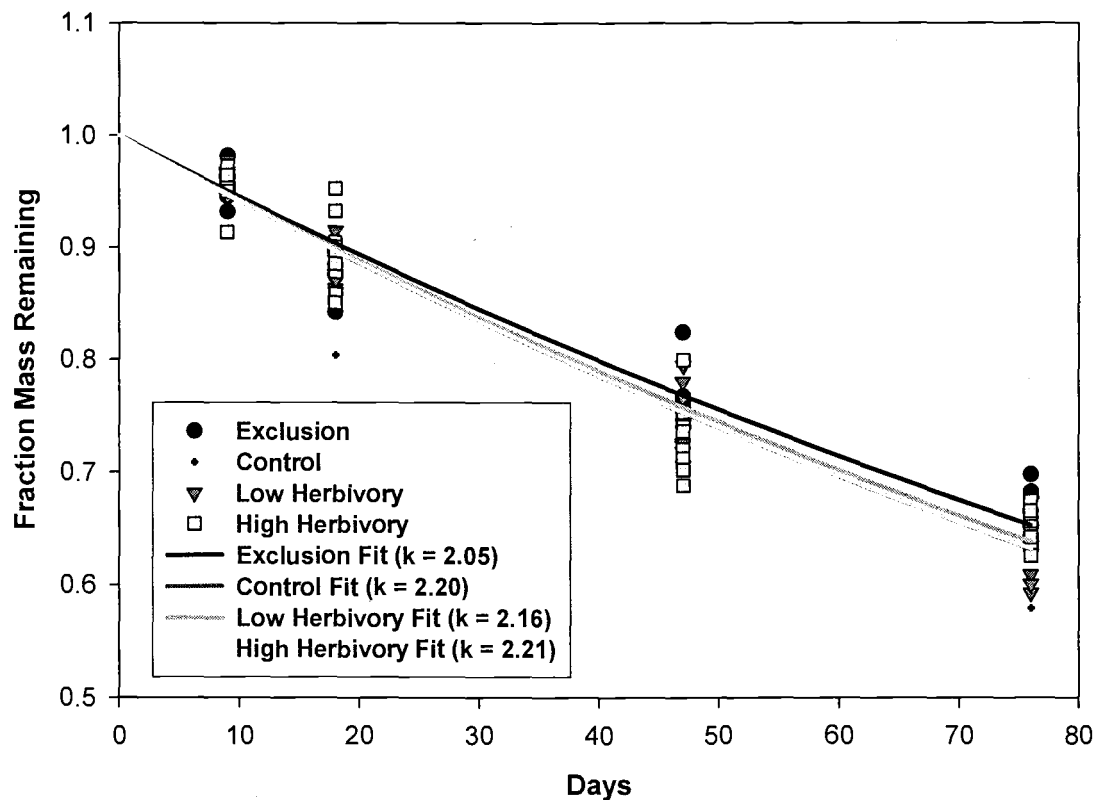
Figure 3.5 Comparison of mass loss in litterbags on the forest floor under four treatments of varying herbivory by *Lamponius portoricensis* feeding on *Piper glabrescens* during a 76-day experiment in a lower montane rainforest in Puerto Rico in 2002. Data points shown with lines fit from regression model.

Discussion

This study demonstrates that herbivores can influence nutrient cycling and key soil processes in tropical forest ecosystems. Although previous studies have shown herbivory to alter to nutrient flow (Kimmins 1972, Hollinger 1986, Schowalter et al. 1991) and soil biota (Schowalter and Sabin 1991, Reynolds and Hunter 2001, Reynolds et al. 2003), this is the first study to suggest a direct link between canopy herbivory and litter decomposition in a forest ecosystem.

Nutrient Flow to the Soil: The clearest effect of herbivory from this study was the increased transfer of NO_3 to the soil. Several factors may explain the herbivore effect on NO_3, but not PO_4 or NH_4 concentrations in the resin bags. Background concentrations of NH_4 and P in throughfall are higher than that of NO_3 in this system (McDowell 1998), and these greater inputs may have masked any treatment effects for NH_4 and P. The higher concentrations of NH_4 and the increased variability observed for NH_4 and PO_4 in the resin bags (Figure 3.2) are similar to previous differences recorded in throughfall by McDowell (1998), thus lending support to this hypothesis. Of the previous studies exploring the effect of herbivory on throughfall nutrient concentrations, none has shown increases in P resulting from herbivory, and of those that have suggested increases in N, only total N or NO_3 was reported (Schowalter et al. 1991, Reynolds et al. 2000). Hence there is no evidence from previous studies of throughfall to suggest an effect of herbivory on PO_4 or NH_4.

Variability of the forest floor and overstory tree composition also may have affected results. The soil surface at the study site was extremely heterogeneous, with patches of roots, rock, woody debris, exposed soil and leaf litter. In addition to substrate variability, intensive precipitation events occur with high frequency in this forest and the volume of water flowing across any particular surface can vary greatly depending on overstory tree architecture and micro-topography. Large variability in all response variables was anticipated and potentially masked some herbivore-induced effects.

Frass vs. Greenfall Inputs: Of the various herbivore-generated components analyzed in this study, frass-related inputs (total leaf area removed – greenfall) appeared to have the most significant effects on soil processes, influencing both nitrate levels and decomposition rates. Comprised principally of insect frass and small greenfall fragments, the frass related inputs would be expected to leach nutrients more rapidly than large greenfall material or leaf litter due to much greater surface area to volume ratios. Leaching losses from chewed leaves remaining on the plant should be highly correlated with frass and small greenfall fragments as well, since the production of both materials is associated with more intensive leaf damage and subsequent exposure of inner leaf tissues. We might expect the greenfall component to play a less active role in the short-term nutrient dynamics investigated in this study due its relatively large size and intact nature. The higher mobility of frass-N compared to that of leaf litter-N, as observed by Christenson et al. (2002), further supports the short-term importance of frass.

The potential for compounded error associated in the calculation of the frass component (combined error from greenfall and total leaf area removed calculations) warrants caution in the interpretation of these results. However, since the greenfall area calculation involved a direct measurement of fragment, and these leaves appeared to be representative of the entire plant, we suspect that error derived from greenfall area measurements contributed relatively little to the total error associated with the calculation of frass related inputs.

Decomposition: Despite the apparent correlation between frass inputs and litter decay, the mechanism responsible for the effect on decomposition rates remains unclear. The correlation between NO_3 levels and herbivore inputs suggests that increased availability of N may have played a role in accelerating decay rates. However, the lack of correlation between decay rates and NO_3, as well the other nutrient ions, indicates that something other than, or in addition to, nitrate may be regulating decomposition processes. Simple forms of organic N were not measured in the resin bags, and considering that soil microbial communities can utilize various forms of organic N (Zeller et al. 2000), this N source has the potential to

affect decay processes. In addition to organic compounds, a number of essential nutrient ions also were not measured in the resin bags, but may play a significant role in influencing decay rates. For example, Mg and Ca have both been recognized as important predictors of decay in this ecosystem (Bloomfield 1993, Bloomfield et al. 1993). Given that Ca flow from the canopy has been linked with herbivory in other studies (Schowalter et al. 1991), these other nutrients may be more important than originally anticipated. Decay processes may have also been affected by alterations to soil fauna populations. Several studies have demonstrated an influence of canopy herbivore inputs on soil microarthropod and nematode populations (Schowalter and Sabin 1991, Reynolds et al. 2003) and changes to these communities could very well have an effect on decomposition rates (Coleman and Crossley 1996, Wardle and Lavelle 1997, Heneghan et al. 1999). Hence, the apparent acceleration of decay processes by herbivore inputs in this study may be a product of multiple, complementary factors.

Ecosystem Considerations: Why have previous studies failed to find an effect of herbivore inputs on decomposition? Although the results from this study are far from conclusive, there is reason to expect an effect. Differences may be a matter of pure chance, study design, the organisms involved, or as suggested in this study, the particular manner in which herbivory was measured. However, given that this study was the first of its kind in a tropical system, the difference may stem from more fundamental distinctions between ecosystems. In contrast to temperate systems where climate is generally considered the dominant control on rates of organic matter turnover (Meentemeyer 1978, Coûteaux et al. 1995), decomposition is thought to be governed primarily by substrate quality in the wet tropics (Lavelle et al. 1993, Aerts 1997, Loranger et al. 2002). Hence, litterfall enrichment by herbivores may have a disproportionately greater effect on decomposition in this system than in temperate forests. Precipitation may play an important role as well. In the temperate systems studied previously (Seastedt et al. 1983, Schowalter et al. 1991), annual precipitation was significantly lower than that of the Luquillo Experimental forest and did not necessarily coincide with peaks in herbivore

activity (Schowalter et al. 1991). Therefore tropical rainforests such as this one, with consistent year round, high rainfall events and year round herbivory, are likely to be associated with greater potential leaching losses from herbivore-damaged leaves. Finally, the level of herbivory tested in this study greatly exceeded levels herbivory attained in previous experiments (Seastedt et al. 1983, Schowalter et al. 1991), and therefore would be expected to have a greater effect. Schowalter et al. (1991) reported that herbivores removed a maximum of 20% leaf area from the Douglas fir saplings used in their study, whereas leaf area removal in this study ranged up to100%.

The levels of herbivory attained in this experiment may seem severe, since tropical forests are not commonly associated with large scale insect outbreaks. However, such intense herbivory is not uncommon following disturbance events (Torres 1992) or on the scale of an individual plant (Lawrence 1996). Herbivory may be higher than previously considered in the tropics due to inadequate techniques for measuring herbivory (Lowman 1984, 1985, Coley and Barone 1996). Furthermore, the complete defoliation of a single *P. glabrescens* in the understory represents only a fraction of the total leaf area contained in a vertical column of tropical forest canopy (Lawrence 1996, Richards 1996). Hence even low or moderate levels of herbivory spread throughout the canopy may supply quantities of herbivore-generated inputs similar to those tested in this study and should thus be considered to have a potentially important influence on soil processes.

This study supports previous findings that herbivory can exert an influence on nutrient cycling. Herbivory demonstrated a clear, but modest effect on the flow of NO_3 to the soil subsystem and suggested an influence on decomposition processes. Despite the lack of frequent, large-scale insect herbivore outbreaks in tropical rainforest systems, herbivory remains a significant ecosystem process and climatic factors may intensify the effects of the herbivory levels present in these systems. This study suggests that insect herbivores may play a significant role in

ecosystem nutrient dynamics and emphasizes the need to further consider herbivory in the management and general understanding of tropical forest ecosystems.

Chapter 4

Conclusion

Results from these experiments clearly demonstrate the potential influence that insect folivores can have on the nutrient cycling dynamics of a tropical forest ecosystem. Although the exact mechanisms remain unclear, it becomes evident that herbivory can alter soil processes by affecting both N flow to the soil and rates of litter decomposition. The results from chapter 3 suggested that frass production or herbivore induced throughfall enrichment may be the principal mechanisms influencing decomposition and N flow from the sub-canopy plants tested. However, results from chapter 2 suggested that greenfall may play an important role as well, since the increased rates of decay and higher nutrient concentrations found for the green litter likely translate into more rapid mineralization rates for essential nutrients. Both studies indicate the potential for herbivory to affect soil nutrient status and possibly ecosystem productivity.

The findings presented here support the incorporation of new elements into nutrient cycling models and forest management practices. In the past, greenfall has been all but ignored in natural systems. Given the diverse mechanisms for greenfall production, it may be more prevalent in forest systems than originally assumed. With the considerably higher decomposition rates and litter quality differences reported here, one would expect large-scale greenfall deposition to significantly influence forest floor nutrient dynamics. The role of insect herbivores also requires reconsideration. In the past these organisms have generally been considered to have negative impacts on forest production. However, most of this evidence comes from managed forest systems or involves introduced species. Unmanaged systems generally have more diverse species assemblages, fewer exotics and greater age stratification among trees. These conditions are generally associated with decreased susceptibility to large-scale outbreaks and less obvious overall impacts resulting from herbivory. The studies presented here suggest that

herbivores have the potential to accelerate rates of nutrient cycling and increase soil nutrient availability, thus playing a potentially beneficial role to the ecosystem.

In light of the evidence provided by these studies, further research is needed to better assess and quantify herbivore-generated inputs throughout a variety of forest systems. Due to the difficulty in accessing some of these inputs, new techniques must be developed to better measure herbivory products, under a variety of conditions. Because ecosystems vary so greatly in nutrient status, climate and the types of organisms involved, herbivore inputs and ecosystem responses are likely to show large contrasts. Hence, in order to more fully comprehend the role of insect herbivores in a global context, studies that test the effects of these inputs on ecosystem processes need to be carried out across an array of ecosystems.

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