Effects of an Invasive Plant Species, Celastrus orbiculatus, on Soil Composition and Processes

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ABSTRACT.—*Celastrus orbiculatus* is a non-native, invasive liana that was introduced to the United States in the 1860s and has spread rapidly throughout the Northeast. Several attributes contribute to the invasiveness of *C. orbiculatus*, including tolerance to a wide range of light levels and habitat types. We compared soil characteristics in seven sets of adjacent, paired plots, spanning a range of habitats and soil types, with and without *C. orbiculatus*. The paired plots were similar other than the presence or absence of *Celastrus*. Plots with *C. orbiculatus* had significantly higher soil pH, potassium, calcium and magnesium levels. Furthermore, nitrogen mineralization and litter decomposition rates were higher in plots with *C. orbiculatus*. Phosphorus levels were not significantly different between the paired plots. The results of this study contribute to the growing body of research of the effects of invasive species on ecosystem processes.

INTRODUCTION

Exotic invasive plant species threaten biodiversity and ecosystem processes and can change community compositions and abundance of native species (Ehrenfeld, 2003; Wolfe and Klironomos, 2005; Callaway and Maron, 2006). Almost every type of ecosystem in North America has been affected by invasive exotic species (Ehrenfeld, 1997). Invasiveness of exotic species has most often been attributed to reproductive and life-history characteristics, as well as physical attributes of the exotic, such as aboveground biomass and specific leaf area (Baruch and Goldstein, 1999; Ehrenfeld *et al.*, 2001; Gerlach and Rice, 2003). Most research has focused on the characteristics that make an invasive species successful and the varying susceptibility of different plant communities to invasion (Ehrenfeld and Scott, 2001). However, the effects of exotic plant species on soil composition and ecosystem processes have been studied less commonly and observations have not been consistent across species (Ehrenfeld, 2003; Vanderhoeven *et al.*, 2005; Wolfe and Klironomos, 2005).

Some studies have shown that exotic species can enhance their invasiveness by increasing local nutrient availability, producing nutrient-rich sites (Ehrenfeld, 2003; Wolfe and Klironomos, 2005). Various traits of exotics may cause soil-based ecosystem changes that result in positive feedback processes, further enhancing the exotic's spread (Ehrenfeld *et al.*, 2001; Heneghan *et al.*, 2006; Kulmatiski *et al.*, 2006; Reinhart and Callaway, 2006). Traits such as high growth rates often correlate to leaves with high specific leaf area (SLA) and low construction costs that can lead to faster decomposition (Reich *et al.*, 1997; Baruch and Goldstein, 1999; Ehrenfeld *et al.*, 2001; Ehrenfeld, 2003).

In the Northeastern United States, there have been few studies relating soil attributes to invasions. Some of these studies have examined possible effects of soil characteristics in an indirect manner by comparing environmental attributes of sites not containing exotic

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species to sites containing exotic species (Howard *et al.*, 2004; Ashton *et al.*, 2005). Other studies have focused on specific species, including *Berberis thunbergii* (Japanese barberry) and *Microstegium vimineum* (Japanese stilt grass). Significant differences in soil properties were found in plots with these exotics, including higher pH values and higher nitrification and litter decomposition rates (Ehrenfeld *et al.*, 2001). There are many other invasive species in the Northeastern U.S. that negatively affect composition and function of Northeastern forests, but which have not been examined for possible effects on soil ecosystem process.

One prominent problem invasive in New England is *Celastrus orbiculatus* (Oriental bittersweet), an invasive liana that was introduced from East Asia into the northeastern United States in the 1860s (Patterson, 1974). *Celastrus orbiculatus* can grow taller than 30 m, with a stem exceeding 18 cm in diameter. It can damage trees by girdling (Lutz, 1943), increasing tree susceptibility to ice damage (Sperry *et al.*, 1987), or interfering with forest regeneration by shading out smaller native seedlings and saplings. Currently, its distribution in North America is from the east coast of the U.S. north to Quebec and Ontario, south to Georgia and west to Wisconsin (Ma and Moore, 2004; USDA NRCS, 2008). Dispersal by birds, mammals and humans (it is used in ornamental horticulture and in cut flower displays) probably accounts for its rapid expansion (Dreyer *et al.*, 1987; LaFleur *et al.*, 2007). *Celastrus orbiculatus* can grow in a variety of habitats including forests, open fields and sandy areas. This adaptability of *C. orbiculatus* can partly be attributed to its ability to withstand a range of light levels, including heavy shade (Dreyer *et al.*, 1987; Leicht and Silander, 2006; Leicht-Young *et al.*, 2007b).

The objective of this study was to determine how *Celastrus orbiculatus* might affect soil chemical and biological properties and processes. Prior studies of the effect of invasives on soil properties have focused on soil nitrogen, pH, or phosphorus; here, we included soil cations (calcium and magnesium) plus litter decomposition processes. This is the first detailed study of the effects of a temperate invasive liana on soil properties and processes. To examine the effects of *C. orbiculatus* on soil and litter decomposition, we selected adjacent plots that were similar except for the presence or absence of *C. orbiculatus*. These paired plots spanned a broad range of soil and habitat conditions in the landscape where *C. orbiculatus* occurs. We hypothesized, based on previous work on temperate exotic species, that plots containing *C. orbiculatus* would have increased nutrient availability (Blank and Young, 2002; Vanderhoeven *et al.*, 2005), mineralization rates (Ehrenfeld *et al.*, 2001; Ehrenfeld, 2003), and litter decomposition rates (Grout *et al.*, 1997; Kourtev *et al.*, 1998; Ehrenfeld, 2003; Ashton *et al.*, 2005; Heneghan *et al.*, 2007).

METHODS

To investigate soil responses to the presence and absence of the invasive species *Celastrus orbiculatus*, seven paired plots (3 × 3 m) were selected across Mansfield, Connecticut (in the vicinity of 41°48′30″N, 72°15′00″W). The seven paired plots were chosen to span a range of possible soil and environmental conditions in the areas in which *C. orbiculatus* occurs and which is representative of much of southern New England (Leicht-Young *et al.*, 2007b). Site conditions varied from coarse-textured xeric soils to gravely, sandy, excessively well-drained loams, (classified as typic Udorthents and Dystrochrepts) over coarse parent material (esker or kame desposits) to fine, sandy, more mesic loams (moderately well-drained to well-drained—typically over thin glacial till, and classified mostly as typic Dystrochrepts, but also aquic or oxyaquic Dystrochrepts and one fluventic Dystrudept). Some sites had never been cultivated for agriculture; other sites had some evidence of long past agriculture, and one site had recent (10–15 y ago) agricultural activities. Sites also varied in openness and

community composition. Each of the paired plots consisted of one plot with one or more *C. orbiculatus* plants present and an adjacent plot without the invasive. Each of the paired plots were otherwise selected to be similar in soil and other environmental attributes and were separated by an average distance of 11.3 m. In addition, to control for multi-species effects, none of the plots had any other invasive plant species present.

Four soil samples were randomly taken from each of the paired plots. A spade was used to collect the A plus B (or Ap) mineral horizons of the soil to a depth of about 10 cm; organic horizons were discarded. The soil samples were sealed in bags, placed in a cooler on ice to minimize further microbial activity on the soil, and transported to the University of Connecticut Soil Testing Lab for analysis.

At the end of the day's collections, approximately half of each soil sample was spread thinly on sheets of paper to dry overnight at room temperature. The rest of the sample was left to incubate in a controlled environment (22 C) in a sealed bag for 28 d. The dried portion of the soil was then sieved prior to pH, nitrogen, phosphorus, potassium, calcium and magnesium analyses. Soil pH was measured from an equal-mixture slurry of soil and distilled water using an Accumet Model 50 pH meter. A Modified Morgan extraction technique (McIntosh, 1969) was used to assay the macronutrient (P, K, Ca, Mg) content of the soils. We placed 4 g of the air-dried, sieved soil into 50 mL extraction flasks. Next, 20 mL of Modified Morgan extractant (0.62 N NH_4OH + 1.25 N CH_3COOH) was added to each flask. The flasks were allowed to shake at 180 oscillations per minute for 15 min on a reciprocating shaker. The solutions were then filtered through Whatman No. 2 filter paper.

Potassium, calcium and magnesium content were all analyzed by an Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES) machine (Spectro Ciros Vision model). Phosphorus and nitrate concentrations were analyzed colorimetrically using a Technicon Autoanalyzer II and a Scientific AC 200 colorimeter, respectively. To extract soil nitrogen, a 2 M KCl solution was used. Nitrate content of both field-collected and incubated soils was determined. Nitrification rates were calculated as:

$$N_{nitrification} = (Nitrate_{final} - Nitrate_0)/T_{days}$$

(Robertson *et al.*, 1999).

The procedure used for litter decomposition measurements followed that outlined by Gartner and Cardon (2004, 2006). Fresh leaves of both *Quercus rubra* (red oak) and *Celastrus orbiculatus* were collected in August from one site. The objective was to mimic the mixed species litter conditions that prevail in forests with native species canopies and invasive lianas present. The leaves were placed in a leaf press, dried for 5 d, and finally dried in an oven to ensure constant initial weight. In a 15 cm × 15 cm fiberglass mesh litterbag, 1.5 g of *C. orbiculatus* litter was placed below 1.5 g of *Q. rubra* litter. The bags were sealed with staples. A second set of litterbags were filled with three sheets of 110 mm Whatman filter paper, for a combined weight of approximately 3 g. These filter paper bags were used as a control. Three bags containing the leaf litter and three bags containing the filter paper were placed randomly on the soil mineral surface at each plot in mid-August 2005. The bags were fastened flat to the soil surface with wire. After 90 d, the litter and filter paper bags were retrieved from the sites, and the leaves and filter paper were dried and reweighed (after carefully removing any adhering soil mineral material). The decomposition index was calculated by subtracting the initial weight of the leaves or filter paper from the final weight of the leaves or filter paper, and dividing by 90 d. To compare the general chemical composition of the leaves used in the litter bags, we took three samples of undecomposed leaves of each species (*C. orbiculatus* and *Q. rubra*) and had them analyzed for percentage of

potassium, calcium, magnesium, phosphorus, nitrogen, C:N and pH (A & L Great Lakes Laboratories Inc., Fort Wayne, Indiana).

A detailed description of each site containing the paired plots (10 m radius plots) was recorded using the field protocol established by the Invasive Plant Atlas of New England (IPANE) project (Mehrhoff *et al.*, 2003). *Celastrus orbiculatus*, abundance, distribution and percent cover were recorded. The distribution of *C. orbiculatus* was recorded as a single plant, evenly sparse, a single patch, multiple patches or dense throughout. The abundance and percent cover of *C. orbiculatus* were obtained, respectively, by counting or visual estimation of the number of *C. orbiculatus* individuals in the plot (scale: 1, <20, 20–99, 100–999, >1000) and estimating the percentage of ground shaded by *C. orbiculatus* (scale: <1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–100%). Habitat/community type was characterized by the dominant vegetation type at the site. Canopy closure was reported as an ocular estimate of the percentage of sky covered by foliage within a given site. Slope aspect was determined by GPS, and soil moisture was categorized by visual inspection of the soils or underlying surficial geology to be either xeric (*e.g.*, coarse sands, or esker/kame deposits), mesic (*e.g.*, find sandy loams), or intermediate; no wetland sites were sampled, as *C. orbiculatus* does not occur in wetlands.

To determine if the amount of soil pH, potassium, calcium, magnesium, phosphorus, nitrogen mineralization, as well as if litter and filter paper decomposition differed in plots with and without *Celastrus orbiculatus* present, we analyzed our data using a linear mixed effects model in S-Plus (Insightful Corporation, 2003). We chose this model because both fixed and random effects were studied (Pinheiro and Bates, 2000). These models also allow for grouped data (*i.e.*, the four soil samples in each plot) to be analyzed taking into account correlations between observations within the same group (Pinheiro and Bates, 2000). Presence or absence of *C. orbiculatus* was treated as a fixed-effect, explanatory variable. Plot number was treated as a random effect explanatory variable because each site was considered to be a random sample from the population of habitat types and *Celastrus* locations. The response variables, pH, potassium, calcium, magnesium, phosphorous, nitrogen mineralization, litter and filter paper decomposition were then dependent (response) fixed effects. Since the eight response variables being quantified using the linear mixed models cannot be considered completely independent of one another, the analyses could be subject to Type I errors. To correct for this, we used a Benjamini-Hochberg correction (Benjamini and Hochberg, 1995) to adjust the P-values. We examined whether the addition of the site random effect significantly improved the model using a likelihood ratio test that compared the model with and without the random effect. Additionally we analyzed the specific locations to see if there were any that were significantly different from the others for each response variable. Calcium and magnesium were log-transformed to normalize the data. Numerous nulls (non-detectable levels) were present in the phosphorus data; therefore, all data that were below the detection limit of 0.04 mg/kg of phosphorus were censored to equal the detection limit. A Box-Cox transformation was used to find the best transformation of the phosphorus data in terms of normality and homogeneity of variance.

To compare the initial leaf chemistry measures of *Celastrus orbiculatus* and *Quercus rubra* used in the decomposition experiment, we used independent samples *t*-tests followed by the same Benjamini-Hochberg correction to correct for the seven response variables (*see* methods above) that were quantified.

Results

The most common habitat type we observed was northern hardwood forest, which comprised four out of the seven sites. Other habitat types included a field/forest edge, an

TABLE 1.—Site description data for the seven plot pairs. a) general habitat information about the plots. b) abundance, distribution and percent cover for the plot pairs with *Celastrus orbiculatus*

a) Site attribute data				
Site pair	Habitat/community type	Canopy closure	Aspect	Soil moisture
1	Field/forest edge	26–50%	Flat	Xeric
2	Open field	0–25%	Flat	Mesic
3	N. hardwood	76–100%	NE	Mesic
4	N. hardwood	51–75%	Flat	Mesic
5	N. hardwood	51–75%	Flat	Mesic
6	White pine	51–75%	Flat	Xeric-Mesic
7	N. hardwood	76–100%	SE	Xeric-Mesic

b) *Celastrus orbiculatus* plot data			
Site pair	Abundance	Distribution	Percent cover
1	20–99	Multiple patches	26–50%
2	100–999	Single patch	76–100%
3	20–99	Evenly sparse	26–50%
4	1	Single patch	51–75%
5	20–99	Multiple patches	51–75%
6	20–99	Evenly sparse	26–50%
7	20–99	Dense throughout	51–75%

open field and white pine forest. The most frequent canopy closure category was 76–100%, occurring in three out of the seven sites. The slope of five out of the seven pairs of sites was flat. Soil moisture in most of the sites was mesic and ranged to xeric (Table 1a).

The abundance and dispersion of *Celastrus orbiculatus* was variable among plots. It was present as a single patch, multiple patches, evenly sparse or dense throughout in at least one of the seven sites. The percent cover of *C. orbiculatus* was most commonly 26–50% to 51–75% (Table 1b).

Overall, plots with *Celastrus orbiculatus* are significantly different in soil attributes than sites without *C. orbiculatus*. Only filter paper (as litter) decomposition and phosphorus concentrations were not statistically different among sites (Table 2). Positive coefficient values were determined for all other variables, indicating a positive trend: sites with *C. orbiculatus* are more likely to have higher nutrient values or decomposition rates than sites without. We also found that the addition of the site random variable significantly improved the model except for the leaf and filter paper decomposition responses (Table 3). In terms of the individual sites, there were very few that had significant random effects. However, there were three exceptions. Plot pair one was significantly different in terms of soil magnesium ($P = 0.001$), plot pair six for soil pH ($P = 0.003$) and plot pair two for phosphorous ($P = 0.043$, although overall, the amount of phosphorous was not significantly related to presence of *C. orbiculatus*).

In nearly all of the paired sites, potassium, calcium and magnesium were significantly greater in plots with *Celastrus orbiculatus* than without (Figs. 1A–C). Phosphorus, however, was quite variable among the seven sites and individual plots, with no detectable trend among them (Fig. 1D). pH values were always greater in *C. orbiculatus* plots than in plots without *C. orbiculatus* (Fig. 1E). Mean nitrogen mineralization values were always higher in plots with *C. orbiculatus* than without, except at site 4 (Fig. 1F). The standard error bars at sites 1 and 6 (Fig. 1F) reflect negative nitrogen mineralization values for some plots without

TABLE 2.—Linear mixed effects models of pH, potassium, log_{10}(calcium), log_{10}(magnesium), phosphorus$^{-0.5}$, nitrogen mineralization rate, and litter and filter paper decomposition as a function of *Celastrus orbiculatus* presence and plot number

	Term	Coefficient	Std. error	df	T	P
Potassium	Intercept	55.9055	5.6925	48	9.8209	<0.0001
	Celastrus	17.0031	4.4639	48	3.8090	0.0004
log_{10}(calcium)	Intercept	2.2154	0.1552	48	14.2759	<0.0001
	Celastrus	0.2734	0.0693	48	3.9475	0.0003
log_{10}(magnesium)	Intercept	1.4445	0.1303	48	11.0873	<0.0001
	Celastrus	0.2090	0.0473	48	4.4220	0.0001
Phosphorus$^{-0.5}$	Intercept	3.4364	0.5354	48	6.4189	<0.0001
	Celastrus	−0.0374	0.2828	48	−0.1322	0.8954
pH	Intercept	5.0286	0.1528	48	32.9111	<0.0001
	Celastrus	0.3253	0.0513	48	6.3430	<0.0001
Nitrogen	Intercept	0.2134	0.0743	48	2.8715	0.0061
mineralization	*Celastrus*	0.1786	0.0456	48	3.9201	0.0003
Litter decomposition	Intercept	0.0144	0.0011	33	13.0263	<0.0001
	Celastrus	0.0027	0.0008	33	3.3979	0.0018
Filter paper	Intercept	0.0055	0.0015	28	3.6872	0.0010
decomposition	*Celastrus*	0.0028	0.0018	28	1.5782	0.1258

C. orbiculatus. Decomposition rates (especially filter paper decomposition) were more variable than other effects tested, except for phosphorus. However, overall, litter decomposition was significantly greater in plots with *C. orbiculatus* (Figs. 1G–H).

Leaf litter of *Celastrus orbiculatus* had significantly greater levels of potassium and calcium, while *Quercus rubra* had greater C:N. There was no difference in percentage of magnesium, phosphorus and nitrogen (Table 4). The pH of the leaves of *C. orbiculatus* was clearly higher than that of *Q. rubra*. However, since there was no variability in the three leaf replicates of both species (all were identical), statistical significance could not be specifically determined (Table 4).

DISCUSSION

Our results indicate that many of the soil attributes that were measured between adjacent plots were significantly different from each other across a spectrum of soil types. Although

TABLE 3.—Likelihood ratio tests of linear mixed effects models with and without the random site effect included of pH, potassium, log_{10}(calcium), log_{10}(magnesium), phosphorus$^{-0.5}$, nitrogen mineralization rate, and litter and filter paper decomposition as a function of *Celastrus orbiculatus* presence and plot number

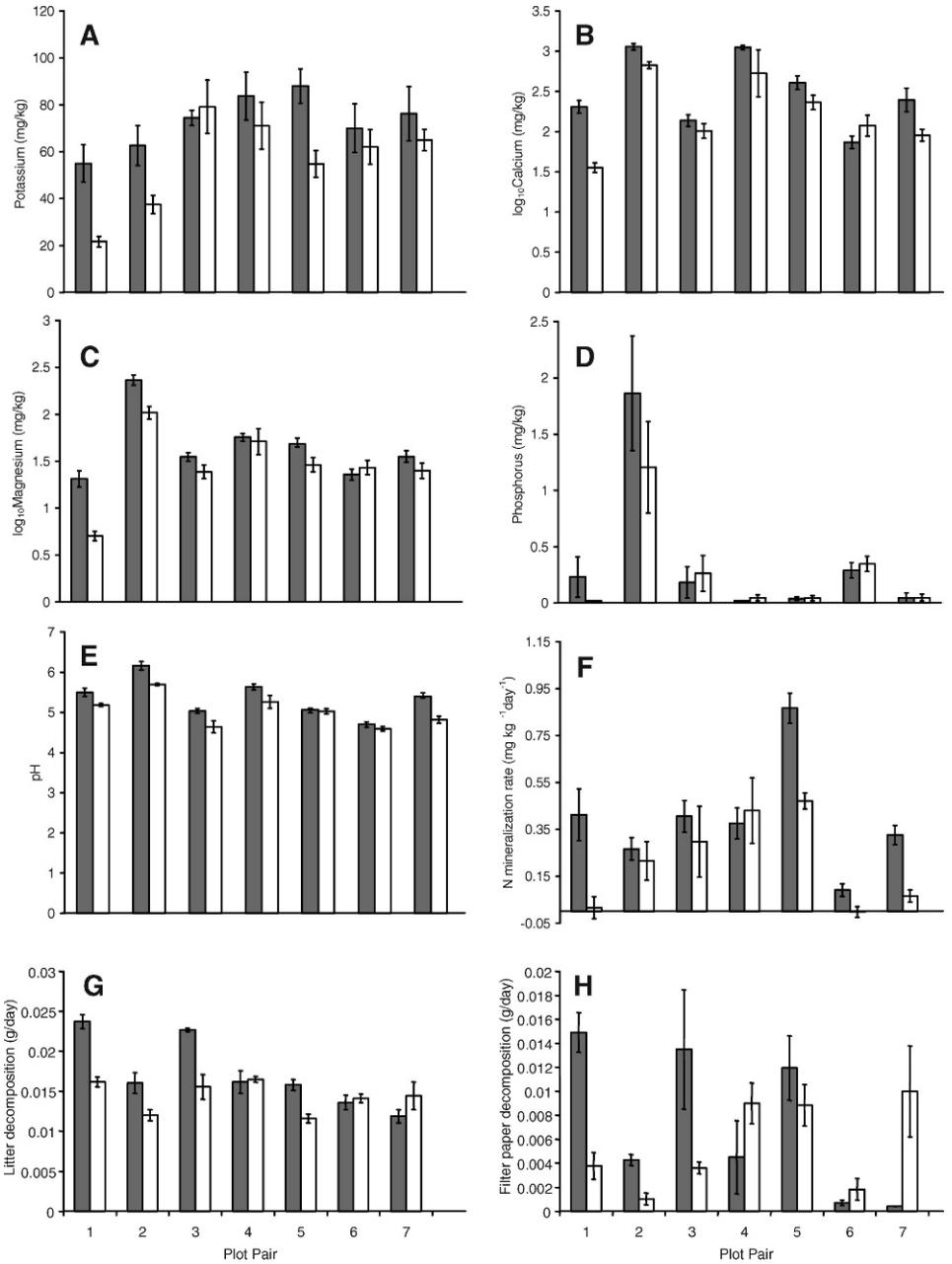| Term	df	AIC	Likelihood ratio	P-value
Potassium	4, 6	483, 501	13.93	0.0009
log_{10}(calcium)	4, 6	41, 91	46.17	<0.0001
log_{10}(magnesium)	4, 6	2, 68	61.57	<0.0001
Phosphorus$^{-0.5}$	4, 6	229, 263	29.42	<0.0001
pH	4, 6	12, 84	67.71	<0.0001
Nitrogen mineralization	4, 6	−8, 22	25.98	<0.0001
Litter decomposition	4, 6	−313, −306	2.62	0.2701
Filter paper decomposition	4, 6	−283, −277	1.74	0.4197

FIG. 1.—Mean values of (A) potassium, (B) log$_{10}$magnesium, (C) log$_{10}$calcium and (D) phosphorus (E) pH, (F) nitrogen mineralization, (G) litter decomposition and (H) filter paper decomposition for the seven paired plots. Untransformed values of phosphorus are shown for ease of interpretation. Gray bars are plots with *Celastrus orbiculatus* present and white bars are plots without. Error bars represent the standard error of the mean

TABLE 4.—Leaf chemistry results for *Celastrus orbiculatus* and *Quercus rubra*. Values are mean ± SE. Different letters indicate significant differences at the α = 0.05 level. For pH there was no variability in the three replicates so statistical tests could not be performed

	Celastrus orbiculatus	*Quercus rubra*
% potassium	2.517 ± 0.102[a]	0.997 ± 0.038[b]
% calcium	3.84 ± 0.068[a]	1.273 ± 0.033[b]
% magnesium	0.51 ± 0.01[a]	0.477 ± 0.009[a]
% phosphorus	0.193 ± 0.003[a]	0.197 ± 0.003[a]
% nitrogen	2.733 ± 0.052[a]	2.643 ± 0.015[a]
C:N	18.270 ± 0.354[a]	20.809 ± 0.146[b]
pH	5.6	5.3

we cannot say definitively that *Celastrus orbiculatus* is causing these differences, the presence or absence of the plant was the major difference between these plots. Thus, it is likely that *C. orbiculatus*, similar to other invasive species, can appreciably influence the local soil environment.

We found that the inclusion of a random site effect significantly improved our model. This random site effect took into account soil and other local environmental differences. Despite these differences in the sites themselves, the same differences in soil chemistry and decomposition were observed in the plots containing *Celastrus orbiculatus* compared to those without. We also determined that some site random effects in particular were significant for specific soil chemistry measures. Plot pair one had a significant negative random effect in the model for soil magnesium, most likely because the plot without *C. orbiculatus* had very low magnesium. Plot pair six, with a significant negative random effect in the pH model, had the least amount of variability and was the only site in which white pine was the dominant overstory species. Finally, plot pair two had a significant positive effect in the model for phosphorous, most likely because it was located in an open, abandoned field that had been farmed in the past and that has finely textured soils (J. Silander, pers. obs.).

Compared across plots, those with *Celastrus orbiculatus* had significantly higher nitrogen mineralization rates than those without. Similar results have been found among other invasive plant species (Ehrenfeld *et al.*, 2001; Hawkes *et al.*, 2005; Heneghan *et al.*, 2006). In a review of studies encompassing 56 invasive plant species worldwide, Ehrenfeld (2003) found that nitrogen mineralization and nitrification rates were more commonly higher where invasive species were present. Changes in microbial communities associated with the introduction of invasive species can account for higher nitrification rates (Hawkes *et al.*, 2005). Ehrenfeld *et al.* (2001) and Kourtev *et al.* (2002, 2003) for example, showed that plots with *Berberis thunbergii* and *Microstegium vimineum* compared to adjacent plots with native species each had structurally and functionally distinct soil microbial communities. Sites 1 and 6 show that some nitrogen mineralization values were negative in plots lacking *C. orbiculatus*. This could be a result of microbial uptake and immobilization of ammonium and nitrate. Indeed, this mechanism was implicated in a study that showed that increased nitrification rates of *M. vimineum* were associated with decreases in the concentration of available nitrate (Kourtev *et al.*, 2003).

The quantities of three cations, potassium, calcium and magnesium, were also measured and found to be greater in plots with *Celastrus orbiculatus*. In the case of plot 1, the difference in magnesium was so great that it resulted in a significant plot effect. Rarely are soil cations

measured in species-specific studies (but *see* Vanderhoeven *et al.* 2005, 2006). Unlike nitrogen, which is mostly obtained from organic matter, these nutrients tend to be derived from the mineral soil fraction (Thompson and Troeh, 1993). Similar results were shown with increased potassium, calcium and magnesium with *Lepidium latifolium* (perennial pepperweed) (Blank and Young, 2002), increased potassium and magnesium with *Fallopia japonica* (Japanese knotweed), increased potassium with *Heracleum mantegazzianum* (giant hogweed) and increased calcium with *Prunus serotina* (Vanderhoeven *et al.*, 2005). Uplift of minerals from deep soil or parent material by deep-rooted plants (Jobbagy and Jackson, 2004) could explain these patterns. This seems unlikely at our sites because this system contains deep-rooted native species on shallow glacial till covering ancient, nutrient poor gneisses and schists.

Besides these cations, we also measured phosphorus which was the only element that was not greater in the plots with *Celastrus orbiculatus*. There was great variation in the values of phosphorus within and among plots (Fig. 1D). This is in contrast to studies by Vanderhoeven *et al.* (2005, 2006) and Chapuis-Lardy *et al.* (2006) who showed an increase in phosphorus under *Solidago gigantea* (giant goldenrod). The review by Ehrenfeld (2003) showed that, in the few studies that examined phosphorus, concentrations of this element are quite variable, showing both increases and decreases in the presence of invasive.

Plots containing *Celastrus orbiculatus* had significantly greater pH than those without. Soil pH can be used to predict the availability of essential nutrients (Carter, 1993). pH influences the rate of nutrient release by weathering, the solubility of all materials in the soil, and the amounts of nutrients stored on cation-exchange sites. The effect of other invasive plants on pH has been examined in several different systems (Ehrenfeld, 2003). Kourtev *et al.* (1998) found that pH was significantly higher at sites with *Berberis thunbergii* and *Microstegium vimineum* adjacent to plots without the invasives. The same has been shown for *Rhamnus cathartica* (European buckthorn) in Midwestern forests (Heneghan *et al.*, 2006) and *Prunus serotina* (black cherry) in European sites (Vanderhoeven *et al.*, 2005). Changes in the pH of the soil are especially concerning because these effects can potentially be long-term, promoting a continuous invasion of these and other exotic species (Kourtev *et al.*, 2003).

The mechanisms for the increase in pH with invasive species present remain unclear, although several potential mechanisms have been proposed. One possibility is that increased nitrification and the preferential uptake of nitrate over ammonium to support the typically larger biomass of invasive species can increase pH (Ehrenfeld *et al.*, 2001). Finzi *et al.* (1998) have suggested several ways that the native tree *Acer saccharum* (sugar maple) may increase pH. First, leaf chemical attributes can feedback directly on soil mineral composition through leaf decomposition processes. Second, species take up cations differently and allocate them to biomass with different turnover times (*cf.*, Reich *et al.* 2005). Finally, the parent material that the plant is growing in can differ in mineral content (Finizi *et al.*, 1998). *Celastrus orbiculatus* and other exotic species could act on the soil by any one, or a combination of these mechanisms, thus altering the local soil pH and nutrients. It seems unlikely that differences in parent material among seven pairs of closely adjacent sites could be responsible for the differences we observed. However, this possibility cannot be ruled out. The litter of *C. orbiculatus* had more than three times the percentage of calcium (3.8% *versus* 1.3%) in its leaves compared to *Quercus rubra*, as well as a higher pH. The greater percentage of calcium may have led to higher soil pH in plots with *C. orbiculatus* present. In another study, the leaves of *A. saccharum* similarly has a high percentage (~1.35%) of calcium in their leaves, which likely resulted in higher pH under the canopy of this species (Finizi *et al.*, 1998).

Plant litter decomposition is an indicator of the rate and timing of nutrient release in forms available for uptake by plants and soil biota. Despite large differences among sites, litter decomposition rates were significantly higher in all *Celastrus orbiculatus* plots relative to control plots (*cf.*, Fig. 1G). This has also been shown to be the case for areas invaded by *Berberis thunbergii* (Kourtev *et al.*, 1998), as well as in other invaded forest sites in the Northeast (Ashton *et al.*, 2005). Decomposition rates can increase with an increased density of earthworms and other soil fauna (Kourtev *et al.*, 1998; Kourtev *et al.*, 2002, 2003; Hawkes *et al.*, 2005; Heneghan *et al.*, 2007). It is possible that the high levels of calcium in the leaves of *C. orbiculatus* had a positive influence on earthworm densities (Reich *et al.*, 2005). Changes in soil fauna alone may not only increase decomposition, but differences in litter quality, productivity and rooting depth can also influence decomposition rates (Scowcroft, 1997; Jobbagy and Jackson, 2004; Vanderhoeven *et al.*, 2006). For instance, high growth rates, such as those found for *C. orbiculatus* (Leicht, 2005), high specific leaf area (Leicht, 2005; Leicht and Silander, 2006) and low carbon-to-nitrogen ratio (Scowcroft, 1997) can equal lower construction costs (Baruch and Goldstein, 1999) and faster leaf litter decomposition.

An important concept to consider when measuring the soil composition and processes associated in sites with *Celastrus orbiculatus* is whether the invasive has caused the changes or simply grows preferentially where soil composition is ideal. A field study of *Berberis thunbergii* and *Microstegium vimineum* in adjacent plots of close proximity (10–20 m) to plots with native flora showed that there were significant differences in microbes, nitrogen mineralization and litter decomposition across all three conditions. This is especially remarkable because the plots had the same land-use history and a uniform tree canopy (Kourtev *et al.*, 2002). These same exotics were also tested under greenhouse conditions. Differences in soil processes and microbes were once again found to be significant (Kourtev *et al.*, 2003). The experimental conditions had identical soils; therefore, any changes in the soil must have been due to the plants and their associated microbial communities. In our study, it is possible that prior conditions, such as agricultural histories, could have an influence on current invasive species distributions (Kulmatiski *et al.*, 2006; DeGasperis and Motzkin, 2007). However, *C. orbiculatus* is known to grow in a very wide range of habitats both with and without agricultural histories, ranging from sand dunes (Leicht-Young *et al.*, 2007a) to wet and dry forests and is fairly ubiquitous on the New England landscape (Leicht-Young *et al.*, 2007b). Thus, based on paired plot proximity and previous greenhouse experiments with other exotics, it is most parsimonious to conclude that soil alterations were caused by the presence of *C. orbiculatus* (*cf.*, Vanderhoeven *et al.* 2005, 2006). However, further manipulative studies would be needed to prove this definitively.

Quantifying how *Celastrus orbiculatus* changes soil composition and processes is an important step in the management and restoration of native ecosystems. The changes observed in this study could have an impact on the re-introduction of native plants to areas that previously contained *C. orbiculatus* (Heneghan *et al.*, 2006). Further research is still needed in understanding the mechanisms by which this species and other invasives alter soil ecosystems processes. Additional research on the structure and function of microbial communities that accompany *C. orbiculatus* is also necessary. Finally, the effects of *C. orbiculatus* abundance, particularly threshold effects that result in significant ecosystem-level changes, need to be examined.

LITERATURE CITED

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. *Ecol. Appl.*, **15**:1263–1272.

BARUCH, Z. AND G. GOLDSTEIN. 1999. Leaf construction cost, nutrient concentration and net CO_2 assimilation of native and invasive species in Hawaii. *Oecologia*, **121**:183–192.

BENJAMINI, Y. AND Y. HOCHBERG. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. Roy. Stat. Soc. B*, **57**:289–300.

BLANK, R. R. AND J. A. YOUNG. 2002. Influence of the exotic invasive crucifer, *Lepidium latifolium* on soil properties and elemental cycling. *Soil Sci.*, **167**:821–829.

CALLAWAY, R. M. AND J. L. MARON. 2006. What have exotic plant invasions taught us over the past 20 years? *Trends Ecol. Evol.*, **21**:369–374.

CARTER, M. R. 1993. Soil Sampling and Methods of Analysis. Lewis Publishers, Boca Raton, Florida.

CHAPUIS-LARDY, L., S. VANDERHOEVEN, N. DASSONVILLE, L. S. KOUTIKA AND P. MEERTS. 2006. Effect of the exotic invasive plant *Solidago gigantea* on soil phosphorus status. *Biol. Fertil. Soils*, **42**:481–489.

DEGASPERIS, B. G. AND G. MOTZKIN. 2007. Windows of opportunity: Historical and ecological controls on *Berberis thunbergii* invasions. *Ecology*, **88**:3115–3125.

DREYER, G. D., L. M. BAIRD AND C. FICKLER. 1987. *Celastrus scandens* and *Celastrus orbiculatus*: comparisons of reproductive potential between a native and an introduced woody vine. *B. Torrey Bot. Club*, **114**:260–264.

EHRENFELD, J. G. 1997. Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC). *J. Torrey Bot. Soc.*, **124**:210–215.

———, P. KOURTEV AND W. Z. HUANG. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecol. Appl.*, **11**:1287–1300.

——— AND N. SCOTT. 2001. Invasive species and the soil: Effects on organisms and ecosystem processes. *Ecol. Appl.*, **11**:1259–1260.

———. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**:503–523.

FINIZI, A., C. D. CANHAM AND N. VAN BREEMEN. 1998. Canopy tree soil interactions within temperate forests: species effects on pH and cations. *Ecol. Appl.*, **8**:447–454.

GARTNER, T. B. AND Z. G. CARDON. 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos*, **104**:230–246.

——— AND ———. 2006. Site of leaf origin affects how mixed litter decomposes. *Soil Biol. Biochem.*, **38**:2307–2317.

GERLACH, JR., J. D. AND K. J. RICE. 2003. Testing life history correlates of invasiveness using congeneric plant species. *Ecol. Appl.*, **13**:167–179.

GROUT, J. A., C. D. LEVINS AND J. S. RICHARDSON. 1997. Decomposition rates of purple loosestrife (*Lythrum salicaria*) and Lyngbei's sedge (*Carex lyngbyei*) in the Fraser River estuary. *Estuaries*, **20**:96–102.

HAWKES, C. V., I. F. WREN, D. J. HERMAN AND M. K. FIRESTONE. 2005. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecol. Lett.*, **8**:976–985.

HENEGHAN, L., F. FATEMI, L. UMEK, K. GRADY, K. FAGEN AND M. WORKMAN. 2006. The invasive shrub European buckthorn (*Rhamnus cathartica*, L.) alters soil properties in Midwestern U.S. woodlands. *Appl. Soil Ecol.*, **32**:142–148.

———, J. STEFFEN AND K. FAGEN. 2007. Interactions of an introduced shrub and introduced earthworms in an Illinois urban woodland: Impact on leaf litter decomposition. *Pedobiologia*, **50**:543–551.

HOWARD, T. G., J. GUREVITCH, L. HYATT, M. CARREIRO AND M. LERDAU. 2004. Forest invasibility in communities in southeastern New York. *Biol. Invasions*, **6**:393–410.

INSIGHTFUL CORPORATION. 2003. S-PLUS 6.2 for Windows.

JOBBAGY, E. G. AND R. B. JACKSON. 2004. The uplift of soil nutrients by plants: biogeochemical consequences across scales. *Ecology*, **85**:2380–2389.

KOURTEV, P. S., J. G. EHRENFELD AND W. Z. HUANG. 1998. Effects of exotic plant species on soil properties in hardwood forests of New Jersey. *Water Air Soil Poll.*, **105**:493–501.

———, ——— AND M. M. HAGGBLOM. 2002. Exotic plant species alter the microbial community structure and function in the soil. *Ecology*, **83**:3152–3166.

———, ——— AND ———. 2003. Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biol. Biochem.*, **35**:895–905.

KULMATISKI, A., K. H. BEARD AND J. M. STARK. 2006. Soil history as a primary control on plant invasion in abandoned agricultural fields. *J. Appl. Ecol.*, **43**:868–876.

LAFLEUR, N. E., M. A. RUBEGA AND C. S. ELPHICK. 2007. Invasive fruits, novel foods, and choice: An investigation of European starling and American Robin frugivory. *Wilson J. Ornithol.*, **119**:429–438.

LEICHT, S. A. 2005. The comparitive ecology of an invasive bittersweet species (*Celastrus orbiculatus*) and its native congener (*C. scandens*). PhD Dissertation, University of Connecticut, Storrs, Connecticut.

——— AND J. A. SILANDER, JR. 2006. Differential responses of invasive *Celastrus orbiculatus* (Celastraceae) and native *C. scandens* to changes in light quality. *Am. J. Bot.*, **93**:972–977.

LEICHT-YOUNG, S. A., N. B. PAVLOVIC, R. GRUNDEL AND K. J. FROHNAPPLE. 2007a. Distinguishing native (*Celastrus scandens* L.) and invasive (*C. orbiculatus* Thunb.) bittersweet species using morphological characteristics. *J. Torrey Bot. Soc.*, **134**:441–450.

———, J. A. SILANDER, JR. AND A. M. LATIMER. 2007b. Comparative performance of invasive and native *Celastrus* species across environmental gradients. *Oecologia*, **154**:273–282.

LUTZ, H. J. 1943. Injuries to trees caused by *Celastrus* and *Vitis*. *B. Torrey Bot. Club*, **70**:436–439.

MA, J. AND G. MOORE. 2004. *Celastrus orbiculatus* Thunb., Wildland shrubs of the United States and its territories: Thamnic descriptions. General Technical Report IIFT-WB-I. United States Department of Agriculture, Forest Service Institute of Tropical Forestry and Shrub Sciences Lab.

MCINTOSH, J. L. 1969. Bray and Morgan soil test extractants modified for testing acid soils from different parent materials. *Agron. J.*, **6**:259–265.

MEHRHOFF, L. J., J. A. SILANDER, JR., S. A. LEICHT, E. MOSHER AND N. M. TABAK. 2003. IPANE: Invasive Plant Atlas of New England (http://www.ipane.org).

PATTERSON, D. T. 1974. The ecology of oriental bittersweet, *Celastrus orbiculatus*, a weedy introduced ornamental vine. PhD Dissertation, Duke University, Durham, North Carolina.

PINHEIRO, J. C. AND D. M. BATES. 2000. Mixed-effects models in S and S-PLUS. Springer-Verlag, New York.

REICH, P. B., M. B. WALTERS AND D. S. ELLSWORTH. 1997. From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. U.S.A.*, **94**:13730–13734.

———, J. OLEKSYN, J. MODRZYNSKI, P. MROZINSKI, S. E. HOBBIE, D. M. EISSENSTAT, J. CHOROVER, O. A. CHADWICK, C. M. HALE AND M. G. TJOELKER. 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecol. Lett.*, **8**:811–818.

REINHART, K. O. AND R. M. CALLAWAY. 2006. Soil biota and invasive plants. *New Phytol.*, **170**:445–457.

ROBERTSON, G. P., D. C. COLEMAN, C. S. BLEDSOE AND P. SOLLINS. 1999. Standard soil methods for long-term ecological research. Oxford University Press, New York, New York.

SCOWCROFT, P. G. 1997. Mass and nutrient dynamics of decaying litter from *Passiflora mollissima* and selected native species in a Hawaiian montane rain forest. *J. Trop. Ecol.*, **13**:407–426.

SPERRY, J. S., N. M. HOLLBROOK, M. H. ZIMMERMAN AND M. T. TYREE. 1987. Spring filling of xylem vessels in wild grapevine. *Plant Physiol.*, **83**:414–417.

THOMPSON, L. M. AND F. R. TROEH. 1993. Soils and soil fertility. Oxford University Press, New York, New York.

USDA NRCS. 2008. The PLANTS Database (http://plants.usda.gov). National Plant Data Center, Baton Rouge, Louisiana 70874-4490 USA.

VANDERHOEVEN, S., N. DASSONVILLE AND P. MEERTS. 2005. Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. *Plant Soil*, **275**:169–179.

———, ———, L. CHAPUIS-LARDY, M. HAYEZ AND P. MEERTS. 2006. Impact of the invasive alien plant *Solidago gigantea* on primary productivity, plant nutrient content and soil mineral nutrient concentrations. *Plant Soil*, **286**:259–268.

WOLFE, B. E. AND J. N. KLIRONOMOS. 2005. Breaking new ground: Soil communities and exotic plant invasion. *Bioscience*, **55**:477–487.