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Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes

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ABSTRACT

Although it is generally acknowledged that invasions by exotic plant species represent a major threat to biodiversity and ecosystem stability, little attention has been paid to the potential impacts of these invasions on nutrient cycling processes in the soil. The literature on plant–soil interactions strongly suggests that the introduction of a new plant species, such as an invasive exotic, has the potential to change many components of the carbon (C), nitrogen (N), water, and other cycles of an ecosystem. I have reviewed studies that compare pool sizes and flux rates of the major nutrient cycles in invaded and noninvaded systems for invasions of 56 species. The available data suggest that invasive plant species frequently increase biomass and net primary production, increase N availability, alter N fixation rates, and produce litter with higher decomposition rates than co-occurring natives. However, the opposite patterns also occur, and patterns of difference between exotics and native species show no trends in some other components of nutrient cycles (for example, the size of soil pools of C and N). In some cases, a given species has different effects at different sites, suggesting that the composition of the invaded community and/or environmental factors such as soil type may determine the direction and magnitude of ecosystem-level impacts. Exotic plants alter soil nutrient dynamics by differing from native species in biomass and productivity, tissue chemistry, plant morphology, and phenology. Future research is needed to (a) experimentally test the patterns suggested by this data set; (b) examine fluxes and pools for which few data are available, including whole-site budgets; and (c) determine the magnitude of the difference in plant characteristics and in plant dominance within a community that is needed to alter ecosystem processes. Such research should be an integral component of the evaluation of the impacts of invasive species.

Key words: exotic species; invasion ecology; ecosystem process; carbon; nitrogen; water; soil; soil organic matter; net primary productivity; nutrients; litter.

INTRODUCTION

Invasions of exotic species are widely recognized as one of the major threats to biodiversity and ecosystem stability (Wilcove and others 1998; Mack and others 2000) and are consequently attracting an exponentially increasing amount of attention from ecologists. The central research questions have been: What makes a species capable of a successful invasion? What makes a community invasible? What are the consequences of exotic invasions? Simple answers to these questions continue to elude researchers, even as the diversity of invasive situations becomes more apparent (Londsdale 1999; Kolar and Lodge 2001).

Answers to the first question have focused on individual, population, and community ecology—that is, reproduction, dispersal, and physiology

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(Huston 1994; Londsdale 1999; Mack and others 2000; Durand and Goldstein 2001; L. Windham and J.G. Ehrenfeld unpublished). The second question has been approached through studies of competition, disturbance, predation, and community composition (Mack and D'Antonio 1998; Levine and D'Antonio 1999; Davis and others 2000; Richardson 2000; Durand and Goldstein 2001). The third question is most commonly answered with evidence of changes in community composition, in the abundance of native species, and in disturbance regimes (Wilcove and others 1998; Cox 1999; Levine and D'Antonio 1999). The consequences of exotic invasions may, however, include less obvious changes below ground—that is, in the soil (Ehrenfeld and Scott 2001)—and these consequences may in turn have impacts on the invasibility of ecosystems and the invasiveness of species.

The potential for plant invasions to alter ecosystem dynamics was initially shown in a classic work by Vitousek et al. (Vitousek and others 1987) and has been summarized periodically (Vitousek 1990; Walker and Smith 1997; Gordon 1998; Cox 1999). These summaries have repeatedly cited the same small number of examples. However, the potential for plant invasions to alter soil nutrient dynamics may be much greater than these summaries suggest, as there are extensive data from natural communities and experimental systems to show the linkage between plant species composition and these ecosystem processes (Ehrenfeld 2001). Individual species have been shown to affect a variety of components of the carbon (C) and nutrient cycles, including pools of aboveground and belowground C, nitrogen (N), and other elements; net primary productivity and plant growth rates; chemical quality and rates of litterfall; and nutrient and C mineralization rates (Tilman and others 1997; Hooper and Vitousek 1998; van Breeman 1998; Hector and others 1999; Chapin and others 2000). This body of evidence strongly suggests that when the species composition of a community changes due to the invasion and spread of an exotic, there are likely to be consequent changes in nutrient cycling processes.

Changes in nutrient cycling processes that arise due to changes in a flora may reflect alterations in the soil microbial community related to differences in the quantities and qualities of inputs to the soil by different species of plants (Borga and others 1994; Garland 1996; Grayston and others 1996; Westover and Kelley 1997; Grayston and Campbell 1998; Grierson and Adams 2000). Nutrient dynamics may also become altered as a result of changes in the physical properties of the soil caused by the introduction of new species (Boettcher and Kalisz 1989; Finzi and others 1998; Kelly and others 1998; Ehrenfeld 2001). Changes may also result from alterations in the patterns of species dominance within the plant community, since the effects of a given species on ecosystem processes are modulated by its relative abundance within the community (Grime 1998). Finally, changes in plant functional types—herbaceous versus woody plants, N-fixing versus nonfixing species, C3 versus C4 species, and so on—are also associated with changes in the distribution and dynamics of soil nutrients (Gill and Burke 1999). There are thus a variety of mechanisms through which changes in the species composition of a community may alter nutrient cycling processes (McLendon and Redente 1992; Berendse 1998; van Breeman 1998; Hodge and others 2000; Ehrenfeld 2001).

The invasion of exotic species is a special case of change in plant community composition in which the substitution of one species (an exotic) for one or more native species or the addition of a new species has important consequences for conservation and the human utilization of ecosystem services. An examination of the impacts of exotic plants on nutrient cycling should thus be part of any evaluation of the consequences of an invasion. Furthermore, plant invasions provide natural experiments that test the impact of individual species on ecosystem function (Grime 1998; Hector and others 1999; Diaz and Cabido 2001).

Plants can affect nutrient and C dynamics through a variety of mechanisms (Table 1). These mechanisms reflect the ways in which plants interact with both the physical medium and the biota of the soil. Some traits are described as "qualitative," because they are either present or absent within a given species (Chapin and others 1996; Mack and others 2001); these include the ability to fix atmospheric N, the presence of perennial tissues, and the photosynthetic pathway. Other traits vary quantitatively among species; examples include the concentrations of N, phosphorus (P), and lignin; the size of an individual; and the transpiration rate. Both quantitative and qualitative traits underlie the concept of "functional group" (Smith and others 1997).

When a new species is introduced, its effects on nutrient cycling will depend on how different it is from the constellation of traits present within the existing plant community. Although a number of studies have found that soil properties change in response to the introduction of new traits and new functional groups (Aguiar and others 1996; Gill and Burke 1999), others have not found such effects. McCarron and Knapp (2001), for instance, found no difference in soil moisture between a C4 grass

Table 1. Plant Traits Thought to Affect Soil Nutrient Cycling Processes

Trait	Attribute	Mode of Action
Structure	Size	Relative size of exotics and natives; "size" can be height, biomass, or leaf area
	Canopy architecture	Shading, interception of precipitation and/or particulates
	Leaf area index	Ability to intercept light resources, assimilation rate; total amount of water transpired
Life history	Annual versus perennial	Presence of perennial tissues, allowing nutrient and C storage, retranslocation
	Phenology	Timing of growth and resource acquisition relative to timing of resource supply; timing of leaf fall and/or mortality; timing of canopy development relative to co-occurring species
Tissue type	Herbaceous versus woody	Presence of lignin-rich, high C:N woody material
Photosynthetic pathway	C3 versus C4 versus CAM	Phenology, response to drought and/or high light intensity
Physiology	Nutrient-use efficiency Transpiration rate Photosynthesis rate	Growth rate, resource use relative to availability
Symbionts	N fixation	Ability to acquire N beyond the soil source; additions of high N-containing litter to the soil; changes in soil chemistry resulting from high rates of nitrification
	Mycorrhizae	Presence/absence; type; effectiveness in resource capture
Vegetative spread	Presence/absence	Spatial extent of an "individual" re resource preemption; spatial extent of rhizosphere effects on soil microbial communities
	Clonal growth	Clonal subsidy of ramet growth; storage of photosynthate
Roots	Depth and architecture	Access to soil resources
	Rhizosphere biology	Effects on rhizosphere biota and physical conditions; amount and composition of exudate
Tissue chemistry	Concentrations of nutrients, lignin, polyphenols, and so on	Nutrient demand; effects on decomposition, nutrient and C mineralization rates
	Secondary plant substances	Allelopathic effects; effects on decomposition rate

C, carbon; N, nitrogen

and several species of C3 shrubs, but soil moisture differed beneath the various shrub species. This example shows that even though it is likely that exotic plant invasions will alter soil and ecosystem properties, it is not always the case, as was also shown in a recent group of papers on the topic (Ehrenfeld and Scott 2001).

In this paper, I review the evidence for changes in soil processes in response to plant invasions and evaluate possible generalities in the patterns of response. I consider the dynamics of C, N, and water from the perspective of the ecosystem as a system of pools linked by fluxes (Rodhe 1992). From this perspective, the size of a pool is determined by the balance of input and output rates; each of these fluxes in turn is set by one or more controlling biological, physical, and/or chemical factors; and the system of pools and fluxes describes both the cycling of the substance or element of interest within an ecosystem and also the net balance (loss, accretion, steady state) of the material with respect to an environment defined as external to the ecosystem of interest. To determine if and how the cycling of these substances is altered by the invasion, I have identified those pools and fluxes for the cycles of C, N, and water for which data were located on the effects of exotic plant invasions, in order to determine if and how the cycling of these substances is altered by the invasion.

DATA SOURCES

I have focused this review on soil-associated processes that are involved in the dynamics of C and nutrient elements, because they form a coherent, well-defined set of phenomena that are based on plant–microbial interactions and that can be related to the existing literature on plant–soil interactions. I have included changes in soil moisture because this property strongly affects the dynamics of C and nutrient elements, and the uptake and utilization of water by plants is linked to their use of C and nutrients. Changes in nutrient dynamics resulting from changes in disturbance have been excluded, in part because changes in disturbance regimes associated with exotic invasions have recently been reviewed (Mack and D'Antonio 1998; D'Antonio and others 1999) and because it is the disturbance event, rather than the interaction of the plant with the soil, that changes nutrient cycling.

I have examined the available literature in which an exotic species is directly compared with native species, either co-occurring species or those that the exotic is displacing. I searched for papers using combinations of the terms "exotic," "invasive," "invasion," "nonnative," and "plant" in the following electronic indexes: Web of Science, ingenta, Agricola, Biological and Agricultural Index, and JSTOR. However, many studies involving soils and nonnative species are not oriented toward the analysis of exotic plant invasions and thus are not identified by such searches. Additional searching was done using web-based compendia of literature for specific common or economically important exotic species available through exotic plant web sites and general plant web sites (such as http://plants.usda.gov) and their linking pages. Finally, literature was obtained through conventional searches of the bibliographies of papers and reports. Unfortunately, many studies of soil properties and processes in invaded areas lack any comparison with native species or communities; these studies cannot be used to determine whether soil properties have been altered by the invasion. Many other studies of exotic and co-occuring native species offer only qualitative or anecdotal comparisons. Finally, many studies assess the response of exotics to experimentally added nutrients but do not address the effects of the exotics on unamended soils.

Of the 79 papers identified by the review, 70% were based on observational studies of invaded and uninvaded areas or extant populations of invasive and native species. Information about the time since invasion, the causes of invasion, and plant densities was available in very few cases. Review papers, summarizing known information about particular species or biomes, comprised another 12%. The remaining 18% were primarily based on experimental approaches, most commonly pot or mesocosm studies in which the exotic(s) and native(s) were planted into a common soil in greenhouse or field containers; however, a few studies involved experimental removal or manipulations of the exotics. A substantial number of the studies were not designed to test exotic versus native effects, but the inclusion of an exotic among the species studied for other purposes allowed comparative data to be extracted.

Data were obtained for a total of 56 species. Two papers (Baruch and Goldstein 1999; Pattison and others 1999) described contrasts between native and exotic species in C acquisition and leaf nutrient content, but they reported statistical comparisons only for the two classes of species and not for the individual species comparisons; these studies are included in the tables, but the species are not listed separately.

The diversity of these approaches and the authors' reliance on observations of preexisting invasions may affect the reliability of the patterns described here. I have therefore identified the type of data available from each cited study by using the following codes in the References section: O—observational study in which soils under adjacent or nearby invaded and native species or communities are sampled; EM—experimental study in which the exotic is added, removed, or otherwise manipulated and the response of the soils measured, EP—experimental study in which the exotic and natives are grown in pots or mesocosms, R—review article summarizing the results of several other studies. Citations in Tables 2–5 are identified by number, also listed in the References section.

In addition to this heterogeneity in the methods of observation, there are many limitations to the data that are available. Studies that provide quantitative comparisons of pools and fluxes vary greatly in the analytic methods used, the units in which the results are reported, and the frequency and temporal and spatial scales of sampling, making quantitative comparisons among studies difficult. I have therefore reported only the direction of change: + indicates that the value under the exotic is greater than under the native(s), – indicates that the value under the exotic is less than under the native(s), = signifies that the value under the exotic is not significantly different from that under the native(s).

Moreover, each study reports data for only a small subset of the possible pools and fluxes in a particular element or material cycle; therefore, there are few studies for any particular pool or flux. The latter problem is apparent in the tables (Tables 2–5); the numbers of studies identified for each component under consideration ranged from five to

Table 2. Changes in Standing Crops of Biomass and Nutrients, Net Primary Productivity, and Litterfall Masses Associated with Exotic Species Invasions

Species	Plant Biomass	NPP	Litter Mass	Litter Chemistry	Root–Shoot	Growth Rate	Reference
Acacia ssp.			+				78
Acacia cyclops			+	p+			79
Acacia longifolia	+					+	61
Acacia saligna	+		+	N+			60, 78
Arundo donax	+	+					20
Berberis thunbergii	+		–				22, 36
Bromus diandrus	–				–	+	35
Bromus diandrus	+						29
Bromus madritensis		+					54
Bromis mollis	+						29
Bromus tectorum			–	N+	–		9
Bromus tectorum		X[a]					5
Bromus tectorum			+	C:N +; lignin:N+[b]			25
Eucalyptus grandis	+				–	+	51, 61
Gunnera tinctoria	+	+					34
Hakea ericea	+		=			+	60, 61
Hieracium pilosella				Phenolic C+; P+; Lignin:N–			54
Kochia scoparia							62
Lantana camara	–	=	–	Nutrient–			6
Lepidium latifolium			+	N+			7
Lythrum salicaria	–						23
Lythrum salicaria	+						26
Lythrum salicaria					+		47
Lythrum salicaria		+					72
Microstegium vimineum	–						22
Melinus minutiflora			N+				2
Myrica faya			Lignin, N+; Cellulose, P–				65
Phragmites australis	+	+					44, 74, 77
Pinus spp.	+				–		51, 61
Pinus contorta	+	+	–	Lignin, P, Mg, Mn+ +	–		1
Pinus patula	+		+				61
Pinus pinaster		+		N–		+	51, 61
Pinus radiata	+		=			+	27
Sapium sebiferum	+						31
Senecio madagascariensis						+	50
Sphaeropteris cooperi		P_{max}[c]+				+	21
Mixture[d]		=	–	Litter N–			42
30 species		P_{max}[c]+				+	4
5 species[e]		P_{max}[c]+			=	+	49

P, phosphorus; N, nitrogen; C, carbon; Mg, magnesium; Mn, manganese; NPP, net primary productivity; +, exotic higher than native(s); –, exotic lower than native(s); x^n, variable pattern as indicated in footnote; =, exotic not different from native.

No entry means no data available. "Growth rate" includes measurements of relative growth rate, assimilation rates, construction costs per leaf (+ = lower cost).

See References section for citation numbers and type of study.

[a] *Change in timing, continuity of cover*

[b] *Difference for Bromus versus Stipa but not versus Hilaria*

[c] *P_{max} = maximum photosynthetic rate*

[d] *Melinis minutiflora, Schizachyrium condensatum, small amounts of Andropogon virginicus*

[e] *Schinus terebinthifolius, Chitharexylum caudatum, Cestrum nocturnum, Psidium cattleiamum, Bidens pilosa*

21. In the few cases in which there were 15 or more observations for a given flux or pool, the null hypothesis that the frequencies of "exotic greater than native(s)," "exotic less than native(s)," and "no

Table 3. Changes in Soil Carbon Pools and Fluxes

Species	Soil Organic C	C Mineralization Rate	Decomposition Rate	Microbial Biomass C	Reference
Acacia cyclops	+				78
					56
Acacia saligna	+				56
Agropyron cristatum	–				15
Agropyron repens	–				71
Berberis thunbergii			++		22
Bromus japonicum	–				63
Bromus tectorum	+	+		+	9
Bromus tectorum				X[a]	5
Bromus tectorum		0			25
Hieracium pilosella	+				43
Hieracium pilosella		+		+	52
Hieracium pilosella	X[b]	+[c]		–[b]	54
Imperata cylindrica			+		33
Kochia scoparia		+		+	62
Lantana camara			+		6
Lythrum salicaria			leaf +; stem–		24
Lythrum salicaria			+		30
Myrica faya			+		65
Phragmites australis	0		leaf +; stem–		43, 73, 74
Pinus contorta	X[d]		–		1
Pinus patula	–	–			61
Pinus pinaster	–	–	–		78
Piper aduncum			+		33
Sapium sebiferum			+		13
Senecio jacobaea		0		X[e]	68
Taianiatherum caput-medusae	–			0	59
Mixture[f]			X[g]		42

Symbols and reference numbers as in Table 2.

C mineralization rate includes measurements of soil respiration.

[a] *Higher than under Stipa, lower than under Hilaria (the two co-occurring native species)*

[b] *Large difference on south-facing slope; small difference on north-facing slope*

[c] *Reduced in soil adjacent to exotic*

[d] *About equal in current (initial) stand; P. contorta larger at steady state in simulation study but not by a large amount*

[e] *Difference present at small spatial scales but not when averaged across different slope exposures and grazing regimes*

[f] *Melinis minutiflora, Schizachyrium condensatum, small amounts of Andropogon virginicus*

[g] *Decomposition rate on areal basis faster in mixed native–exotic community, lower in exotic-only community due to low litter amounts; litter decomposition rate per species is higher for exotics*

change under the exotic" were equal was tested using the log-likelihood ratio test (*G* test) (Sokal and Rohlf 1995). For the more common cases in which the expected frequency of each class was less than five (that is, less than 15 cases altogether), no statistical test was made and the observed frequencies of each class of response are merely noted in the text.

The comparisons include contrasts with both particular native species and whole communities. I have excluded studies of nutrient-related properties and processes of species in their native ranges (for example, *Melaleuca* in Australia or *Phragmites australis* in Europe) (Although *P. australis* is commonly considered a native species in North America, recent genetic evidence shows that most *Phragmites* stands in the United States are an exotic [European] genotype [Saltonstall 2002]). Few studies included information about plant traits that would permit associations to be deduced between the characteristics listed in Table 1 and observed changes in ecosystem processes. Most of the available research is restricted to abundant species that cause economic or apparent ecological harm; thus, there are multiple studies available for a very small number of species. If and how species that are not perceived as pests affect ecosystem processes is impossible to determine. Finally, this review is restricted to terrestrial and wetland habitats because the focus is on soil- or sediment-based changes; therefore, I have excluded aquatic plants whose effects on water column properties have been examined.

CARBON

Net primary production and the resulting standing crop biomass (Table 2) drive other ecosystem processes, particularly C dynamics (Table 3). In most cases, exotics cause increases in standing crop biomass (14 of 18 cases; $G = 20.48$, $P < 0.001$) and net primary productivity (10 of 12 cases). Many qualitative and anecdotal descriptions of invasive plants (not included in Table 2) also emphasize the larger size and/or spatial extent and/or growth rate of exotics compared with co-occurring native species; indeed, Darwin noted this contrast in describing the invasion of an exotic thistle in Argentina (as cited in Huston 1994). Large size (tall plants with large leaves) is one of the few physical traits that is correlated with invasion success in the British flora (Williamson and Fitter 1996). However, contrary cases are also recorded (four of 18 cases); for example, oak–pine forests in the Himalayas are replaced by invasions of a shrub, *Lantana camara* (Bhatt and others 1994).

Exotic plants most commonly affect net primary productivity (C acquisition) by differing from native species in overall size, morphology, phenology, or growth rate. The presence of storage organs (for example, thick rhizomes) either not present in any native species or substantially larger than those of native species can have a dramatic effect on C stocks, not only through their own biomass but also because they supply photosynthate for the growth of tall, thick stems. This phenomenon is well illustrated by *Arundo donax* (giant reed), in which the extensive system of large rhizomes fuels the growth of stems to nearly 10 m, almost an order of magnitude larger than native herbaceous plants. The large biomass of rhizomes as well as aboveground tissues results in much greater biomass than any native community containing a mixture of herbs and cottonwood trees (Dudley 2000). Similar combinations of differences in size and clonal spread account for the much higher standing crop biomass and net primary productivity of invasions of *Phragmites* into brackish and freshwater marshes (Meyerson and others 2000; Windham 2001) and *Gunnera tinctoria* invasions into meadows (Hickey and Osborne 1998). Invasions of trees into shrubland or grassland (Rutherford and others 1986) also clearly involve the replacement of small plants with large ones; differences in rooting biology and tissue types, and sometimes the substitution of perennials for annuals, also accompany these invasions. Frequently, a decrease in the root–shoot ratio (five of six cases) (Table 2) is associated with the change in the size of plants and their spatial extent.

Differences between invasives species and natives in C stocks may also result from physiological properties. Invaders had faster growth rates than native species in nine of nine studies of individual species. Baruch and Goldstein (1999) found that a sample of 30 invasive species had, as a group, higher specific leaf area, net carbon dioxide assimilation rate, foliar [N], and foliar [P] than a sample of 34 native species in Hawaii, as well as lower leaf construction costs (in units of glucose equivalents per unit mass and per unit area). Pattison and other (1999) similarly found that a group of five invasive species in Hawaiian rainforests had higher relative growth rates and maximum photosynthetic rates than a matched group of four native species in both sunlit and shaded conditions, although these species (again, as two groups) were not different in biomass allocation to shoots versus roots or in specific leaf area. In only four studies, however, were higher growth rates and higher standing crop biomasses both found, whereas in one study (Holmes and Rice 1996) higher growth rates in *Bromus diandrus* were associated with lower standing crop biomass than the native species. Thus, it is unclear whether higher per-plant growth rates always generate site-level differences in total standing crop and/or net primary production. Finally, in some cases (for example, invasions of *Bromus tectorum* in arid and semiarid grasslands of the southwestern United States) (Belnap and Phillips 2001), the total standing crop biomass or net production is not altered, but the spatial distribution of the exotic biomass (continuously distributed) is very different from that of the native flora ("islands" of plant growth separated by bare soil).

The presence of larger plants is not necessarily associated with a greater mass of litter on the soil surface. Litter mass was increased over the native amount in only half of the reported cases (six of 12 cases) (Table 2); it was decreased in five of 12 cases and remained unchanged in one study. Furthermore, reports of increased biomass are not necessarily associated with cases of increased litter mass. For example, forest floors in hardwood forest stands invaded by the shrub *Berberis thunbergii* have much thinner litter layers, despite input rates that are approximately similar to the native shrubs (Kourtev and others 1998; Ehrenfeld and others 2001). Similarly, exotic *Pinus contorta* forests have a lower litter mass than the native *P. sylvestris* stands (Agren and

Table 4. Soil Nitrogen Pools and Fluxes

Species	Soil TKN	Extr. N_{inorg}	Mineralization and Nitrification	N fixation	Biomass [N]	Other	Reference
Abrus precatorius				+			28
Acacia spp.	+			+	+		51, 61, 78
Acacia auriculiformis				+			28
Acacia cyclops	+	+	+		+		56
Acacia saligna	+	=	=		+		56
Agropyron cristatum	–	–					15
Agropyron repens		+	X^a				70, 71
Berberis thunbergii	=	+	+			Nred.+	22, 36, 37
Bromus japonicum			+				63
Bromus tectorum	+	+	X^b			Pot. Denit.–	8, 9
Bromus tectorum		=	–		–	= for C, cellulose, lignin	25
Bromus tectorum	=	=				Mineralizable N =	5
Carduus nutans				$-^c$			68
Casuarina glauca				+			28
Gunnera tinctoria	=		+	+	+		34
Hieracium pilosella		–					52
Hieracium pilosella	+						43
Hieracium pilosella	$+^d$	$-^e$	–		+		54
Kochia scoparia			+				62
Lantana camara	–				+		6
Lepidium latifolium	+	+					7
Lythrum salicaria	–		=		+	Pot. Denit. =, Micr. N =	48
Lythrum salicaria					5 spp. =, 1 spp. +		47
Melinus minutiflora	+	+	+		+		2
Melinus minutiflora				$-^f$		40	
Mesembryanthemum crystallinum		+					66
Microstegium vimineum	=		+		=	Nred. +	22, 37
Mimosa pingra				+			41
Myrica faya	+	+	+	+			64, 65

Table 4. (Continued)

Species	Soil TKN	Extr. N_{inorg}	Mineralization and Nitrification	N fixation	Biomass [N]	Other	Reference
Phragmites australis[g]	=	–Br, = Fw	+		+ or =	Br: Pot. Denit. +, Fw: Pot. Denit. = Biomass N/area +	14, 44, 48, 58, 73, 75
Pinus patula	=						61
Pinus pinaster	–						61
Pinus radiata	–					Leaching +, Total biomass N +	27
Poa pratensis			X[b]				69
Pueraria montana				+			28
Rhododendron ponticum		+					45
Sphaeropteris cooperi					+	NUE_{inst} +, NUE over lf lifetime =	21
T. caput-medusae	–		–				59
Tamarix spp.			X[h]				57
Mixture[i]			+			N in litter mass, N immob., total N uptake =	42
30 species, various					+	Leaf [P] +	4

TKN, total Kjeldahl nitrogen; Extr. N_{inorg}, sum of NH_4^+, NO_3^{N}, and NO_2^{N}; Nred., concentration of nitrate reductase enzyme in leaf tissues; Pot. Denit., potential denitrification as measured by the denitrification enzyme assay; NUE, nitrogen-use efficiency; Micr. N, microbial biomass N. Symbols and reference numbers as in Table 2.

[a] *% N nitrified, initial N mineralization rates intermediate relative to natives, but total annual net N mineralization higher than natives*

[b] *Total N mineralized in lab assay greater than natives; N mineralization potential lower than one native, higher than others*

[c] *Exotic reduces N fixation in adjacent Trifolium plants*

[d] *Different in north-facing and south-facing fields*

[e] *Larger difference on north-facing than south-facing slope*

[f] *Exotic reduces abundance of leaf litter of native tree, which supports nonsymbiotic N-fixers*

[g] *Br, comparison with brackish marsh plants; Fw, comparison with freshwater wetland plants*

[h] *Concentrations similar, but temporal patterns of availability different*

[i] *Melinis minutiflora, Schizachyrium condensatum, small amounts of Andropogon virginicus*

Table 5. Other Soil Properties and Fluxes

Species	Salinity	Water Flow Soil Moisture	pH	Soil C:N	Other	Reference
Acacia spp.		Higher ET, drier soils	−			61, 51
Acacia cyclops				−	P_{tot} +	56, 79
Acacia saligna				−		56
Agropyron cristata				=		15
Andropogon virginicus		Lower ET, higher water table				46
Arundo donax		Lower water table, higher ET				20
Berberis thunbergii			+			22, 36, 37, 38, 39
Bromus diandrus		Uses only shallow soil				35
Bromus diandrus		Less water use per plant and per unit of root length				29
Bromus mollis		Less water use per plant and per unit of root length				29
Bromus tectorum		Higher soil moisture				16
Bromus tectorum					Higher Fe, Mn, Cu; Ca lower versus *Stipa* but not versus *Hilaria*; Higher K, Mg	5
Carpobrotus edulis		Higher water use	+			18
Centaurea diffusa					Root exudate effect	12
Erodium botrys		Less water use per plant and per unit of root length				29
Gunnera tinctoria		Higher ET—drier soils	+			34
Halogeton glomeratus	+				Na_{exch} +	32
Hieracium pilosella			−	+	P_{tot}, exch =; Ca, Mg, K+	43, 52
Hieracium pilosella			−		Higher Al, P, cations	10
Hieracium pilosella			−		Lower base sat.	54
Hieracium pilosella					Higher exch. Ca, Mg	43
Lepidium latifolium	+					7
Leptospermum laevigatum		Higher water use				51
Lythrum salicaria					Lower porewater PO_4	58
Lythrum salicaria					Higher tissue [P], Equal st. crop P	23

Table 5. (Continued)

Species	Salinity	Water Flow Soil Moisture	pH	Soil C:N	Other	Reference
Mesembryanthemum crystallinum	+					66
Microstegium vimineum			+			22, 36, 37, 38, 39
Phragmites australis	–	Lower water table			Higher Eh	3, 76
Phragmites australis					Lower porewater S^{2-}	3
Phragmites australis					Lower leaf Pb, Zn	11, 76
Pinus contorta			–			1
Pinus patula					P, K, Ca, Mg_{exch}–	61
Pinus radiata			–		P_{tot}, K_{exch}, Ca_{exch} +; CEC, % base st.–; leaching loss K +; leaching loss Mg, Ca–	27
Pittosporum undulatum		Similar to natives				55
Prosopis glandulosa		Higher water use				51
Rhododendron ponticum					Higher Na than heath	45
T. caput-medusae			+			59
Tamarix spp.	+	Higher ET from higher leaf area index				19, 53
Ulex europaeus					P_{extr}, K, Na higher than heathland	45

Symbols and references as in Table 2

Knecht 2001). Since the mass of litter on the forest floor reflects the combination of several characteristics—allocation of biomass to leaves and annual stems or small twigs and the decomposition rate of this material—it is perhaps not surprising that both increases and decreases have been observed.

Differences in litterfall mass interact with differences in the litter decomposition rate to affect the net flux of C into the soil. Many exotic plants have more rapidly decomposing litter than the natives they replace (10 of 14 cases, considering decomposition rates of stems and leaves as separate cases) (Table 3). However, in addition to cases in which decomposition rates are slower than natives (for example, *P. contorta*) (Agren and Knecht 2001), there are important interactions among decomposition rates, litter mass, and plant morphology. Decomposition rates may vary with the plant tissue, so that differences in plant morphology ultimately control litter dynamics. For example, the leaves of both *Lythrum salicaria* and *Phragmites australis* decompose more rapidly than co-occuring native species, whereas the stems decompose more slowly (Emery and Perry 1996; Meyerson and others 2000; Windham 2001). In such cases, a high ratio of stem–leaf biomass ultimately will control the C fluxes associated with litter deposition. In other cases (for example, *Sapium sebiferum*), large quantities of rapidly decomposing litter deposition yield only small standing crops of litter (Cameron and Spencer 1989).

However, some invasive plants have notably slow rates of decomposition, possibly due to the presence of secondary plant substances in high concentrations. For example, the leaves of *Melaleuca* spp. contain essential oils (monoterpenes) that dramatically slow the decomposition rate to a mass loss of less than 10% during the first year of decomposition (Boon and Johnstone 1997). A number of common exotics are well known for their medicinal properties (often antimicrobial activity), but the decomposition rates of the tissues, particularly in comparison with native species within invaded communities, are unknown. The role played by the secondary plant compounds of exotics in mediating changes in litter dynamics is essentially completely unknown.

Soil C—the mass of organic C in the mineral soil, the mineralization rate of this C, and the amount of microbial biomass C—has received less attention than primary production or litter dynamics. Not surprisingly, both increases and decreases have been documented (six of 13 cases showing decreases and four of 13 showing increases) (Table 3). The few studies of microbial biomass C (six studies) (Table 3) and soil C mineralization rates (eight studies) do not clearly show patterns of increase or decrease under exotics. The mechanisms accounting for these differences have been variously identified as differences in size, degree, and mode of vegetative spread; tissue chemistry; and root distribution; a different set of interacting factors appears to be involved in each case. Notably, differences in litter mass or the litter decomposition rate are not always, or even often, accompanied by changes in soil organic C dynamics; for example, no differences in the soil organic matter content have been found in comparisons of *Phragmites*-invaded and uninvaded *Spartina patens* marshes (Windham 1999a), despite large differences in standing crop biomass and litter dynamics.

Soil C quantities and flux rates may also reflect changes in the mass and species composition of the soil biota, as suggested by several recent studies. Under recent *B. tectorum* invasions in desert grassland, the fungal and mesofaunal communities of soils have been shown to change in size and species composition, but the nature of the changes depends on the preexisting species of native grass. Furthermore, the altered communities resemble native communities in preferentially invaded sites (Belnap and Phillips 2001). Yeates and Williams (2001) also found differences in the species composition of the soil fauna (copepods, tardigrades, rotifers, nematodes, and enchytraeids) between adjacent areas of exotic and native plants in New Zealand, but the specific compositional changes for a given exotic species–native vegetation comparison varied among sites. Gremmen and others (1998) found that the invasion of *Agrostis stolonifera* onto a sub-Antarctic island was associated with few changes in the macroinvertebrate fauna, but there was an increase in the number of species of mites and in the densities of some of them. Although these changes in the soil biota are likely to be linked to changes in C dynamics, given the important role of the soil fauna in C and nutrient cycling (Coleman and Hendrix 2000), the issue of C dynamics was not explicitly addressed in any of these studies. In another study, changes in the composition of the soil microbiota were linked to alterations in both the metabolism of simple C compounds and the expression of enzymes involved in C mineralization (b-glucosidase, cellulase, phenol oxidase, and peroxidase) in the invasions of both a shrub (*Berberis thunbergii*) and a grass (*Microstegium vimineum*) into deciduous forest understories (Kourtev and others c 2002). Similar changes in microbial enzyme activities in the sediment have also been found at a site where *Phragmites australis* has replaced *Spartina alterniflora* in undisturbed brackish marshes (Ravit and others 2003). Although these cases are suggestive of a causative chain among plant invasions, the soil biota, and C dynamics, they clearly will need to be supplemented by studies of other invasive plant–soil systems before general patterns can be discerned.

NITROGEN

The differences in plant size, spatial distribution, and tissue chemistry that lead to changes in C cycling are also likely to cause changes in N cycling; these have been reported for a wide range of exotic plant invasions (Table 4). Invasions have been associated with increases (nine of 21 cases), decreases (six of 21 cases), and no change in total soil N (TKN) (also six of 21 cases) (*G* test not significant), suggesting that there is no discernible pattern in the response of TKN to exotic invasions. However, of the 10 studies that measured microbial biomass N, eight found increases in this pool, mostly (but not entirely) associated with increased TKN. The complex relationships between these two pools is reflected in these patterns of soil response to plant invasions.

Extractable inorganic N (NH_4^+ + NO_3^-) may increase (nine of 17 cases), decrease (four of 17 cases), or show no change (four of 17 cases) (*G* test not significant). However, N mineralization and nitrification rates more commonly increased in response to invasions (11 of 16 cases; $G = 8.751$, $P < 0.05$), which may in some cases explain the increases in extractable N that have been observed. Changes in mineralization and/or nitrification rates are not, however, necessarily associated with changes in total soil N or solution N concentrations. The observed changes have been attributed to differences in the amount and spatial distribution of biomass and fine roots and differences in the N concentration in litter. In addition, an increased demand for N, which is associated with a larger standing crop biomass, has also been implicated as a cause of changes in other components of the N cycle (for example, in *Phragmites* invasions into brackish marshes, where the greater demand for N in the large biomass was associated with decreased porewater pools of NH_4^+) (L. Windham and J.G. Ehrenfeld unpublished). In addition to differences in the magnitudes of pools and fluxes, there can be differences in the seasonal patterns of increasing and decreasing quantities, even though the concentrations or flux rates are not different. For example, such differences in seasonal patterns of extractable N were documented for riparian sites invaded by *Tamarix* spp. (Stromberg 1998). Notably, changes in TKN, extractable inorganic N, and measured N mineralization rates are often not well correlated (Witkowski 1991).

N fixation is most obviously altered by the invasion of symbiotic N = fixing species into ecosystems in which such species are uncommon or absent. This change has been particularly well documented for the extensive invasions of *Acacia* spp. into South African ecosystems (Versfeld and van Wilgren 1986; Stock and others 1995). Almost 10% of the invasive species listed for North America by the US Department of Agriculture are in the Fabaceae, suggesting that increased inputs of N from symbiotic fixation may not be uncommon. However, although the effects of invasions by thicket-forming or commonly occurring N-fixing plants are clear, the threshold density of plants at which site-level impacts occur is unknown. Moreover, non–N-fixing exotics can affect the rate of N fixation in co-occuring native symbiotic N-fixers. Invasives can affect the abundance and activity of nonsymbiotic N-fixing bacteria, as was demonstrated for the invasion of fire-promoting African grasses in Hawaii (Ley and D'Antonio 1998). These grasses eliminate the fire-sensitive native tree (*Metrosideros polymorpha*) on whose litter nonsymbiotic N-fixers are active; the invasion results in substantial decreases in N inputs through this route. Invasive species that do not themselves fix N may also indirectly affect the rate of fixation in co-occurring N-fixing species (Wardle and others 1994, 1995), possibly through an allelopathic mechanism.

Other components of the N cycle are less well studied. In particular, the relative denitrification rates of native and exotic invasives have seldom been compared although the frequency with which extractable NO_3, is increased suggests that denitrification may increase following many invasions. There are preliminary data to suggest that the denitrification rate was higher under *Phragmites* than the native *Spartina patens* in a brackish marsh (L. Windham and J.G. Ehrenfeld unpublished). In contrast, Otto and others (1999) detected no change in denitrification rates among *Phragmites*, *Lythrum*, and the native *Typha* in a freshwater marsh, and Bolton and others (1990) found a decrease in potential denitrification rates under *Bromus tectorum*. There have been no studies examining changes in the leaching losses of N (or other nutrients) and no whole-site N budgets, with the exception of an estimated budget for the *Phragmites*/*Spartina* system (L. Windham and J.G. Ehrenfeld unpublished).

OTHER SOIL POOLS AND FLUXES

One of the most widely studied effects of exotic plants on ecosystem processes is the modification of soil moisture and water flow (probably because of the large economic consequences of these changes). Equal numbers of increases and decreases in soil moisture and/or evapotranspiration rates were reported in the literature (Table 5). Higher evapotranspiration rates may occur as the result of larger plant size, greater leaf area on plants of equal stature, or differences in rooting depth (and consequently the volume of soil from which water is extracted). Conversely, lower evapotranspiration rates and/or lower water extraction from soil have been associated with shallower or smaller root systems. Plant morphology—the size, timing of growth, and spatial extent of the plant—appears to be more important than differences in physiological performance (for example, transpiration rates per unit of leaf area or water-use efficiency). For example, *Tamarix*, an exotic well known for its ability to alter whole-ecosystem water budgets, affects water dynamics by producing a much greater leaf area, rather than by having a higher transpiration rate or higher water use per unit of leaf area (Sala and others 1996).

Differences in water use between natives and exotics may be related to differences in salt uptake and changes in the salinity of surface soils (Table 5). Some exotics—for example, *Halogeton glomeratus*—may salinize the soil directly by absorbing salts and depositing them on the surface through the shedding of salt-laden leaf litter (Harper and others 1996); in such cases, physiological differences between natives and exotics drive the change in ecosystem properties. In other cases—for example, *Phragmites australis* invasions into brackish marshes—the decrease in salinity is due to differences in both physiology (the exotic does not translocate and excrete salts through the leaves, as does the native species) and in growth (the exotic shades the ground more effectively, thereby reducing evaporation).

Changes in soil pH have also been noted in a variety of invasions (Table 5). Again, both increases and decreases occurred in equal numbers in the studies reviewed here. Decreases in pH can be attributed to increased nitrification, high rates of uptake of NH_4^+, and/or changes in litter quality (that is, more acidic, base-poor litter tissues). Increases in pH may reflect the preferential uptake of nitrate as an N source or increased base cation concentrations in the litter. However, the mechanisms of pH change have not been clearly identified in any of the cases cited.

Exotic plant invasions have also been observed to affect the fluxes of a variety of other elements (Table 5), including P, cations, and metal pollutants. Decreases in soil-extractable pools may be associated with the high uptake of these elements, which is driven by a large biomass or high tissue nutrient concentrations. Physiological differences between natives and exotics may also be implicated. For example, salt glands on the leaves of *Spartina* spp. are associated with high flux rates of cations, including pollutant metals, from the roots to the shoots; because the glands are not present in the invasive *Phragmites* populations that supplant the *Spartinas*, metal cations remain associated with root tissues (Burke and others 2000; Windham and others 2001). However, in most cases, the mechanisms underlying the observed changes are unknown.

DISCUSSION

This survey clearly shows that exotic plant invasions can greatly alter ecosystem processes. However, the invasion may result in increases, decreases, or no difference between the exotic and the natives in any of the soil nutrient variables. Furthermore, the alteration of one process does not necessarily result in changes in related processes; that is, significant differences between exotics and natives for C cycling processes do not necessarily entail changes in N cycling, and vice versa. Similarly, differences in one component of a cycle do not necessarily imply differences in linked components of the same cycle. That said, however, a few general trends emerge from this survey. These patterns, and the ensuing presentation of less–well-documented trends, are offered heuristically as hypotheses to be tested in well-designed experimental studies, rather than as firm conclusions.

1. Invasive exotic species tend to have higher standing crop biomass, higher net primary production, and faster growth rates than the native species that they displace. Associated with the increased size and growth rate is an increase in the shoot–root ratio (that is, greater allocation of C to aboveground tissues).
2. Invasive exotic species tend to produce litter that decays more rapidly than that of the co-occurring native species.
3. More extractable inorganic N is found under invasive exotics than under native species.

4. Increased rates of N mineralization, and in particular nitrification, are associated with exotic invasive plants.
5. The invasion of plants that support symbiotic N-fixers has a large effect on N cycling.
6. Non–N-fixing exotic species can alter N fixation rates indirectly by affecting the activities of both symbiotic and nonsymbiotic N-fixing organisms associated with native species.
7. Exotics may cause changes in the timing of nutrient fluxes and the spatial distribution of soil pools even when there are no changes in the absolute quantities involved.
8. Soil pools of C, N, and water often respond to exotic invasions, but the direction of change cannot as yet be predicted because increases and decreases have been observed in roughly equal numbers.

These tentative patterns are based on a data set beset with limitations: few comparative studies of each pool and flux, the lack of comparative whole-system budgets, few experimental tests of the hypothesis of difference between exotic and native species and communities, variable methods and units of reporting, and little information about the history and extent of each invasion. These limitations underscore the need for well-designed experimental tests of the hypothesized patterns.

The occurrence of changes in both pool sizes and flux rates across the studies of 56 species reviewed here suggests that exotic species may enhance their invasiveness by altering nutrient availability in the invaded ecosystem. Recent research has suggested that invasions are promoted by increases in nutrient availability (usually accomplished by the addition of fertilizer) and by the presence of nutrient-rich sites within ecosystems (Huenneke and others 1990; Levine and D'Antonio 1999; Maron and Jefferies 1999; Stohlgren 1999). The possibility that exotic species can create their own nutrient-rich sites has been demonstrated experimentally for two exotic plants, *Berberis thunbergii* and *Microstegium vimineum* (Ehrenfeld and others 2001; Kourtev and others (a) 2002), but it has not been similarly tested for other invasives. In two separate experiments, Ehrenfeld and others (2001) and Kourtev and others (b) forthcoming observed increases in nitrification in controlled greenhouse experiments when these two species were grown in a common, previously uninvaded soil; this finding strongly suggests that plant species can directly alter microbial functions. The studies by Vitousek and others (1987) of *Myrica faya* similarly suggest that the exotic invasion creates conditions that promote its own growth. It seems likely, (but is as yet unproven) that exotic plants create positive feedback loops that enhance their invasiveness (Ehrenfeld and others 2001).

All of the changes noted here reflect one or more of the plant traits listed in Table 1. Perhaps the most important causative factor is a difference between the invading exotic and the native flora in the size and spatial extent of the invading species. Ecosystem properties change when an exotic is substantially bigger or smaller than native vegetation, sends roots into a larger or smaller soil volume than the natives, and/or uses clonal spread to fill space more effectively than natives. This pattern is in line with the finding of Williamson and Fitter (1996), who noted an association between large size and high leaf area and invasiveness in the British flora. Although these features are sufficient to cause ecosystem change, they may not be absolutely necessary, since ecosystem-level impacts of plant invasions are also observed at sites where there is no large change; examples include the invasion of *Kochia scoparia* grass into shortgrass praire (Vinton and Burke 1995) and the replacement of native shrubs by *Berberis thunbergii* (Ehrenfeld and others 2001). Differences in phenology can also cause ecosystem processes to change, as can marked differences in tissue chemistry, even where there are no differences in size. These are traits that vary continuously among species. Discrete, "qualitative" traits are much less likely to be factors that drive changes in soil nutrient dynamics. If quantitative, continuously varying traits are the most frequent drivers of changes in nutrient dynamics, then the most important questions are how much of a difference from native vegetation is required in a given trait to cause ecosystem-level changes in function and how abundant a species must be before it can change site-level properties.

The mechanisms by which plants can alter nutrient dynamics have rarely been examined within the context of exotic plant invasions; thus, their importance is unknown. One example is rhizosphere biology (Grayston and others 1996). The reports reviewed here of changes in the soil micro- and mesobiota following invasions suggest that such changes may be widespread and may alter nutrient dynamics. Further research is needed to determine whether plant-driven changes in the composition of the microbiota translates into ecosystem-level changes in C and nutrient dynamics.

The only discrete, qualitative characteristic that has been shown to reliably cause changes in ecosystem-level processes is N fixation. When an N-fixing species invades a community in which N-fixers are absent or rare, there are large, readilydocumented changes in many aspects of both C and N dynamics. Other qualitative traits are less clearly linked with ecosystem changes. For example, the substitution of grasses for woody plants (as in the Hawaiian invasions) does not necessarily result in measurable changes in all of the fluxes in the N cycle (Mack and others 2001).

Another qualitative change that may be important is the introduction of exotic species with novel compounds in their tissues. For example, *Melaleuca* spp. have large concentrations of essential oils (monoterpenes) in their leaves that comprise up to 7% of the dry mass, as well as large litterfall masses (Boon and Johnstone 1997); these compounds strongly inhibit the microbial colonization of leaf litter and are associated with very slow decomposition rates in its native habitat (Boon and Johnstone 1997). Some exotics are well known in the medical literature for their bioactive secondary compounds; these compounds may be novel substances when the plant producing them invades new ecosystems and consequently exert an affect on ecosystem processes. The importance of such compounds in plant invasions should also be a priority for future research.

The degree of change in quantitative characteristics necessary to precipitate ecosystem changes actually can involve two components. First, there is the perindividual degree of difference: relative amounts of aboveground and belowground biomass per plant, tissue concentrations of nutrients, lignin, polyphenols, and so on. A second question involves the relative and absolute abundance of individuals within a community. At the beginning of an invasion, when the exotic plant is still rare or only sparsely distributed throughout a community, it probably has little effect on stand-level functions even if its per-individual traits differ greatly from the natives. But at some unknown threshold of relative abundance, the difference in quantitative traits will start to affect stand-level processes. The threshold density of invasive plants necessary for such changes to take place is thus another important unknown factor that needs to be defined before the impact of exotic invasions on ecosystem function can be evaluated. Because most of the studies comparing invaded and uninvaded sites have specifically selected the invaded sites for their high dominance of exotic plants and supplied no information about the abundance or density of the exotic, there is currently little basis for determining how much change in continuously varying characteristics is needed to precipitate ecosystemwide changes. Defining this threshold should be a high priority for future research.

The data also suggest that the impact of an exotic plant invasion depends on the particular ecological context within which an invasion occurs, rather than reflecting a species-specific effect that can be expected for all invasions of that species. A number of studies have documented the variable effects of a given species in different environments. For example, *Bromus tectorum* increases the rates of N mineralization and nitrification in cool deserts (Bolton and others 1990) but decreases these rates in warm, arid grasslands (Evans and others 2001). *Phragmites australis* decreases extractable NH_4^+ concentrations in porewater in brackish marshes but not in freshwater marshes (Meyerson and others 2000; L. Windham and J.G. Ehrenfeld unpublished). The impact of *Hieraceium pilosella* invasions into degraded pasture in New Zealand depends on both the grazing intensity and the exposure of the site (Scott and others 2001). In South Africa, *Acacia* spp., which are N-fixing trees, alter available N in strandveld communities but not fynbos (Stock and others 1995). Changes in the abundance of many groups of soil fauna under several invasive species in New Zealand varies among sites, with patterns of response to the "site × plant species" interaction itself varying among taxa (Yeates and Williams 2001).

Given the frequency with which site-specific results have been reported, more research is needed to assess the generality of the observed impacts of a given species across a variety of environments. It is possible that the impacts of an invasive species depend on its characteristics relative to those of the system into which it enters, as well as the degree of difference in key traits between the exotic and the native species. Thus, a given invasive species might have a large impact on a community with native species that differ in key traits but little impact on another community whose native species have traits similar to the invasive one. Furthermore, the impact of an invasive species may depend on the specifies of the landscape setting, such as soil characteristics or moisture regime.

Finally, it should be noted that under some circumstances, the changes in ecosystem processes triggered by exotic plant invasions may be viewed as beneficial rather than adverse. Invasions of *Hieracium pilosella* in overgrazed pastures in New Zealand cause increases in soil organic matter, thus helping to improve productivity at these sites (Scott and others 2001). In Papua New Guinea, the exotic plant *Piper aduncum* increases nutrient stocks in the surface soil, and the high evapotranspiration rate of *Imperata cylindrica* causes sufficient drying of the soil to allow crop growth (Hartemink and O'Sullivan 2001).

In summary, this analysis shows that the impacts of exotic plant invasions on soil nutrient cycling is an important research priority, given that changes in nutrient dynamics after such invasions are widespread. A review of the pertinent literature has allowed some general patterns of ecosystem response to invasion to be identified, but these conclusions cannot be accepted as definitive without more extensive experimental testing. A number of critical aspects of ecosystem change remain unknown, including the sensitivity of many of the fluxes that make up nutrient cycles and the potential response of whole-site budgets. Feedback, both positive and negative, resulting from plant–soil interactions is often invoked to explain vegetation patterns (Bever and others 1997; van den Putten 1997; Berendse 1998; van Breeman 1998; Petraitis and Latham 1999; Ehrenfeld and others 2001). Soil-based feedback, acting either to accelerate the invasions or to stabilize them once they are under way, could make the restoration of native communities more difficult. The evidence summarized here suggests that such feedback systems are a prominent feature of exotic invasions, but their presence requires verification by experimental studies. A full investigation into the impact of exotic invasions on soil process and plant–soil feedbacks should be undertaken as part of any assessment of particular species before expensive, resource-demanding control programs are undertaken (Anderson 1995; Hager and McCoy 1998; Zavaleta and others 2001). The evidence presented here that invasions of exotic plants can extensively affect the storage and release of C, N, and other substances indicates that the impacts of exotics on soil nutrient dynamics could be as important, or more important, than some of the more frequently monitored effects, such as plant diversity and animal abundance. This review should help to stimulate the research needed to explore and substantiate this possibility.

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Note: numbers refer to citations in Tables 2–5; letters denote the type of study (O = observational, EM = experimental manipulation of exotic populations, EP = experimental growth of plants in pots or mesocosms, R = review or literature-based study).

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