Stony Brook University

The Impact of Plant Invasions on Nitrogen Cycling and Trace Gas Emissions

A Dissertation Presented

by

Jonathan Edward Hickman

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Ecology and Evolution

Stony Brook University

May 2009

Stony Brook University

The Graduate School

Jonathan Edward Hickman

We, the dissertation committee for the above candidate for the Doctor of

Philosophy degree, hereby recommend acceptance of this dissertation.

Manuel T. Lerdau, Dissertation Advisor
Professor, Department of Ecology and Evolution, Stony Brook University

Catherine Graham, Chairperson of Defense
Assistant Professor, Department of Ecology and Evolution, Stony Brook University

Jessica Gurevitch
Professor, Department of Ecology and Evolution, Stony Brook University

Peter Groffman
Senior Scientist, Cary Institute of Ecosystem Studies

This dissertation is accepted by the Graduate School

Lawrence Martin
Dean of the Graduate School

Abstract of the Dissertation

The Impact of Plant Invasions on Nitrogen Cycling and Trace Gas Emissions

by

Jonathan Edward Hickman

Doctor of Philosophy

in

Ecology and Evolution

Stony Brook University

2009

If a shift in species composition, as occurs during the spread of an invasive species, includes a change in the ecophysiological characteristics of the community, the invasion may alter a range of ecosystem processes. Invasion by the nitrogen-fixing legume kudzu (Pueraria montana) across the southeastern United States has the potential to increase nitrogen (N) cycling and nitric oxide (NO) emissions from soils, thus raising ozone concentrations in regions where ozone formation is limited by NO availability. Furthermore, kudzu is expected to move northward by 100's of kilometers as global temperatures increase. I studied kudzu invasions in Georgia and found that rates of N-turnover in soils increased up to 1000%, and NO emissions from soils were more than 100% higher (2.81 vs. 1.24 ng NO-N cm-2 h-1) in invaded vs. uninvaded sites. Atmospheric modeling suggests that these higher NO emissions will raise ozone concentrations substantially. To understand the impacts of a northward migration, I examined how kudzu invasion affects soil nitrogen and microbial dynamics in Maryland. I found that net nitrogen mineralization was 10 times higher and net nitrification was 5 times higher in invaded soils at one site in Edgewater, MD, but not at two other sites. Nitric oxide from invaded soils were over 5 times higher than fluxes from uninvaded soils in Edgwater, but only half as large in a second site. I propose that kudzu invasion in the southeastern United States represents a novel threat to air quality and could increase the frequency with which federal ozone standards are exceeded. In a second set of experiments, I used litter from congeneric pairs of native and invasive species to investigate 1) whether leaf litter from invasive species loses mass and N more quickly than litter from native species and 2) whether mixtures of litter from native and invasive litters lose mass and N additively. Litter from invasive species decomposed more quickly, and mixtures of native and invasive litters decomposed nonadditively, at a slower rate

than expected. These results suggest that, while invasive species are likely to alter decomposition and nutrient cycling, the presence of native species may buffer ecosystems against these changes.

In memory of Carter & Marion Hickman and Lois & Lester Saipe

Table of Contents

List of Tables

Chapter 3

Chapter 4

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Acknowledgments

First I would like to thank my advisor, Manuel Lerdau. He has provided years of thoughtful encouragement and critiques, and I am profoundly grateful that I have had the opportunity to be his student for the past six years. If I am in any measure a scientist, it is due in no small part to Manuel; he has provided a model of critical, insightful thinking that I can only aspire to. Perhaps more importantly, he has opened an engaging, inviting world of research to me.

Much of this research would not have been possible without the generosity of Peter Groffman. I was trained in many of the techniques I used in Peter's lab, which became something of a home away from home, and Peter has been a steadying and encouraging presence over the last few years. The other members of my committee--Jessica Gurevitch and Catherine Graham--provided guidance and thoughtful critiques that made my dissertation and research stronger than it would have without their presence.

I would also like to acknowledge the invaluable assistance of Sharon Hall, who helped guide me through the gas sampling which plays a central role in this research, and without whom this essential part of the dissertation may not have been completed. Charles Canham has provided patient, thoughtful advice on statistical issues and career questions. I am also grateful for the assistance of Dennis Whigham, who has been a reliable resource in my research, Lisa Donovan, who provided resources and lab space for my Georgia field campaign, and to Karen McGlathery, for use of her Lachat autoanalyzer.

Special thanks go to Lisa Martel and particularly to David Lewis in Peter Groffman's lab, who showed me unflagging patience and assistance throughout my sample analyses. Thanks also to Meg Miller in Karen McGlathery's lab, who provided much needed support during my analyses in Virginia.

Finally, I would like to thank the members of the Lerdau lab (Kate Howe, Beth Leger, Isabel Ashton, Ramona Walls, Sue Natali, Sybil Gotsch, Dennis Grey, Patty Oikawa, Jennifer Funk, and Nina Theis), who provided advice and a stimulating environment in which to work, and to my family, who have been supported me throughout my graduate school experience. The staff of the Department of Ecology and Evolution has been extremely patient and helpful: Martha Nolan, Iris Roth, Donna DiGiovanni, Fumio Aoki, and Mike Doall.

This work was supported by the National Science Foundation, the Environmental Protection Agency, the National Aeronautics and Space Administration, and fellowships from the Garden Club of America and Stony Brook University.

Chapter 1 The effects of invasive species on ecosystems and the atmosphere

Introduction

The role of individual species and species' traits in the context of communities and ecosystems is a central issue in ecology. Individual species can have a huge influence on the surrounding community and ecosystem, whether it is a keystone species such as *Pisaster ochraceus*, which can determine community structure, or an ecosystem engineer like the *Castor Canadensis*, the beaver, which can create a novel environment (Paine 1969, Odling-Smee 2003). In the plant community, species may alter their environment in a variety of ways, such as by determining the availability of nutrients (*e.g.*, through the presence of N-fixing legumes or through the production of recalcitrant plant litter), the availability of water (*e.g.*, through the redistribution of water from lower to upper soil profiles), fire frequency, light availability, the frequency of disturbance, and even the chemical composition of the atmosphere (Vitousek and Walker 1989, Lerdau and Keller 1997, D'Antonio 2000, Chapin 2002, Schnitzer and Bongers 2002). In some of these cases, a single species may be responsible for the observed environmental effects; in others, traits that are shared by multiple species in a community may have a cumulative effect. The ability of individual invasive species to alter a range of ecosystem processes is well documented. Largely, this ability can be attributed to species' physiology in a particular context—*e.g.*, the presence of a nitrogen-fixing plant species may play a key role in nitrogen cycling in an ecosystem where other species of N-fixers are absent or rare. Traits that are shared by species can also influence ecosystem processes. For example, plant species that have rapidly decomposing litter tend to reinforce high rates of decomposition and nutrient cycling within an ecosystem, while the opposite is true for species with recalcitrant litter (Hobbie 1992).

Impacts of invasive species on ecosystems and the atmosphere

Invasions by exotic plant species can be a valuable tool for understanding how individual species or traits shared among multiple species can affect higher-level processes.

These “natural experiments” in which community composition is changed—manipulated not by design, but as a consequence of historical contingency—provide an opportunity for studying the ecosystem effects that follow a change in species composition. Many studies of invaders have identified how both individual species and suites of species have influenced ecosystems in important ways. The effects of invaders are typically the consequence of how their physiology differs from the physiology of the native species present in a community before the invasion occurred. Perhaps best known is the example of invasion by the nitrogen (N) fixing tree *Myrica faya* in Hawai’I (Vitousek and Walker 1989). *M. faya*’s ability to fix N lead to substantial changes to the development of young volcanic soils, increases in nitrogen cycling rates, and the spread of numerous other invasive species whose establishment had been prevented previously by limited nitrogen availability. The potential for traits shared by multiple invasive species to affect communities and ecosystems has also been well documented for grass invasions in western North America, where invasion by multiple species has been shown to have altered the fire regime of some ecosystems (D'Antonio 2000).

Few parts of the world remain free of these often destructive plants, which can cause the extirpation of native species, the disruption of entire ecosystems, and appear likely to influence other agents of global change (Pimentel et al. 2000). However, some of the broader impacts of invaders—including changes to atmospheric chemistry—have received less attention than their impacts on other ecosystem properties (Hall 2005). One way in which an invasive species can dramatically change ecosystems and atmospheric chemistry is through the production of “keystone molecules”—compounds that can have an impact on ecosystems and communities far out of proportion to their relative abundance in the environment (Lerdau 2003). For example, isoprene (C_5H_8), a volatile organic compound (VOC) is produced in the leaves of many plant species (Lerdau and Keller 1997, Keller and Lerdau 1999). It is also an important reactant in the atmosphere, notably in the production of tropospheric ozone, an important pollutant (National Research Council 1991). Similarly, the signaling compounds produced by legumes and other nitrogen-fixers to attract N-fixing microbial symbionts, and the enzyme nitrogenase, which the symbionts use to fix N, can result in substantial increases in nitrogen cycling and trace gas fluxes that could potentially affect air quality (Erickson et al. 2001, Martin et al. 2003, Hall and Asner 2007).

For my dissertation, I have investigated both of these categories of potential changes—those caused by traits shared across invasive species, as well as impacts caused by the unique physiology of an individual invasive species, the N-fixing ability of the invader kudzu (*Pueraria montana*). I have focused specifically on how both individual and groups of invasive species may alter nitrogen cycling and, in the case of kudzu, trace gas byproducts of the nitrogen cycle. The ability of invasive N-fixing species to disrupt N cycling in invaded ecosystems is well known, and in the case of kudzu, this will be the first investigation of this aggressive invader's impacts on ecosystems. In contrast to kudzu, which tends to form monospecific stands, many invaders in the northeastern United States become established as part of more diverse communities—multiple invasive and native species often co-occur in the same location (Howard et al. 2004). These invaders are not physiologically distinct from the native species in the region, and many of them are in the same genus or family as many native species. Nevertheless, these invasions may cause changes in nutrient cycling in the invaded ecosystems if invaders as a group tend to produce leaf litter that is more rapidly decomposed than that of native species. Understanding these two different modes of ecosystem disruption that can accompany two very different modes of invasion will help provide a more complete picture of how plant invasions and the effects of a single species and groups of species can influence the nitrogen cycle.

Trace gas fluxes: VOC's and nitrogen oxides

Among the broader impacts that may follow an invasion by a single species are changes in the emissions of certain trace gases and the reactivity of the atmosphere. Two classes of trace gases, nitrogen oxides and VOC's can profoundly alter the radiative and chemical balance of the atmosphere. Nitrous oxide (N_2O) is a powerful greenhouse gas that also contributes to the destruction of ozone in the stratosphere (upper atmosphere). Nitric oxide (NO) and VOC's are the critical precursors to ozone formation in the troposphere (lower atmosphere), and can also be involved in the formation of organic and nitrate aerosols (Schlesinger 1997). Tropospheric ozone is the single most important air pollutant in terms of impacts on agricultural crops and human health, and it is also a major greenhouse gas (EPA 2002). Atmospheric concentrations of N_2O rose considerably during the 20^{th} century, and continue to increase by3.5 Tg, or 0.3%, annually (Matson and Vitousek 1990, Matson et al. 2002). In the stratosphere, N_2O contributes to the

destruction of the ozone that acts to protect the earth's surface from damaging ultraviolet radiation (Schlesinger 1997).

Over much of the earth, including the regions where my research was conducted in the eastern United States, biogenic reactive compounds emitted from plants (e.g., isoprene), and soils (*e.g.*, NO) make major contributions to the atmosphere's reactivity (Guenther et al. 1995, Pierce et al. 1998, Fiore et al. 2005). The size of biogenic fluxes is determined by a number of factors, including climate, soil nitrogen dynamics, and plant species composition; for example, emissions of photochemically-active reduced carbon compounds such as isoprene are sensitive to temperature and light, while emission rates of reactive nitrogen oxides from soils vary as a function of soil moisture and nitrogen transformation rates (Lerdau and Keller 1997, Keller and Lerdau 1999, Davidson et al. 2000). Legumes and other nitrogen-fixing plants are linked to substantial increases in NO fluxes from soils, presumably as a consequence of root exudation and depositing nitrogen-rich litter, which increases N cycling rates and the trace N gas fluxes that are byproducts of the soil nitrogen cycle (Erickson et al. 2001, Martin et al. 2003, Hall and Asner 2007). In tropical environments, these plants may also be contributing to substantial increases in N_2O emissions from soils (Erickson et al. 2001).

Kudzu: potential impacts

Kudzu is among the most well-recognized invasive plants, yet the fact that it is both a large isoprene emitter and a nitrogen-fixer—and thus a novel source of both VOC *and* nitrogen oxide emissions—has received little attention from an atmospheric chemistry perspective. As noted above, these compounds are the key precursors to tropospheric ozone formation and a major natural source of organic and nitrate aerosols, which gives kudzu the distinction of being as close to a 'polluting plant' as one can find. Its extensive cover in the southeastern US--which at over 3 million ha rivals soybean--and its ability to spread rapidly (over 50,000 ha yr^{-1}) serve to bring the implications for regional air quality into even greater relief (USDA 2002, Forseth and Innis 2004).

In the United States, kudzu is projected to be fixing up to 235 kg N ha^{-1} yr^{-1} in the United States, an order of magnitude more than *Myrica faya* in Hawai'i, and potentially a vastly larger input of biologically-available nitrogen than atmospheric nitrogen

deposition, which ranges from roughly 7 kg N ha^{-1} yr^{-1} in the southeastern United States to about 10-13 kg N ha^{-1} yr^{-1} in the northeast (Vitousek and Walker 1989, Forseth and Innis 2004, Holland et al. 2005). Because ecosystems in the eastern United States tend to be N-limited, kudzu invasion has the potential to dramatically increase nitrogen cycling and trace gas fluxes. The particulars of tropospheric chemistry in the southeast US may make understanding NO fluxes resulting from kudzu invasion particularly important. Ozone formation in the Southeast is generally NO_x limited--in the warm summer months, large biogenic emissions of VOC's (notably isoprene) create a high VOC/NO_x ratio in the troposhere, so that small changes in NO_x concentrations can play a large role in ozone formation (Chameides 1988, National Research Council 1991, Trainer et al. 1993, Kleinman et al. 1994, Jacob et al. 1995, Daum et al. 2000). The unique confluence of an extensive and growing N-fixer invasion and a relatively VOC-rich/NO_x-poor atmosphere may lead to substantially increased tropospheric ozone levels in the southeastern United States as a direct result of the invasion, with detrimental effects on human health and agriculture.

Preliminary investigation of kudzu's potential to alter ecosystems

In August and September, 2005, I collected preliminary data to determine how kudzu invasion is affecting the plant community and ecosystems at two sites in the Maryland Department of Natural Resources' McKee-Beshers Wildlife Management Area in Montgomery County, MD, just a few miles from the Potomac River. Kudzu has formed dense carpets and thoroughly covers trees in several spots along the edge of the oak/hardwood forest typical of this region, where white and red oaks (*Quercus alba*) and *Q. rubra*), box elder (*Acer negundo*), sassafras (*Sassifras albidum*), American elm (*Ulmus Americana*), and hickory (*Carya* spp.) are common. I paired plots invaded by kudzu with nearby uninvaded plots that were similar in slope, aspect, topography, and land-use history. I attempted to obtain an initial impression of the impacts of kudzu invasion by comparing community and ecosystem variables in the invaded sites to those in the uninvaded sites. In each site, I used standard quadrat methods to estimate species composition and cover, took leaves from kudzu and the common tree species listed above to measure foliar nutrient concentrations, and took soil samples to measure the soil pools

of carbon and nitrogen as well as the microbial processes responsible for nitrogen cycling in the soil (potential net nitrogen mineralization, potential net nitrification, and denitrification).

The results of this preliminary investigation support my hypothesis that kudzu invasion is altering community composition as well as nutrient pools and cycling. Kudzu appears to be preventing the establishment of trees in invaded sites, where there were only 20% as many juvenile trees as in uninvaded sites. In planned contrasts following a one-way ANOVA, foliar nitrogen concentrations were significantly higher in kudzu leaves than in the leaves of the common tree species ($P<0.05$), suggesting that kudzu is indeed contributing high levels of nitrogen to invaded sites (Figure 1). I also found suggestions that nitrogen cycling was higher in the sites invaded by kudzu, though no statistically significant results (Figure 2). Net N mineralization, in which the decomposition of organic N-containing compounds releases inorganic forms of N, trended higher in invaded plots, as did net nitrification, the transformation of ammonium (NH_4^+) to nitrate (NO_3^-), which is also the main source of NO emissions in temperate soils. However, my statistical tests had very low power because I only sampled two site pairs, and I made no direct measurements of gas fluxes. Additionally, these sites in Maryland are at the northern limit of kudzu's range, and may not be representative of the invader's impact further south.

Research approach and summary

In order to understand how the extensive invasion of kudzu may influence ecosystems and atmospheric chemistry in the southeastern United States, I conducted a combination of field and modeling experiments. In chapter 2, I present my study of the impact of kudzu on nitrogen cycling and NO gas fluxes in Georgia, and the potential impacts on ozone formation across a 9-state region. I found that kudzu invasion had large impacts on net nitrogen mineralization and net nitrification, and doubled emissions of NO. In collaboration with atmospheric chemists, these results were used to parameterize a model of ozone formation across the region. I determined that under the extreme, but not unreasonable case in which kudzu spreads across all non-agricultural and non-urban soils, ozone concentrations could increase by up to 2ppb, and parts of the

southeastern United States would fail to meet EPA Clean Air Act ozone standards by an additional 7 days from June through August.

Researchers have predicted that that kudzu will migrate northward by 100's of kilometers in response to rising temperatures and elevated atmospheric CO_2, and empirical evidence suggests that this range expansion may be underway already (Sasek and Strain 1990, Lamont and Young 2004, Holmgren 2008). However, the ecosystem impacts of such a range expansion can be difficult to predict, especially when factors affecting nitrogen fixation rates—such as growing season length, temperature, and nitrogen deposition—can be very different in more northern regions than in the heart of its current distribution. In chapter 3, I examine the potential ecosystem and atmospheric consequences of a northward expansion by kudzu. I studied the effects of kudzu invasion on nitrogen cycling and trace gas fluxes in Maryland, along most northern portion of kudzu's distribution, and where temperatures and growing seasons mimic those projected for the higher latitudes where kudzu is expected to migrate as temperatures and atmospheric CO_2 increase (Hayhoe 2008, NOAA/ESRL 2008). Effects similar to those in Georgia were found, but only in some sites, and only during one of the two years of the experiment, suggesting that kudzu range expansion has the potential to have large impacts on northern ecosystems and atmospheric chemistry, but the timing and location of those effects may be difficult to predict.

In the final chapter, I shift from investigations of the effects of a single species on ecosystems to the effects of a group of species that may share common traits related to their ability to invade. Until recently, scientists have depended largely on vote-counting and narrative literature reviews for a window into general patterns of ecosystem impacts of invasion (Ehrenfeld 2003, Levine et al. 2003, Dukes and Mooney 2004), with some exceptions (Ashton 2005, Liao et al. 2008). One valuable tool for studying general properties of invaders is phylogenetic pairing. Phylogenetic pairing—of invasive species either with related exotic species that are not invasive or related native species--has been put to use to great effect in studies of general properties associated with invasive success (e.g., Agrawal et al. 2005, Muth and Pigliucci 2006, Funk and Vitousek 2007), but it has been used less frequently in assessments of general impacts of invaders (Levine et al. 2003). Many of those properties that are often touted as typical of a successful invader—

high growth rates, high nitrogen concentrations—can have impacts on ecosystem properties such as evapotranspiration or nutrient cycling. In the final chapter, I conducted two decomposition experiments to investigate whether there are traits shared by invasive species in the northeastern United States cause changes to nutrient cycling and availability in invaded ecosystems. Using a phylogenetically-paired design, I found that invasive litter decomposes and releases N more quickly than native litter. Because leaf litter in eastern forests is often decomposing in the presence of other species, I also examined the decomposition of litter in combination of species to better understand decomposition dynamics, and found that in the presence of native litter, rates of decomposition in invasive litters slows; the presence of native species may provide a temporary buffer against invasive impacts on nutrient cycling.

Figures

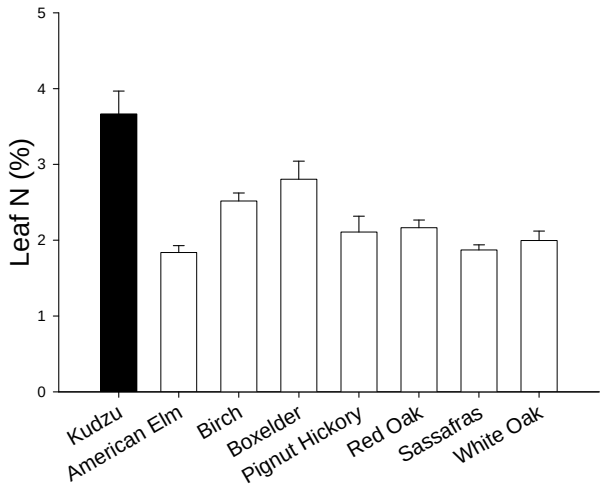


Figure 1. Bar plot of nitrogen concentration (+/- SE) of kudzu (black bar) and 7 co-occurring woody species (white bars) from Montgomery County, MD in September, 2005 ($P<0.05$).

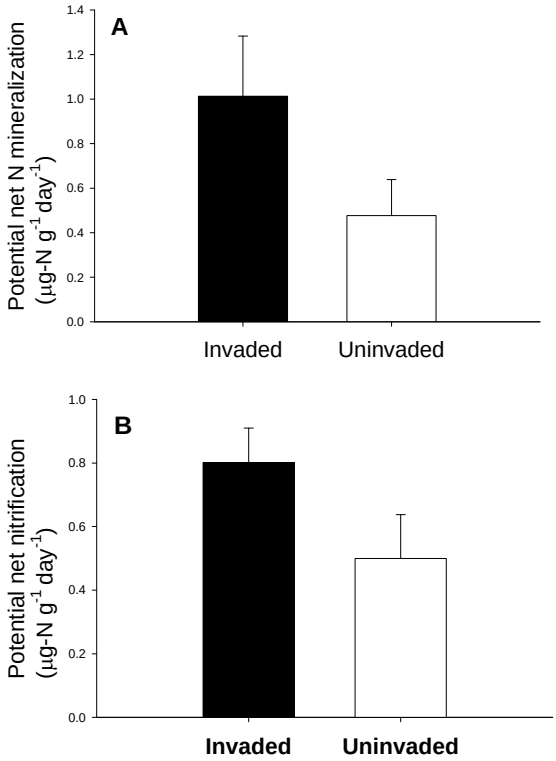


Figure 2. Bar plots of mean (+/- SE) net N mineralization (A) and net nitrification (B) in soils invaded by kudzu (black bars) and in uninvaded soils (white bars) in two pairs of plots Montgomery County, MD in September, 2005. There were no significant effects of invasion.

Chapter 2 Kudzu (*Pueraria montana*) invasion doubles emissions of nitric oxide, a precursor to tropospheric ozone

Abstract

Invasion by the nitrogen-fixing legume kudzu (*Pueraria montana*) across the southeastern United States has the potential to increase nitrogen (N) cycling and nitric oxide (NO) emissions from soils, thus raising ozone concentrations in regions where ozone formation is limited by NO availability. I studied kudzu invasions in Georgia and found that rates of N-turnover in soils increased up to 1000%, and NO emissions from soils were more than 100% higher (2.81 vs. 1.24 ng NO-N cm-2 h-1) in invaded vs. uninvaded sites. Atmospheric modeling suggests that these higher NO emissions will raise ozone concentrations substantially. I propose that kudzu invasion in the southeastern United States represents a novel threat to air quality and could increase the frequency with which federal ozone standards are exceeded.

Introduction

Although the ability of exotic invasive species to alter community, ecosystem and biogeochemical processes is well documented (Vitousek and Walker 1989, D'Antonio 2000, Zavaleta 2000), the impacts of invasion on the chemical and radiative balance of the atmosphere have received less attention (but see Hall and Asner 2007 (Hall and Asner 2007)). Whenever the physiology of an invasive species includes metabolic processes that involve biosphere/atmosphere exchange—such as the reduction of N_2 or the production of a chemically reactive hydrocarbon—the spread of that species has the potential to affect the atmosphere. This is particularly likely to be the case when the metabolic process in question is rare or absent from the ecosystem being invaded, and when the invader is abundant enough that the magnitude of its impact is larger than the natural variation already present in the invaded ecosystem. I investigated the impacts of the nitrogen (N) kudzu (*Pueraria montana*), the most abundant invasive terrestrial plant in the southeastern United States, on soil emissions of the greenhouse gas nitrous oxide (N_2O), and the chemically reactive species nitric oxide (NO), one of the precursors to

tropospheric ozone formation. Like most other legumes, kudzu develops symbiotic associations in its roots with bacteria capable of transforming atmospheric N_2 into biologically available NH_4^+ (Forseth and Innis 2004). When it is released to the soil from decomposing tissues or leaked from roots, the symbiotically-fixed N can be taken up by plants and microbes (Forseth and Innis 2004). Because of these additions of fixed N to soils, invasions by N-fixing plants tend to cause the overall rate of N-cycling in the invaded ecosystem to increase, including rates of nitrification (the oxidation of NH_4^+ to NO_3^-) and denitrification (the reduction of NO_3^- to N_2) (Erickson et al. 2001, Martin et al. 2003, Hall and Asner 2007). As a consequence, emissions of NO and N_2O, gas by-products produced during nitrification and denitrification, tend to increase as well (Forseth and Innis 2004).

Tropospheric ozone is among the most damaging of air pollutants, affecting respiratory health and reducing crop production. In the southeastern United States, where kudzu invasion is most severe, formation of tropospheric ozone is generally limited by atmospheric concentrations of NO and NO_2 (collectively referred to as NO_x), and soil emissions of NO can be an important determinant of ozone concentrations in the region (Williams and Fehsenfeld 1991, Davidson et al. 1998). Kudzu is also a strong emitter of isoprene (C_5H_8), a photochemically reactive hydrocarbon that plays an important role in tropospheric ozone formation (Sharkey and Loreto 1993a, b).

With a current distribution of over 3 million ha, and spreading by over 50,000 ha yr^{-1}, kudzu coverage in the southeastern United States exceeds that of cultivated soybean, making it the dominant N-fixing plant in the region (USDA 2002, Forseth and Innis 2004). Although high levels of N fixation have been documented in U.S. populations of kudzu, N fixation in kudzu and its effects on invaded ecosystems have received limited attention (Lynd and Ansman 1990). Projections based on N fixation rates in kudzu's native range suggest that it may be fixing up to 235kg N ha^{-1} yr^{-1} in the U.S., an order of magnitude more than the invasive N-fixing tree *Myrica faya* in Hawai'i (20 kg N $ha^{-1}yr^{-1}$) or atmospheric deposition in the eastern U.S. (7-13 kg N $ha^{-1}yr^{-1}$) (Vitousek and Walker 1989, Forseth and Innis 2004, Holland et al. 2005). Because kudzu also emits the VOC isoprene at high rates (Sharkey and Loreto 1993b), its rapid expansion has the potential to be a growing source of tropospheric ozone production in the region.

Methods

To take the first step in determining how kudzu invasion may be affecting air quality in the Southeast, I tested the hypotheses that kudzu is accelerating microbial production and emission of NO and N_2O from invaded soils. I then used a chemical model of the troposphere to estimate the potential impacts that these changes in gas fluxes can have on ozone in the region. In July and September 2007, I conducted measurements in paired plots at three locations in Madison County, Georgia, a common experimental design for investigations of impacts of invasions on soil processes (*15-17*). At each site, one plot was established within a stand of kudzu, and a second plot established in an area where kudzu had not invaded, within 50m of the kudzu plot. The uninvaded plots were former pasture that had not been grazed for at least 10 years, and contained a combination of blackberry shrubs (*Rubus occidentalis*) and herbaceous species, though there were a few juvenile sweetgum (*Liquidambar styraciflua*) individuals inside or adjacent to the plots at 2 of the 3 sites. There were fewer than 7 trees in any 50m x 20m area, and only 1 to 3 trees within the $10m^2$ plots; each tree was approximately 3m to 5m tall. At the time of my measurements, kudzu represented 100% of the canopy in invaded plots and 0% in uninvaded plots. All plots were located on Madison sandy loam soils, derived from mica schist and/or gneiss. Plots within a site had similar slopes and aspects; additional information on soils and land-use history can be found in the online supporting material (methods detailed at the end of the chapter).

Understanding the real-world ecosystem impacts of kudzu invasion requires field studies that are necessarily less controlled than manipulative experiments (Ashton 2005). I recognize that in field experiments of this nature, it is impossible to completely rule out the possibility that factors other than kudzu—such as land use history—may influence nitrogen cycling and trace gases in these sites. Although it limits my ability to control potentially important factors, I believe it is important to understand the potential impacts of kudzu invasion in a field setting, where the effects of a kudzu "treatment" are representative of what is actually occurring with kudzu invasion in the region. To that end, I have worked to reduce the effects of potential confounding factors in the field as much as possible. I have worked to control land-use history, slope, aspect, and soil type

by locating each pair of invaded and uninvaded plots in close proximity to one another within the same former pasture, with similar slopes, aspects, and soils.

To test the hypothesis that kudzu is increasing NO emissions, I conducted dynamic chamber-based flux measurements of NO fluxes using a portable chemiluminscent NO_x analyzer (Unisearch model LMA-3D). Fluxes were measured from four rings placed randomly within each plot in July. I also took a separate series of gas samples from a static chamber fitted to each ring for lab analysis of N_2O concentrations using a gas chromatograph fitted with an electron capture detector. After completing gas measurements for each ring in July, I removed a 12-cm soil core for lab analysis of net N mineralization, net nitrification, denitrification enzyme activity, total carbon (C) and N pools, inorganic N pools, and microbial biomass; a second set of soil samples were taken for analysis in mid-September. I analyzed the data using split-plot ANOVA. When necessary, data were log transformed or rank transformed to meet the assumptions of ANOVA. The reported P values are based on one-tailed tests unless otherwise indicated.

Results & Discussion

NO fluxes were larger in sites invaded by kudzu (P=0.032, figure 1). Averaged across the four rings sampled in each plot, fluxes were 127% higher in invaded plots. The measured NO emissions varied from 2.19 to 3.70 ng NO-N cm^{-2} h^{-1} in invaded plots compared to a much narrower range of 1.21 to 1.26 ng NO-N cm^{-2} h^{-1} in uninvaded plots. Fluxes of N_2O showed a trend towards increasing under kudzu (Figure 1; P=0.107)). Soil moisture, which can have substantial effects on trace N gas fluxes (Davidson and Verchot 2000), did not differ between invaded and un-invaded plots in July (P=0.43) or September (P=0.48, two-tailed tests).

The results of the laboratory soil assays demonstrated a clear and consistent association between kudzu invasion and increased N cycling rates in both mid-summer and early autumn. I found large increases in net N mineralization rates under kudzu, with as much as an order of magnitude difference between invaded and uninvaded plots in both July (P=0.003) and September (P=0.007, Figure 2). Net rates of nitrification, which is typically the primary source of NO production in well-drained soils (Davidson et al.

2000), were 110% to 532% higher in soils invaded by kudzu across the two sampling times (July: P=0.012, September: P=0.031, Figure 2). There were no differences in my measurements of denitrification enzyme activity, microbial biomass, total C, or total N in soils during either season.

Soil inorganic N pools are an unreliable indicator for changes in N cycling rates because inorganic N in soils can turn over in a matter of hours under high rates of plant uptake and microbial immobilization (Schlesinger 1997), but they can provide insight into N availability in relation to plant demand. Soil pools of inorganic N were also higher in invaded sites, though by a smaller factor than the N cycling rates (Figure 3). On average, invaded sites had 69% more NH_4^+ (P=0.028), and 220% more NO_3^-/NO_2^- (P=0.0025) in July. In September, invaded sites had an average of 10% more NH_4^+(P=0.0085), though the difference may have been strongly affected by an outlying core taken from the uninvaded Carey Pasture plot, which contained 20 μg N g^{-1} dry soil, considerably more than the average of 4.3 μg N g^{-1} dry soil for all other cores taken from both invaded and uninvaded soils. Pools of NO_3^- and NO_2^- were 550% larger in invaded plots (P=0.02). An excess of soil NO_3^- can contribute to aluminum mobilization, soil acidification, and increased rates of NO_3^- leaching to aquatic ecosystems (Matson et al. 2002).

In order to develop a first order estimate of the annual NO emissions from these soils, I assumed that A) the measured fluxes are representative of fluxes from these soils throughout the growing season; B) fluxes don't vary diurnally; and C) the growing season length is 260 days with a base temperature of 28^{o}C (SRCC 1997). Although more extensive sampling throughout the southern United States and measurements of seasonal and diurnal variation would provide the basis for more accurate estimates of annual NO emissions, these assumptions allow me to make an initial, transparent estimate. Based on these assumptions and my field measurements, I calculated that the kudzu-invaded soils emit 1750 g NO-N ha-1 yr-1. In contrast, the mixed-vegetation uninvaded soils emit only 761 g NO-N ha-1 yr-1. This second estimate is very close to the (Davidson et al. 1998) estimate that 523 g NO-N ha-1 yr-1 are emitted from non-agricultural soils in the southeastern United States, suggesting that the estimates from this current study represent

a reliable first cut at estimating kudzu's influence on annual NO emissions (Davidson et al. 1998).

Ozone formation in the Southeast is generally NO_x limited: in the warm summer months, large biogenic emissions of volatile organic compounds (VOCs) (notably isoprene) create a high VOC/NO_x ratio in the atmosphere, and under these conditions, ozone production is very sensitive to perturbations in NO_x (Chameides 1988, National Research Council 1991, Trainer et al. 1993, Kleinman 1994, Jacob et al. 1995, Daum et al. 2000). Assuming that the increases in NO fluxes observed at my Georgia sites are representative of the impacts of kudzu across the southeastern United States, the doubling of NO emissions under kudzu could increase regional ozone concentrations and the frequency of high ozone events.

To investigate the potential effects of a kudzu invasion on regional ozone levels, I used the global chemical transport model (CTM) GEOS-Chem model, focusing on the summer season (June–August) when ozone levels are highest. For the sensitivity analysis, I assumed an extreme case in which kudzu covers all non-agricultural, non-urban soils. In this scenario, kudzu produced a 28% increase in soil NO emissions and a subsequent spike in ozone concentrations. This increase occured against a background of decreasing NO_x emissions nationally; NO_x emissions in the United States decreased by 29% between 1990 and 2006, due to a 17% decrease in NO_x emissions from transportation, and a 38% decrease from fuel combustion (EPA 2002). The areas most vulnerable to kudzu-induced NO fluxes are Mississippi, Arkansas, and Tennessee, where ozone increases by up to 1.6 ppb (Figure 4). As a consequence, the summer days with daily maximum 8 hour average ozone exceeding 70 ppb would increase in these areas by up to 7 days/summer due to kudzu invasion. The warm temperatures that spawn high ozone events (*e.g.*, events in the 90th percentile) also increase NO fluxes from invaded soils, so that kudzu invasion becomes most important during the worst pollution episodes, increasing ozone concentrations by up to 2 ppb. This increase has the potential to partly or entirely offset national reductions in ozone concentrations of 2-15ppb under the A1B scenario in the GEOS Chem simulation. Given the unexpected difficulty many regions have had in meeting ambient ozone standards in spite of efforts to reduce anthropogenic production of NOx and VOCs (Hall et al. 1996), the potential for kudzu invasion to

further offset benefits from anthropogenic emission reductions could constitute an obstacle to meeting the future air quality standards in the United States.

The continuing invasion by kudzu represents a novel and growing source of ozone precursors. Increasing temperatures will allow kudzu to survive at higher elevations and to expand its range to the north by 100s of kilometers; an observed trebling in the number of populations on Long Island, NY may represent early evidence of that expansion (Sasek and Strain 1990, Lamont and Young 2004). Kudzu's impact on the atmosphere will be most important in areas that are distant from urban centers, and particularly in landscapes where little fertilizer is added to soils, such as the forested areas of southern Appalachia. My model results suggest that kudzu spreads further into these and other areas, the accompanying increase in NO emissions may increase ozone concentrations and the frequency of high ozone events in the southeastern United States. These air quality impacts of an invasive species should be taken into account during both scientific and economic analyses of invasive species' impacts.

Figures

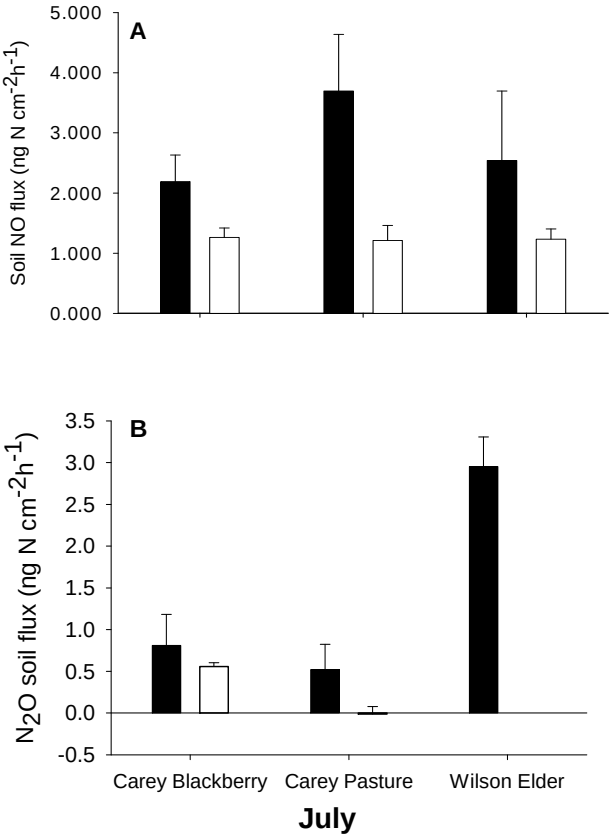


Figure 1. Bar plots showing mean (+SE) NO (A) and N_2O (B) emissions from soils supporting kudzu (black bars) and native vegetation (white bars) at each of 3 Georgia sites in July, 2007. Soil NO emissions were larger across soils invaded by kudzu ($P=0.032$); N_2O emissions showed a trend towards increasing under kudzu ($P=0.107$).

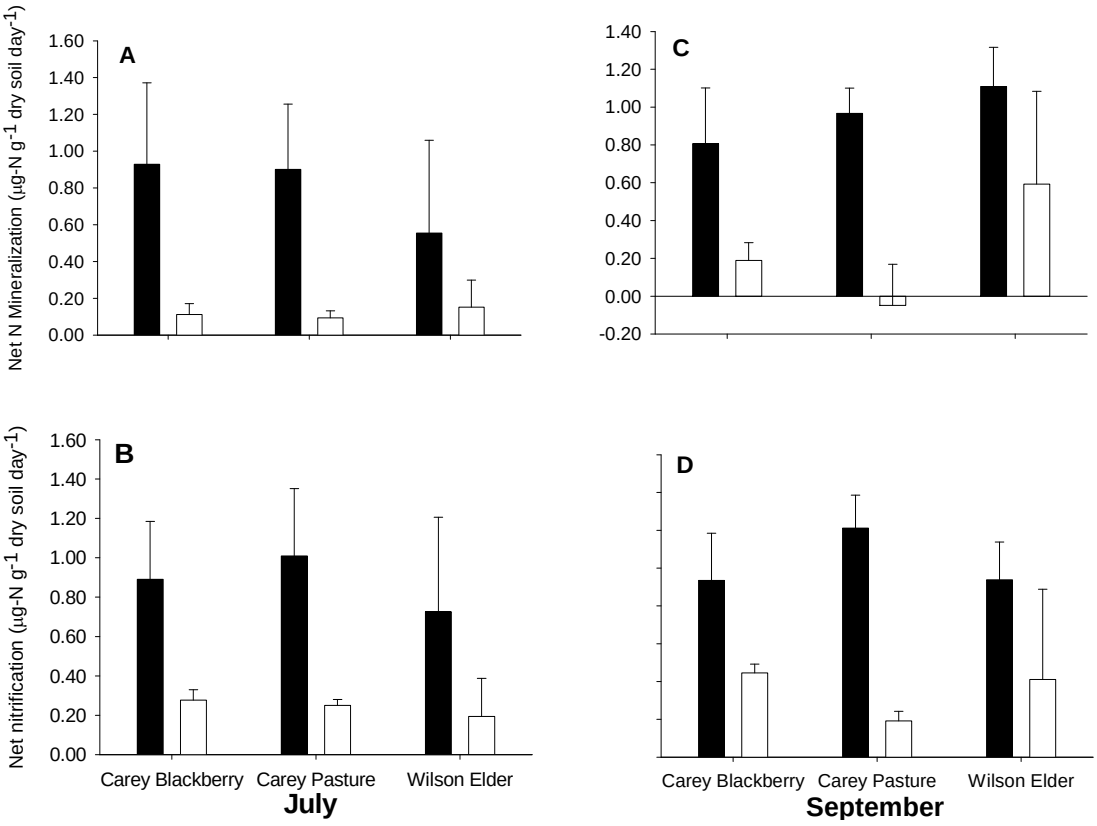


Figure 2. Bar plots of mean (+SE) net N mineralization and net nitrification from lab assays of soils supporting kudzu (black bars) and native vegetation (white bars) at each of 3 Georgia sites in July (A and B), and September (C and D), 2007. Net N mineralization rates were higher in invaded sites July (A; P=0.003) and September(C; P=0.007); net nitrification rates were also higher in both July (B; P=0.012) and September (D; P=0.031).

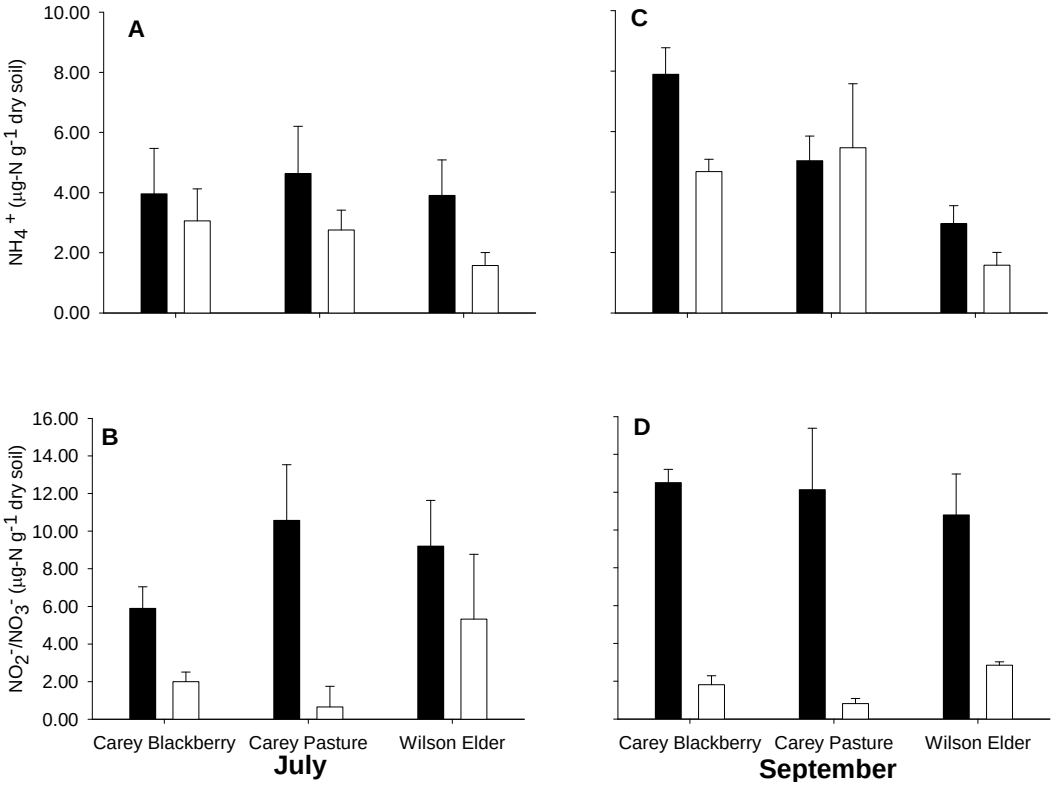


Figure 3. Bar plots of mean (+SE) inorganic nitrogen pools from soils supporting kudzu (black bars) and native vegetation (white bars) at each of 3 Georgia sites in July (A and B), and September (C and D), 2007. Soil pools of NH4+ were higher in invaded sites in July (A, P=0.028) and September (C, P=0.0085). Pools of NO2-/NO3- were higher in both July (B, P=0.0025) and September (D, P=0.020).

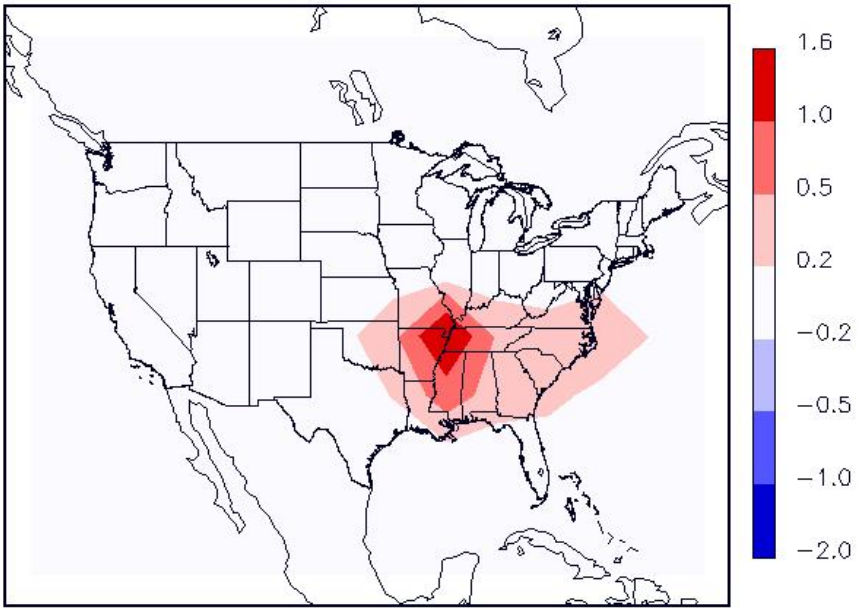


Figure 4. Changes in summer (June-August) average surface ozone (in ppb) due to the 28% increase in soil NO_x emissions accompanying kudzu cover of all non-agricultural, non-urban soils in a 9-state region. Simulated with the GEOS-Chem model.

Supporting Material: Materials and Methods

Sites

The paired-site design has become common in studies of the effects of N-fixers on soil nitrogen studies and gas fluxes (Rice et al. 2004, Yelenik et al. 2004). The paired uninvaded site is used as a control or reference for determining the relative impact of kudzu invasion.

Three sites were selected in Madison County, Georgia. Two sites were located on private property along Buford Carey Road (34.14659, -83.32646 and 34.14460, -83.32422) and one on private property along Stone Stewart Road (34.09457, -83.30870). Each site was selected to contain an area invaded by kudzu that could be paired with an uninvaded area within 50m of the invaded site. Sites were selected so that soils, slopes, aspects, and land-use history was similar between paired uninvaded and invaded areas within each site. The soils at all three sites were well-drained Madison sandy loam, with some variation in slope among sites. At the first Buford Carey site ("Carey blackberry"), the invaded and uninvaded plots were located on an east-facing 10-15% slope. Plots at the second Buford Carey site ("Carey Pasture") were located on a north-east facing 6-10% slopes, while plots at the Stone Stewart site ("Wilson Elder") were located on south-facing 6-10% slopes. Aerial photos from the Digital Library of Georgia, which collects aerial photography of Madison County produced by the Agricultural Stabilization and Conservation Service (USDA 1944-1980). The first Buford Carey site is located in an area which appears shrubby at least as far back as 1951, during which time they display no signs of agricultural activity. The second Buford Carey site is located on land that was used as pasture starting as far back as the 1940's. After 1973, the land was no longer managed, though one area abutting the kudzu patch was mowed occasionally. The Stone Stewart site was farmed at least until 1951, but farming in the plots ceased prior to 1967.

Sample collection and preparation

Soil sampling was conducted from July 20-22 and September 15, 2007. At each sampling time, soil cores were taken from paired invaded and uninvaded plots on the same day. Locations for soil cores were selected randomly in each plot. The top litter

layer was removed, and a PVC pipe (5 cm internal diameter x 20 cm long) was driven 12 cm into the ground and removed with the core intact. The cores contained little or no organic layer, so they were not separated into different horizons before being placed in separate polyethylene bags. The cores were kept cool until transferred to a refrigerator in the lab. Most lab analyses were started within 3 days of soil collection, but the denitrification assays were usually conducted 4-6 days after sampling. Since precipitation can stimulate microbial activity (Paul 1996), samples were taken at least 24 hours after any major rain event.

Soils were homgenized by hand in plastic bags, and major rocks, roots, and invertebrates were removed. Subsamples from each core were taken for laboratory analysis of moisture content, total C and N, initial nitrate and ammonium, microbial biomass, net mineralization and nitrification potential, and dentirification enzyme assays (details below). Soil moisture content (g H_2O g^{-1} dry soil) was determined by drying a subsample at 60 C until soils were no longer decreasing in weight. Total carbon and nitrogen content of dried, ground samples was determined using a CE Flash EA 1112 Elemental Analyzer (CE Instruments, Milan, Italy).

Inorganic N pools

Inorganic N was extracted from soils by placing a 10g subsample of soil from each core in a 120 ml polypropylene specimen cup with 50ml 2M KCl, and shaking the cups for 60 minutes to ensure that all the inorganic N bound to soil surfaces can exchange with the KCl. The soils were allowed to settle for another 60 minutes after shaking. The KCl solution from each cup was filtered using Whatman #42 filter paper and stored below freezing in a 40ml glass scintillation vial. Determinations of NO_3^-/NO_2^---N and NH_4^+--N content were made using a Lachat autoanalyzer (Lachat Quickchem Systems, Milwaukee, WI). These measurements also represent the initial or “pre-incubation” inorganic N concentrations for the calculations of net N mineralization and net nitrification rates.

Net N mineralization and net nitrification

Concurrent with subsampling for the initial KCl extractions, a second 10g subsample was taken from each homogenized core and placed in a 120 ml specimen cup, which in turn was placed in a mason jar and sealed with a gas-tight lid fitted with a rubber septum. The jars were incubated at 20-22 C. After 10 days, the specimen cups were removed, and inorganic N was extracted and analyzed as described above; these extractions represent the "post-incubation" inorganic N content. Net mineralization was calculated as the difference in total inorganic N concentrations in the pre-incubation and post-incubation extractions; net nitrification was calculated similarly, as the difference in NO_3^--N and NO_2^--N concentrations in pre- and post-incubation soil extractions (Matson et al. 1987).

Soil microbial biomass

The determination of total microbial biomass was made using the chloroform fumigation incubation method (Jenkinson and Powlson 1976, Voroney and Paul 1984). 10g soil samples were fumigated with chloroform to kill the microbes, innoculated with 0.1g soil from the same sample, and using measurements of the CO_2 evolved to estimate the microbial C present.

A 10g subsample of soil from each core was fumigated for 12-18 hours. The 10g samples of fumigated soils and a 0.1g fresh soil inocculum from the same core were placed in a quart-sized mason jar and sealed with a gas-tight lid fitted with a rubber septum. A second 10.1g fresh sample from the same core was sealed in a second mason jar. After incubating for 10 days at 20-22^oC, a 9ml gas sample from the headspace of each mason jar was transferred to an evacuated glass vials. The vials were stored at room temperature until CO_2 concentrations were determined using a gas chromatograph fitted with a thermal conductivity detector. Headspace concentrations of CO_2-C were calculated. Microbial biomass-C was calculated as the difference in CO_2-C per unit dry weight of soil in fumigated and unfumigated samples, divided by a constant (0.41) representing the fraction of biomass mineralized to CO_2.

Denitrification enzyme activity assays

I determined the denitrification potential of soils using the Dentrification Enzyme Activity method (Smith et al. 1978). A slurry of soil and a medium containing a surfeit of nitrate and glucose was created, so that the denitrification process was limited only by the amount of denitrifying bacteria in the sample. Choloramphenicol, an inhibitor of microbial growth, was added to ensure the assay is measuring activity of the microbial community present in the soil at the time of sampling. A 5g subsample was taken from each homogenized soil core and placed with 10 ml medium into a 125ml erlenmeyer flask with a ground glass joint and sealed with a rubber stopper. The flasks were placed under negative pressure for 3-minutes followed by a 1-minute flush with N_2 gas. This process was repeated 2 more times to ensure that the soils were anaerobic. Following the third flush with N2, the flasks were vented, and 4ml acetylene was added to each flask to inhibit the transformation of N_2O to N_2 by denitrifying bacteria. The flasks were placed on an orbital shaker, and 9ml samples of the headspace of each flask were taken using a polypropylene syringe and transferred to evacuated gas vials after 1 and 3 hours. The N_2O concentration of each vial was determined using a gas chromatograph fitted with an electron capture detector.

Trace N gas emissions

Plots were sampled for NO and N_2O emissions from July 20-22, 2007. Gas measurements for each set of paired uninvaded and invaded plots were conducted on the same day, and all sampling was conducted between 10am and 6pm to limit any variation in temperature between plots. In each plot, four beveled, Teflon-coated PVC rings (25.5cm diameter) were randomly inserted several centimeters into the soil. At least 30 minutes after inserting the ring, a Teflon-coated, molded PVC chamber top fitted with a gas-sampling port was inserted over the ring and made gas-tight. Emissions of NO were measured *in situ* using a portable chemiluminescent detector equipped with a CrO_3 filter that converts all NO to NO_2 (Unisearch Associates, Concord, Ontario, Canada)(Matson 1996 *8*). Standard curves were conducted in the field before and after each set of four measurements using a standard gas with a known NO_2 concentration (0.0992 ppm, Scott-Marin Co., Riverside, CA). Ambient NO_2 concentrations were low but detectable, so

NO_2 concentrations within the chamber were measured immediately before and after NO measurements in order to measure the consumption of ambient NO2 by soils, which was assumed to be linear. NO emissions were measured as the linear increase in NO concentrations in the chamber over 4 minutes, and were corrected for the consumption of ambient NO_2 during that 4-minute period (Hall and Matson 2003).

To measure N_2O emissions, a Teflon-coated, molded PVC chamber top fitted with a septum was placed over each ring and made gas-tight. Using polypropylene syringes, 9ml gas samples were taken from the chamber at 0, 10, 20, and 30 minutes, and transferred to evacuated glass vials. The vials were stored at room temperature until analysis for N_2O using a gas chromatograph fitted with an electron capture detector. The N_2O flux was calculated using the linear increase in N_2O concentration, the chamber volume, and the soil surface area.

Ozone Sensitivity Analysis

To investigate the potential effects of a kudzu invasion on regional ozone levels, I used the global chemical transport model (CTM) GEOS-Chem model focusing on the summer season (June–August) when ozone levels are highest. The GEOS-Chem model has been extensively used in past studies on tropospheric ozone and its precursors, both globally (Bey et al. 2001, Martin et al. 2002, Sauvage et al. 2007, Wu et al. 2007) and for the United States (Fiore et al. 2002, Fiore et al. 2003a, Fiore et al. 2003b, Hudman et al. 2004, Hudman et al. 2007, Wu et al. 2008). I used GEOS-Chem version 8.01.01 (http://www.as.harvard.edu/chemistry/trop/geos/) with the meteorological input from the NASA/GISS general circulation model (GCM). More detailed model description is available in Wu *et al.* (Wu et al. 2007, Wu et al. 2008).

The soil NO_x inventory in the standard version of GEOS-Chem follows Yienger and Levy (Yienger and Levy 1995). For this study, I scaled the calculated soil NO_x emission in the SE by a factor of 3 in order to match observed NO fluxes in this region (Davidson et al. 1998). I followed the IPCC A1B scenario for 2050 in which the U.S. NO_x emissions from fossil fuel are projected to decrease by 40% due to technological improvements. The meteorology was simulated for 2050 which enhances the soil NO_x

emissions by 8% compared to 2000 due to higher temperatures (Wu et al. 2008). NO flux from non-agriculture soils account for about 1/3 of the total soil NO emissions over the SE (Davidson et al. 1998). As a sensitivity test, I assumed full kudzu coverage over the non-agriculture land area over SE, which increased the total soil NO_x emission by 28%.

Chapter 3 Range expansion of invasive species under climate change: understanding the potential impacts of a northward expansion of kudzu (*Pueraria montana*) on ecosystems and atmospheric chemistry

Abstract

Kudzu (*Pueraria montana*), a leguminous vine native to Asia, is expected to move northward by 100's of kilometers as global temperatures increase. As a nitrogen-fixer, kudzu has demonstrated the ability to accelerate nitrogen (N) cycling and increase production of both nitric oxide (NO), a precursor to tropospheric ozone, and nitrous oxide (N_2O), a powerful greenhouse gas. Though there is a strong theoretical and empirical foundation for predicting kudzu's expansion northward, it is more difficult to predict how that expansion will affect ecosystems in the northeastern United States in coming decades. Kudzu's range in the northern United States is limited by winter temperatures, and even in places where kudzu is able to establish, both soil temperature and growing season length can influence N-fixing activity in legumes, and may serve to diminish the potential impact of kudzu on invaded ecosystems and atmospheric chemistry. In order to understand the wider impacts of kudzu's expansion into the northeastern region in coming decades, I examined how kudzu invasion affects soil N and microbial dynamics from April, 2006 through September, 2007 at 3 sites in Maryland that currently experience winter temperatures within the range expected for the Northeast within the next 100 years. I also measured fluxes of NO and N_2O at 2 of the sites in September, 2007. Kudzu's impact on soils in Maryland appears to be subject to considerable interannual and spatial variability. Across all three sites, kudzu invasion only caused a significant increase in the sizes of soil nitrate and ammonium pools, and only on certain dates. Though there were no differences in N cycling through most of 2006, in 2007, net N mineralization was 10 times higher and net nitrification was 5 times higher in invaded soils at one site in Edgewater, MD, but not at the two other sites. Trace gas flux

measurements showed a similar pattern: NO fluxes from invaded soils were over 5 times higher than fluxes from uninvaded soils in Edgwater, but only half as large in a Poolesville, MD site. Kudzu leaf litter decomposed more quickly than litter from co-occurring species, providing one possible mechanism for the observed impacts on soil N dynamics. There were only occasional differences in denitrification activity, microbial biomass, and soil moisture in invaded and uninvaded soils, and no difference in N_2O fluxes. This study suggests that when experiencing lower temperatures and shorter growing seasons than are found closer to the center of its North American distribution, kudzu continues to have the potential to disrupt ecosystem processes, but the presence of an impact is subject to interannual and spatial variability, making these impacts less predictable than in lower latitudes. Although kudzu may not soon be the threat to northeastern ecosystems and regional air quality that it is in the southeastern U.S., it is possible that its establishment in the northeast may be accompanied by changes in N cycling and trace gas fluxes, at least in some places during certain, probably mild, years.

Introduction

Considerable attention has been paid to the impacts of a changing climate on the distribution of plant species. Much work has focused on documenting how climate change has already altered species distributions and to predict its impacts on communities and endangered or threatened species in coming decades (e.g., Benning et al. 2002, Parmesan and Yohe 2003, Root et al. 2005). Populations are generally expected to migrate to higher latitudes or higher elevations as increasing temperatures remove restrictions imposed by winter temperatures, and warmer summer temperatures may make lower latitudes or elevations less habitable (Kingsolver 1992). One question in this reshuffling of species is how plant species that play important roles in ecosystem processes will respond to the changing climate, including invasive species that have the potential to disrupt or damage communities and ecosystems as populations migrate under changing temperature and precipitation regimes. While field, greenhouse, and modeling studies have examined the responses of species and communities to global change factors (e.g., Sasek and Strain 1988, Higgins and Harte 2006, Mohan et al. 2006), the question of how these key species will interact with ecosystems at higher latitudes has received less

attention. Because climatic conditions at the northern edge of a species distribution in North America are likely both to be different from those at the center of the distribution and also closer to emerging conditions in more northern latitudes under a changing climate, understanding the ecosystem impacts of these populations can provide a window into the potential impacts of a northern expansion of the species in coming decades.

Kudzu (*Pueraria montana*), a leguminous vine native to Asia, is expected to move northward by 100's of kilometers as global temperatures increase, and it is likely to have a range of ecosystem impacts throughout its new distribution (Sasek and Strain 1991). Currently estimated to be spreading by 50,000 ha yr-1, this invasive vine already covers over 3 million ha in the southeastern United States, roughly equivalent to the acreage of soybean agriculture in the region, making it the likely dominant nitrogen-fixer in Southeast (USDA 2002, Forseth and Innis 2004). It has demonstrated a capacity for high rates of nitrogen (N) fixation in its native range and has shown a high degree of nodulation and nitrogenase activity in the United States (Lynd and Ansman 1990, Forseth and Innis 2004). Although fixation rates have not been measured in the U.S., kudzu is accelerating N mineralization and nitrification rates in soils at sites in Georgia, sometimes by an order of magnitude, and more than doubling emissions of nitric oxide (NO), a precursor to ozone formation, and nitrous oxide (N_2O), a powerful greenhouse gas (Hickman, in preparation).

There are numerous examples of how the species-specific physiology of plants can determine or strongly influence a number of ecosystem properties, including fire regime, water availability, nutrient cycling, and atmospheric chemistry (e.g., Vitousek and Walker 1989, Hobbie 1992, D'Antonio 2000, Zavaleta 2000, Hall and Asner 2007). In the area of atmospheric chemistry, of critical concern is the central role species-specific physiology can play in controlling fluxes of both volatile organic compounds (VOC's) and NO, the two key precursors to the formation of tropospheric ozone, which is often regarded as the most important air pollutant in terms of its impacts on public health and agriculture (EPA 2002). Biogenic emissions of the VOC isoprene (C_5H_8) are strongly controlled by species identity (Lerdau and Keller 1997, Keller and Lerdau 1999), while a key group of species—legumes and other N-fixing plants—are linked to substantial increases in NO fluxes from soils, presumably as a consequence of the

decomposition of their N-rich litter (Erickson et al. 2001, Martin et al. 2003, Hall and Asner 2007, Hickman in preparation). Because species identity is so important to the emissions of N oxides and isoprene, a shift in plant community composition, as would occur with changes in species distributions under climate change, can result in large shifts in an ecosystem's capacity to produce and emit these reactive compounds. The unusual physiological combination found in kudzu--moderate- to high-emissions of isoprene and a high N-fixation capacity that has been shown to double soil NO fluxes in Georgia--means that the vine is responsible for increasing emissions of both precursors to tropospheric ozone, making it as close to a "polluting plant" as one can find (Hickman in preparation). The northern expansion of kudzu, which already appears to be underway (see below), has the potential to profoundly change northeastern ecosystems and atmospheric chemistry. Understanding how kudzu's physiology will interact with the new environment it encounters in the ecosystems of the northeast is essential to understanding its potential impact on soils, communities, and the atmosphere.

Two key environmental factors are behind the expected range expansion of kudzu: ambient CO_2 concentrations and winter temperatures, both of which are expected to increase substantially in the 21st century. Vines in general have shown larger and more sustained growth responses to increased CO_2 than trees have (Hattenschwiler and Korner 2003), and the growth responses of N-fixers such as soybean have shown little acclimation to elevated CO_2 (Ainsworth et al. 2002).

Though there is a strong theoretical and empirical foundation for predicting kudzu's expansion northward (Wechsler 1977, Sasek and Strain 1991, Jones et al. 1994, Soussana and Hartwig 1996, Hartwig et al. 2000, Ainsworth et al. 2002, Lamont and Young 2004), it is more difficult to predict how that expansion will affect ecosystems in the northeastern United States, at least during the 21st century. In regions where winters are not severe enough to prevent the establishment of kudzu, season length and cold temperatures are still likely to diminish rates of N fixation in kudzu and limit changes to soil N cycling. Reductions in soil temperature of as little as 5° C have been shown both to delay the onset and reduce the degree of nodulation in several legumes (e.g., *Glycine max* (L.) Merr., *Lupinus angustifolius*, *Vicia faba* L., *Trifolium repens*, *Medicago doliata*), so that plants growing in soils that remain cooler longer into the growing season

exhibit diminished rates of N fixation relative to plants growing in warmer soils (Lindemann and Ham 1979, Fyson and Sprent 1982, Ryle et al. 1989, Peltzer et al. 2002, Robin et al. 2005). Freezing temperatures during the winter can induce embolisms in vines, and may reduce the amount of kudzu biomass surviving to the next growing season. Consequently, even as temperatures permit a northward expansion of kudzu, its impact on the N cycle may not mirror those observed closer to the center of its distribution. Even so, growing seasons in the Northeast are expected to increase by roughly 20 to 60 days by the end of the century, and average temperatures by 2.5° to 5.5° C, creating a climate likely to be considerably more hospitable to kudzu, and more conducive to high rates of N fixation (Jones et al. 1994).

Another factor that has the potential to influence an impact of kudzu on soil N dynamics is atmospheric N deposition. Rates of N deposition tend to be higher in the northeastern United States than in southern states (Holland et al. 2005). When soil pools of inorganic N are large, N-fixers may reduce investment in N fixation, and N fixation itself can be inhibited (Lucinski et al. 2002). Additionally, N additions to uninvaded soils may reduce any differences that may have emerged between invaded and uninvaded soils as a consequence of kudzu invasion.

Because of these complicating factors, predicting the impacts of a northern expansion by kudzu is not simply a matter of mapping out where kudzu is expected to establish and assuming that the impacts observed in kudzu's current distribution will be replicated in its new range. Instead, these various factors make predicting kudzu's impact on soils in higher latitudes more difficult. It is possible that delayed onset of N fixation and reduced nodulation in cooler soils as well as winter die-back can reduce the amount of N added to soils by kudzu, while higher rates of N-deposition to both invaded and uninvaded soils in the northeastern United States could reduce the magnitude of any differences in N dynamics in invaded and uninvaded soils that may have emerged as a consequence of kudzu alone. However, projections of kudzu's N fixation rates under ideal climatic conditions are an order of magnitude larger than N deposition rates (Forseth and Innis 2004, Holland et al. 2005), leaving the possibility that kudzu could have sizable impacts even under the conditions of cooler temperatures and higher N

deposition prevalent in the northeastern United States expected to continue during coming decades.

In order to understand the wider impacts of kudzu's move north in coming decades, I examined how well-established kudzu populations at the northern limit of its current distribution affect a range of community and ecosystem properties. I expect the cooler temperatures that predominate in the northern part of kudzu's distribution to limit kudzu productivity, particularly in years with multiple freezing events, and consequently to reduce N-fixation rates on an per unit area basis. These increases, combined with higher levels of N deposition, are likely to reduce potential differences in N cycling and trace N gas in invaded and uninvaded soils. However, I expect the large differences observed in Georgia (Hickman in preparation), the large observed and estimated N-fixation activity of kudzu, and the generally high N lifestyle of legumes (Hickman in preparation) to increase N cycling rates and trace gas emissions even in these more northern soils, particularly in soils where kudzu density approaches levels typically observed in the southeastern United States.

Materials and Methods

Sites

I selected sites where winter temperatures tend to be colder than in the center of kudzu's current distribution, and have been within the range that northeastern temperatures are expected to reach within the next 100 years. Averaged over 1961 to 1990, January minimum temperatures in the southeastern United States, where kudzu thrives, tended to hover around or slightly above freezing; Athens, GA and Montgomery, AL averaged -0.056° and 1.83°C, respectively. Minimum January temperatures were considerably lower in Northeastern states, averaging –9.78° to –9.167°C in Poughkeepsie, NY, Worcester, MA, and Hartford, CT. In Baltimore, MD, at a latitude where kudzu has long been successfully established, average minimum January temperatures were –4.72°C from 1961 to 1990, roughly intermediate between the Southern and Northern averages (NOAA/ESRL 2008). Minimum temperatures in the northeastern United States are expected to increase by roughly 2-6 degrees by the end of

the century, making northeastern winters much closer in temperature to those currently experienced in Maryland (Jones et al. 1994).

Because changes in ecosystem processes (including trace gas fluxes) can lag behind changes in community composition (Chapin 2002), I selected three sites where kudzu was well-established: McKee-Beshers Wildlife Management Area in western Montgomery County, MD (N 39 05.107, W 077 25.871), the Summit Hall Turf Farm, also in Montgomery County (N 39 05.315, W 077 26.556), and the Smithsonian Environmental Research Center (SERC) in Anne Arundel County, MD (N 38 51.945, W 076 33.815).

Experimental design

The paired-site design has become common in studies of the effects of N-fixers on soil N studies and gas fluxes (Rice et al. 2004, Yelenik et al. 2004, Ashton 2005). The paired uninvaded site is used as a control or reference for determining the relative impact of kudzu invasion. In this case, the paired-site structure is preferable to a transect design because kudzu typically invades along a forest edge, and transects running from invaded into uninvaded habitat would also run from the forest edge into the forest interior, confounding degree of kudzu invasion with edge effects. At each site, one plot was established within a stand of kudzu, and a second plot was established in an area where kudzu had not invaded, within 40-200m of the kudzu plot, for a total of 6 plots. At SERC, the invaded plot was located within a former agricultural field where kudzu has been present for over 30 years. The uninvaded plot was established on a former agricultural field abandoned 30 years ago, cleared 10 years later, and allowed to return to succession during the last 20 years (Dennis Whigham, personal communication). Soils in both the invaded and uninvaded plots at SERC were a well-drained Marr-Dodon complex, derived from loamy fluviomarine deposits, with a slope of 2 to 5 degrees (USDA). Soils at all plots in McKee-Beshers and Summit Hall were well-drained Penn silt loam. At McKee-Beshers, both plots had 3 to 8 degree south-facing slopes; the plots at Summit Hall had 15 to 25 degree slopes (USDA). The area adjacent to these plots has been managed as a flooded bottomland swamp for over 40 years; the plots themselves are unmanaged (Ken D'Loughy personal communication). Plant cover at the sites was

characterized in September, 2005 and was described by Hickman and Lerdau (Hickman 2006). In invaded plots at all three sites, kudzu cover ranged from 80% to 100%. Uninvaded plots at all three sites contained primarily herbaceous species, though the woody shrub *Rosa multiflora* was present in the uninvaded plot at SERC. Additionally, succession had proceeded further in the area around the uninvaded plot at McKee-Beshers was located—though the plot itself contained only herbaceous species, the surrounding area contained more and larger trees than the other plots.

Sample collection and preparation

Soil sampling was conducted 9 times starting in March, 2006: bimonthly from March through September 2006 and 2007, and once in December, 2006. At each sampling time, soil cores were always taken from all sites within a single day, with the exception of September, 2007, when soils from SERC were taken on September 5th, and soils from the other sites were taken on September 6th. Locations for soil cores were selected randomly in each plot; 3 cores were taken per plot, for a total of 18 cores per sampling time. The one exception was sampling in September, 2007, when 4 cores were taken per plot, for a total of 24 soil cores. The top litter layer was removed, and a PVC pipe (5 cm internal diameter x 20 cm long) was driven 12 cm into the ground and removed with the core intact. The cores contained little or no organic layer, so they were not separated into different horizons before being placed in separate polyethylene bags. The cores were kept cool until transferred to a refrigerator in the lab. Most lab analyses were started within 3 days of soil collection, but the denitrification assays were usually conducted 4-6 days after sampling, and analysis of soils from September, 2007 were conducted approximately 2-3 weeks after sampling. Since precipitation can stimulate microbial activity (Paul 1996), samples were taken at least 24 hours after any major rain event.

Soils were homogenized by hand in plastic bags, and major rocks, roots, and invertebrates were removed. Subsamples from each core were taken for laboratory analysis of moisture content, total C and N, initial nitrate and ammonium, microbial biomass, net mineralization and nitrification potential, and denitrification enzyme assays (details below). Soil moisture content (g H_2O g^{-1} dry soil) was determined by drying a

subsample at 60° C until soils were no longer decreasing in weight. Total carbon (C) and N content of dried, ground samples was determined using a CE Flash EA 1112 Elemental Analyzer (CE Instruments, Milan, Italy).

Inorganic N pools

Inorganic N was extracted from soils by placing a 10g subsample of soil from each core in a 120 ml polypropylene specimen cup with 50ml 2M KCl, and shaking the cups for 60 minutes to ensure that all the inorganic N bound to soil surfaces can exchange with the KCl. The soils were allowed to settle for another 60 minutes after shaking. The KCl solution from each cup was filtered using Whatman #42 filter paper and frozen in a 40ml glass scintillation vial until determinations of NO_3^-/NO_2^--N and NH_4^+-N content were made using a Lachat autoanalyzer (Lachat Quickchem Systems, Milwaukee, WI). These measurements also represent the initial or "pre-incubation" inorganic N concentrations for the calculations of net N mineralization and net nitrification rates.

Net N mineralization and net nitrification

Concurrent with subsampling for the initial KCl extractions, a second 10g subsample was taken from each homogenized core and placed in a 120 ml specimen cup, which in turn was placed in a mason jar and sealed with a gas-tight lid fitted with a rubber septum. The jars were incubated at 20-22° C. After 10 days, the specimen cups were removed, and inorganic N was extracted and analyzed as described above; these extractions represent the "post-incubation" inorganic N content. Net mineralization was calculated as the difference in total inorganic N concentrations in the pre-incubation and post-incubation extractions; net nitrification was calculated similarly, as the difference in NO_3^--N and NO_2^--N concentrations in pre- and post-incubation soil extractions (Matson et al. 1987).

Soil microbial biomass

The determination of total microbial biomass was made using the chloroform fumigation incubation method (Jenkinson and Powlson 1976, Voroney and Paul 1984). A 10g subsample of soil from each core was fumigated for 12-18 hours. The 10g samples of fumigated soils and a 0.1g fresh soil inoculum from the same core were

placed in a quart-sized mason jar and sealed with a gas-tight lid fitted with a rubber septum. A second 10.1g fresh sample from the same core was sealed in a second mason jar. After a 10 day incubation at 20-22^{o} C, a 9ml gas sample from the headspace of each mason jar was transferred to an evacuated glass vial. The vials were stored at room temperature until CO_2 concentrations were determined using a gas chromatograph fitted with a thermal conductivity detector. Microbial biomass-C was calculated as the CO_2-C per unit dry weight of soil in fumigated samples, divided by a constant (0.41) representing the fraction of biomass mineralized to CO_2.

Denitrification enzyme activity

I determined the denitrification potential of soils using the Dentrification Enzyme Activity method (Smith et al. 1978). A slurry of soil and a medium containing a surfeit of nitrate and glucose was created, so that the denitrification process was limited only by the amount of denitrifying bacteria in the sample. Choloramphenicol, an inhibitor of microbial growth, was added to ensure the assay was measuring activity of the microbial community present in the soil at the time of sampling. A 5g subsample was taken from each homogenized soil core and placed with 10 ml medium into a 125ml Erlenmeyer flask with a ground glass neck and sealed with a rubber stopper. The flasks were placed under negative pressure for 3-minutes followed by a 1-minute flush with N_2 gas. This process was repeated 2 more times to ensure that the soils were anaerobic. Following the third flush with N_2, the flasks were vented to room pressure, and 4ml acetylene was added to each flask to inhibit the transformation of N_2O to N_2 by denitrifying bacteria. The flasks were placed on an orbital shaker, and 9ml samples of the headspace of each flask were taken using a polypropylene syringe and transferred to evacuated gas vials after 1 and 3 hours. The N_2O concentration of each vial was determined using a gas chromatograph fitted with an electron capture detector. The change in N_2O concentration from time 0 through 3 hours was used to calculate the denitrification rates.

Trace N gas emissions

Plots were sampled for NO and N_2O emissions on September 5th and 6th, 2007. Gas measurements for each set of paired uninvaded and invaded plots were conducted on

the same day, and all sampling was conducted between 10am and 6pm to limit variation in temperature between plots. In each plot, four beveled, Teflon-coated PVC rings (25.5cm diameter) were randomly inserted several centimeters into the soil. At least 30 minutes after inserting the ring, a Teflon-coated, molded PVC chamber top fitted with a gas-sampling port was inserted over the ring and made gas-tight. Emissions of NO were measured *in situ* using a portable chemiluminescent detector equipped with a CrO_3 filter that converts all NO to NO_2 (Unisearch Associates, Concord, Ontario, Canada). Standard curves were conducted in the field before and after each set of four measurements using a standard gas with a known NO_2 concentration (Scott-Marin Co., Riverside, CA). Ambient NO_2 concentrations were low but detectable, so NO_2 concentrations within the chamber were measured immediately before and after NO measurements in order to measure the consumption of ambient NO_2 by soils, which was assumed to be linear. NO emissions were measured as the linear increase in NO concentrations in the chamber over 4 minutes, and were corrected for the consumption of ambient NO_2 during that 4-minute period (Hall and Matson 2003).

To measure N_2O emissions, a Teflon-coated, molded PVC chamber top fitted with a septum was placed over each ring and made gas-tight. Using polypropylene syringes, 9ml gas samples were taken from the chamber at 0, 10, 20, and 30 minutes, and transferred to evacuated glass vials. The vials were stored at room temperature until analysis for N_2O using a gas chromatograph fitted with an electron capture detector. The N_2O flux was calculated using the linear increase in N_2O concentration, the chamber volume, and the soil surface area.

Litter decomposition

In October, 2006, newly senesced leaf litter was collected from kudzu and 7 co-occurring woody species (Table 1). Litter was collected along a transect approximately 500m in length encompassing both invaded and uninvaded areas in the McKee-Beshers Wildlife Management Area, and running across Penn silt loam soils. Litter bags were constructed from nylon 1/32 inch square mesh, measuring 15.5cm by 12cm along the interior edges. Enough bags were constructed to allow for the destructive sampling of three replicates of each species at 18, 32, 44, and 53 weeks. Leaves were dried at room

temperature, and 2.5g of dried litter from a single species was placed in each mesh bag and weighed. Three 2.5g samples from each species were dried at 60°C and weighed to calculate the weight difference between air-dried and oven-dried litter. Each bag was sealed with three staples of known weight, which was later subtracted from the final weight after harvesting.

The litter bags were placed in the field December 6th, 2006. Replicates were allocated randomly to each of 3 blocks located approximately 10m apart from one another in an area of uninvaded forest in McKee-Beshers. Within a block, litter bags were placed randomly on a 3 m^2 grid at 0.5m intervals. At each harvest time, bags were collected, dried at 60°C, weighed, and ground for analysis of C and N content using a CE Flash EA 1112 Elemental Analyzer (CE Instruments, Milan, Italy).

Statistical analyses

Because of several site disturbances in which plot markers were removed or destroyed, it was necessary for me to establish new plots for sampling on several occasions over the course of the 2-year experiment. Consequently, I was unable to conduct a repeated measures analysis of the soil data. Instead, I conducted separate split-plot ANOVAs at each time point to avoid non-independence of samples within any single analysis; site was included as a random factor, and kudzu invasion as a fixed factor.

Analyses of the NO and N_2O fluxes were conducted using split plot ANOVA, including site and kudzu invasion whole and within plot factors. For the decomposition experiment, mass loss and N loss were analyzed in 3-way mixed model ANOVAS, including block as the random factor, and species and harvest date as the fixed factors. When necessary, data were log transformed or rank transformed to meet the assumptions of ANOVA.

Results

Across all three sites, kudzu invasion only caused a significant increase on the sizes of soil nitrate pools, nitrification rates, and denitrification enzyme activity, and only on certain dates, and trends towards an increase in some of these variables on several dates as well as on microbial biomass on one date (Table 2, Figures 1 through 8). Nitrate

levels in invaded areas were an average of over 1.5 times higher on dates where the difference was significant. The difference actually increased to just over 2 times when summed across all sampling times, and invasion may have had a significant effect on nitrate pools across sampling times with the greater statistical power of a repeated measures analysis (Figure 1). There were no differences in total soil N.

There were no differences between the kudzu and uninvaded plots in net N mineralization, and differences in net nitrification on only two dates (Figure 2). Tests of significance for interactions are not possible in split plot analyses, but visual inspection of the data suggests that in 2007, net N mineralization was an average of 10 times higher in invaded soils at SERC than in uninvaded soils, while net nitrification was 5 times higher (Figure 3). It appears that while kudzu had no impact on net N mineralization and nitrification in 2006 at any of the sites, it may have been accelerating N cycling at the SERC site in 2007, but not at the other two sites.

September, 2007 measurements of trace N gas fluxes followed the pattern for soil N cycling; there was no significant difference, but examination of the data shows that NO fluxes were over 5 times higher in invaded soils at SERC; in contrast, fluxes in invaded soils at Summit Hall were only half as high as in uninvaded soils (Figure 4A). There were no differences in N_2O fluxes, though N_2O emissions from invaded soils at SERC were more than 3 times higher than emissions from uninvaded soils (Figure 4B).

Laboratory assays of denitrification enzyme activity, which provides an index for potential denitrification rates, showed differences due to kudzu invasion only in May, 2007, when enzyme activity was higher in soils from uninvaded sites (Figure 5, $P=0.023$ in a two-tailed test).

There was no significant effect of invasion on microbial biomass at any of the sampling times (Figure 6). With the single exception of September, 2007, when soil moisture was higher in uninvaded soils ($P=0.024$), soil moisture did not differ between invaded and uninvaded areas. (Figure 7). There were no differences in total soil C.

Leaf litter from kudzu lost mass more quickly than 7 co-occurring tree species in 2007 ($P<0.0001$, Figure 8). By the end of one year, kudzu had lost most of its mass (56.2% +/-2.3% of starting mass), while on average, litter from each of the other species lost between 38.0 +/-3.0% and 14.0 +/- 1.0% of their initial mass. Patterns of N loss

matched those for mass loss, with kudzu losing a greater percentage of its starting N and more N mass over the course of the year than the native species ($P<0.05$).

Discussion

Warming temperatures are expected to promote the expansion of kudzu into the northeastern United States, which may result in the disruption of ecosystem processes and increases in the emissions of harmful trace gases. Both soil temperature and growing season length can influence N-fixing activity in legumes, and may serve to diminish the potential impact of kudzu on invaded ecosystems and atmospheric chemistry. My study in Maryland suggests that when experiencing lower temperatures and shorter growing seasons than are found closer to the center of its distribution, kudzu continues to have the potential to disrupt ecosystem processes, but the presence of an impact is subject to large inter-annual and spatial variability, making these impacts less predictable than in lower latitudes.

The most striking of the results is evidence of increased trace N gas fluxes and N cycling in invaded soils and NO fluxes at one site in 2007, but not in others. Visual examination of the data suggests that N cycling rates were higher in invaded soils at the SERC site throughout 2007 (Figure 4), and that both NO and N_2O fluxes were higher in September 2007 (Figure 4). Though NO fluxes were actually only half as large from invaded soils as uninvaded soils at Summit Hall, invaded soils at SERC emitted NO 5 times faster than in uninvaded soils—a much larger difference than the approximate doubling observed in Georgia. Since I only made measurements in September, 2007, it is impossible for me to draw any direct conclusions about the potential inter-annual variability in gas fluxes from invaded and uninvaded soils in Maryland. However, because NO is produced largely as a byproduct of nitrification, it is likely that differences in NO emissions from invaded and uninvaded soils were absent at all sites in 2006, emerging only at SERC in 2007. At the very least, the September, 2007 gas flux measurements suggest that kudzu may have the potential to cause dramatic increases in NO fluxes from some soils as it migrates north, with the potential for unwelcome changes to regional air chemistry.

While environmental conditions in Maryland appear often to inhibit the kinds of ecosystem and atmospheric impacts kudzu is having in ecosystems farther south (Hickman in preparation), this inhibition is not universal. The degree to which the 2007 increases in N cycling and gas emissions at SERC may be an anomaly is unclear. Periods of unusually mild temperatures during winter 2006-2007 may have played a contributing role to these increases, but daily and monthly temperature records provide little support for the possibility that the interannual variability can be attributed to temperature differences. Average winter temperatures (December through February) in Maryland weren't any higher in 2006-2007 (2.39° C) than they were the previous winter (2.56° C). March temperatures were slightly higher in 2007 (6.89° C) than in 2006 (6.56° C), but April was 3.06° C warmer in 2006 than 2007 (NCDC 2008). There was also little change in the number of days experiencing below-freezing temperatures in Upper Marlboro, MD (near the SERC site) from October through April for the two years: 94 days experienced below-freezing temperatures in 2005-2006, and 97 days in 2006-2007 (NCDC 2008).

Whatever the driving factor for the observed differences at SERC, these results suggest that kudzu retains the ability to disrupt ecosystems and increase emissions of dangerous trace gases in a region where average minimum January temperatures are roughly 4.5° C colder on average than in Georgia, and within the range of temperatures expected for much of the northeastern region by the end of the century. Although kudzu may not soon be the threat to northeastern ecosystems and regional air quality that it is in the southeastern U.S., it is impossible to dismiss the possibility that its establishment in the northeast may be accompanied by changes in N cycling and trace gas fluxes, at least in some places during certain, probably mild, years. One may also expect regions where kudzu is now established but where it does consistently alter N cycling may experience greater impacts of invasion as temperatures warm. An increase of 2 to 6° C by 2100 would raise winter temperatures in Maryland above those currently experienced in Georgia, where kudzu's impact on N cycling is large and consistent.

Alternatively, it is possible that atmospheric N deposition, which is generally higher in the Mid-Atlantic region than in southeastern states (Holland et al. 2005), and can enrich the inorganic N content of soils, may be reducing N fixation in kudzu at the Maryland sites. Since N-fixation is energetically expensive, N-fixers may switch to

uptake of NH_4^+ and NO_3^- if there are high concentrations of inorganic N in soils; nitrate can also inhibit nitrogenase activity and rhizobial infection of legume roots (Munns 1977, Kwon and Beevers 1993, Lucinski et al. 2002). Because there are differences in both temperatures and atmospheric N deposition with latitude, it is impossible to eliminate N deposition as a contributing factor to the different patterns of N cycling observed in Maryland and Georgia. However, if there was little variation in N deposition between sites in Maryland, the presence of a difference at SERC in 2007 suggests that N deposition was not responsible for the absence of an effect of kudzu invasion in 2006. Using measurements in 2005 and 2006 as replicates, there were no differences in annual wet NO_3^- and NH_4^+ deposition among 5 National Atmospheric Deposition Program monitoring locations in Maryland and Virginia, though there were differences among locations when analyzing just summer deposition (P=0.52 and P=0.06, respectively; analysis not shown) (NADP 2008).

Additionally, if N deposition were contributing to greater N availability in Maryland than in Georgia, I would expect to find faster N cycling rates and possibly larger pools of inorganic N in uninvaded soils in Maryland. However, net N mineralization, net nitrification, and denitrification enzyme activity did not differ in uninvaded soils in the two states (P=0.56, P=0.55, an P=0.28 respectively; analysis not shown) or in pool sizes of inorganic N (P=0.51; analysis not shown). While I can't rule out a role for atmospheric N deposition completely, it appears to be an unlikely source of the site differences I observed. Even if N deposition is contributing to reduced N-fixation in kudzu, that effect can be expected to decrease under increasing atmospheric CO_2 concentrations. Elevated CO_2 acts as a drain on inorganic N pools in soil, limiting growth responses in non-N-fixers, while the growth response to elevated CO_2 in N-fixers is unaffected (Soussana and Hartwig 1996, Hartwig et al. 2000, Lee et al. 2003). Resolution of these questions would be aided by direct measurements of N-fixation rates in kudzu in both Maryland and Georgia and comparisons of N inputs from kudzu to N inputs in uninvaded areas.

It is certainly possible that interactions in N deposition, temperature, and competition for soil N could play a role in controlling N-fixation in kudzu, and controlled experiments incorporating these factors will be needed to determine exactly what factors

and interactions are important. The possible confounding effect of N deposition is a necessary consequence of conducting paired field experiments like this one. However, in studying the ecosystem effects of invasion, and especially in trying to understand the possible real-world impacts of kudzu's northward expansion on variables such as NO emissions, field studies are an essential tool (see discussion in Ashton et al, 2005 (Ashton 2005)). Ultimately, a combination of controlled field experiments and manipulative studies focusing on factors of interest will provide more complete understanding of how various factors may interact with kudzu invasion to influence gas fluxes and N cycling.

In contrast to 2007, sampling throughout the 2006 growing season revealed only a mild effect of kudzu invasion—a sporadic increase in the size of NO_3^- pools in invaded soils, which continued in 2007, and a smaller, less consistent difference in NH_4^+ over the two years (Figure 1). The absence of differences in net N mineralization, net nitrification, and denitrification enzyme activity in 2006 suggests that differences in N cycling rates were not responsible for the increased NO_3^- in invaded plots. Although kudzu plots were not significantly drier than uninvaded plots, it may be possible that increased water use by kudzu had some drying effect on soils, reducing leaching of nitrate. Additionally, pools of NO_3^- can increase in dry soils when sub-surface NO_3^- is carried to the surface with the movement of capillary water (Paul 1996). N-fixation activity by kudzu may also reduce the plant's demand for other sources of N, so that differences in soil inorganic N pools may reflect differential plant uptake in invaded and uninvaded plots.

Even when net N mineralization and net nitrification were higher in invaded plots, no differences emerged in denitrification enzyme activity. Denitrification depends on a source of reduced C and anoxic conditions in addition to NO_3^- (Davidson et al. 2000), and it is possible that these factors limited denitrification in both invaded and uninvaded sites rather than NO_3^- pools.

The markedly faster decomposition of kudzu leaf litter is consistent with the idea that labile, N-rich litter is responsible for kudzu's impact on soil N dynamics. Kudzu's more labile leaf litter began to lose mass more quickly than other species within the first few months of decomposition, and extended that difference throughout the year. These faster rates of mass and nutrient loss represent a faster input of nutrients into these

ecosystems than is typical of co-occurring woody species, and provide a probable mechanism for observed increases in N cycling rates. Root exudation and turnover may also play an important role.

Soil moisture, which can be an important determinant of microbial activity (Paul 1996), differed as a consequence of invasion only in September, 2007. The significant effect of invasion in September, 2007 is worth noting, however, since I took gas samples on this date, and soil moisture can affect both the size of trace gas fluxes and the proportion of NO to N_2O emitted (Davidson and Verchot 2000). Oxygen diffuses more slowly into soils with high moisture levels, favoring the anoxic process of denitrification, the major source of N_2O production, over nitrification, which produces larger amounts of NO. Additionally, high soil water content slows the diffusion of NO out of soils, providing microbes with more opportunities to further reduce NO to N_2O or N_2 (Davidson et al. 2000). These soils were relatively dry, with only 10-15% moisture by mass, however, and though present, the differences between invaded and uninvaded soils were very small: 10.3% and 11.0% moisture by mass, respectively. Though soil moisture is essential for substrate transport and availability (and thus can help promote rates of N cycling and gas fluxes), the direction of difference in moisture at these sites (including SERC) was opposite that of N cycling and gas fluxes, indicating that other factors—such as kudzu invasion--were more important to the differences in N cycling at SERC.

Many invasive species, such as *Myrica faya* in Hawai'i, or kudzu in the southeastern U.S., can have dramatic impacts on the ecosystems they invade. The environmental context of an invasion can be an important determinant of the magnitude of that invasion's impact on an ecosystem. In Hawai'i, the absence of any N fixers combined with a N-poor substrate provide an environment in which invasion by the N-fixer *M. faya* can fundamentally alter the trajectory of community development (Vitousek and Walker 1989). In the eastern U.S., the replacement of chestnut, a species that does not emit the VOC isoprene, by species of oak, which does, likely resulted in a net increase of biogenic VOC production in the region (Lerdau 2003). The impacts of kudzu, both an N-fixer and a large emitter of isoprene, may likewise be dependent on the environmental context of invasion as it migrates north.

My research suggests that in a climate typical of the northern limits of its current distribution, kudzu retains the ability to increase N cycling and fluxes of trace N gases, though this ability may often be inhibited, presumably as a consequence of cooler soil temperatures, shorter growing seasons, and freezing events that may damage above-ground biomass. As often as not, establishment of kudzu in the northeast may not be accompanied by changes in N cycling, but my understanding of kudzu's impacts at these higher latitudes is not complete enough to predict where and when it may affect ecosystems, other than to say that some, sometimes large, changes to N cycling and emissions of dangerous trace gases are likely to result. Over time, one can expect the frequency of ecosystem impacts to increase as northeastern winters grow milder and growing seasons become longer, creating an environment more suitable to kudzu establishment and N-fixing activity. Elevated CO_2 concentrations may enhance this effect, both by having a fertilizing effect on kudzu growth and by depleting soil N, giving kudzu a stronger competitive advantage over non-N-fixers. Though kudzu's full impact on the ecosystems and atmosphere of northeastern states may not be experienced for years or decades after it invades, preventing its establishment will be essential to avoiding these potentially damaging impacts in the long term.

Tables & Figures

Species
Acer rubrum
Acer negundo
Carya glabra
Fagus grandifolia
Pueraria montana
Quercus alba
Sassafras albidum

Table 1. Plant species used in litter decomposition experiment.

	2006					2007			
	April	May	July	Sept	Dec	March	May	July	Sept
Net N mineralization	0.710	0.350	0.785	0.998	0.820	0.521	0.832	0.145	0.440
Net nitrification	0.137	0.945	0.511	***0.0558***	0.608	0.675	0.696	0.223	0.593
Soil NO_3^-	***0.0867***	0.328	**0.00422**	0.403	0.430	***0.0962***	**0.0434**	0.460	0.161
Soil NH_4^+	0.376	0.580	0.894	0.825	0.261	0.120	0.140	0.910	0.768
DEA	0.828	0.955	0.957	0.422	0.127	0.179	**0.0229**	0.690	0.525
Microbial biomass			0.434	0.151	0.623	0.476	0.421	0.308	0.201
Moisture	0.364	0.510	0.646	0.793	0.923	0.519	0.484	0.455	***0.074***

Table 2. Results of split plot ANOVA F tests for the effect of kudzu invasion ANOVA for each sampling time. Results that are significant at $P<0.05$ are in bold, and for $0.05<P<0.10$ are in bold italics. P values for significant tests of kudzu invasion on variables involving N are presented as one-tailed tests.

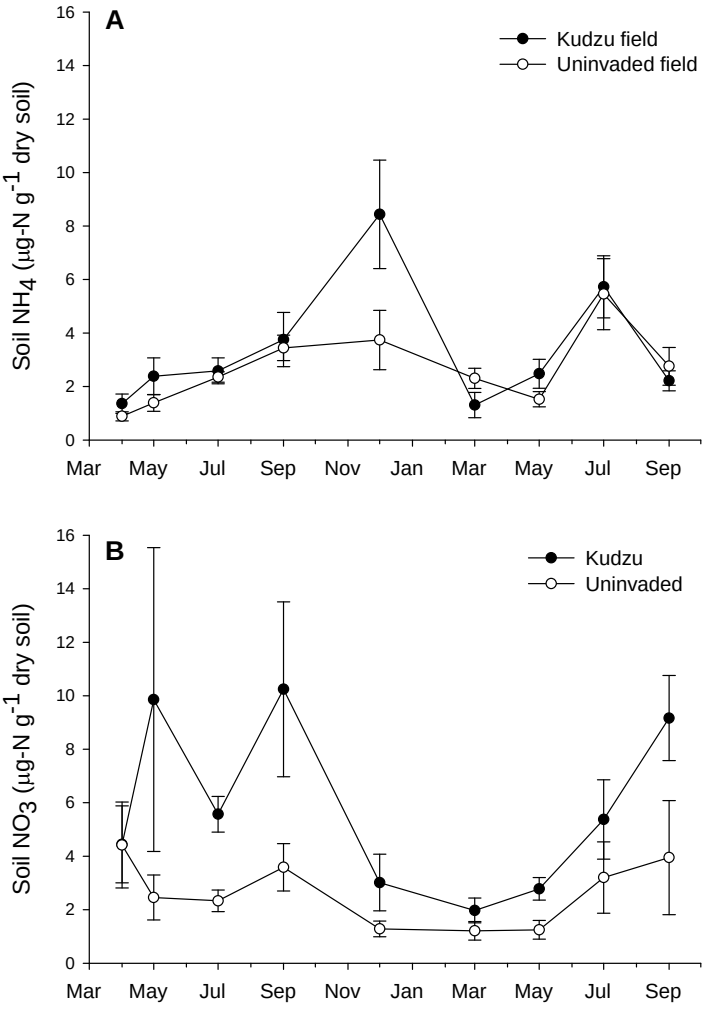


Figure 1. Soil pools of inorganic nitrogen at three sites in Maryland from April, 2006 through September, 2007. Values are means +/- 1 SE. Pools of nitrate tended to be higher in areas invaded by kudzu throughout the sampling period (B, $P<0.05$ for 4 of 9 sampling times in one-tailed tests, $P=0.08$ for a 5th).

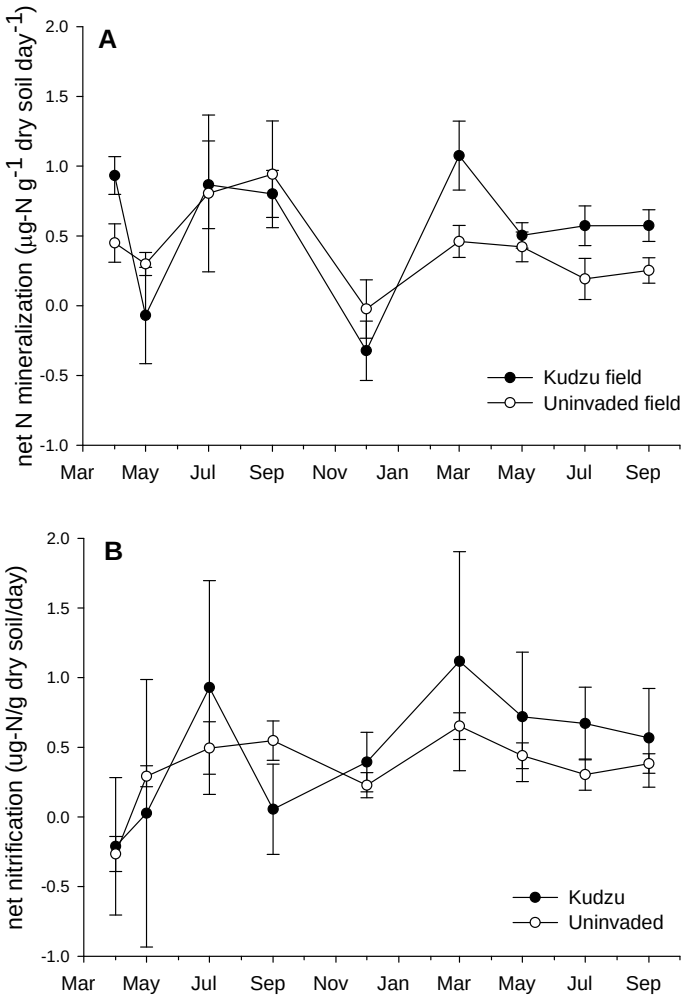


Figure 2. Net N mineralization (A) and net nitrification rates (B) at three sites in Maryland from April, 2006 through September, 2007. Values are means +/- 1 SE. There are significant interactions between site and kudzu presence throughout 2007 for net nitrification rates ($P<0.05$ in one-way tests), and for x of the 4 sampling times in 2007 for net mineralization ($P<0.05$ in one-way tests).

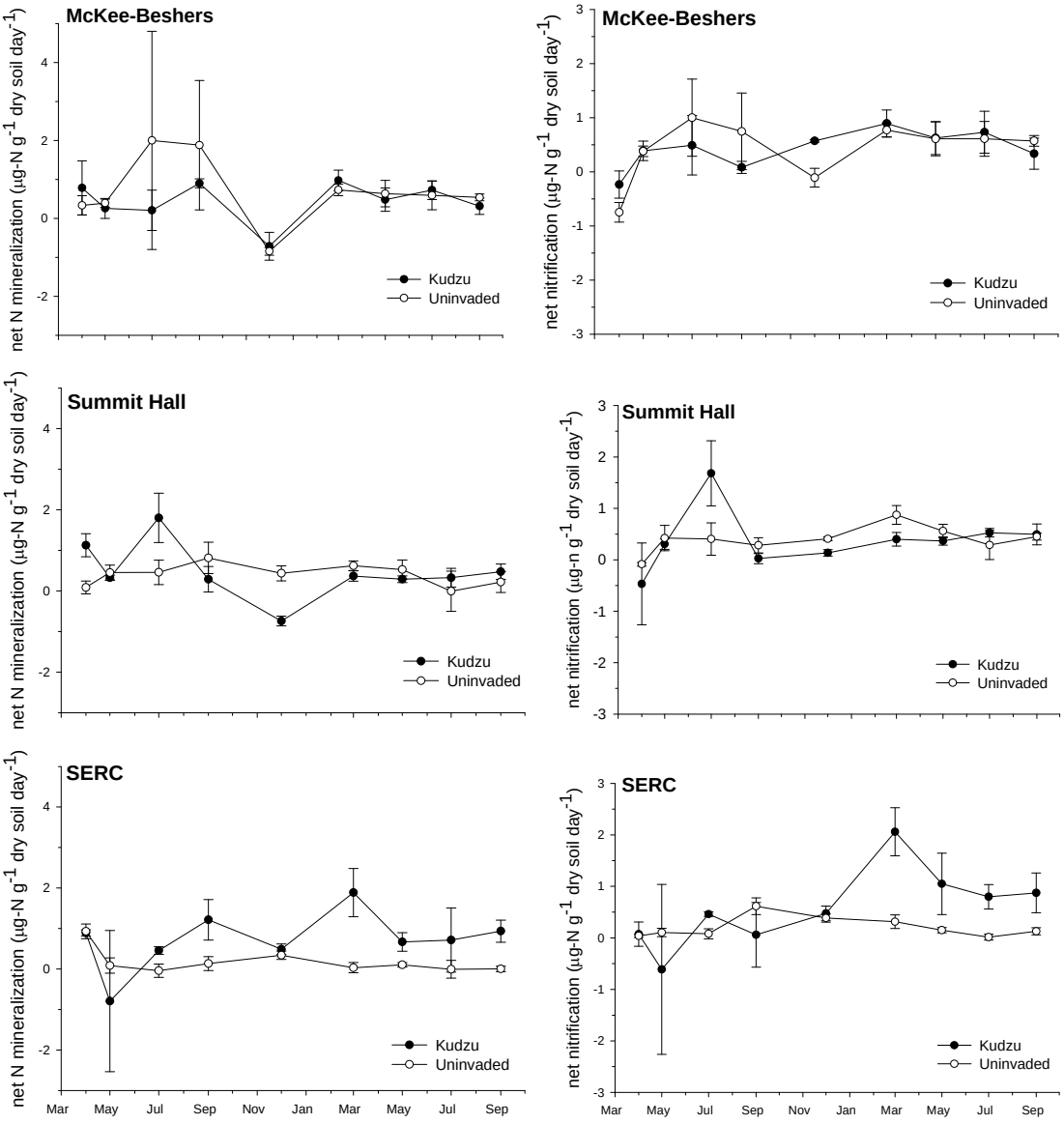


Figure 3. Net N mineralization (left) and net nitrification (right) at each of the three sites in Maryland from April, 2006 through September, 2007. Values are means +/- 1 SE. Significant interactions between site and kudzu presence in 2007 suggest

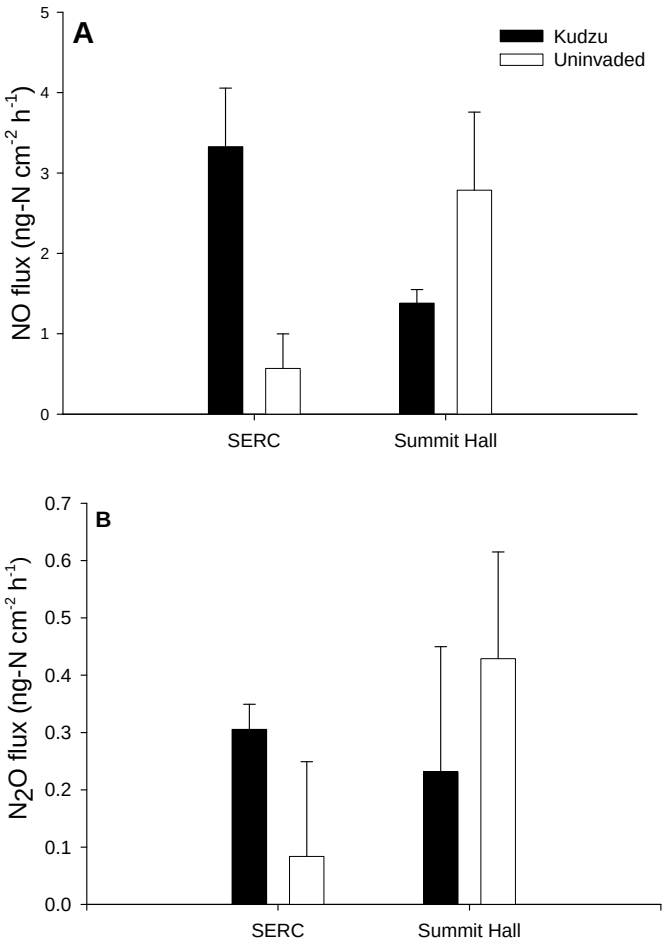


Figure 4. Emissions of NO (A) and N_2O (B) at two sites in Maryland in September, 2007. Values are means +/- 1 SE.

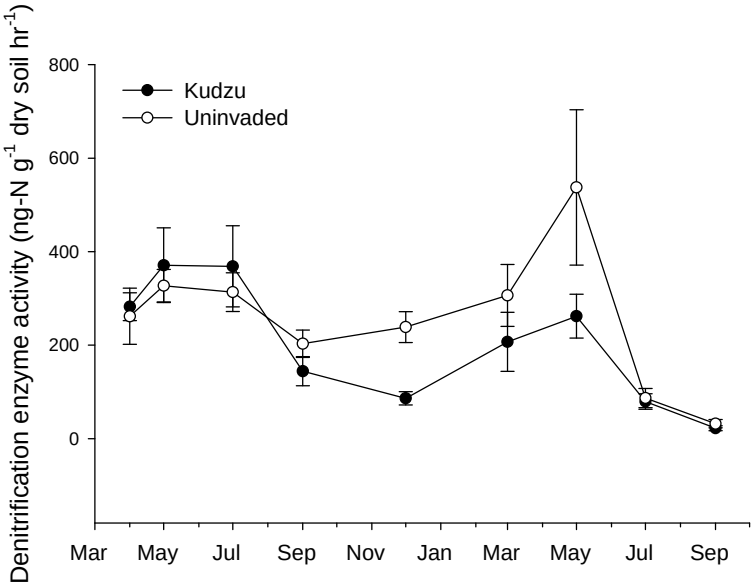


Figure 5. Denitrification enzyme activity at 3 sites in Maryland from April, 2006 through September, 2007. Values are means +/- 1 SE.

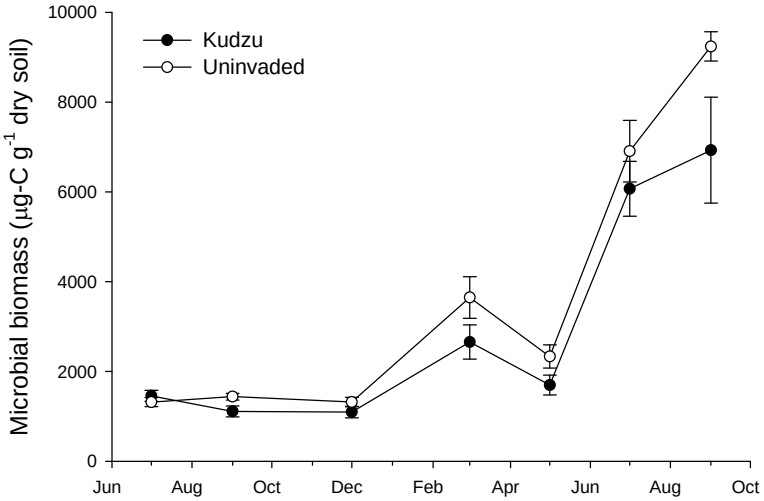


Figure 6. Microbial biomass at 3 sites in Maryland from July, 2006 through September, 2007. Values are means +/- 1 SE.

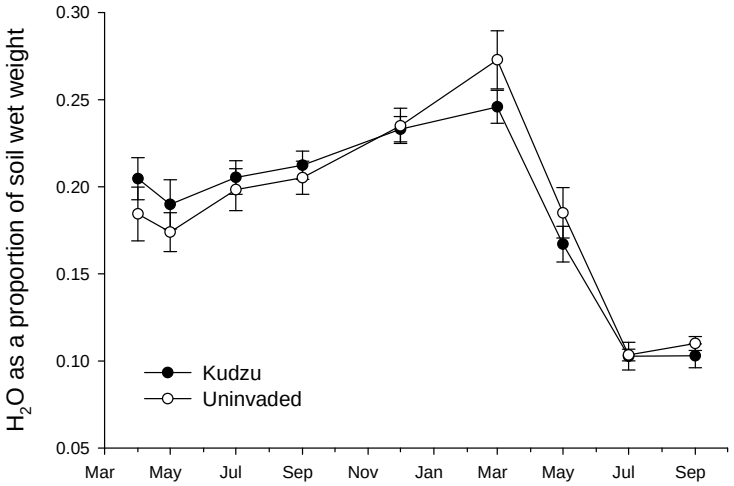


Figure 7. Soil moisture at 3 sites in Maryland from April, 2006 through September, 2007. Values are means +/- 1 SE.

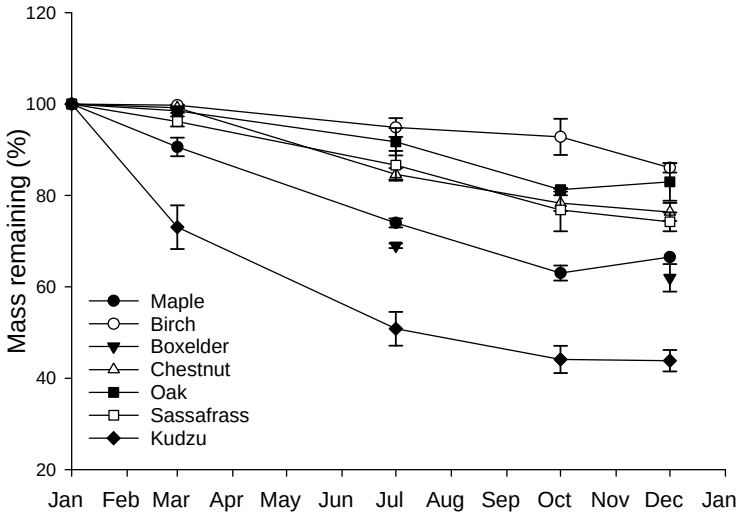


Figure 8. Mass loss during decomposition for leaf litter from 7 co-occurring woody species in Maryland during 2007. Values are means +/- 1 SE.

Chapter 4 Interactions in the decomposition of leaf litter from native and invasive species may buffer ecosystems against invader-induced acceleration of nutrient cycling

Abstract

If a shift in species composition, as occurs during the spread of an invasive species, includes a shift in litter chemistry, it may be accompanied by changes in leaf litter decomposition dynamics that can determine rates of nutrient cycling and productivity in the community. Because litter from two different species often exhibit non-additive rates of mass and nutrient loss when decomposing together rather than separately, the rate of change in ecosystem processes following a shift in plant community composition may depend in part on whether litter is decomposing separately or in combination. I selected pairs of native and invasive species from the same genus or family and common to Long Island, NY for two litterbag decomposition experiments to determine: 1) whether leaf litter from invasive species loses mass and nitrogen (N) more quickly than litter from native species and 2) whether mixtures of litter from native and invasive litters lose mass and N additively. Litter from invasive species lost more mass and N than native species in both experiments, with some notable exceptions among late successional species in and vines in the *Vitaceae*. While mixtures containing litter from only native or only invasive species decomposed in an additive fashion, mixtures of native and invasive species decomposed at the slower rate typical of the native species decomposing alone. These results suggest that, while invasive species are likely to alter decomposition and nutrient cycling, the presence of native species may buffer ecosystems against these changes, and consideration of a species' successional status and growth form may be necessary for reliably predicting the effects of invasion on ecosystem processes.

Introduction

Most studies on the ecosystem impacts of invasive species have concentrated on the effects of particular invaders rather than on the impacts of invasive species as a group or on whether native and invasive species might interact to affect ecosystem properties (e.g., Witkowski 1991, Levine et al. 2003, Haubensak et al. 2004, Rice et al. 2004, but see Ashton 2005). One way that invaders might alter ecosystems is through the deposition of leaf litter with distinctive chemical composition. Because leaf litter is the largest annual nutrient source in most terrestrial systems, differences in the litter chemistry of invasive species can change nutrient availability and future productivity (Swift 1979, Hobbie 1992, Schlesinger 1997, Ehrenfeld et al. 2001, Ashton 2005).

Species with high rates of nutrient uptake and readily decomposable, nutrient-rich litter tend to reinforce high rates of nutrient cycling, while species with lower rates of nutrient uptake and more recalcitrant litter maintain slower rates of nutrient cycling (Hobbie 1992). Plant invasions are known to cause changes in nutrient cycling when a key aspect of the invader's physiology differs from members of the invaded community, as with the invasion of Hawaiian ecosystems by the nitrogen-fixer *Myrica faya* (Vitousek and Walker 1989). But invasions could also change nutrient cycling rates if a community is invaded by a group of species with litter that decomposes either more quickly or more slowly than the species they are replacing. Such a group of invaders could change nutrient cycling in an ecosystem even if the functional diversity of the community remains unaltered by the invasion.

Recent studies suggest that litter from invasive species often has higher nutrient contents and decomposes faster than litter from co-occurring natives, potentially leading to increased rates of nutrient cycling (Ehrenfeld 2003, Ashton 2005, Liao et al. 2008). In many cases, there are *a priori* reasons for expecting these changes; for example, many studies include invasive N-fixing plants, which are expected to have more N-rich, faster decomposing litter. Invasions in which a new growth form is introduced into an ecosystem are also likely to cause changes in litter decomposition rates (Vitousek and Walker 1989, Wedin and Tilman 1990, Hobbie 1996, Scowcroft 1997). Because many

invaders are early successional or ruderal species (D'Antonio 1999), they may also be expected to have N-rich, labile litter associated with rapid growth (Lambers 1998).

If changes to ecosystem properties occur because an invader is functionally different from the community it is invading, it can be difficult to conclude that invasion *per se* is likely to cause changes to an ecosystem; instead, these changes may only happen when a novel function is introduced to an ecosystem. In other words, it is difficult to determine whether there are general properties shared by invaders that are likely to change ecosystems, or whether such changes should be expected only for certain species in certain contexts (e.g., a nitrogen-fixing species invading a community where nitrogen fixers are absent). One way to determine whether there may be general properties shared by invasive species that may change ecosystem processes is by controlling for factors other than a species' identity as native or invasive that are likely to influence litter decomposition dynamics. By controlling for factors such as phylogeny and growth form, I can ensure that differences observed are indeed differences due to a species identity as invasive.

The rate at which ecosystem dynamics change after plant invasions may be complicated by interactions during the decomposition of litter from native and invasive species. Litter from two different species often exhibits non-additive rates of mass and nutrient loss when decomposing in mixtures as opposed to in isolation, and these interactions may play an important role in determining how quickly ecosystem processes change following a shift in plant community composition (Gartner and Cardon 2004). While the deposition of more rapidly decomposed leaf litter from invasive species may result in increased rates of nutrient cycling, interactions with litter from native species or other invasive species may ameliorate or exacerbate this impact, depending on whether interactions are non-additive, and if so, in what direction. In the northeastern United States, where invasion by multiple exotic species is common (Howard et al. 2004), understanding the potential interactions among leaf litter from different species and different origins (native v. exotic) is essential to understanding how invasions affect ecosystem processes.

To assess how the decomposition dynamics of litter from invasive species may impact ecosystem processes, I conducted two experiments. In the first I used litter from

three invasive species and three co-occurring congeneric or confamilial native species in Long Island, NY. By tracking mass and N loss for each species individually and in each possible 2-species combination, I was able to determine whether and to what extent the presence of other species affects the decomposition dynamics of litter from native and invasive species. An earlier study by Ashton *et al.* investigating differences in decomposition in invaded and uninvaded sites found evidence suggesting that litter from invasive species decomposed faster than litter from native species (Ashton 2005). To investigate whether litter from invasive species as a group decomposes more quickly than litter from native species (which the results of Ashton *et al.* suggest may be the case (Ashton 2005)), I conducted an additional litter decomposition experiment using closer phylogenetic pairing between invasive and native species than used by Ashton *et al.* and expanding the number of species studied from 8 to 11.

Materials & Methods

Site description

I examined decomposition of native and exotic invasive leaf litter in the East Farm Preserve along the north shore of Long Island, Suffolk County, New York, USA (40degrees54.3' N, 73deg08.9'W). The Preserve was cleared in the early 1900s, historically used for agriculture and pasture, abandoned, and donated to The Nature Conservancy. The Preserve is a mixed deciduous hardwood forest with loamy soils. I selected a plot in a relatively uninvaded, native-dominated forest, with less than 1% exotic species cover (Ashton 2005). The most common native species in the plots were *Acer rubrum* L. (red maple), *Fagus grandifolia* Ehrh. (American beech), *Quercus rubra* L. (red oak), *Quercus alba* L. (white oak), *Prunus serotina* Ehrh. (black cherry), and *Viburnum acerifolium* (maple-leaf viburnum).

Experimental design

I conducted two experiments: in 2003, I examined the effects of species origin (invasive vs. native) on leaf litter decomposition, and in 2004, I examined the effects of mixing litter from different species and origins on decomposition. In autumn, 2002, I

collected newly senesced leaf litter from 11 woody species common to Long Island for my experiment comparing native and invasive litter decomposition rates, which ran from December 2002 through December 2003 (Table 1). In autumn, 2003, I collected newly senesced leaf litter from 6 woody species common to Long Island for the mixed litter experiment, which ran from December 2003 to December 2004 (Table 2). All the species selected were common on Long Island and present in the East Farm preserve. In each experiment, half of the selected species were invasive species not native to North America (hereafter referred to as invasive), and half were native species. Each native species selected was paired with a corresponding invasive species by growth form (though one pair in 2003—*Prunus serotina* and *Rosa multiflora*—included species with different growth forms), which can influence rates of decomposition (Hobbie 1996), and by phylogentic relatedness; all pairs represent native and invasive species within the same genus, or, where within-genus pairing was not possible, within the same family. Decomposition is strongly influenced by the chemical and physical structure of leaf litter, and litter from related species exhibits less variation in these traits (Swift 1979, Becerra 1997). By selecting related taxa of native and invasive species, I can help ensure that any differences between species are due to species origin rather than differences in phylogeny.

Sample preparation and analysis

For all species, litter was collected from at least three sites on Long Island, within an area of approximately 100 km^2, and from multiple individuals within each site. The litter selected was derived from plants and leaves grown in full sun. Within each experiment, litter from all sites was pooled for each species.

All litterbags were constructed from 1mm^2 mesh, with interior dimensions of 15.5 x 12 cm. For the 2003 species origin experiment, litter was dried at 38°C before bags were filled. A subsample of litter from each species was weighed, dried at 60°C, and reweighed to calculate 38°C to 60°C conversion factors. I filled each bag with a total of 2.5-3.5g of litter from a single species; enough bags were filled with each species to allow for the destructive harvest of 3 replicates at 0, 3, 15, 25, 35, and 52 weeks. An additional set of bags was filled with 3g of polyester material to quantify the amount of

organic and inorganic mass gained by the bags over time. The mean mass gain by the polyester bags collected at each harvest time was subtracted from the litterbags to quantify the amount of organic and inorganic matter accumulating in the bags over time (Harmon 1999).

For the 2004 litter mixture experiment, litter was dried at 60°C. I filled each bag with a total of 2.5-3.5g of litter from a single species, or with equal amounts of litter from two different species. Enough bags were filled with every possible one- and two-species combination to allow for the destructive harvest of 3 replicates at 0, 3, 15, 25, 40, and 52 weeks, for a total of 378 litter bags. No polyester-filled bags were used, but subsamples of harvested litter were placed overnight in a muffle furnace at 550°C for the determination of ash-free dry weight to correct for any soil contamination of the samples.

In both years, replicates for each harvest were randomly placed in each of 3 blocks spaced 10 m apart from each other; over 50m separated the sites for the two experiments. Within each block, the bags were randomly placed 0.5 m from each other in a grid, and pinned to the soil surface, below the existing litter layer. The random allocation to blocks and grid locations was intended to prevent any confounding effects of spatial variation on litter decomposition. At each of the 6 harvest times, bags were collected, gently cleaned of introduced soil and organic matter, dried at 60C, and weighed to calculate mass loss. A Wiley mill was used to grind the dried litter, which was then analyzed for C and N concentration using a CE Flash EA 1112 Elemental Analyzer (CE Instruments, Milan, Italy).

Statistical Analysis

To examine differences in mass and N loss in the 2003 species origin experiment, I conducted a 3-way full-factorial, mixed-model ANOVAs, with one random factor (block) and two fixed factors (time and litter type (2 levels: native and invasive)). Because newly senesced litter from different species has different concentrations of N, most tests of N loss used the percent of initial N remaining as a response variable. However, I also conducted some tests on the total loss of N by weight from decomposing litter.

To examine differences in mass and N loss in the 2004 mixed litter experiment, I conducted a 3-way full-factorial, mixed-model ANOVAs, with one random factor (block) and two fixed factors (time and litter type (5 levels: single native species, single invasive species, mixture of two invasive species, mixture of two native species, and mixture of one native and one invasive species)). As with the 2003 experiment, most tests of N loss used the percent of initial N remaining as a response variable, but I once again conducted some tests on the total loss of N by weight from decomposing litter.

For the 2004 mixed litter experiment, I also conducted a series of planned contrasts to determine whether mixtures of litter from different species decomposed more quickly or more slowly than species decomposing alone. I conducted 4 separate contrasts (Table 3). First I conducted 2 contrasts to determine whether mixing litter from different native species together or mixing litter from different invasive species together had any effect on decomposition rates (i.e., one contrast compared mixtures of native species to single native species, and a second compared mixtures of invasive species to single invasive species). I conducted 2 additional contrasts to determine whether mixing litter from native species with litter from invasive species had a synergistic or antagonistic effect on decomposition rates. These contrasts consisted of comparing the mixtures of native and invasive litters with either the native litters decomposing alone or the invasive litters decomposing alone. Because the mixtures of native and invasive litters were used for both of these contrasts, these tests are not strictly orthogonal. They do, however, represent a set of reasonable contrasts in line with my hypotheses regarding the effects of litter mixtures, and following the recommendation of Quinn and Keough (Quinn and Keough 2002), I did not adjust my α for the tests.

The contrasts were conducted for the response variables (proportion total mass remaining and proportion N remaining, corrected using the polyester fill or AFDW technique for the respective experiments) at week 52, since replicates from this date exhibit the cumulative differences in mass and N loss among the various litter types, and thus provides the best metric for understanding how these differences may affect ecosystem processes over a longer time scale. An additional analysis of the absolute amount of N lost by week 52 was conducted, because although litter types may not exhibit differences in the proportion of initial N lost, higher starting N concentrations in

invasive or native litters could still result in larger N fluxes to ecosystems. In the mixed litter experiment, a series of unplanned contrasts among the individual single and mixed litter types was made also to identify any differences between species. Data were rank-transformed as necessary to meet the assumptions of ANOVA. Because I used % mass remaining and % N remaining as response variables, variances often increased over time. In order to meet the assumption of homogeneity of variances even after transformations were employed, the first sampling time was excluded from the ANOVA of %N remaining in 2003, and the first two sampling times were excluded from the ANOVA of % mass remaining in 2004.

Likelihood estimates of the decomposition constants (k) for the decomposition equation: $x=e^{-kt}$ were determined by simulated annealing using the anneal function in the likelihood package developed for R by Lora Murphy (http://www.ecostudies.org/lme_R_code_tutorials.html) .

Results

2003

Mass loss

There was considerable variation in mass loss among species in 2003: *Rosa multiflora* and *Rubus phoenicolasius* had lost over 96% of their starting mass by the end of the experiment, in contrast to both *Acer* species, which lost slightly less than 50% of their mass after one year. I found a nearly significant interaction between time and litter type (Figure 1, P=0.074, where litter type is a factor with 2 levels: native and invasive), demonstrating that invasive species exhibit faster rates of mass loss, in keeping with the results of earlier studies. There were significant effects of the family by time interaction (P=0.0067), and for family, time, and family by litter type interaction (P<0.001 for each), the latter of which suggests that in some families, invaders may not lose mass faster than natives (Table 4). An analysis of the estimated decomposition constant k for each litter type also revealed faster rates of mass loss for litter from invasive species (F=96.9, P=0.01, Table 5).

N loss

Patterns of N-loss echoed those of mass loss (Figure 1), with a significant litter type by time interaction (Table 6, P=0.0006), where invasive litter appears to lose N more quickly than native litter. After relatively little change in N concentrations through week 15, both litter types exhibited immobilization of N at week 25, followed by rapid N loss. In keeping with the presence of a significant litter type by family interaction (P=0.022), when each pair was analyzed separately, I found that invaders lost more nitrogen than natives in 3 of the 5 cases, while the pattern was reversed in a fourth case (Figure 2).

Within-family comparisons

In comparisons within families, there were some exceptions to the overall patterns among the Sapindaceae and the Vitaceae. In the family Sapindaceae, the invader *A. platanoides* lost mass more slowly than its native congener *A. rubrum* (P=0.046) in 2003, though there were no differences in the proportion of N lost by the end of the year. There were no differences between the species in starting litter N concentrations or C:N ratios. Results were different in the 2004 experiment, when *A. platanoides* litter had higher N concentrations (P=0.0431) and a lower C:N ratio (P=0.0074). The native *A. rubrum* litter exhibited considerably more immobilization of N over the course of the year than did *A. platanoides* (P=0.014), though there was effectively no net N loss in either species by the end of they year, and no differences in mass loss between the species (Figure 2 and Figure 3). Though there were no differences in starting N concentration or C:N, *A. platanoides* had higher N concentrations in 2004.

In 2003, the general pattern of greater mass loss among invaders was also reversed in the Vitaceae, when litter from the native *V. novae-angliae* exhibited greater mass loss (P=0.0074) and %N loss (P=0.0015)) than the confamilial invader *A. brevipedunculata*. Starting concentrations of N in litter from the two species were not significantly different (P=0.0736; though *A. brevipedunculata* had a lower starting C:N ratio (P=0.0182)). Results were different in 2004, when *A. brevipedunculata* litter had both higher starting N concentrations and a lower C:N ratio, there were no differences in N loss between the two species, and early increases in mass loss in *V. novae-angliae* disappeared by the end of the year (Figure 3).

2004

Mass loss

Variation in mass loss was also substantial in 2004, ranging from 86% of starting mass lost in *R. phoenicolasius* to 46% of starting mass lost in *R. allegheniensis* after a year. I found no effect of litter type in 2004 (where litter type is a factor with 5 levels: three mixture types (invasive/invasive, native/native, and native/invasive) and the two single species types (native and invasive)), but like in 2003, there was a significant time by litter type interaction (Figure 1, P=0.0336). Decomposition constants were calculated, and are listed in Table 5. The main effects for time (P<0.0001) and block (P=0.0038) were also significant (Table 7).

My planned contrasts revealed two significant effects. First, invasive litter lost more mass after one year than native litter (P=0.0013), as was the case in my 2003 experiment. Secondly, mixtures containing litter from both native and invasive species lost less mass by the end of the experiment than invasive species decomposing alone (P=0.0497). These mixtures did not lose more mass than native species decomposing alone, indicating mixtures of native and invasive species lost mass in a non-additive fashion.

In contrast, there was no effect of mixing litter from different species when only invasive litters were included in the mixture or when only native litters where included in the mixtures—in both cases, litter lost the same proportion of mass whether it was decomposing alone or in a mixture.

In a set of unplanned contrasts comparing the mass lost after one year from all the different individual and mixed species combinations used, I found one set of significant differences: the invasive species *R. phoenicolasius* lost more mass than 9 other types of litter bags, including 3 species decomposing alone, and 6 mixtures of species. The greater mass loss in *R. phoenicolasisus* suggests that it may be an important contributor to the differences in mass loss between native and invasive litters.

I did not consider plant family as an explicit factor in my analysis of the 2004 experiment, but I did conduct tests to determine whether mixing native and invasive litters within a family or genus had the same non-additive effect observed in the larger

analysis (Figure 3). Tests of the *Rubus* species revealed the same pattern as the overall analysis, where invasive litter alone lost more mass than the mixture (P=0.031, analysis not shown). This pattern was reversed in *Vitaceae*, where the native species decomposing alone lost more mass than the mixture (P=0.0091, analysis not shown).

N loss

There was great variation in the proportion of N remaining among species, ranging from losses of 87.8% in the invader *R. phoenensis* to an increase of 32% in the native *A. rubrum* after one year (Figure 1). Significant effects were found for the litter type main effect (Table 8, P=0.0004) as well as the time by litter type interaction (P=0.0003), suggesting differences in the N loss dynamics of different litter types. Unlike with mass loss, planned comparisons among litter types at week 52 provided no evidence for non-additive effects on the proportion of N lost for any of the mixture types. However, two of the three ANOVAs examining the proportion of N lost at week 52 within each family provided some evidence for the same non-additive effects seen for mass loss in native/invasive mixtures: the *A. brevipedunculata* / *V. novae-engliae* and the *R. phoenicolasius* / *R. allegheniensis* mixtures were no different from the native component of the mixture alone in %N remaining, but had lost less N than the invasive component (Figure 3, P=0.0216 and P=0.00604, respectively, analysis not shown).

In both 2003 and 2004, starting N concentrations in invasive litter were higher in invasive species than in native species (P=0.01056, Figure 4). Consequently, faster declines in the proportion of N in invasive litters (or mixtures containing invasive litter) actually represent an even larger absolute flux of N to the ecosystem. In 2003, net loss of N by weight was higher for the invaders in parings of species within Caprifoliaceae (P=0.0153), and Rosaceae (P=0.0009), though there were no differences in the *Rubus* and species, and the pattern was reversed for the Vitaceae (P=0.0129). In 2004, Aceraeceae species again showed no difference, but in both the *Rubus* (P=0.0032) and Vitaceae (P-=0.0016) pairings, the invader lost more N over the course of the year.

Unplanned contrasts of the proportion N lost were similar in some respects to those for overall mass loss, with *R. phoenicolasius* losing a greater proportion of its starting N concentration by week 52 than 11 other species groups, none of which

included *R. phoenicolsius*. But *A. rubrum*, which experienced a net increase in N content by week 52, had significantly larger proportion of its starting N concentration than 5 other species groups, including one mixture that included *A. rubrum* (*A. rubrum* with *R. phoensis*).

Discussion

Decomposition of native and invasive litter

Previous research suggests that litter from invasive species tends to decompose faster than that of co-occurring natives, potentially leading to increased rates of nutrient cycling, and my results generally, but not uniformly, support this suggestion (Scowcroft 1997, Ehrenfeld 2003, Ashton 2005, Liao et al. 2008). In both experiments reported here, invasive species as a group lost more mass by the end of the experiment than did native species, and N loss generally followed the same pattern. This pattern, however, was reversed in the Vitaceae and Sapindaceae, suggesting that invasiveness, *per se*, is not responsible for faster decomposition and nutrient release (Figure 2 and Figure 3).

Differences in litter chemistry are likely to be driving the differences in decomposition rates observed here. In Lavelle *et al.*'s hierarchical model of the controls on decomposition in terrestrial ecosystems, litter chemistry follows climate and soil properties as the chief determinants of decomposition (Lavelle et al. 1993). The higher N concentrations and lower C:N in invasive litters appear to be responsible for the overall patterns of increased mass and N loss among those species. This conclusion is borne out in comparisons of litters within species—for those families where invaders decomposed more quickly (Caprifoliaceae and the two Roseaceae pairs), the invasive litter also had lower C:N and higher N concentrations.

The higher N concentrations and faster decomposition of invasive litter may be explained by the early-successional or disturbance-favoring strategy used by many invaders (D'Antonio 1999). These species tend to exhibit fast growth, produce N-rich litter, and reinforce high rates of nutrient cycling, which favors their continued success over natives or other exotics (Grime 1988, Hobbie 1992). In these cases, invasive species

may successfully invade by being a more extreme early-successional species than their confamilial native species, increasing nutrient cycling as a result (Ashton 2005).

The reversal of this pattern in the Vitaceae may be the result of the native species matching the invader at its own game as a successful early-successional species. *Vitis* species are widely recognized as early pioneer species favoring moderately and highly disturbed habitats, with an ability to grow quickly and choke out other vegetation, characteristics commonly associated with successful invasive species (Lutz 1943, Siccama et al. 1976, Huenneke and Sharitz 1986, Locasio 1991), and *V. novae-angliae* is the only native species in this study that is listed as a noxious weed in the United States (though *P. serotina*, *A. rubrum*, and *P. quinquefolia* have all been identified as potentially weedy species in the northeastern U.S. (Uva 1997)). Additionally, because they are structural parasites, vines such as *V. novae-angliae* can devote more resources to growth (Schnitzer and Bongers 2002), and many vines have exhibited greater growth responses to CO_2 than other woody species (Phillips et al. 2002). Their physiology may make vines an exception to the overall pattern of faster decomposition among invaders.

In contrast, the slower decomposition of the invasive *A. platanoides* adds to several lines of evidence suggesting that its success is more likely due to its performance as a shade-tolerant tree competing with other late-successional species. Earlier studies have depicted *A. platanoides* as a more extreme late-successional species than its native congener: *A. platanoides* is more shade tolerant than *A. rubrum*, and N mineralization under *A. platanoides* proceeds more slowly than it does under *A. rubrum* (Fang 2005), traits consistent with a species that produces recalcitrant leaf litter. Much as the invasive *Rubus* species succeed by being more extreme early-successional species than their native counterparts, it appears that *A. platanoides* may succeed by being a more extreme late-successional species.

Though I conclude that as a group, litter from invaders in the northeastern United States exhibits increased rates of mass and N loss during decomposition, it appears that consideration of the biology of the invader—in particular, the plant's physiology and successional status—is critical to predicting whether invasion is likely to be accompanied by a change in decomposition rates.

Effects of mixing litter

The mixed litter experiment can provide a more nuanced and realistic understanding of the impact of invasive species on ecosystem processes, particularly early in an invasion. In the northeastern United States, terrestrial ecosystems are commonly invaded by multiple exotic species, creating an environment in which leaf litter from a particular species is often decomposing in association with litter from other native and invasive species (Howard et al. 2004). Consequently, understanding the potential interactions between litters from different species and origins (native v. exotic) when they decompose in mixtures will be essential to understanding how an ecosystem responds to invasion.

The mixture of native and invasive litters was the only one of the three mixture classes to exhibit non-additive effects in decomposition. These native/invasive mixtures decomposed at the same rate as native species, which was significantly slower than the decomposition rates of invasive litters. The same effects were seen for N loss within the *Rubus* and *Vitaceae* pairings, but more time may be needed to see the same general patterns for N loss across all the species mixtures: N was largely immobilized in native litters, while invaders lost N at about half the rate they lost mass suggesting that considerable immobilization was also occurring in invasive litters. But if the observed interaction in mass loss of the native/invasive mixture persists until decomposition is complete, the same effect could be expected to emerge for N loss as well.

The slower-than-expected decomposition of native and invasive litter mixtures has several implications for invaded ecosystems in the northeastern United States. Early in an invasion, invaders are likely to be less common than native members of a community, so invasive litter will usually be decomposing in association with native litters. As long as this association continues, the increased decomposition rates typically exhibited by invasive litter is held in check, preventing or moderating the impacts of fast-decomposing invaders on soils as a consequence of the interaction present in native/invasive litter mixtures. As the abundance of invaders in a community increases, the chances that litter from a given invasive species is decomposing alone or in combination with another invader will increase, ultimately removing the check that native litter provides on rapid decomposition and leading to increases in nutrient cycling rates.

This moderating effect of native litter effectively buffers uninvaded ecosystems against changes caused by invasive litter, and if litter-mediated changes in nutrient cycling and soil communities are an important factor contributing to invasive success, the moderating effect of native litter may also indirectly buffer the native community against invasion. The strength of this buffering effect can be expected to be inversely related to invader abundance, and strongest during the early stages of an invasion.

The slow decomposition of native and invasive mixtures is likely caused by litter-mediated changes in the decomposer community. Phenolic compounds or secondary metabolites transferred from one litter type to another can slow decomposition in a mixture (Fyles and Fyles 1993, McArthur et al. 1994, Salamanca et al. 1998, Nilsson 1999), in this case, presumably from the native to the invasive litter. *A. rubrum* generally has higher phenolic concentrations than faster-growing native trees, and also has higher concentrations of hydrolysable tannins (Shure and Wilson 1993). Relatively high concentrations of polyphenolics have also been found in *V. riparia*, of which *V. novae-angliae* is a hybrid, in comparison to other species in the genus *Vitis* (Kortekamp 2006). Though unlikely, it is also conceivable that high N release from an N-rich invader could have an inhibitory effect on lignin-degrading enzymes, resulting in slower decomposition of more recalcitrant native litter types (Carreiro et al. 2000). Empirically, the rapid decomposition of *R. phoenicolasisus* demonstrated in the unplanned comparisons suggests that this species may have had an important influence on the differences between native and invasive species decomposing alone, but these comparisons do not provide sufficient evidence to conclude that interactions involving *R. phoenicolasisus* were driving non-additive mass loss of the native/invasive litter mixture.

The fact that mixtures containing two native species decompose in a purely additive fashion suggests that ecosystem processes in uninvaded communities are likely to be sensitive to the more rapidly decomposing invasive species. If the alternate had been true, and mixing native species had synergistic effects on decomposition, decomposition dynamics in uninvaded ecosystems may have already proceeded at a rate comparable or closer to that of litter from invasive species (providing that mixtures of invasive litters decompose additively), reducing the potential impact of invasion on ecosystem processes. While multiple invaders may help promote invasive success by

altering soils to favor faster-growing species with more nutrient-rich litter, it appears that they will do so in a purely additive fashion, at least for effects mediated by litter decomposition.

While this research supports the general conclusion that litter from invasive species tends to decompose more quickly than that from native species, the exceptions to that pattern are equally important to the development of the theory and prediction of the impacts of plant invasions. Here, the ecosystem impacts of an invasive species can be linked to the tendency of plants with a certain successional status to have a characteristic litter chemistry, though as was seen with the Vitaceae pair, the physiology of certain growth forms may present an exception to the general pattern of differences between native and invasive litters. Davis *et al*. (2001) argued that greater consideration of successional status is needed in research on the mechanisms and predictability of species invasions (Davis 2001); my research suggests that it is also important for understanding and predicting the ecosystem impacts of invasion.

The environmental context of decomposing invasive litter is also important to understanding its impacts on ecosystems—both the identity of any litter it is decomposing with, and the history of the site where decomposition is occurring. Because the more rapid decomposition of invasive litter tends to slow to rates typical of native species in mixtures of the two, the ecosystem impacts of invasion may be reduced or ameliorated, at least early in an invasion when native leaf litter is abundant. As invader abundance increases, however, these ameliorating effects will gradually disappear as invasive litter is increasingly likely to decompose in association with litter from the same or other invasive species. Additional research into understanding the mechanism behind these interactions and the role that species, genus, or family-specific biology plays will be needed to better understand the degree to which a buffering effect is likely to occur with any given invasion.

Additionally, since my experiments were conducted in an uninvaded site, by default I was examining properties of the litter independent of the long-term effects invasion may have on the environment. I was also implicitly examining the potential effects of exotic species at the early stage of an invasion, when invaders have had as yet little or no impact on soil properties. As an invasion proceeds, soil properties such as

nutrient cycling and microbial community composition can change as a consequence (Vitousek and Walker 1989, Kourtev et al. 2002a, Kourtev et al. 2002b, Kourtev et al. 2003); these changes, in turn, can influence decomposition rates, with decomposition proceeding much more rapidly in invaded sites (Ashton 2005). It is further possible that over time, the decomposer community may adapt to the chemical differences in invasive litters, leading both to more rapid decomposition of both invasive litter generally and litter mixtures.

Tables and Figures

Table 1. Species used in the 2003 decomposition experiment

Native Species	Invasive species	Growth form	Family
Acer rubrum L.	*Acer platanoides* L.	tree	Sapindaceae
Vitis novae-angliae Fern.	*Ampelopsis brevipedunculata* (Maxim.) Trautv.	vine	Vitaceae
Rubus occidentalis	*Rubus phoenicolasius*	shrub	Rosaceae
Prunus serotina	*Rosa multiflora*	shrub	Rosaceae
Parthenocissus quinquefolia,	*Lonicera morrowii*	shrub	Caprifoliaceae
Viburnum acerifolium		shrub	Caprifoliaceae

Table 2. Species used in the 2004 mixed-litter decomposition experiment

Native Species	Invasive species	Growth form	Family
Acer rubrum L.	*Acer platanoides* L.	tree	Sapindaceae
Vitis novae-angliae Fern.	*Ampelopsis brevipedunculata* (Maxim.) Trautv.	vine	Vitaceae
Rubus allegheniensis	*Rubus phoenicolasius*	shrub	Roseaceae

Table 3. Planned comparisons for the 2004 mixed-litter decomposition experiment

Comparisons	Groups used in comparison		
Test 1	Native species alone	vs.	Native/Native species mixture
Test 2	Invasive species alone	vs.	Invasive/Invasive species mixture
Test 3	Native species alone	vs.	Native/Invasive species mixture
Test 4	Invasive species alone	vs.	Native/Invasive species mixture

Table 4. ANOVA of mass loss from native and invasive litter, weeks 3 through 52, 2003

Source	SS	MS	df	*F*	*P*
Time	271747.83	271747.83	1	884.110933	**2.34e-52**
Litter type	19.6182483	19.6182483	1	0.65038061	0.50425821
Family	31591.805	7897.95126	4	73.0831019	**0.00000234**
Block	1402.77291	701.386454	2	12.136976	0.15013419
Time x litter type	795.120421	795.120421	1	11.8576062	0.07388866
Time x family	5598.03397	1399.50849	4	7.91105542	**0.00673079**
Time x block	79.0063853	39.5031927	2	0.26295978	0.78384923
Litter type x Family	8740.50344	2185.12586	4	27.4112257	**0.00009673**
Litter type x block	60.1902128	30.0951064	2	0.36741405	0.70279922
Family x block	863.096334	107.887042	8	1.3520794	0.33927961
Time x litter type x family	1877.62155	469.405387	4	5.07672979	**0.02372951**
Time x litter type x block	133.572185	66.7860923	2	0.70288118	0.52079654
Time x family x block	1411.50316	176.437894	8	1.92424439	0.18681915
Litter type x family x block	636.077245	79.5096557	8	0.25928784	0.97735485
Time x litter type x family x block	733.536323	91.6920403	8	0.29831309	0.96503387

Notes: "Time" refers to harvest date and "litter type" refers to whether litter was from a native or invasive species. Significant differences are marked in boldface type. Data were rank transformed to meet the assumption of homogeneity of variances.

Table 5. Initial nitrogen contents and likelihood estimates of decay constants for all species

Species	Initial N content (%)		Initial C:N		*k* (1/yr)	
	2003	2004	2003	2004	2003	2004
Native						
Acer rubrum L.	1.14+/-0.03	0.61+/-0.03	40.85+/-1.11	80.5+/-4.15	0.98+/-0.04	0.91+/-0.19
Vitis novae-angliae Fern.	1.30+/-0.02	1.46+/-0.08	34.43+/-0.38	32.60+/-1.63	1.25+/-0.08	1.00+/-0.13
Prunus serotina	1.35+/-0.07		33.37+/-1.50		1.38+/-0.03	
Parthenocissus quinquefolia	1.66+/-0.04		27.23+/-0.65		1.19+/-0.15	
Viburnum acerifolium	0.86+/-0.05		54.37+/-3.32		1.35+/-0.10	
Rubus allegheniensis		1.55+/-0.05		31.11+/-0.95		0.82+/-0.16
Rubus occidentalis	1.60+/-0.03		28.13+/-0.46		1.82+/-0.13	
Invasive						
Acer platanoides L.	1.04+/-0.07	1.03+/-0.14	42.68+/-3.04	44.87+/-5.75	0.77+/-0.07	0.83+/-0.05
Ampelopsis brevipedunculata (Maxim.) Trautv.	1.47+/-0.07	2.09+/-0.22	29.58+/-1.20	23.15+/-2.07	0.94+/-0.05	0.68+/-0.04
Rosa multiflora	2.11+/-0.04		20.77+/-0.43		1.83+/-0.08	
Lonicera morrowii	1.44+/-0.05		30.93+/-1.03		2.12+/-0.11	
Rubus phoenicolasius	1.39+/-0.03	2.06+/-0.01	30.72+/-0.79	22.40+/-0.22	2.10+/-0.03	1.76+/-0.16

Notes: All values are means +/- 1 SE; n=3 for initial N content and initial C:N; n=3 bags per time point over 6 harvest times for calculation of *k*.

Table 6. ANOVA of nitrogen loss from native and invasive litter, weeks 15 through 52, 2003

Source	SS	MS	df	*F*	*P*
Time	75483.6622	75483.6622	1	32.0588977	**3.165e-7**
Litter type	4.41048616	4.41048616	1	0.25686326	0.64954066
Block	3905.29959	1952.64979	2	7.96392233	0.08128209
Family	39487.4627	9871.86567	4	23.8217472	**0.00011926**
Time x litter type	761.085828	761.085828	1	25.5723852	**0.00060513**
Time x family	8857.96639	2214.4916	4	4.51744445	**0.02701656**
Time x block	681.0849	1340.54245	2	12.7734157	0.53816288
Litter type x family	3681.44556	920.361389	4	4.88072294	**0.02223377**
Litter type x block	29.0685918	14.5342959	2	0.07056144	0.93228708
Family x block	3235.5245	404.440562	8	2.2726237	0.13279295
Time x litter type x family	2712.65886	678.164715	4	1.70943513	0.22662727
Time x litter type x block	27.1303614	13.5651807	2	0.03077011	0.96977256
Time x family x block	3696.49186	462.061483	8	1.25847568	0.3764504
Litter type x family x block	1419.56567	177.445709	8	0.07571114	0.9996828
Time x litter type x family x block	2937.27716	367.159645	8	0.1559375	0.9956775

Notes: "Time" refers to harvest date and "litter type" refers to whether litter was from a native or invasive species. Significant differences are marked in boldface type. Data were rank transformed to meet the assumption of homogeneity of variances.

Table 7. ANOVA of % mass remaining in native and invasive litter and litter mixtures, weeks 25 through 52, 2004

Source	SS	MS	df	*F*	*P*
Time	121106.081	121106.081	1	41.5103083	**1.348e-9**
Litter type	35870.9328	8967.73319	4	3.86078965	**0.04923858**
Block	16315.0301	8157.51503	2	3.43073221	0.07153104
Litter type x block	18580.3608	2322.5451	8	0.80024574	0.60320306
Time x litter type	4881.9111	1220.47778	4	1.13685516	0.40452564
Time x block	798.66208	399.33104	2	0.31469803	0.73504772
Time x litter type x block	8574.45471	1071.80684	8	0.3673724	0.93641759

Notes: "Time" refers to harvest date and "litter type" refers to the 5 different types of single and mixed litter bags: a single native species, a single invasive species, a mixture of two native species, a mixture of two invasive species, and a mixture of one native species and one invasive species. Significant differences are marked in boldface type.

Table 8. ANOVA of % N remaining in native and invasive litter and litter mixtures, weeks 3 through 52, 2004

Source	SS	MS	df	*F*	*P*
Time	6204.00806	6204.00806	1	8.72663469	**0.00340228**
Litter type	28517.5589	7129.38973	4	33.0094292	**0.00005037**
Block	1008.16051	504.080253	2	1.87986732	0.1862458
Time x litter type	4785.10703	1196.27676	4	8.2689496	**0.00606511**
Time x block	1099.04612	549.523058	2	2.72383512	0.09106844
Litter type x block	1727.07272	215.88409	8	0.30445756	0.9639769
Time x litter type x block	1157.13746	144.642182	8	0.20345549	0.99012678

Notes: "Time" refers to harvest date and "litter type" refers to the 5 different types of single and mixed litter bags: a single native species, a single invasive species, a mixture of two native species, a mixture of two invasive species, and a mixture of one native species and one invasive species. Significant differences are marked in boldface type.

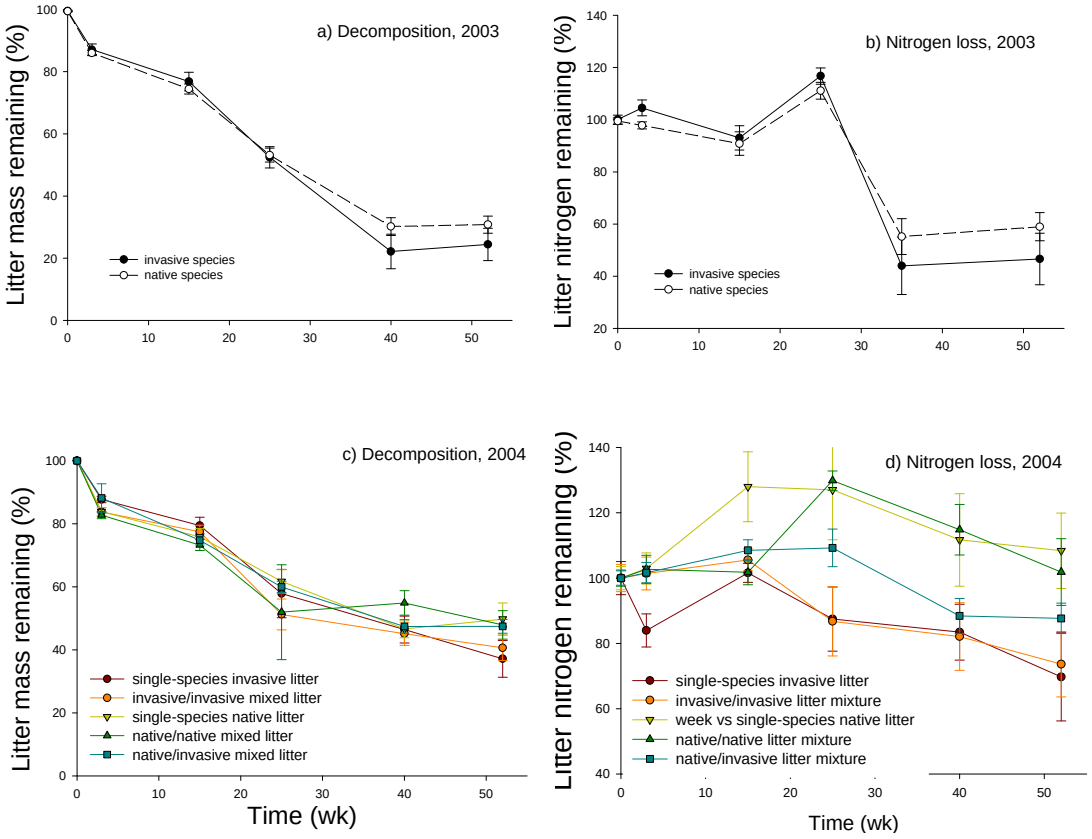
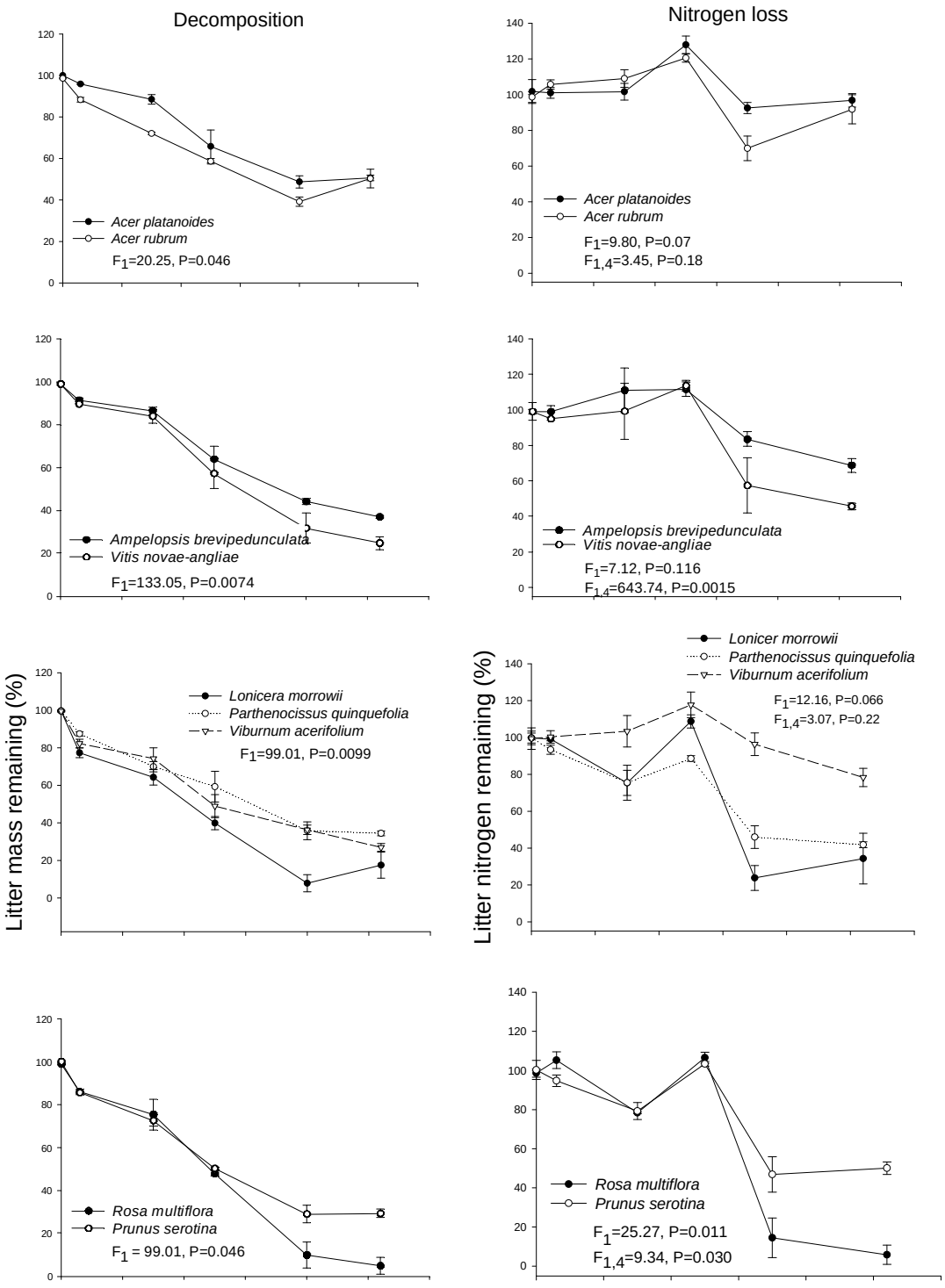


Figure 1. Decomposition (percentage of initial mass remaining) and nitrogen loss (percentage of initial nitrogen remaining) of leaf litter from native and invasive species in 2003 (top two graphs) and 2004 (bottom two graphs). Open symbols represent native species and filled symbols represent invasive species (n=3 plots, n=5 invasive species, n=6 native species, and n=3 bags per species per time point). Error bars are +/- 1 SE.


Decomposition
Nitrogen loss
Litter mass remaining (%)
Litter nitrogen remaining (%)
Acer platanoides
Acer rubrum
F1=20.25, P=0.046
F1=9.80, P=0.07
F1,4=3.45, P=0.18
Ampelopsis brevipedunculata
Vitis novae-angliae
F1=133.05, P=0.0074
F1=7.12, P=0.116
F1,4=643.74, P=0.0015
Lonicera morrowii
Parthenocissus quinquefolia
Viburnum acerifolium
F1=99.01, P=0.0099
Lonicer morrowii
F1=12.16, P=0.066
F1,4=3.07, P=0.22
Rosa multiflora
Prunus serotina
F1 = 99.01, P=0.046
F1=25.27, P=0.011
F1,4=9.34, P=0.030

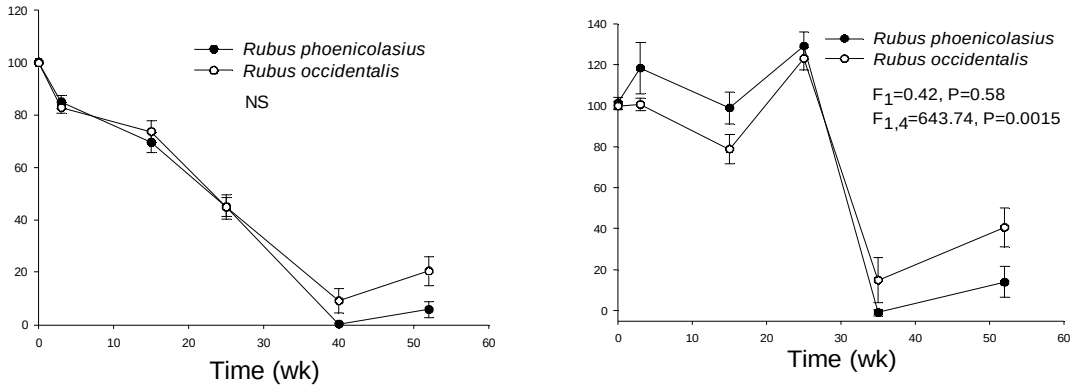


Figure 2. Decomposition (percentage of initial mass remaining) and nitrogen loss (percentage of initial nitrogen content remaining) of litter from native and invasive species by genus or family. Open symbols represent native species, and filled symbols represent invasive species (n=3 blocks and n=3 bags per species per time point). Error bars are +/- SE. ANOVA results for the main effect of species are printed below each key in decomposition graphs, and for the main effect of species and the interaction between time and species in the graphs of nitrogen loss.

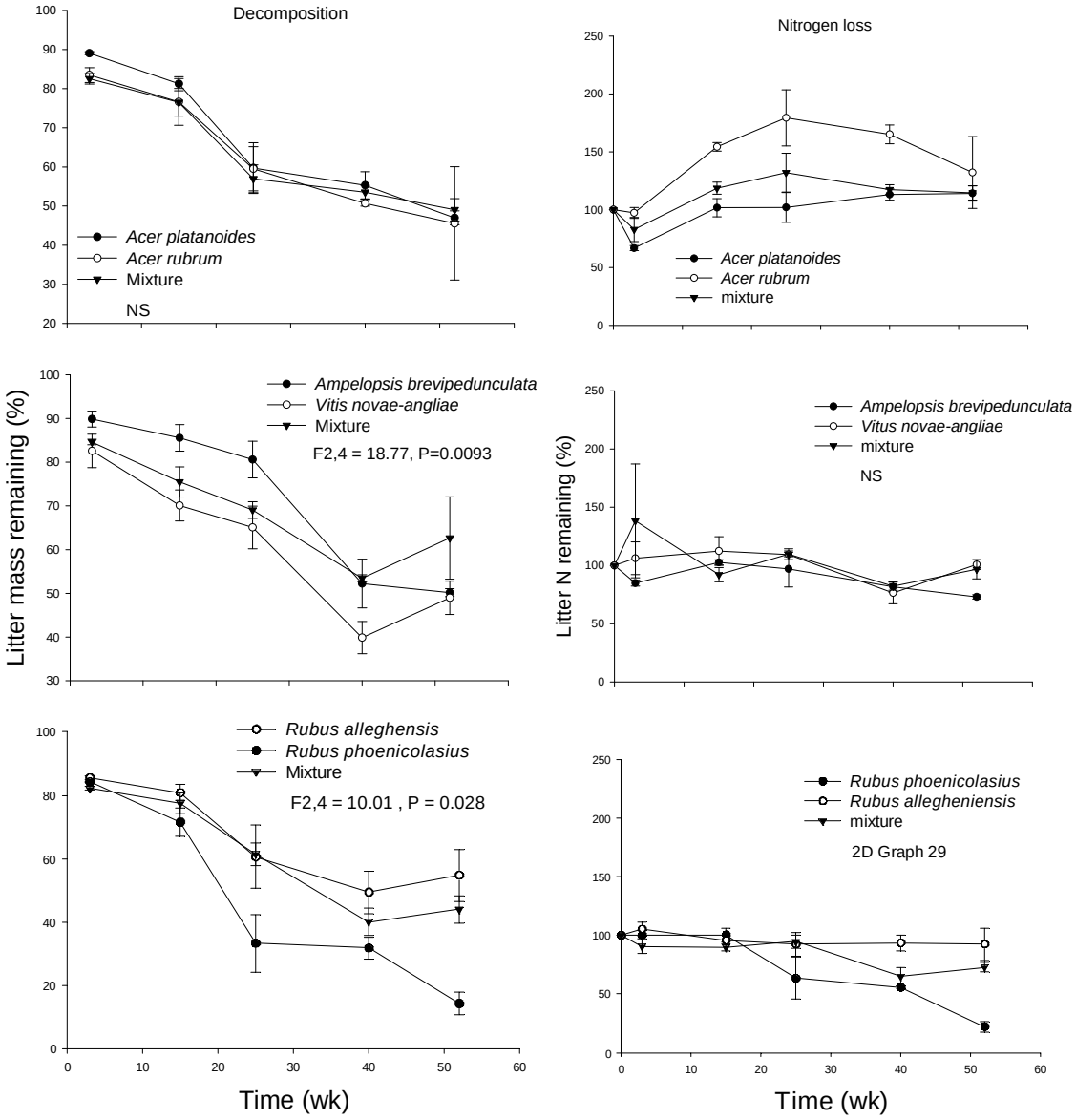


Figure 3. Decomposition (percentage of initial mass remaining) and nitrogen loss (percentage of initial nitrogen content remaining) of litter from single native and invasive species and mixtures by genus or family. Open symbols represent native species, and filled symbols represent invasive species (n=3 blocks and n=3 bags per species per time point). Error bars are +/- SE. ANOVA results for the main effect of species are printed below each key in decomposition graphs, and for the main effect of species and the interaction between time and species in the graphs of nitrogen loss.

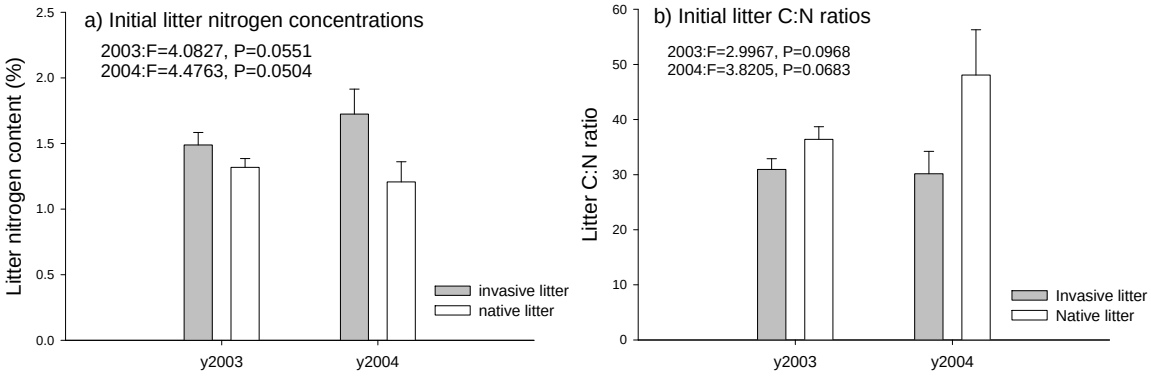


Figure 4. Initial nitrogen concentrations and C:N ratios of leaf litter from native and invasive species. White bars represent native species, and grey bars represent invasive species (2003: n=5 invasive species and n=6 native species, with n=3 replicates per species; 2004: n=3 species per origin, with n=3 replicates per species). Error bars are +/- 1 SE.

Bibliography

Agrawal, A. A., P. M. Kotanen, C. E. Mitchell, A. G. Power, W. Godsoe, and J. Klironomos. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology **86**:2979-2989.

Ainsworth, E. A., P. A. Davey, C. J. Bernacchi, O. C. Dermody, E. A. Heaton, D. J. Moore, P. B. Morgan, S. L. Naidu, H. S. Y. Ra, X. G. Zhu, P. S. Curtis, and S. P. Long. 2002. A meta-analysis of elevated [CO2] effects on soybean (Glycine max) physiology, growth and yield. Global Change Biology **8**:695-709.

Ashton, I. W., L.A. Hyatt, K.M. Howe, J. Gurevitch, and M.T. Lerdau. 2005. Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. Ecological Applications **15**:1263-1272.

Becerra, J. X. 1997. Insects on plants: Macroevolutionary chemical trends in host use. Science **276**:253-256.

Benning, T. L., D. LaPointe, C. T. Atkinson, and P. M. Vitousek. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. Proceedings of the National Academy of Sciences of the United States of America **99**:14246-14249.

Bey, I., D. J. Jacob, R. M. Yantosca, J. A. Logan, B. D. Field, A. M. Fiore, Q. B. Li, H. G. Y. Liu, L. J. Mickley, and M. G. Schultz. 2001. Global modeling of tropospheric chemistry with assimilated meteorology: Model description and evaluation. Journal of Geophysical Research-Atmospheres **106**:23073-23095.

Carreiro, M. M., R. L. Sinsabaugh, D. A. Repert, and D. F. Parkhurst. 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology **81**:2359-2365.

Chameides, W. L., Lindsay, R.W., Richardson, J., and C.S. Kang. 1988. The role of biogenic hydrocarbons in urban photochemical smog--Atlanta as a case study. Science **241**:1473-1475.

Chapin, F. S., Matson, P.A., Mooney, H.A. 2002. Principles of Terrestrial Ecosystem Ecology. Springer-Verlag, New York.

D'Antonio, C. M. 2000. Fire, plant invasions, and global change. Pages 65-93 *in* H. a. R. H. Mooney, editor. Invasive species in a changing world. Island Press, Washington, DC.

D'Antonio, C. M., T.L. Dudley, and M. Mack. 1999. Disturbance and biological invasions: direct effects and feedbacks. Pages 413-452 *in* L. R. Walker, editor. Ecosystems of disturbed ground. Elsevier, Amsterdam.

Daum, P. H., L. I. Kleinman, D. Imre, L. J. Nunnermacker, Y. N. Lee, S. R. Springston, L. Newman, J. Weinstein-Lloyd, R. J. Valente, R. E. Imhoff, R. L. Tanner, and J. F. Meagher. 2000. Analysis of O-3 formation during a stagnation episode in central Tennessee in summer 1995. Journal of Geophysical Research--Atmospheres **105**:9107-9119.

Davidson, E. A., M. Keller, H. E. Erickson, L. V. Verchot, and E. Veldkamp. 2000. Testing a conceptual model of soil emissions of nitrous and nitric oxides. Bioscience **50**:667-680.

Davidson, E. A., C. S. Potter, P. Schlesinger, and S. A. Klooster. 1998. Model estimates of regional nitric oxide emissions from soils of the southeastern United States. Ecological Applications **8**:748-759.

Davidson, E. A., and L. V. Verchot. 2000. Testing the hole-in-the-pipe model of nitric and nitrous oxide emissions from soils using the TRAGNET database. Global Biogeochemical Cycles **14**:1035-1043.

Davis, M. A., K. Tompson, and J.P. Grime. 2001. Chales S. Elton and the dissociation of invasion ecology from the rest of ecology. Diversity and Distributions **7**:97-102.

Dukes, J. S., and H. A. Mooney. 2004. Disruption of ecosystem processes in western North America by invasive species. Revista Chilena De Historia Natural **77**:411-437.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems **6**:503-523.

Ehrenfeld, J. G., P. Kourtev, and W. Z. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. Ecological Applications **11**:1287-1300.

Ehrlich, P. R., and L. C. Birch. 1967. Balance of Nature and Population Control. American Naturalist **101**:97-107.

EPA. 2002. Nitrogen: Multiple and Regional Impacts. EPA-R-01-006, U.S. Environmental Protection Agency, Clean Air Market Programs, Washington, D.C.

Erickson, H., M. Keller, and E. A. Davidson. 2001. Nitrogen oxide fluxes and nitrogen cycling during postagricultural succession and forest fertilization in the humid tropics. Ecosystems **4**:67-84.

Fang, W. 2005. Spatial analysis of an invasion front of Acer platanoides: dynamic inferences from static data. Ecography **28**:283-294.

Fiore, A., D. J. Jacob, H. Liu, R. M. Yantosca, T. D. Fairlie, and Q. Li. 2003a. Variability in surface ozone background over the United States: Implications for air quality policy. Journal of Geophysical Research-Atmospheres **108**:D04308.

Fiore, A. M., L. W. Horowitz, D. W. Purves, H. Levy, M. J. Evans, Y. X. Wang, Q. B. Li, and R. M. Yantosca. 2005. Evaluating the contribution of changes in isoprene emissions to surface ozone trends over the eastern United States. Journal of Geophysical Research--Atmospheres **110**:D12303.

Fiore, A. M., D. J. Jacob, I. Bey, R. M. Yantosca, B. D. Field, A. C. Fusco, and J. G. Wilkinson. 2002. Background ozone over the United States in summer: Origin, trend, and contribution to pollution episodes. Journal of Geophysical Research-Atmospheres **107**:4275.

Fiore, A. M., D. J. Jacob, R. Mathur, and R. V. Martin. 2003b. Application of empirical orthogonal functions to evaluate ozone simulations with regional and global models. Journal of Geophysical Research-Atmospheres **108**:4431.

Forseth, I. N., and A. F. Innis. 2004. Kudzu (Pueraria montana): History, physiology, and ecology combine to make a major ecosystem threat. Critical Reviews in Plant Sciences **23**:401-413.

Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature **446**:1079-1081.

Fyles, J. W., and I. H. Fyles. 1993. Interaction of douglas fir with red alder and salal foliage litter during decomposition Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **23**:358-361.

Fyson, A., and J. I. Sprent. 1982. The development of primary root nodules on *Vicia faba* L. grown at 2 temperatures Annals of Botany **50**:681-692.

Gartner, T. B., and Z. G. Cardon. 2004. Decomposition dynamics in mixed-species leaf litter. Oikos **104**:230-246.

Grime, J. P. 1988. The C-S-R model of primary plant strategies: origins, implications, and tests. Pages 371-393 *in* L. D. G. a. S. K. Jain, editor. Plant evolutionary biology. Chapman & Hall, London.

Guenther, A., C. N. Hewitt, D. Erickson, R. Fall, C. Geron, T. Graedel, P. Harley, L. Klinger, M. Lerdau, W. A. McKay, T. Pierce, B. Scholes, R. Steinbrecher, R. Tallamraju, J. Taylor, and P. Zimmerman. 1995. A Global-Model Of Natural Volatile Organic-Compound Emissions. Journal of Geophysical Research--Atmospheres **100**:8873-8892.

Hall, S. J., and G. P. Asner. 2005. Scaling biogenic trace gas emissions from plots to regions: Effects of *Morella faya* (Fire tree) stand size on soil N_20 and NO_x fluxes in Hawaii Volcanoes National Park. Ecological Society of America, Montreal, Canada.

Hall, S. J., and G. P. Asner. 2007. Biological invasion alters regional nitrogen-oxide emissions from tropical rainforests. Global Change Biology **13**:2143-2160.

Hall, S. J., and P. A. Matson. 2003. Nutrient status of tropical rain forests influences soil N dynamics after N additions. Ecological Monographs **73**:107-129.

Hall, S. J., P. A. Matson, and P. M. Roth. 1996. NOx emissions from soil: Implications for air quality modeling in agricultural regions. Annual Review of Energy and the Environment **21**:311-346.

Harmon, M. E., K. Nadelhoffer, and J.M. Blair. 1999. Measuring decomposition, nutrient turnover, and stores in plant litter. Pages 220-240 *in* D. C. C. G.P. Robertson, C.S. Bledsoe, and P. Sollins, editor. Standard soil methods for long-term ecological research. Oxford University Press, New York.

Hartwig, U. A., A. Luscher, M. Daepp, H. Blum, J. F. Soussana, and J. Nosberger. 2000. Due to symbiotic N-2 fixation, five years of elevated atmospheric pCO(2) had no effect on the N concentration of plant litter in fertile, mixed grassland. Plant and Soil **224**:43-50.

Hattenschwiler, S., and C. Korner. 2003. Does elevated CO2 facilitate naturalization of the non-indigenous Prunus laurocerasus in Swiss temperate forests? Functional Ecology **17**:778-785.

Haubensak, K. A., C. M. D'Antonio, and J. Alexander. 2004. Effects of nitrogen-fixing shrubs in Washington and coastal California. Weed Technology **18**:1475-1479.

Hayhoe, K., C. Wake, B. Anderson, X.-L. Liang, E. Maurer, J. Zhu, J. Bradbury, A. DeGaetano, A. Stoner, and D. Wuebbles. 2008. Regional Climate Change Projections for the Northeast USA. Mitigation and Adaptation Strategies for Global Change.

Hickman, J. E. a. M. T. L. 2006. Nitrogen fixation by kudzu: impacts on invaded communities and ecosystems. Ecological Restoration **24**:200-201.

Hickman, J. E. and M. T. Lerdau. in preparation. Kudzu (Pueraria montana) invasion increases emissions of precursors to tropospheric ozone pollution.
Higgins, P. A. T., and J. Harte. 2006. Biophysical and biogeochemical responses to climate change depend on dispersal and migration. Bioscience **56**:407-417.
Hobbie, S. E. 1992. Effects Of Plant-Species On Nutrient Cycling. **7**:336-339.
Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. Ecological Monographs **66**:503-522.
Holland, E. A., B. H. Braswell, J. Sulzman, and J. F. Lamarque. 2005. Nitrogen deposition onto the United States and western Europe: Synthesis of observations and models. Ecological Applications **15**:38-57.
Holmgren, P. K., and N.H. Holmgren. 2008. Index Herbarium. New York Botanical Garden.
Howard, T. G., J. Gurevitch, L. Hyatt, M. Carreiro, and M. Lerdau. 2004. Forest invasibility in communities in southeastern New York. Biological Invasions **6**:393-410.
Hudman, R. C., D. J. Jacob, O. R. Cooper, M. J. Evans, C. L. Heald, R. J. Park, F. Fehsenfeld, F. Flocke, J. Holloway, G. Hubler, K. Kita, M. Koike, Y. Kondo, A. Neuman, J. Nowak, S. Oltmans, D. Parrish, J. M. Roberts, and T. Ryerson. 2004. Ozone production in transpacific Asian pollution plumes and implications for ozone air quality in California. Journal of Geophysical Research-Atmospheres **109**:D23S10.
Hudman, R. C., D. J. Jacob, S. Turquety, E. M. Leibensperger, L. T. Murray, S. Wu, A. B. Gilliland, M. Avery, T. H. Bertram, W. Brune, R. C. Cohen, J. E. Dibb, F. M. Flocke, A. Fried, J. Holloway, J. A. Neuman, R. Orville, A. Perring, X. Ren, G. W. Sachse, H. B. Singh, A. Swanson, and P. J. Wooldridge. 2007. Surface and lightning sources of nitrogen oxides over the United States: Magnitudes, chemical evolution, and outflow. Journal of Geophysical Research-Atmospheres **112**:D12S05.
Huenneke, L. F., and R. R. Sharitz. 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. American Midland Naturalist **115**:328-335.
Jacob, D. J., L. W. Horowitz, J. W. Munger, B. G. Heikes, R. R. Dickerson, R. S. Artz, and W. C. Keene. 1995. Seasonal Transition From Nox- To Hydrocarbon-Limited Conditions For Ozone Production Over The Eastern United-States In September. Journal of Geophysical Research--Atmospheres **100**:9315-9324.
Jenkinson, D. S., and D. S. Powlson. 1976. Effects Of Biocidal Treatments On Metabolism In Soil .1. Fumigation With Chloroform. Soil Biology & Biochemistry **8**:167-177.
Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as Ecosystem Engineers. Oikos **69**:373-386.
Keller, M., and M. Lerdau. 1999. Isoprene emission from tropical forest canopy leaves. Global Biogeochemical Cycles **13**:19-29.
Kingsolver, J. G., P.M. Kareiva, R.B. Huey. 1992. Biotic Interactions and Global Change. Sinauer Associates, Sunderland, MA.

Kleinman, L., Y. N. Lee, S. R. Springston, L. Nunnermacker, X. L. Zhou, R. Brown, K. Hallock, P. Klotz, D. Leahy, J. H. Lee, and L. Newman. 1994. Ozone Formation At A Rural Site In The Southeastern United-States. **99**:3469-3482.

Kleinman, L. I. 1994. Low And High Nox Tropospheric Photochemistry. Journal Of Geophysical Research--Atmospheres **99**:16831-16838.

Kortekamp, A. 2006. Expression analysis of defence-related genes in grapevine leaves after inoculation with a host and a non-host pathogen. Plant Physiology and Biochemistry **44**:58-67.

Kourtev, P. S., J. G. Ehrenfeld, and M. Haggblom. 2002a. Exotic plant species alter the microbial community structure and function in the soil. Ecology **83**:3152-3166.

Kourtev, P. S., J. G. Ehrenfeld, and M. Haggblom. 2003. Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. Soil Biology & Biochemistry **35**:895-905.

Kourtev, P. S., J. G. Ehrenfeld, and W. Z. Huang. 2002b. Enzyme activities during litter decomposition of two exotic and two native plant species in hardwood forests of New Jersey. Soil Biology & Biochemistry **34**:1207-1218.

Kwon, D. K., and H. Beevers. 1993. Adverse effects of nitrate on stem nodules of *Sesbania rostrata* Brem. New Phytologist **125**:345-350.

Lambers, H., Chapin, F.S., Pons, T.L. 1998. Plant Physiological Ecology. Springer-Verlag, New York.

Lamont, E. E., and S. M. Young. 2004. Noteworthy plants reported from the Torrey Range - 2002 and 2003. Journal of the Torrey Botanical Society **131**:394-402.

Lavelle, P., E. Blanchart, A. Martin, S. Martin, A. Spain, F. Toutain, I. Barois, and R. Schaefer. 1993. A hierarchical model for decomposition in terrestrial ecosystems--application to soils of the humid tropics Biotropica **25**:130-150.

Lee, T. D., M. G. Tjoelker, P. B. Reich, and M. P. Russelle. 2003. Contrasting growth response of an N-2-fixing and non-fixing forb to elevated CO2: dependence on soil N supply. Plant and Soil **255**:475-486.

Lerdau, M. 2003. Keystone Molecules and Organic Chemical Flux from Plants. Pages 177-192 *in* J. M. Melillo, C.B. Field, and B. Moldan, editor. Interactions of the Major Biogeochemical Cycles. Island Press, Washington, D.C.

Lerdau, M., and M. Keller. 1997. Controls on isoprene emission from trees in a subtropical dry forest. Plant Cell and Environment **20**:569-578.

Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London Series B-Biological Sciences **270**:775-781.

Liao, C. Z., R. H. Peng, Y. Q. Luo, X. H. Zhou, X. W. Wu, C. M. Fang, J. K. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytologist **177**:706-714.

Lindemann, W. C., and G. E. Ham. 1979. Soybean plant growth, nodulation, and nitrogen fixation as affected by root temperature. Soil Science Society of America Journal **43**:1134-1137.

Locasio, C. G., B.G. Lockaby, J.P. Caulfield, M.B. Edwards, M. K. Causey. 1991. Mechanical site preparation effects on understory plant diversity in the piedmont of southern USA. New Forests **4**:261-269.

Lucinski, R., W. Polcyn, and L. Ratajczak. 2002. Nitrate reduction and nitrogen fixation in symbiotic association Rhizobium - legumes. Acta Biochimica Polonica **49**:537-546.

Lutz, H. J. 1943. Injuries to trees caused by *Celastrus* and *Vitis*. Bulletin of the Torrey Botanical Club **70**:436-439.

Lynd, J. Q., and T. R. Ansman. 1990. Exceptional Forage Regrowth, Nodulation And Nitrogenase Activity Of Kudzu (Puearia-Lobata (Willd) Ohivi) Grown On Eroded Dougherty Loam Subsoil. Journal of Plant Nutrition **13**:861-885.

Martin, R. E., G. P. Asner, R. J. Ansley, and A. R. Mosier. 2003. Effects of woody vegetation encroachment on soil nitrogen oxide emissions in a temperate savanna. Ecological Applications **13**:897-910.

Martin, R. V., D. J. Jacob, J. A. Logan, I. Bey, R. M. Yantosca, A. C. Staudt, Q. B. Li, A. M. Fiore, B. N. Duncan, H. Y. Liu, P. Ginoux, and V. Thouret. 2002. Interpretation of TOMS observations of tropical tropospheric ozone with a global model and in situ observations. Journal of Geophysical Research-Atmospheres **107**:4351.

Matson, P., K. A. Lohse, and S. J. Hall. 2002. The globalization of nitrogen deposition: Consequences for terrestrial ecosystems. Ambio **31**:113-119.

Matson, P. A., and P. M. Vitousek. 1990. Ecosystem Approach To A Global Nitrous-Oxide Budget. Bioscience **40**:667-671.

Matson, P. A., P. M. Vitousek, J. J. Ewel, M. J. Mazzarino, and G. P. Robertson. 1987. Nitrogen Transformations Following Tropical Forest Felling And Burning On A Volcanic Soil. Ecology **68**:491-502.

McArthur, J. V., J. M. Aho, R. B. Rader, and G. L. Mills. 1994. Interspecific leaf interactions during decomposition in aquatic and floodplain ecosystems. Journal of the North American Benthological Society **13**:57-67.

Mohan, J. E., L. H. Ziska, W. H. Schlesinger, R. B. Thomas, R. C. Sicher, K. George, and J. S. Clark. 2006. Biomass and toxicity responses of poison ivy (Toxicodendron radicans) to elevated atmospheric CO2. Proceedings of the National Academy of Sciences of the United States of America **103**:9086-9089.

Munns, D. N., Fox, R. L., and Koch, B. L. 1977. Influence of lime on nitrogen fixation by tropical and temperate legumes. Plant and Soil **46**:591-601.

Muth, N. Z., and M. Pigliucci. 2006. Traits of invasives reconsidered: Phenotypic comparisons of introduced invasive and introduced noninvasive plant species within two closely related clades. American Journal of Botany **93**:188-196.

NADP. 2008. National Atmospheric Deposition Program (NRSP-3). NADP Program Office, Illinois State Water Survey, Champaign, IL. .

National Research Council. 1991. Rethinking the ozone problem in urban and regional air pollution. National Academy Press, Washington, D.C.

NCDC. 2008. COOP Data/Record of Climatological Observations. National Climatic Data Center, Federal Building, 151 Patton Avenue, Asheville, NC.

Nilsson, M. C., Wardle, D. A., and Dahlberg, A. 1999. Effects of plant litter species composition and diversity on the boreal forest plant-soil system. Oikos **86**:16-26.

NOAA/ESRL. 2008. US station data climate data set. NOAA/ESRL Physical Sciences Division, Boulder, Colorado.

Odling-Smee, F. J. L., KN; and Feldman, MW. 2003. Niche Construction: The Neglected Process in Evolution. Princeton University Press, Princeton.
Paine, R. T. 1969. *Pisaster-Tegula* interaction--prey patches, predator food preference, and intertidal community structure. Ecology **50**:950-961.
Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**:37-42.
Paul, E. A., Clark, F.E. 1996. Soil microbiology and biochemistry. Academic Press, San Diego.
Peltzer, S. C., L. K. Abbott, and C. A. Atkins. 2002. Effect of low root-zone temperature on nodule initiation in narrow-leafed lupin (Lupinus angustifolius L.). Australian Journal of Agricultural Research **53**:355-365.
Phillips, O. L., R. V. Martinez, L. Arroyo, T. R. Baker, T. Killeen, S. L. Lewis, Y. Malhi, A. M. Mendoza, D. Neill, P. N. Vargas, M. Alexiades, C. Ceron, A. Di Fiore, T. Erwin, A. Jardim, W. Palacios, M. Saldias, and B. Vinceti. 2002. Increasing dominance of large lianas in Amazonian forests. Nature **418**:770-774.
Pierce, T., C. Geron, L. Bender, R. Dennis, G. Tonnesen, and A. Guenther. 1998. Influence of increased isoprene emissions on regional ozone modeling. Journal of Geophysical Research--Atmospheres **103**:25611-25629.
Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience **50**:53-65.
Quinn, G. P. a. M. J. K. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University PRess, Cambridge.
Rice, S. K., B. Westerman, and R. Federici. 2004. Impacts of the exotic, nitrogen-fixing black locust (Robinia pseudoacacia) on nitrogen-cycling in a pine-oak ecosystem. Plant Ecology **174**:97-107.
Robin, C., K. Sultan-Tubeileh, M. Obaton, and A. Guckert. 2005. Nitrogen fixation and growth of annual Medicago-Sinorhizobium associations at low temperature. European Journal of Agronomy **22**:267-275.
Root, T. L., D. P. MacMynowski, M. D. Mastrandrea, and S. H. Schneider. 2005. Human-modified temperatures induce species changes: Joint attribution. Proceedings of the National Academy of Sciences of the United States of America **102**:7465-7469.
Ryle, G. J. A., C. E. Powell, M. K. Timbrell, and A. J. Gordon. 1989. Effect of temperature on nitrogenase activity in white clover. Journal of Experimental Botany **40**:733-739.
Salamanca, E. F., N. Kaneko, and S. Katagiri. 1998. Effects of leaf litter mixtures on the decomposition of Quercus serrata and Pinus densiflora using field and laboratory microcosm methods. Ecological Engineering **10**:53-73.
Sasek, T. W., and B. R. Strain. 1988. Effects of Carbon-Dioxide Enrichment on the Growth and Morphology of Kudzu (Pueraria-Lobata). Weed Science **36**:28-36.
Sasek, T. W., and B. R. Strain. 1990. Implications of atmospheric CO2 enrichment and climatic change for the geographical distribution of 2 introduced vines in the USA. Climatic Change **16**:31-51.
Sasek, T. W., and B. R. Strain. 1991. Effects of Co2 Enrichment on the Growth and Morphology of a Native and an Introduced Honeysuckle Vine. American Journal of Botany **78**:69-75.

Sauvage, B., R. V. Martin, A. van Donkelaar, X. Liu, K. Chance, L. Jaegle, P. I. Palmer, S. Wu, and T. M. Fu. 2007. Remote sensed and in situ constraints on processes affecting tropical tropospheric ozone. Atmospheric Chemistry and Physics **7**:815-838.

Schlesinger, W. H. 1997. Biogeochemistry: an analysis of global change. Academic Press, San Diego.

Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. Trends in Ecology & Evolution **17**:223-230.

Scowcroft, P. G. 1997. Mass and nutrient dynamics of decaying litter from Passiflora mollissima and selected native species in a Hawaiian montane rain forest. Journal of Tropical Ecology **13**:407-426.

Sharkey, T. D., and F. Loreto. 1993a. Water-Stress, Temperature, And Light Effects On Isoprene Emission And Photosynthesis Of Kudzu Leaves. Plant Physiology **102**:159-159.

Sharkey, T. D., and F. Loreto. 1993b. Water-Stress, Temperature, And Light Effects On The Capacity For Isoprene Emission And Photosynthesis Of Kudzu Leaves. Oecologia **95**:328-333.

Shure, D. J., and L. A. Wilson. 1993. Patch-size effects on plant phenolics in successional openings of the southern Appalachians. Ecology **74**:55-67.

Siccama, T. G., G. Weir, and K. Wallace. 1976. Ice damage in a mixed hardwood forest in Connecticut in relation to *Vitis* infestation. Bulletin of the Torrey Botanical Club **103**:180-183.

Smith, M. S., M. K. Firestone, and J. M. Tiedje. 1978. Acetylene Inhibition Method For Short-Term Measurement Of Soil Denitrification And Its Evaluation Using N-13. Soil Science Society of America Journal **42**:611-615.

Soussana, J. F., and U. A. Hartwig. 1996. The effects of elevated CO2 on symbiotic N-2 fixation: A link between the carbon and nitrogen cycles in grassland ecosystems. Plant and Soil **187**:321-332.

SRCC. 1997. Growing Season Summary. Southeast Regional Climate Center.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in Terrestrial Ecosystems. Blackwell Scientific, Oxford, UK.

Trainer, M., D. D. Parrish, M. P. Buhr, R. B. Norton, F. C. Fehsenfeld, K. G. Anlauf, J. W. Bottenheim, Y. Z. Tang, H. A. Wiebe, J. M. Roberts, R. L. Tanner, L. Newman, V. C. Bowersox, J. F. Meagher, K. J. Olszyna, M. O. Rodgers, T. Wang, H. Berresheim, K. L. Demerjian, and U. K. Roychowdhury. 1993. Correlation Of Ozone With Noy In Photochemically Aged Air. Journal of Geophysical Research--Atmospheres **98**:2917-2925.

USDA. Web Soil Survey. Accessed 9-2008.

USDA. 1944-1980. Georgia Aerial Photographs. Digital Library of Georgia. Accessed 9-2008.

USDA National Agricultural Statistics Service. 2002. 2002 Census of Agriculture.

Uva, R. H., Neal, J.C., Ditomaso, J.M. 1997. Weeds of the Northeast. Cornell University Press, Ithaca, NY.

Vitousek, P. M., and L. R. Walker. 1989. Biological Invasion by Myrica-Faya in Hawaii - Plant Demography, Nitrogen-Fixation, Ecosystem Effects. Ecological Monographs **59**:247-265.

Voroney, R. P., and E. A. Paul. 1984. Determination Of Kc And Kn Insitu For Calibration Of The Chloroform Fumigation Incubation Method. Soil Biology & Biochemistry **16**:9-14.

Wechsler, N. R. 1977. Growth and physiological characteristics of kudzu, *Pueraria lobata* (Willd.) Ohwi, in relation to its competitive success. University of Georgia, Athens, GA.

Wedin, D. A., and D. Tilman. 1990. Species effects on nitrogen cycling--a test with perennial grasses Oecologia **84**:433-441.

Williams, E. J., and F. C. Fehsenfeld. 1991. Measurement of soil nitrogen oxide emissions at 3 North American ecosystems. Journal of Geophysical Research-Atmospheres **96**:1033-1042.

Witkowski, E. T. F. 1991. Effects Of Invasive Alien Acacias On Nutrient Cycling In The Coastal Lowlands Of The Cape Fynbos. Journal of Applied Ecology **28**:1-15.

Wu, S. L., L. J. Mickley, D. J. Jacob, J. A. Logan, R. M. Yantosca, and D. Rind. 2007. Why are there large differences between models in global budgets of tropospheric ozone? Journal of Geophysical Research-Atmospheres **112**:D05302.

Wu, S. L., L. J. Mickley, E. M. Leibensperger, D. J. Jacob, D. Rind, and D. G. Streets. 2008. Effects of 2000-2050 global change on ozone air quality in the United States. Journal of Geophysical Research-Atmospheres **113**:D06302.

Yelenik, S. G., W. D. Stock, and D. M. Richardson. 2004. Ecosystem level impacts of invasive Acacia saligna in the South African fynbos. Restoration Ecology **12**:44-51.

Yienger, J. J., and H. Levy. 1995. Empirical model of global soil biogenic NO_x emissions. Journal of Geophysical Research-Atmospheres **100**:11447-11464.

Zavaleta, E. 2000. The economic value of controlling an invasive shrub. Ambio **29**:462-467.