THE EFFECTS OF GYPSY MOTH DEFOLIATION ON NITROGEN CYCLING IN AN OAK-PINE FOREST IN THE NEW JERSEY PINE BARRENS

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ABSTRACT OF THE THESIS

The effects of gypsy moth defoliation on nitrogen cycling in an oak-pine forest in the New Jersey Pine Barrens

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Insect herbivory that results in extensive defoliation has the potential to affect forest nitrogen dynamics. High-nitrogen leaf materials and insect excrement (frass) are deposited on the forest floor during the growing season, potentially providing a pulse of labile carbon and nitrogen. Whether the released nitrogen is retained by or lost from the forest system has important implications for nitrogen dynamics within the forest, as well as across the larger landscape. Invasion of forests in the New Jersey Pine Barrens by the gypsy moth (*Lymantria dispar* L.) during the summer months of 2006 and 2007 provided the opportunity to study the impact of defoliation on nitrogen cycling in an oak-pine stand. Nitrogen budgets were produced for a non-defoliated year, 2005, and a year in which forest plots were completely defoliated, 2007, in order to assess the ecosystem-level effects of defoliation. The two budgets were not as distinct as expected. This was due, in part, to the lack of adequate forest floor data for 2005. It is likely that the forest floor is the site of altered nitrogen cycling and that microbial activity is a key component of nitrogen retention and/or loss. Future studies should focus on filling the gaps in our understanding of the Pine Barrens nitrogen budget.

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Introduction

Forest ecosystem function can be altered by herbivore invasion. Defoliating insects, for example, are expected to have both immediate and long-term effects on ecosystem process rates as well as the interaction between organisms and the abiotic environment. Studies of defoliation in forest systems have documented: reduced photosynthesis, tree growth, and productivity; increased cycling or leaching of nutrients; stimulated decomposition; altered light and microclimatic conditions; reduced transpiration, followed by increased water drainage; a reduced seed crop; and a pulse of nitrogen (N) and labile carbon (C) (see Lovett *et al.* 2002). The longer-term effects of defoliation are primarily related to the changes in community composition which follow mortality and reduced seed crops (Lovett *et al.* 2006). Altered species abundances and spatial patterns will impact litter quality and amount, decomposition rate, and long-term productivity (Lovett *et al.* 2006). There is also some evidence of a feedback between ecosystem function and pest success (e.g. Frost and Hunter 2007; Throop and Lerdau 2004).

One of the expected ecosystem effects of extensive defoliation is altered timing and quantities of nitrogen cycled within the system. Foliar nitrogen that is normally cycled tightly within an individual tree is consumed by insects, often during the growing season when foliar biomass and nitrogen content are at their peak. Most of this nitrogen – the portion which does not leave the system in the form of dispersing insects or their predators – is redeposited on the forest floor in the form of frass (insect excrement), dead insects, and unconsumed particles of foliage. This is in contrast to the usual retranslocation of N from leaves to roots, followed by the deposition of senesced leaves and needles that are lower in N than live foliage. While the carbon to nitrogen (C:N) ratio of frass is

similar to that of live oak leaves (Lovett and Ruesink 1995), the quality of nutrients other than N and soil moisture at the time of deposition may be factors affecting frass mineralization rates.

Initial decomposition of insect frass is assumed to result in a nitrogen pulse (Lovett and Ruesink 1995), a short-duration increase in bioavailable, or extractable, forms of nitrogen. This effect has been documented in mesocosm studies using oak seedlings (Frost and Hunter 2004) and in laboratory incubations of insect frass and soil (Lovett and Ruesink 1995). Whether, and under what conditions, nitrogen mobilized by defoliation and initial decomposition is retained within a forested ecosystem is an important aspect of long-term nutrient dynamics. The nitrogen may be retained through immobilization by soil microbes, incorporation into soil organic matter, and/or plant uptake. Alternatively, nitrogen may be lost from the system if it is leached in drainage water or volatilized. This result was found in a watershed-scale study of gypsy moth defoliation, which documented increased nitrate export to streams (Eshleman *et al.* 1998). Other studies have indicated, however, that nitrate export is highly variable and that conclusions cannot be drawn without long-term study (reviewed in Aber *et al.* 2003). Regardless of the fate of the mobilized N, it is clear that the flow of nitrogen through the system is changed by defoliation, and that the consequences of the altered flow may not be immediately evident.

The nitrogen retention capacity of forests is of interest, due to concern about excess nitrogen inputs in the form of atmospheric deposition and surface runoff (Groffman *et al.* 1993). Excess nitrogen can have wide-reaching effects on forest health and has been shown, for example, to decrease soil microbial diversity (Dighton *et al.* 2004); de-

crease plant diversity (Vitousek *et al.* 1997); and encourage plant invasion (Gilliam 2006) in nitrogen-limited systems. N deposition may result in decreased soil pH and base cation availability, as well as in increased availability of toxic metals (Dighton *et al.* 2004). In addition, loss of nitrogen in the form of leachate is a component of stream acidification (Townsend *et al.* 2004) and coastal eutrophication (Driscoll 2003). Very few nitrogen budgets, however, have been calculated for forests in the eastern United States. This lack of basic information makes it difficult if not impossible to assess the magnitude or importance of specific perturbations to nitrogen cycling.

During the summer months of 2006 and 2007, invasion of southern New Jersey forests by the gypsy moth (*Lymantria dispar* L.) resulted in mid-season defoliation of forest canopy and understory species. An oak-pine stand, located at the Rutgers Pinelands Field Station in the New Jersey Pine Barrens, was partially defoliated by gypsy moth larvae in 2006 and completely defoliated by reinvasion in 2007. In 2007, field plots within this stand were essentially leafless from June 1 to July 15. The field plots had been established in 2003 by the US Forest Service Global Change Program for the study of carbon dynamics in this ecosystem, so forest productivity had been documented prior to the defoliation event. The availability of productivity data and the occasion of a large-scale natural disturbance provided the opportunity to study the effects of defoliation on nutrient cycling through comparison.

Study objectives

The overall objective of this project was to produce forest nitrogen budgets for non-defoliated and defoliated years (2005 and 2007, respectively) based on measure-

ments within an oak-pine stand located near the Rutgers Pinelands Field Station, New Lisbon, NJ. I compared the two budgets to test hypotheses regarding the effects of gypsy moth invasion on N dynamics in this forest ecosystem and to explore mechanisms of N retention or loss following extensive insect disturbance.

Biometric measurements, soil data, and litterfall data have been collected annually in forest census plots. I collected forest inventory and litterfall data in 2007, the year of defoliation, and used data collected by the US Forest Service (USFS) in 2005 to calculate biomass and productivity for both years. I collected samples of live foliage, wood, leaf litter, and gypsy moth frass to analyze for nitrogen content. While awaiting laboratory analysis of these samples, I conducted a literature search for data pertaining to the nitrogen content of these ecosystem components. I substituted literature values for actual values where possible, to produce estimated budgets until the actual data are available. I calculated ecosystem nitrogen pools from biomass and nitrogen content data. Litter decomposition, frass decomposition, and microbial biomass have been studied in other contexts, making more data available for calculating a site-specific nitrogen budget. Once we understand the relative sizes of nitrogen pools and the magnitude and timing of nitrogen fluxes in an undisturbed year, we can test hypotheses about the fate of nitrogen deposited by defoliating insects.

I expect gypsy moths to have a large impact on nitrogen cycling. The New Jersey Pine Barrens are an oligotrophic system; such systems tend to have highly efficient mechanisms for conserving nitrogen (Gosz 1981; Publicover 1992). Retranslocation of N from foliage in the fall is likely to be large, as a consequence of internal N conservation. Extensive herbivory by gypsy moths defoliated the canopy in mid-summer, at the time of

maximum foliar N content. Nitrogen, which is normally redistributed, was deposited on the forest floor earlier than usual. The deposition of frass and live leaf material in mid-summer is likely to stimulate microbes that are already active in the soil. Laboratory incubations have shown that microbial activity is stimulated by readily-available carbon in the three months immediately following deposition (Lovett and Ruesink 1995). The moisture content of these materials, as well as the increased soil moisture due to decreased evapotranspiration (Clark *et al.* unpublished), is also likely to encourage microbial activity.

The microbial community should respond to early nitrogen deposition by immobilizing in biomass the nitrogen released from damaged leaves and frass. This response should follow the typical leaching, accumulation, and release phases of leaf litter decomposition (Berg and Staaf 1981). However, the timing of each phase may be shortened if the nitrogen in frass is more readily available than that in senesced leaves. Once carbon becomes limiting, the mineralization rate should decline and microbial biomass should decrease, again releasing nitrogen to soil pools.

I hypothesize that the initial immobilization of N by microbes will be followed by a net loss of nitrogen from the system. Damaged plants undergoing a second flush of growth may benefit from N captured by mycorrhizal fungi, but the rapid N cycling through the microbial pool will likely outpace plant demand. It is likely that plants will use nitrogen stores in order to produce leaves quickly and with minimal energy expenditure. In fact, a study by Christensen *et al.* (2002) indicates that although nitrogen in frass is mobilized more quickly than that in oak litter, the nitrogen is not retained in plant-available pools. Thus, plant uptake should not keep pace with nitrogen supply and much

of that N should be subject to leaching loss, as it is in the spring, before initial leaf-out (Zak *et al.* 1990). The loss of this N should be evident in the annual nitrogen budget.

In order to test my understanding of nitrogen dynamics following defoliation, I have: (1) estimated the amount of nitrogen stored in plants, soil and soil biota, and the forest floor; (2) estimated the annual rate of nitrogen accumulation in and transfer between ecosystem pools; (3) developed a nitrogen budget for the oak-pine stand by combining the data gathered for objectives (1) and (2) above with that from other studies conducted in this system. Further, I have (4) assessed the effect of gypsy moth defoliation on nitrogen cycling by comparing the 2005 and 2007 budgets.

Materials and Methods

Site description

The research site is located at Rutgers Pinelands Field Station in the Pine Barrens of south-central New Jersey. The Pine Barrens are the largest intact forest on the coastal plain of the northeastern United States, consisting of over one-million acres of semi-wilderness to moderately developed land. This is a cool temperate forest, with mean monthly temperatures ranging from 0.1ºC in January to 21.0ºC in June (1895-2008; State Climatologist of NJ). Mean annual precipitation is 1130 mm (1895-2008; State Climatologist of NJ). Soils are derived from the Cohansey and Kirkwood Formations (Lakewood and Sassafras soil series). These are sandy, coarse-grained, and oligotrophic soils with an organic horizon that is rarely more than 5-10 cm thick (Dighton *et al.* 2004). Cation exchange capacity and base saturation of the soils are low (Tedrow 1986). The Pine Barrens are a fire-maintained ecosystem; both wildfires and prescribed burning may further contribute to existing nutrient limitation (Gray and Dighton 2006).

The research plots at the Pinelands Field Station are within a 1 km^2 oak-pine stand – the Silas Little Experimental Forest (SLF) – where the USFS is currently measuring carbon dynamics with an eddy flux tower. The site is described in detail in Skowronski *et al.* (2007). The stand overstory is characterized by pitch pine (*Pinus rigida*), shortleaf pine (*P. echinata*), chestnut oak (*Quercus prinus*), black oak (*Q. velutina*), and white oak (*Q. alba*). Additional *Quercus* sp. make up the understory. The shrub layer is primarily ericaceous, composed of blueberry (*Vaccinium* sp.) and huckleberry (*Gaylusaccia* sp.). Pennsylvania sedge (*Carex pennsylvanica*) is the dominant herb. The stand is representative of other oligotrophic oak-pine forests throughout the Atlantic coastal plain. Within

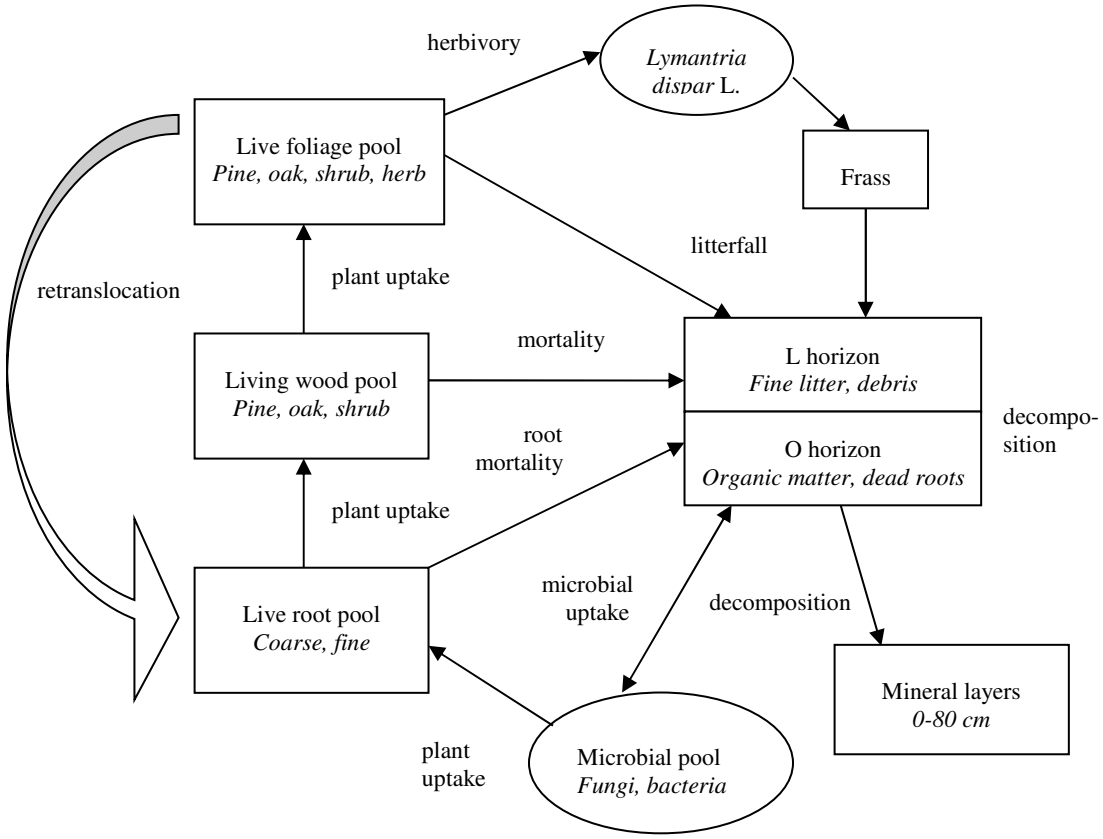
the New Jersey Pine Barrens, oak-pine forest comprises 46% of the approximately 620,000 total upland forest acres (Lathrop and Kaplan 2004).

Methods overview

A systems approach to the effect of defoliation on nitrogen cycling requires quantification of the major nitrogen reservoirs, or pools, and the rates of nitrogen accumulation in and transfer between those pools, or fluxes. I estimated the amount of nitrogen stored in each pool on an annual basis. I compartmentalized the ecosystem as follows: aboveground living pools (pine foliage, pine wood, overstory oak foliage, overstory oak wood, understory oak foliage, understory oak wood, shrub foliage, shrub wood, sedge); forest floor (fine litter, coarse woody debris, soil organic layer, coarse roots, fine roots, microbial biomass); and underground pools (soil mineral layers). I was able to quantify all pools except microbial biomass and the soil mineral layers. In years of herbivore invasion, the herbivores themselves are considered as one of the aboveground pools, while frass is considered a forest floor component. However, herbivore biomass was not measured for this study. Figure 1 presents my conceptual model of nitrogen dynamics in the oak-pine system.

I based the biomass of each ecosystem component on biometric measurements and/or field sampling of forest census plots. I estimated the nitrogen concentration of each material from literature values, pending complete sample analysis. The total nitrogen content of each ecosystem reservoir was calculated by multiplying the biomass of each pool, measured in grams per square meter, by the nitrogen concentration of the material in that pool, measured as percent nitrogen (dry weight basis).

FIGURE 1: General model of forest nitrogen dynamics.



Nitrogen fluxes were also estimated on an annual basis. Ecosystem fluxes that are relevant to my model of this system include: herbivory; primary productivity (foliage production, woody biomass accumulation, and root growth); plant uptake and retranslocation; litterfall; litter decomposition; microbial uptake; and mortality. The major nitrogen input to this system is in the form of atmospheric deposition. Output is likely to be in the form of leachate and/or volatilization. I calculated the transfer rate of each internal flux differently, and subsequent sections will explain these methods in detail. Not all of these fluxes could be calculated with the information at hand, so where appropriate, I substituted values from the literature.

Biometric measurements for living biomass

Overstory trees: Five 201 m^2 randomly located forest census plots were established by the USFS within 200 m of the eddy flux tower at SLF. In 2005, the USFS measured the diameter at 1.3 m (dbh in cm) and height of each pine and oak tree with a stem diameter ≥ 2.5 cm. The trees were tagged and numbered to facilitate remeasurement. I repeated the measures in 2007. I estimated tree biomass and growth increments from published allometric relationships (Whittaker and Woodwell 1968).

The Whittaker and Woodwell equations are based on parabolic volume estimates of biomass for each tree species and follow the form:

$$\log_{10}(y) = A + B \log_{10}(PV)$$

where PV is the parabolic stem volume, based on height and diameter, and y is biomass (Whittaker and Woodwell 1968). These equations were developed by destructive sampling of entire trees (Whittaker and Woodwell 1968). When the species at the Pinelands study site was not one analyzed by Whittaker and Woodwell, a species similar in form was substituted. For example, pitch pine regression coefficients were used for shortleaf pine, and scarlet oak coefficients were used for black oak. The parabolic volume regressions account for site differences in height-diameter relationships (Wang 1984).

The accuracy of the Whittaker and Woodwell (1968) equations was tested by Publicover for a pine-oak stand in the New Jersey Pine Barrens (1992). Publicover determined that the estimated biomass of 12 trees was 8.5% higher than the actual biomass. While Publicover (1992) adjusted the equations for the NJ Pine Barrens, Wang (1984) and others did not. The equations have not been adjusted here.

It should be noted that I could not estimate foliage biomass of overstory trees with any accuracy in 2007, the year of defoliation. As the trees were leafing-out, leaves and needles were simultaneously being consumed by gypsy moths. It cannot be assumed that the foliage biomass reached its full potential, as estimated by the allometric equations. The second flush of leaves, following the disturbance, may not have reached full biomass either. The second flush of overstory foliage biomass for 2007 is therefore estimated as follows: (1) pine foliage is assumed to be 50% of the foliage total estimated by the Whittaker and Woodwell equation and (2) oak foliage is assumed to be approximately 110% of the foliage captured in litterfall traps later that year. These assumptions are based on past experience in this system and are explained below.

Pitch pine standing foliage represents two years of growth. The 50% figure assumes that pitch pines were able to regenerate a full year's crop of needles in the second flush; it is also possible that trees achieved >50% biomass as maximum photosynthetic capability was recovered. I estimated oak foliage from litterfall, because it is known that litterfall traps capture most of the oak foliage pool. The 110% figure is based on the known relationship between shrub foliage and shrub litter; i.e., litter traps capture approximately 90% of shrub foliage (Dr. Kenneth Clark, pers. comm.). It can be assumed that litterfall traps likewise capture at least 90% of oak foliage, although this figure is probably an underestimate based on previous years' figures. Both wood and foliage biomass are calculated per plot; i.e., biomass estimates for individual trees are averaged and the mean of the five plots is taken as the overall stand biomass.

Understory vegetation: The understory vegetation consisted of small or shrubby oaks, ericaceous shrubs, and sedges. The presence of herbaceous plants other than Penn-

sylvania sedge was so rare as to be negligible. I estimated the biomass of understory vegetation by harvesting ten 1.0 m^2 clip plots in 2007 and referring to clip plot data collected by the USFS for 2005. Two plots were selected randomly within the vicinity of each forest census plot in order to minimize disturbance within the plot itself. (Repeated clipping may adversely affect ongoing studies of forest productivity within the plots.) The plots were completely harvested during the time of peak biomass in late summer. I considered standing dead stems to be part of that year's mortality and did not include them in understory biomass. I harvested the 2007 clip plots after defoliation, in the latter part of the growing season; these represent the second flush of understory foliage. After harvest, I removed leaves from woody stems and separated them by species. All materials were oven-dried at 60°C then weighed. I took the average of ten sub-plots, two per forest census plot, as the annual biomass value.

Forest floor biomass

Forest floor materials are those pieces of debris, mostly leaves and wood, that were deposited on the forest floor within the past few years, as well as the organic soil layer. Fine litter and debris are together called the L horizon, while the O horizon is the 5-10 cm layer of partially decomposed humus and roots located between the surface litter and the mineral soil. In the NJ Pine Barrens, the large majority of fine roots and microbial biomass is found in the organic layer.

L and O horizons: The mass of fine litter and the mass of coarse woody debris were estimated twice by the USFS, once in 2003 and once in 2008, and I utilized these data for my budgets. In 2003, two 1.0 m^2 random subplots in the vicinity of each tree

census plot (n = 10 subplots total) were sampled by the USFS for fine litter and woody debris. I used these data for the 2005 budget because 2005 data were not available. There are no O horizon data available for either of these years.

In 2008, three 0.1 m^2 random subplots in the vicinity of each tree census plot, plus nine 0.1 m^2 random subplots (n = 24 subplots total) close to the eddy flux tower were sampled by the USFS for L and O horizons. I used these data for the 2007 budget.

Woody debris was separated from fine litter. For the O horizon materials, roots were first separated from humic materials and then separated according to size. Coarse roots are those which range from 2-5 mm in diameter. Fine roots are those less than 2 mm in diameter. All materials were oven-dried at 60°C then weighed. I calculated the biomass of each forest floor component as the mean across subplots.

Calculation of nitrogen pools

I estimated nitrogen pools in living, forest floor, and underground biomass by multiplying biomass by nitrogen concentration (expressed as g N/100 g dry weight) extracted from the literature. Wang (1984) reported on the nitrogen concentration of live *Pinus rigida* and *Quercus alba* wood and foliage in the NJ Pine Barrens; his values were assumed to be representative of other pine and oak species, pending laboratory analysis of our own samples. The nitrogen concentration of live shrub foliage and wood was not available, so the nitrogen content of pine foliage and wood was used as a proxy.

To calculate forest floor pools, I substituted Wang's (1984) nutrient content values for fine litter, soil organic matter, and roots. I averaged the N content of pine and oak wood to estimate the N content of coarse woody debris. Information on frass nitrogen

content was available from Dr. Dennis Gray of the Pinelands Field Station. Finally, I gleaned root nitrogen content from Wang's study of fire effects on nutrient dynamics (1984). Wang's values for pitch pine roots and oak roots were averaged, because our sampling protocol did not distinguish between species. While none of these substitutions are entirely acceptable, these are the best data available to represent this system at this time and should provide an indication of the magnitude of the disturbance to N cycling.

Nitrogen fluxes

The movement of nitrogen between and rate of accumulation within forest reservoirs is described visually in Figure 1. This general model suggests the major fluxes of nitrogen in the oak-pine system, but it does not differentiate between plant species or between fungal and bacterial functional groups. The modeled fluxes include: herbivory; primary productivity (foliage production, woody biomass accumulation, and root growth); plant uptake and retranslocation; litterfall; litter decomposition (including frass); microbial uptake; and mortality. The internal fluxes for which data is currently available are: primary productivity (foliage production and woody biomass accumulation only); plant uptake and retranslocation; litterfall; and mortality. It is possible that predation of gypsy moth caterpillars and migration of the gypsy moths themselves constitute outputs of nitrogen from the system. Neither of these processes was studied; for the moment it will be assumed that predation and migration have minor impacts on forest nitrogen dynamics.

Herbivory: Data were not collected specifically on herbivory. Due to the timing of caterpillar emergence, it is unclear exactly how much foliage the caterpillars consumed. For the purposes of this study, litterfall in the form of frass and damaged leaves can give us a

rough idea of herbivore consumption. We do not know, however, how the biomass of the caterpillars themselves changed over time.

Foliage production and litterfall: The actual foliage production of tree and shrub species (*Pinus* sp., *Quercus* sp., *Vaccinium angustifolium*, *Gaylusaccia baccata*) and Pennsylvania sedge (*Carex pennsylvanica*) is represented by annual litterfall amounts. Litterfall also provides an estimate of how much nitrogen is transferred to the forest floor annually (excluding atmospheric deposition). Fine litterfall was collected monthly by the USFS from two 0.42 m^2 wire mesh traps adjacent to each tree census plot (n = 10 traps total). In 2007, the year of defoliation, frass was also collected, but on a biweekly rather than monthly basis. We separated litterfall samples into leaves, needles, stems, frass, reproductive material of trees and shrubs, and miscellaneous. All materials were oven-dried at 60°C then weighed. I estimated the total nitrogen in each litterfall compartment by multiplying the biomass of each material by its nitrogen concentration. The nitrogen content of leaf litter, or senescent foliage, was extracted from Gray and Dighton (2006). I substituted nitrogen content of pitch pine (*Pinus rigida*) for all pine litter, N content of white oak (*Quercus alba*) for all overstory and understory oak species, and N content of black huckleberry (*Gaylusaccia baccata*) for shrub litter. Frass N content was gleaned from an ongoing study of frass decomposition (Dr. Dennis Gray, pers. comm.). Nitrogen content of reproductive parts was unavailable.

In 2007, I separated litterfall into two pools. The first pool, or "flush," corresponds to the first flush of leaves, those consumed by the gypsy moths and redeposited mainly as frass. The second litterfall pool represents the flush of leaves which grew after

the gypsy moths laid their egg masses and perished in mid July. The two pools are added together to produce the annual litterfall total.

Shrub species are difficult to sample adequately with litterfall traps, because their low stature prevents their leaves from being captured. For this reason, shrub leaf litter is often estimated as 90% of shrub foliage biomass when calculating litterfall nitrogen flux. This figure is based on long-term data related to the carbon dynamics of this system (Dr. Kenneth Clark, pers. comm.). Pine foliage is also sampled inadequately, because the litterfall traps are located randomly and senescent needles tend to accumulate directly beneath pine trees. Pines replace 50% of their needles annually, so foliage production is typically estimated as 50% of total foliage biomass. However, pine and shrub production could not be estimated in this fashion from the 2007 dataset. Due to the timing of gypsy moth caterpillar emergence, the biomass represented by the first flush of foliage is unknown. Nor can the second flush be inferred; it is unclear whether trees fully leafed-out after July 15, but observation suggests they did not. Due to these uncertainties, the 2005 litterfall data remains in its raw form. The data reflects the foliage actually captured in litter traps; undersampled perhaps, but comparable to the 2007 data.

The two 2007 litterfall pools differ. The first capture was composed of young leaves that were high in nitrogen; the second litterfall collection was composed of senesced leaves that had already retranslocated much of their N to other tissues. I based my calculation of total N in the first sample on the concentration of nitrogen in live foliage. The biomass of the second sample was multiplied by the nitrogen content of senesced foliage, extracted from the literature.

Woody biomass accumulation: Wood productivity can be viewed as the amount of nitrogen accumulated in woody tissue annually. I estimated annual woody biomass accumulation by subtracting the biomass of one year from the biomass of the succeeding year; this figure represents biomass increase due to annual growth. Recall that biomass is estimated from published allometric relationships (Whittaker and Woodwell 1968). The biomass difference was then multiplied by the nitrogen content of wood to estimate annual nitrogen storage in woody plant tissues. *Pinus* sp. and *Quercus* sp. are estimated together, because there were very few pine trees per plot.

Retranslocation: Retranslocation is the movement of nitrogen from senescing leaves to other parts of a plant; it is an internal nitrogen retention mechanism. Retranslocation is quantified as the percent change in nutrient concentration from living leaves to abscissed leaves that have not yet contacted soil. I estimated retranslocation in my plots using literature values for senescent and live foliage nitrogen concentration. At present, data is available for *Pinus rigida*, *Quercus alba*, and *Gaylusaccia baccata* only.

Plant uptake: The amount of nitrogen taken up by a particular plant species is the amount of nitrogen required by that species, minus the amount of nitrogen retranslocated to roots in the fall (Publicover 1992). I determined the plant requirement for nitrogen by multiplying the productivity of each component (foliage, wood, roots) by the nitrogen concentration of that component. I estimated this flux for both overstory and understory species.

Mortality: The nitrogen content of each unit of plant biomass is either returned to the soil as debris/litter or accumulated in growing tissues. For the most part, tree mortality is captured during annual biometric measurements of census plots. Tree and shrub

mortality is also captured as the coarse woody debris component of the forest floor and the wood component of litterfall. Root death may represent a significant flux of nitrogen to the organic soil horizon, but roots were not separated into living and dead pools for the present study. We used a combined measure.

Preliminary results

Annual nitrogen budget for the undisturbed system

Standing pools of nitrogen for 2005 are summarized in Table 1 and presented graphically in Figure 2. The total biomass for the oak-pine system in 2005 (including biomass substitutions) was 11,518.84 g m^{-2}. The total N content was 80.45 g N m^{-2}. The belowground pools are not accurately represented in these numbers; neither the organic horizon nor the soil mineral layers were sampled in 2005. Biomass of the O horizon and root pools are substituted values from the 2007 dataset. Aboveground components were well-sampled.

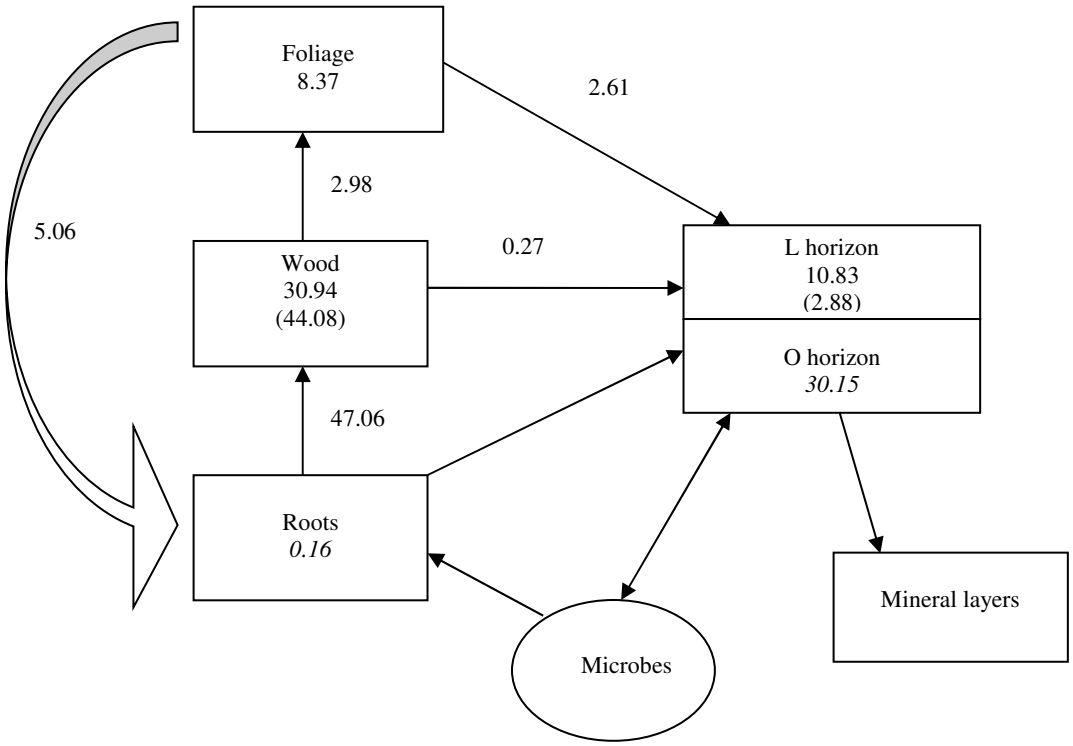
TABLE 1: Biomass summary, 2005.

Nitrogen pools in biomass of oak-pine forest site in the New Jersey Pine Barrens. Biomass data represent peak productivity at mid-summer. *Biomass figures in italics were substituted from the 2007 dataset. Totals in parentheses indicate missing or estimated data in that column.*

Ecosystem component	Mean biomass (± 1SD) ($g\ m^{-2}$)	% N	Total N ($g\ N\ m^{-2}$)
Pine foliage	89.81 (±101.98)	1.0[1]	0.90 (±1.02)
Pine wood	1961.48 (±2333.99)	0.16[1]	3.14 (±3.73)
Oak foliage	373.05 (±77.30)	1.9[1]	7.09 (±1.47)
Oak wood	6116.83 (±1618.97)	0.45[1]	27.53 (±7.29)
Overstory total	**8541.17 (±2616.40)**		**38.65**
Understory oak foliage	2.49 (±4.64)	1.9	0.05 (±0.09)
Understory oak wood	4.55 (±9.50)	0.45	0.02 (±0.04)
Shrub foliage	31.98 (±7.46)	1.0[2]	0.32 (±0.07)
Shrub wood	154.55 (±80.82)	0.16[2]	0.25 (±0.13)
Sedge	1.10 (±1.71)	1.0[2]	0.01 (±0.02)
Understory total	**193.57 (±80.80)**		**(0.65)**
Fine litter	844.70 (±133.60)	1.2[1]	10.14 (±1.60)
Coarse woody debris	223.40 (±141.90)	0.31[3]	0.69 (±0.44)
Soil organic matter	*1603.80 (±509.10)*	1.8[1]	30.15 (±9.57)
Coarse roots	*9.60 (±16.60)*	0.15[1]	0.01 (±0.02)
Fine roots	*102.50 (±65.60)*	0.15[1]	0.15 (±0.10)
Microbial (MBN)	na	0.15[4]	--
Forest floor total	**(2784.00)**		**(41.15)**
Soil mineral layers	na	--	--
Belowground total	**--**	**--**	**--**

[1] Wang 1984.
[2] Pine N content; see text.
[3] Average of pine and oak.
[4] Gray, *personal communication*.

FIGURE 2: Annual nitrogen budget of an oak-pine stand in the NJ Pine Barrens, 2005. The values in boxes are grams of nitrogen per square meter. The values in parentheses are rates of accumulation; these and flux rates, the values adjacent to arrows, are grams of nitrogen per square meter per year. Values in italics are substitutions from the 2007 dataset.



Estimated foliage production, based on allometric equations, totaled 498.43 g m^{-2}, or 5.7% of total aboveground production. Of this, overstory oak foliage was the dominant component; 4.3% of total aboveground production. Leaves of overstory oaks – mainly chestnut oak, black oak, and white oak – contributed 7.09 g N m^{-2} to the living biomass pool. The total nitrogen content of the foliage pool was 8.37 g N m^{-2}. This figure includes estimated nitrogen content for ericaceous shrubs and sedges. Biomass of the shrub and sedge pools was based on clip plot data and is accurate. The % N in foliage, however, was not available, so the 1% N of pine foli-

age was used as an estimate. This is likely to be an underestimate, but it will act as a placeholder until further study is complete.

The nitrogen in living wood biomass totaled 30.94 g N m^{-2}. Again, overstory oak was by far the largest ecosystem component; oak wood represents 70% of total aboveground biomass and 34.2% of total forest nitrogen.

The forest floor was not completely sampled in 2005. Table 1 includes O horizon data from the 2007 dataset (soil organic matter and roots) in order to better estimate the forest floor pool. The L and O horizons represent approximately 41.15 g N m^{-2}. Soil organic matter, if the estimate is truly representative of 2005, is the largest nitrogen reservoir, containing 30.15 g N m^{-2} or 73.3% of forest floor nitrogen. The fine litter fraction, a layer of debris that contains up to five years litterfall, contains 26.4% of forest floor nitrogen. The estimated root pool is relatively small, contributing only 0.16 g N m^{-2} to the total. Aboveground mortality is somewhat represented in the coarse woody debris pool, but belowground mortality is not captured.

In 2005, approximately 2.87 g N m^{-2} fell to the forest floor, mainly as leaf litter (Table 2). 21.6% of leaf litter biomass was in the form of reproductive parts of plants (seeds, cones, etc.), woody debris, and miscellaneous debris. Pine litter, 6.38 g m^{-2}, represents 7.1% of total pine foliage biomass. (In comparison, if the 50% of biomass estimate is substituted for the litterfall value to compensate for undersampling, the biomass of pine litter would be 44.91 g m^{-2}.) The sampled pine litter contributes 1.0% of the total litterfall nitrogen. Oak litter, understory and overstory oaks taken together, represents 88.6% of the biomass estimate, based on allometric equations for *Quercus* species. Oak litter contributes 80.1% of total litterfall nitrogen.

TABLE 2: Annual litterfall in an oak-pine forest site in the NJ Pine Barrens, 2005.

Litterfall component	Mean biomass (± 1SD) ($g\ m^{-2}$)	% N	Total N ($g\ N\ m^{-2}$)	Reference
Pine litter	6.38 (±5.84)	0.43	0.03 (±0.03)	Gray and Dighton 2006
Leaf litter	332.85 (±38.51)	0.69	2.30 (±0.27)	Gray and Dighton 2006
Shrub litter	28.78 (±6.71)	0.97	0.28 (±0.07)	Gray and Dighton 2006
Reproductive parts	8.27 (±5.53)	--	--	
Wood	85.79 (±94.37)	0.31	0.27 (±0.29)	average of pine and oak
Miscellaneous	7.55 (±2.50)	--	--	
Litterfall total	**469.62 (±104.58)**		**(2.87)**	

Estimated aboveground productivity totaled 542.51 $g\ m^{-2}$ biomass in 2005. This figure includes foliage production (Table 1) and woody biomass accumulation (Table 3). Root production is not included, due to lack of growth increment data. As shown in Table 1, foliage production, discounting shrubs and sedges, required a total of 8.04 $g\ N\ m^{-2}$. An estimated 63.7% of oak foliage N, or 4.55 $g\ N\ m^{-2}$, was retranslocated in the fall (Table 4). Retranslocation for pine foliage is estimated at 57% or 0.51 $g\ N\ m^{-2}$. When the 5.06 $g\ N\ m^{-2}$ retranslocation figure is taken into account, annual plant uptake of nitrogen for foliage production totaled 2.98 $g\ N\ m^{-2}$. Woody biomass accumulation of nitrogen in 2005 totaled 44.08 $g\ N\ m^{-2}$; this is the amount of N bound in woody tissue produced in the previous year. This figure was obtained by using the average % N in live pine and oak wood, so it is not accurate. The total plant uptake during an undisturbed year totals 47.06 $g\ N\ m^{-2}$ (Table 5).

TABLE 3: Annual accumulation (storage) of nitrogen in woody plant tissues in an oak-pine forest site in the NJ Pine Barrens, 2005.

Year	Mean biomass in wood (± 1SD) ($g\ m^{-2}$)	Wood production (± 1SD) ($g\ m^{-2}$)	% N	Total N (± 1SD) ($g\ N\ m^{-2}$)
2004	7936.06 (± 2508.75)	--		
2005	8078.31 (± 2510.87)	142.2 (± 86.6)	0.31	**44.08 (± 26.85)**
2006	8271.78(± 2511.32)	--		
2007	8524.89 (± 2542.63)	253.10 (± 165.4)	0.31	**78.46 (± 51.28)**

TABLE 4: Annual movement of nitrogen from foliage to roots for tree and shrub components.

Component	Live foliage % N (g N/100 g biomass)	Senescent foliage % N (g N/100 g biomass)	Difference	Retranslocation (% change)
Oak	1.9	0.69	1.21	63.7%
Pine	1.0	0.43	0.57	57.0%
Shrub	na	0.97	--	--

TABLE 5: Annual uptake of nitrogen by trees and shrubs, 2005. Plant uptake is calculated as plant N requirement minus retranslocation of foliar N. Totals in parentheses indicate missing or estimated data in that column.

Component	Retranslocation (% change)	Foliar N requirement ($g\ N\ m^{-2}$)	Foliage uptake ($g\ N\ m^{-2}\ yr^{-1}$)	Wood production ($g\ m^{-2}$)	Wood uptake ($g\ N\ m^{-2}\ yr^{-1}$)	Total uptake ($g\ N\ m^{-2}\ yr^{-1}$)
Overstory oak	63.7%	7.09	2.57	--	--	--
Understory oak	63.7%	0.05	0.02	--	--	--
Pine	57.0%	0.9	0.39	--	--	--
Shrub	na	na	--	--	--	--
TOTAL	--	--	(2.98)	142.20	44.08	**47.06**

Nitrogen budget for a year with extensive defoliation

The distribution of nitrogen in standing pools for 2007 is summarized in Table 6 and presented graphically in Figure 3. The total biomass for the ecosystem in 2007, the year of mid-summer defoliation, was 11,753.66 g m^{-2}. The total N content of the system was 81.39 g N m^{-2}. The aboveground foliage compartments are split into first and second flush pools to indicate that: (1) the initial flush of leaves was completely consumed and (2) allometric equation estimates were not used for foliage regrowth. There is no clear way to estimate the biomass of the first flush of foliage. The allometric equations used for 2005 estimates would probably overestimate foliar biomass in 2007. As the trees were leafing-out, foliage was being consumed by gypsy moth caterpillars. It is unlikely that trees reached full biomass. Leaf litter captured in litterfall traps provided the basis for estimating the second flush oak foliage. Understory and overstory oak foliage could not be distinguished, and the overstory foliage total represents both compartments. Shrub foliage production was based on clip plots. Pine foliage is 50% of the allometric estimate, due to the difficulty of sampling needles with litterfall traps. This estimate is based on productivity studies in this stand (Dr. Kenneth Clark, pers. comm.).

The estimated productivity of the second flush of foliage is 224.7 g m^{-2} biomass which represents 3.7 g N m^{-2}. The nitrogen content of ericaceous shrubs is an estimate; the 1% N content of pine foliage was used as a proxy for shrub N content because it is the lower of the two available measures. Nitrogen content of aboveground wood totaled 32.73 g N m^{-2}. The 2007 measurements indicate that oak species, understory and overstory, represent 56.6% of total site biomass and 32.3 g N m^{-2}.

TABLE 6: Biomass summary, 2007.

Nitrogen pools in biomass of defoliated oak-pine forest site in the NJ Pine Barrens. Biomass data represent peak productivity at mid-summer. Overstory data is separated into early and post-defoliation compartments. *Totals in parentheses indicate missing or estimated data in that column.*

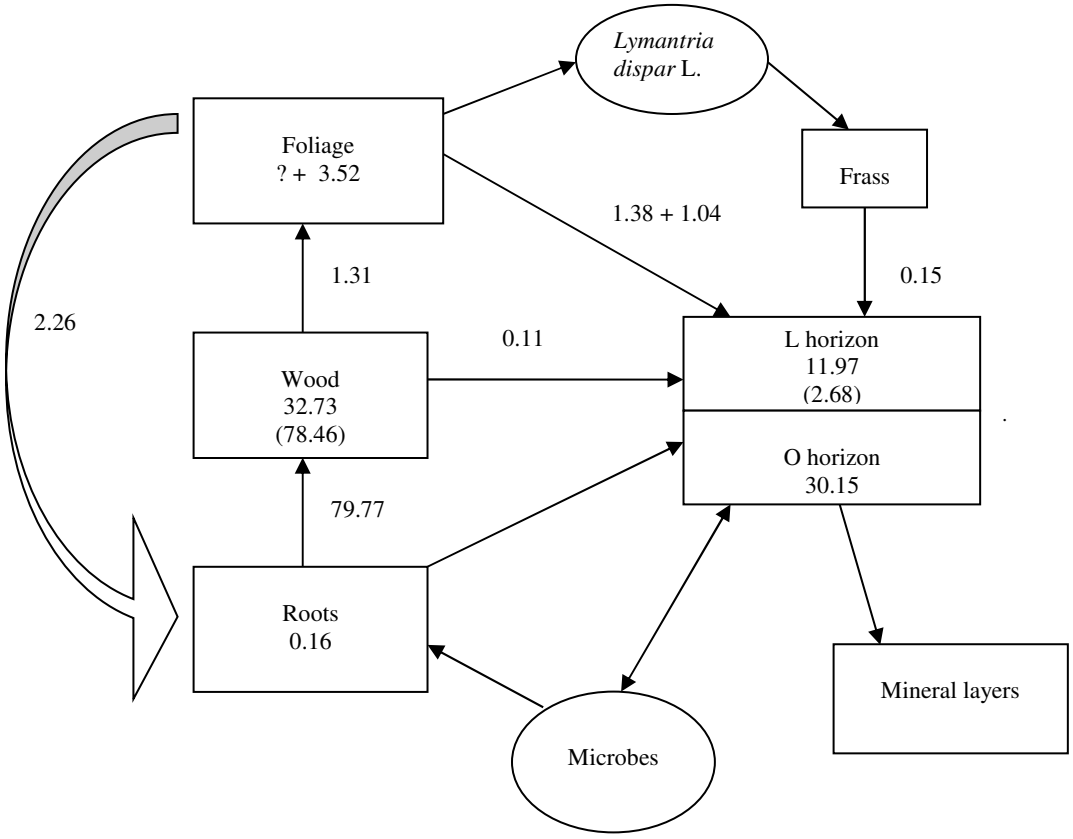
Ecosystem component	Mean biomass (± 1SD) ($g\ m^{-2}$)	% N	Total N ($g\ N\ m^{-2}$)
Pine foliage	0		
Second flush	46.28 (±52.52)	1.0[1]	0.46
Pine wood	2034.42 (±2432.26)	0.16[1]	3.26 (±3.89)
Oak foliage	0		
Second flush	160.85 (±21.84)	1.9[1]	3.06 (±0.41)
Oak wood	6490.44 (±1587.83)	0.45[1]	29.21 (±7.15)
Overstory total	**8778.27**		**38.66**
Understory oak foliage	0		
Second flush	na	1.9	--
Understory oak wood	5.83 (±18.43)	0.45	0.03 (±0.08)
Shrub foliage	0		
Second flush	17.50 (±8.28)	1.0[2]	0.18 (±0.10)
Shrub wood	141.79 (±179.48)	0.16[2]	0.23 (±0.41)
Sedge	0.07 (±0.13)	1.0[2]	0.00 (±0.00)
Understory total	**(165.19)**		**(0.44)**
Fine litter	963.80 (±195.70)	1.2[1]	11.57 (±2.35)
Coarse woody debris	130.50 (±96.80)	0.31[3]	0.40 (±0.30)
Soil organic matter	1603.80 (±509.10)	1.8[1]	30.15 (±9.57)
Coarse roots	9.60 (±16.60)	0.15[1]	0.01 (±0.02)
Fine roots	102.50 (±65.60)	0.15[1]	0.15 (±0.10)
Microbial	na	0.15[4]	--
Forest floor total	**(2810.20)**		**(42.29)**

[1] Wang 1984.
[2] Pine N content; see text.
[3] Average of pine and oak.
[4] Gray, *personal communication*.

TABLE 6: CON'T

Ecosystem component	Mean biomass (± 1SD) ($g\ m^{-2}$)	% N	Total N ($g\ N\ m^{-2}$)
Soil mineral layers	na	--	--
Belowground total	**--**	**--**	**--**

FIGURE 3: Annual nitrogen budget of an oak-pine stand in the NJ Pine Barrens for a year with extensive defoliation, 2007. The values in boxes are grams of nitrogen per square meter. The values in parentheses are rates of accumulation; these and flux rates, the values adjacent to arrows, are grams of nitrogen per square meter per year.



The forest floor L and O horizons were sampled more thoroughly in 2008 than in 2003. (Recall that 2003 data were substituted for 2005 and 2008 data for 2007.) Together, the two horizons contain approximately 42.29 g N m^{-2}. The largest forest floor nitrogen pool is soil organic matter, which holds 30.15 g N m^{-2} or 71.29% of the forest floor total. The fine litter fraction is the second largest pool, representing 27.36% of the total. The root pool, composed of both fine and coarse roots, totals 0.16 g N m^{-2}, and 0.38% of the total.

In 2007, a total of 2.66 g N m^{-2} fell to the forest floor as litter (Table 7). The nitrogen concentration of the foliage in the first litterfall pools is that of live foliage; these are damaged

leaves that fell to the ground during the growing season. The biomass of pre-defoliation litterfall was 171.87 g m^{-2} and contributed 1.53 g N m^{-2} to the forest floor pool. The frass component totaled 0.15 g N m^{-2}; thus, 8.3% of total nitrogen deposited to the forest floor in 2007 was in the form of frass. Herbivory caused 32.2% of the annual litterfall total to be deposited on the forest floor during the growing season. Post-defoliation litterfall was 361.49 g m^{-2} and represented 67.8% of the annual total. The litter in this second pool has lower nitrogen concentrations, because it has undergone retranslocation. Of the second flush total, oak litter is by far the largest pool, contributing 1.01 g N m^{-2} to the forest floor.

TABLE 7: Annual litterfall in an oak-pine forest site in the NJ Pine Barrens, 2007. The data is separated into pre- and post-defoliation collections.

Litterfall component	Mean biomass (± 1SD) (g m^{-2})	% N	Total N (g N m^{-2})	Reference
Pine litter	3.98 (±2.65)	1.0	0.04 (±0.03)	Wang 1984
Leaf litter	69.84 (±19.32)	1.9	1.33 (±0.37)	Wang 1984
Understory litter	0.78 (±1.5)	1.0	0.01 (±0.02)	Wang 1984
Frass	97.27 (±54.49)	0.15	0.15 (±0.08)	Gray, pers. comm.
Early litterfall total	**171.87 (±69.87)**		**1.53**	
Pine litter	1.69 (±1.24)	0.43	0.01 (±0.01)	Gray and Dighton 2006
Leaf litter	146.23 (±19.85)	0.69	1.01 (±0.14)	Gray and Dighton 2006
Shrub litter	1.79 (±2.07)	0.97	0.02 (±0.02)	Gray and Dighton 2006
Reproductive parts	4.00 (±5.83)	--	--	
Wood	35.75 (±18.84)	0.31	0.11 (±0.06)	average of pine and oak
Miscellaneous	0.16 (±0.51)	--	--	
Post-defoliation total	**361.49 (±74.15)**		**(1.15)**	
Litterfall total	**533.36**		**2.68**	

Estimated aboveground productivity totaled 302.77 g m^{-2} biomass in 2007. This total is underestimated for two reasons: (1) it is based on litterfall data, and senesced leaves have lower moisture content than live foliage and (2) frass is not included, because the relationship between

frass weight and amount of foliage consumed is unknown. In comparison, if foliage productivity is estimated with the allometric equations, rather than on litterfall, annual productivity is 574.22 g m^{-2} biomass. Again, this figure represents foliage production and woody biomass accumulation but *not* root production. The production of the second flush of overstory and understory foliage required a total of 3.52 g N m^{-2} (Table 8). Taking into account the 63.7% and 57% retranslocation figures, oak and pine respectively, annual N uptake for foliage production totaled 1.26 g N m^{-2}. Pines retranslocated 0.31 g N m^{-2}, and oaks retranslocated 1.95 g N m^{-2}. Woody biomass accumulation of nitrogen in 2007 totaled 78.46 g N m^{-2} (Table 3). The total plant uptake for a year with insect defoliation totaled 79.77 g N m^{-2}.

TABLE 8: Annual uptake of nitrogen by trees and shrubs, 2007. Plant uptake is calculated as plant N requirement minus retranslocation of foliar N. Totals in parentheses indicate missing or estimated data in that column.

Component	Retranslocation (% change)	Foliar N requirement (g N m^{-2})	Foliage uptake (g N m^{-2} yr^{-1})	Wood production (g m^{-2})	Wood uptake (g N m^{-2} yr^{-1})	Total uptake (g N m^{-2} yr^{-1})
Overstory oak	63.7%	3.06	1.11	--	--	--
Understory oak	63.7%	na	--	--	--	--
Pine	57.0%	0.46	0.2	--	--	--
Shrub	na	na	--	--	--	--
TOTAL	--	--	(1.13)	253.10	78.46	**79.77**

Discussion

The nitrogen budgets for 2005 and 2007 are remarkably similar in terms of aboveground pools and processes. Despite defoliation, the early deposition of high-nitrogen leaf matter and frass, and a second flush of leaves during the same season, the 2007 nitrogen budget does not seem to indicate a large effect of herbivory on short-term nitrogen cycling. Key information is lacking, however, and it is this very information that may be most crucial to our understanding of nitrogen dynamics in the Pine Barrens. The hypothesized pathway of nitrogen loss – initial uptake by microbes followed by release at a time when plant demand is low – is dependent on altered forest floor and belowground processes. While the forest floor was completely sampled in 2008, only the L horizon was sampled in 2003. Literature values cannot compensate for this lack of data.

Aboveground pools and processes

The total biomass of the oak-pine stand is 11,518.84 g m^{-2} in 2005 and 11,753.66 g m^{-2} in 2007. In comparison, for a pine-oak stand in the NJ Pine Barrens, Publicover (1992) calculated a total living biomass of 10,750 g m^{-2}. Wang (1984) also studied a pine-oak stand and calculated a total living biomass of 9,100 g m^{-2}. The foliage pool in 2005 represents 8.37 g N m^{-2}, while the second flush of 2007 is 3.52 g N m^{-2}. The estimates of aboveground nitrogen pools are reasonable, but production of these pools is not as clear.

Plant uptake for foliage production is 2.98 g N m^{-2} in 2005 and 1.13 g N m^{-2} in 2007. Again, uptake is the difference between plant N requirement and retranslocation. Neither of these parameters could be estimated with any certainty. Retranslocation is based on literature values for senescent foliage, and an estimate for shrub retranslocation of N is completely lacking.

Foliage productivity cannot be reasonably estimated for 2007 without an understanding of how much leaf matter the caterpillars actually consumed between June 1 and July 15. The allometric equations would place the 2007 foliage total at 495.76 g m^{-2} biomass. If the estimate for the second flush is correct, 224.70 g m^{-2}, then the herbivores may have consumed up to 271.06 g m^{-2}. This is equivalent to 2.71 to 5.15 g N m^{-2}. This seems possible, given that 1.53 g N m^{-2} was deposited as frass and leaf particles and some amount of nitrogen was incorporated into caterpillar or egg biomass.

Estimating woody biomass accumulation was also problematic. The increase in wood increment is highly variable between plots and between years. For example, one plot showed a 56.02 g m^{-2} biomass increase from 2004 to 2005 and a 420.38 g m^{-2} increase from 2006 to 2007. This seems unlikely, and the pattern does not repeat across the other four plots. The average growth increment across plots was 142.2 ±86.6 g m^{-2} in 2005 and 253.10 ±165.4 g m^{-2} in 2007. The woody biomass accumulation is thus larger than the live wood pool, especially in 2007 when the former was 78.46 g N m^{-2} and the latter was 32.73 g N m^{-2}. Considering the large standard deviations of live wood biomass, especially that of pine, this result is perhaps not that surprising. It does not, however, explain the discrepancy with Wang's data; Wang (1984) estimated a nitrogen accumulation in biomass of 0.25 g N m^{-2}.

Forest floor and litterfall

The litterfall total for 2007 was approximately 63.74 g m^{-2} more than the 2005 total. This slight increase generally agrees with Grace (1986) who found that the total quantity of litter was unchanged in an oak forest defoliated by gypsy moths, but the nutrient composition and seasonal distribution of that litterfall was altered. Grace found that defoliation increased litterfall N from

3.1 to 5.2 g m^{-2}. Here, litterfall N decreased slightly with defoliation, from 2.87 to 2.68 g N m^{-2}. Despite the higher N content of live foliage in the first litterfall collection, the quantity of litter was, of course, low. The quantity of frass in this collection was relatively high – approaching 30% of the 2005 litterfall total – but the nitrogen concentration of frass collected during the defoliation event is only 0.15% (Dr. Dennis Gray, pers. comm.). If we substitute the 1.5% N of frass suggested by Lovett and Ruesink (1995), then the total nitrogen in the frass pool increases to 1.46 ±0.82 g N m^{-2} and the annual litterfall N increases by 1.12 g N m^{-2} with defoliation.

The O horizon, including roots, was not sampled in 2005, and the forest floor data for the 2007 budget were collected in early 2008. This means that the only data available are post-disturbance and very likely show the residual effects of that disturbance. The pool of soil organic matter may be stable from year to year, or the 2007 pool may indicate N accumulation due to the decomposition dynamics of frass. As a point of comparison, Wang (1984) calculated the organic layer biomass of a pine-oak stand as 1,400 g m^{-2} while our 2007 pool is 1,750.9 g m^{-2}.

Root dynamics may also be affected by defoliation. Neither root growth nor root mortality were specifically calculated for this study. It is conceivable that defoliation resulted in immediate fine root death, but also possible that the annual budget would show a net increase in root biomass due to increased extractable nitrogen. Even if dead roots had been separated from live roots during the 2007 sorting process, there are no other data with which to compare these pools. Melillo (1981) indicates that root litter contains more nitrogen than plant litter and is the most important pathway of N transfer between plants and soil. If this is true in the Pine Barrens, then the nitrogen pulse represented by frass deposition may be followed by another pulse due to root mortality.

Belowground pools and processes

Data are completely lacking for microbial biomass nitrogen and nitrogen content of soil mineral layers. While microbial biomass might be expected to fluctuate enormously in response to environmental conditions, the total biomass of this pool at any one time is likely to be extremely small in comparison to other pools. Despite its size, the importance of the microbial pool to nutrient cycling is paramount. Microbial process rates determine the forms of nitrogen available in the soil and the timing of nitrogen availability. I did not measure microbial activity for this study; the preliminary investigation focuses on gross ecosystem pools and fluxes.

I also assumed the nitrogen pool represented by the soil mineral layers to be relatively small. Soil mineral layers seem to have very little organic matter; if true, these are unlikely to accumulate nitrogen. Wang (1984), however, claims that soil layers from at depths of 15-200 cm contain 15,800 g m^{-2} organic matter; this point should be further investigated.

Future study directions

Without a better sense of belowground nitrogen dynamics in this particular stand, it is premature to draw conclusions about the effect of herbivore invasion on nutrient cycling. Future study of this problem should proceed in two stages. First, the nitrogen budgets begun here should be revisited once the chemical analysis of live and litterfall samples is complete. The organic matter content of soil mineral layers should be added to the budgets. Process rates should be reassessed; particularly, litter and frass decomposition rates, woody biomass accumulation, and root growth. Second, the nitrogen budgets should be expanded to include system inputs and outputs. In the Pine Barrens, atmospheric deposition is the major source of nitrogen (as opposed to weathering and/or fixation). Output might occur through leaching loss and/or volatilization.

In years of gypsy moth invasion, migration of the moths or caterpillars and predation on the insects may also constitute outputs from the stand being characterized.

The current nitrogen budgets are based in large part on literature values. Most of these values are representative of the NJ Pine Barrens, but some are averages or generalizations. Current unpublished estimates of nitrogen concentration, for example, often do not agree with published figures. It is not clear whether foliar chemistry is stable enough for older values or estimates from other systems to act as acceptable substitutions. For example, the Tree Chemistry Database lists the nitrogen content of pine wood as 0.3-0.4% N (Pardo *et al.* 1995). These estimates are based on white and red pine measurements, not pitch pine, but the figures are quite different than Wang's (1984) estimate which was used here. Frass nitrogen content, a key component of the study, is estimated at 0.15% N (Dr. Dennis Gray, pers. comm.), 1.5% (Lovett and Ruesink 1995), and, for laboratory-fed insects, 6% (Christenson *et al.* 2002). Much of the literature data are questionable for one reason or another.

At present, field-collected samples have been processed for laboratory analysis of C:N ratios. The USFS collected live foliage samples at the peak of the growing season in 2006 from: pitch pine (*Pinus rigida*), shortleaf pine (*P. echinata*), chestnut oak (*Quercus prinus*), black oak (*Q. velutina*), white oak (*Q. alba*), lowbush blueberry (*Vaccinium pallidum*), black huckleberry (*Gaylusaccia baccata*), and Pennsylvania sedge (*Carex pennsylvanica*). Overstory tree foliage was collected with a pole pruner; trees were selected randomly from within or immediately adjacent to the five forest census plots and branch tips containing two to three years growth were cut. Understory foliage was collected by hand; again, trees and shrubs were randomly selected and branch tips were cut. Leaves were stripped from woody stems and later oven-dried at 60°C. I repeated these methods and prepared additional samples in 2008.

Representative samples of leaf litter, soil organic matter, frass, and roots were also collected. Roots were subsampled from the soil cores described in the Methods section, above. Leaf litter and woody debris samples were obtained from litterfall traps. Frass samples were also obtained from litterfall traps; these were processed within two weeks of deposition. Oven-dry samples of all materials were weighed and ground with a Wiley mill in preparation for nitrogen content analysis.

The lack of data for estimating retranslocation is also more troublesome than expected. Current estimates of retranslocation are high – 57 to 63.7% – which would suggest that the New Jersey Pine Barrens are a nitrogen-limited system. Despite having some indications of nitrogen limitation, it is not entirely clear whether the Pine Barrens ecosystem should be characterized as such. A study of pine seedling growth and ectomycorrhizal diversity under nitrogen fertilization indicated that nitrogen supply could easily exceed seedling nitrogen demand in Pine Barrens soils (Dighton *et al.* 2004). Dighton *et al.* (2004) found that even in treeless soil cores without added nitrogen, microbial immobilization could not keep pace with nitrogen supply. Also, the high C:N ratio of leaf litter in nitrogen-deficient sites is thought to make litter slow to decompose (Gosz 1981). This does not appear to be the case in the New Jersey Pine Barrens where decomposition is relatively rapid as indicated by the stable and shallow (5-10 cm) organic layer.

Both litter and frass decomposition rates should be reassessed. Decomposition data were minimal for this study, yet litter decomposition is a major component of nitrogen dynamics in terrestrial systems. The decomposition rates of various forest floor materials can be calculated using field-placed litterbags. Litterbags containing pine needles, overstory oak foliage, understory oak foliage, or shrub foliage can be placed in the field at random locations near each forest census plot. The bags can be harvested at 12, 24, 36, 48, and 64 months and mass loss can be

estimated. Forest floor mass balance is adjusted by accounting for the decomposition of foliage as estimated from mass. Frass decomposition can be studied in a similar manner if frass is available from captive gypsy moth populations.

Data for 2008 should be incorporated into the calculations of woody biomass accumulation. The estimates of this component of productivity were questionable and should be reassessed with a larger dataset. Root growth and mortality likely represent significant fluxes of nitrogen and should also be investigated further. Publicover (1992) suggests that half of root biomass increase is returned to the system annually (fine root mortality) and half remains in root tissues (coarse root accumulation).

Accurate assessment of the inputs and outputs of nitrogen to the forest system will place the internal nutrient dynamics into a larger context. In order to unravel the mechanisms driving nitrogen retention or loss, it is necessary to have some sense of the amount of nitrogen in soil solution under various conditions. Publicover (1992) found equivalence between atmospheric inputs and leaching losses from the rooting zone of Pine Barrens soils and offers this as evidence of efficient nutrient conservation mechanisms. Yet studies of nitrogen deposition across the northeastern United States show conflicting and variable nitrate leaching patterns. Seasonal fluctuations in surface water nitrate concentration have been documented, and there are complex issues surrounding chronic nitrogen deposition to forest soils (Aber *et al.* 2003). For example, one of the key indicators of nitrogen saturation is soil and water acidification; such a change may not be immediately evident in soils which normally have a low pH, as is the case in the NJ Pine Barrens. Without some knowledge of atmospheric deposition and soil leaching loss in a non-defoliation year, it would not be clear whether nitrogen loss after defoliation is substantial.

It would be beneficial to begin ongoing measurement of nitrogen deposition and nitrogen in soil solution to be able to see long-term patterns. A starting point is the approximately 0.53 g m^{-2} measured by Dighton *et al.* (2004) as the amount of inorganic nitrogen in bulk precipitation for a forest plot not far from the Pinelands Field Station. Similarly, dry deposition, bulk precipitation, and throughfall can be collected to monitor the amount of nitrogen entering the system from the atmosphere. Soil solution can be collected with soil lysimeters and correlated with meteorological data to gain an estimate of hydrological export of nitrogen under specific conditions.

On a final note, it is possible that the most significant effects of gypsy moth defoliation on nitrogen cycling were not apparent during the six months of 2007 following the event but will become evident in subsequent years. Tree mortality in 2008 was extremely high, particularly for black oaks. One possible explanation is nitrogen-deficiency, due to altered retranslocation and uptake patterns or nitrogen loss from the system. However, shrub and sedge biomass appear to be much higher than usual, suggesting that inorganic nitrogen is indeed available or that shrubs and sedges can capture different forms of nitrogen than can oaks. The most interesting avenue to pursue would be the interaction between trees, shrubs, and mycorrhizal fungi under elevated nitrogen conditions. Mycorrhizae and bacteria are often lumped together as "microbial biomass nitrogen," but these groups have very different functions in forest soils. A closer look at decomposition dynamics of both frass and leaf litter may provide the most insight into forest nitrogen dynamics. Ironically, a detailed study of small-scale microbial process rates is likely to lead to the most insight about the effects of defoliation on the ecosystem level.

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