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Quantifying Ecosystem Controls and Their Contextual Interactions on Nutrient Export from Developing Forest Mesocosms

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Abstract

The complexity of natural ecosystems makes it difficult to compare the relative importance of abiotic and biotic factors and to assess the effects of their interactions on ecosystem development. To improve our understanding of ecosystem complexity, we initiated an experiment designed to quantify the main effects and interactions of several factors that are thought to affect nutrient export from developing forest ecosystems. Using a replicated $2 \times 2 \times 4$ factorial experiment, we quantified the main effects of these factors and the factor interactions on annual calcium, magnesium, and potassium export from field mesocosms over 4 years for two Vermont locations, two soils, and four different tree seedling communities. We found that the main effects explained 56%–97% of total variation in nutrient export. Abiotic factors (location and soil) accounted for a greater percentage of the total variation in nutrient export (47%–94%) than the biotic factor (plant community) (2%–15%). However, biotic control over nutrient export was significant, even when biomass was minimal. Factor interactions were often significant, but they explained less of the variation in nutrient export (1%–33%) than the main effects. Year-to-year fluctuations influenced the relative importance of the main effects in determining nutrient export and created factor interactions between most of the explanatory variables. Our study suggests that when research is focused on typically used main effects, such as location and soil, and interactions are aggregated into overall error terms, important information about the factors controlling ecosystem processes can be lost.

Key words: nutrient export; contextual interactions; leachate; calcium; magnesium; potassium; soil; location; climate; plant community; ecosystem development.

Introduction

Quantification of the relative importance of abiotic and biotic controls on ecosystem processes during development is fundamental to our understanding of forest ecosystems. It has generally been accepted that abiotic factors, such as initial source pools and

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climate, control nutrient export, especially during the initial stages of development (Odum 1963). However, persistent questions remain regarding the emergence and extent of biotic control of nutrient export during this time (Bormann and Likens 1979; Gorham and others 1979; Bormann and others 1998; Chadwick and others 1999). Although numerous studies have been conducted on this subject, because of the complexity and size of natural forest ecosystems researchers have found it difficult to use field and experimental research to quantify the relative importance of different abiotic and biotic controls on nutrient export during ecosystem development.

Theoretical research on the controls of nutrient export during forest ecosystem development began over three decades ago, when Odum (1969) suggested that the primary role of the biota in limiting nutrient losses during development was to impose a functional ''strategy'' that resulted in tighter nutrient cycles, thus conserving these important resources. Alternatively, Vitousek and Reiners (1975) took a ''mass balance'' approach. According to this view, biomass accumulation initially contributes to increased storage in the ecosystem, but as the ecosystem matures and net ecosystem production declines, the biota contributes less to storage and consequently increases nutrient losses. Few recent theoretical studies have been conducted on the factors controlling forest nutrient export (for example, Finn 1982), while comparative experimental approaches at several sites have suggested that multiple factors (for example, soil nutrient availability, tree density) are important (for example, Chapman and others 1949; Zirlewagen and von Wilpert 2001).

It is difficulty to identify which combination of factors drives nutrient export because published empirical results often contradict one another. For example, some studies suggest an increase in nutrient losses along successional gradients (Vitousek 1977) but a decline in nutrient availability with age (Bormann and Sidle 1990; Brais and others 1995), whereas others do not demonstrate these monotonic patterns (for example, Allen and others 1997). Another potential complication in the interpretation of these results is nonadditive factor interactions.

Few studies on forest ecosystems have explicitly tested for the role of interactions between factors. Because ecologists use the term ''interaction'' in many different contexts, we need to clarify our use of the term. Our use is statistical: Different combinations of treatment variables influence the outcome of the response variable in a nonadditive manner. In our study, this translates to the following hypothesis: Different combinations of climate, soil, and plant community influence nutrient export from forest ecosystems in a nonadditive manner. We refer to this relationship, measured as statistical interaction, as ''contextual'' interaction to differentiate it from other ecological interactions (for example, competitive interactions between two species or the additive responses of an organism to individual environmental factors) and because it arises out of the context in which a process takes place. Contextual interactions between frequently investigated factors may explain a substantial and significant component of ecological responses at the ecosystem level and may be critical during ecosystem development. However, only by addressing contextual interactions explicitly, using a carefully designed experiment, can their statistical and ecological importance be evaluated quantitatively.

Because a true factor analysis cannot be done using field studies, empirical interpretation of field studies can be misleading (Wootton 1994). Researchers have approached this issue by studying chronosequences or different-aged stands (that is, space-for-time substitutions) (Van Cleve and Viereck 1981; Van Cleve and others 1983; Brais and others 1995); however, these approaches cannot completely control for site- and time-related differences. In this paper, we present an approach that deals with nonadditive factor interactions and uses an experimental design based on mesocosms to provide additional insight into patterns of nutrient dynamics during ecosystem development (Beyers and Odum 1993; Bormann and others 1993; Heltai and others 1995). Although the necessary tradeoff between ''control'' and field relevance over longer periods of time limits the strength of any conclusions involving long-term dynamics, our design can be used to address specific questions regarding the critical stage of stand establishment and fundamental relationships among factors controlling nutrient export.

The goal of this research was to identify, quantify, and interpret variation in total annual nutrient export from forest mesocosms with different abiotic (climate and soil) and biotic (plant community) treatments during early stages of ecosystem development. More specifically, we sought to quantify (a) the magnitude of location, soil, and plant community control of nutrient export during 4-years of primary succession; and (b) the importance of interactions between and among location, soil, and plant community factors in controlling nutrient export during this 4-year period. We chose

sites within a small geographic region that accentuated climatic differences among the experimental units, but we recognize that site differences include more factors than climate. Thus, we hereafter refer to ''location,'' as opposed to climate, as a factor. We focused on calcium (Ca), magnesium (Mg), and potassium (K), so we could observe the response of several plant nutrients to a variety of factors. Using our experiment's ability to quantify sources of variation, we tested three specific predictions: (a) Location and soil factors initially control patterns in nutrient export, (b) plant communities play an increasingly important and strategic role in nutrient export as the ecosystem develops, and (c) interactions among location, soil, and plant community emerge as an important determinant of nutrient export over time. This research is part of a longer-term study of ecosystem development using the same experimental mesocosms.

Methods

Experimental Mesocosms

Mesocosms were constructed in spring and early summer of 1995 from 3,600-L commercially manufactured tanks of linear polyethylene (Polytank, Litchfield, MN, USA). Each tank was 2.4 m in diameter and 1 m deep to the bottom of the soil fill. Each tank held 4.7 m^3 of soil. A conical section at the bottom of each tank, below the soil fill, was filled with 0.7 m^3 of nutrient-poor coarse granite to allow drainage and leachate collection. A fine geotextile cloth was used to keep soil from infiltrating the granite layer. A 15.2-cm–diameter polyvinylchloride (PVC) pipe was placed upright in the center of the tanks and extended to the tank bottom. In addition to providing storage for drainage water, the pipes were outfitted with a vacuum extraction system to enable it water removal from the bottom of the tank.

Experimental Design

The mesocosm experiment was a $2 \times 2 \times 4$ factorial in a split-plot design with location, soil, and plant community treated as factors. There were 40 mesocosms in the design—three replicates (or blocks), each containing eight mesocosms, at the USDA Forest Service Research Laboratory in South Burlington, VT (hereafter referred to as ''SB''), and two replicates, each containing eight mesocosms, at the University of Vermont Wolcott Research Forest in Wolcott, VT (hereafter referred to as ''Wolcott''). Two vegetation-free mesocosms per soil type were included as controls at each location (four mesocosms total), yielding a total of 48 mesocosms in the experiment. Mesocosm-sized plots, not included in the experiments, were planted at each end of mesocosm rows to reduce ''edge effects'' (border plots).

Although the two locations are only about 100 km apart, they are climatically different. The SB site (44°27′ N; 73°12′ W; 60 m elevation), located near Lake Champlain, is more southerly and temperate. Mean annual temperatures for SB in water years 1997–98, 1998–99, 1999–2000, and 2000–01 were 8.41, 8.98, 7.74, and 7.50°C, respectively, and annual precipitation was 1,363, 768, 947, and 679 L m^{-2}, respectively (all climatic data are from NCDC 2002). However, in 1998–99 and 2000–01, 443 L m^{-2} and 104 L m^{-2} of irrigation water was added during a few drought periods. Water years at both locations were estimated from October 1 to September 30 (US Geological Survey Vermont). The Wolcott site (44°36′ N; 72°26′ W; 385 m elevation) is more northerly and colder than the SB site. In nearby Morrisville, VT, the mean annual temperatures for the same 4 water years were 5.71, 6.19, 5.23, and 4.54°C, respectively. Annual precipitation was 1,261, 924, 1,060, and 832 L m^{-2}, respectively. In 1998–99, 73 L m^{-2} of irrigation water was added. Precipitation chemistry data from Underhill, VT (44°31′ N; 72°52′ W; 399 m), near SB, a National Atmospheric Deposition Program (NADP) monitoring site, indicate that Ca, Mg, and K inputs were less than 2% of outputs at both locations during this study (NADP/NTN 2002).

One of two unweathered glacial lake deposit substrates that differed in physical and chemical properties was placed in each mesocosm (Table 1). Soils were selected to provide a contrasting environment for plant growth that would enable us to measure nitrogen (N) accumulation and possible rapid mineral weathering rates. The initial low-N condition gave us a reasonable chance to measure statistically significant changes (and therefore possible interactions) across experimental units. The difference in availability (on exchange sites) of a single element (Ca) between the soils was much greater than the difference of the other major nutrients (including Mg and K), which gave us the opportunity to investigate how this condition might influence the results. We selected soils with low CEC to limit the capacity for abiotic retention of nutrients from this ecosystem and to enable the ecosystem to express its biotic capacity. Although these mined, glacial sands began soil development at the start of this experiment, they are hereafter referred to as ''soils.'' One soil was named after the company that mined the material, Kullman, in

Table 1. Initial Chemical and Physical Properties of the Two Soils

Soil	Bulk Density (g cm^{-3})	CEC (meq 100 g^{-1})	Clay (%)	Silt (%)	Sand (%)	Fine Gravel >2 mm (%)	pH	Ca (mg kg^{-1})[a]	Mg (mg kg^{-1})[a]	K (mg kg^{-1})[a]
Kullman	1.58	18.2	1.15	0.56	63.92	34.26	8.0	3,540	56	5
Milton	1.46	0.9	0.95	0.66	81.17	17.30	7.5	108	43	6

CEC, cation exchange capacity; Ca, calcium; Mg, magnesium; K, potassium
[a]*Ca, Mg, and K values are from ammonium acetate extractions.*

Johnson, VT: the other soil, Milton, was mined in Milton, VT. Ammonium-extractable nutrients were determined in the soils prior to the experiment using methods adapted from McIntosh (1969). Using soil bulk density, concentrations of available nutrients in soil, and the amount of soil in the mesocosms, we determined the percent of initially available nutrients exported from the mesocosms over the course of the experiment.

In spring 1996, a two-species tree ''community'' was planted in each noncontrol mesocosm. The term ''community'' is a convenience, given that two tree species cannot be considered to emulate a natural community and its complex interactions. Species combinations were selected based on our belief that they would survive the initial nutrient conditions of the sands and provide some inherent diversity in response. Planted tree communities were either red pine (*Pinus resinosa* Ait., hereafter referred to as ''RP'') and gray birch (*Betula populifolia* Marsh., hereafter referred to as ''GB''), RP and red maple (*Acer rubrum* L., hereafter referred to as ''RM''), eastern white pine (*P. strobes* L., hereafter referred to as ''WP'') and GB, or WP and RM. Seedlings from each of the two species were planted at random in 18 of 36 planting locations per mesocosm. Two seedlings were planted per planting location, for a total of 72 seedlings per vegetated mesocosm. Reserve plants for replacements and for extra research material were grown in both soils at both locations. Over the course of the experiment, GB, RM, RP, and WP seedlings had the following survivorship: 91%, 93%, 88%, and 94%, respectively. After the spring of 1997, plants were not replaced after their death.

The seedlings of each species derive from two populations. The GB and WP seeds were collected from two populations in Vermont. One population was from Chittenden County, VT (less than 8 km from SB), the other population was from Lamoille County, VT (less than 32 km from Wolcott). The Petawawa Forest Experiment Station in Canada provided RM seeds from two populations in the experimental forest. The RP seedlings were obtained from a Michigan commercial nursery in spring 1996 and included seed sources from two Michigan populations. Both populations of seedlings were represented in each mesocosm. The GB, RM, and WP seedlings were started from seed in January 1995 and grown in a greenhouse. In June 1995, they were moved outside. In November, these seedlings were moved into a large cooler (2°C), with lighting approximating normal day length, to overwinter until spring 1996, when all seedlings were planted into the mesocosms.

Data Collection

Throughout the 1997–2001 water years, the mesocosms were pumped each time 120–375 L of drainage water (leachate) had accumulated in the mesocosm tanks. The total volume of leachate removed from each mesocosm on each pumping date was recorded, and the collected samples were stored at 2°C. Samples were analyzed for Ca, Mg, and K concentrations using an ICP/AES (Leeman Labs PlasmaSpec 2.5). Flux was determined by multiplying the concentrations of the nutrients in the leachate by the volume of water leached (field measurements). Measurements were then summed over each water year to determine the annual flux of each nutrient. Output is expressed as total grams of cation leached per square meter for each year.

In April 1999, 64 seedlings (eight per soil-species combination) were harvested from reserve plants at SB. Plant heights and total oven-dried weights were measured, and relationships were derived between height and total biomass for each species. The relationship between height and total biomass was significant in all cases ($df = 15$, $P \leq 0.001$ for all species; GB: $R^2 = 0.85$, RM: $R^2 = 0.76$, RP: $R^2 = 0.59$, and WP: $R^2 = 0.84$). The maximum height values (in cm) used in the regressions (GB: 67.8, RM: 34.5, RP: 29.6, and WP: 28.0) were similar to the average height values of the plants in 2001 (GB: 60.1, RM: 18.9, RP: 39.4, and WP: 24.6); therefore, estimates of biomass from these regressions were deemed appropriate throughout the experiment. These relationships were used to estimate the total biomass from height measurements taken each year on each seedling.

Above- and belowground biomass of 16 of the harvested seedlings (two seedlings representing each soil–species combination) was analyzed for Ca, Mg, and K concentrations using an ICP/AES. Sample plant leaves and stems were 0.6% Ca, 0.1% Mg, and 0.4% K, and plant roots were 0.7% Ca, 0.2% Mg, and 0.4% K, respectively, which are in the range of expected values (Likens and Bormann 1970; Arthur and others 2001). These percentages were used to estimate annual cation accumulation in plant biomass. In June 2001, two soil cores were taken from the upper 5 cm of each mesocosm. Soil pH was measured in a 2:1 slurry of deionized water and 15.0 g of soil.

Data Analysis

Statistical tests were conducted using SAS v. 8. 1 for Unix (SAS Institute, Cary, NC, USA). Analyses of variance (ANOVA) were performed for each variable (Ca, Mg, K, and volume of leachate) in each of the 4 years using a factorial ($2 \times 2 \times 4$) in a split-plot design. Block was the whole-splot unit; location was the whole-plot factor; mesocosms nested within blocks were the subplot units; and soil and plant community were the subplot factors. A similar analysis was conducted on soil pH. To assess potential interactions between year and the experimental factors, data for all years combined were analyzed using a repeated-measures design (that is, a split-plot in time). Transformations were not deemed necessary to meet model assumptions of normality and homogeneity of variances. A Student-Newman-Keuls (SNK) test was used to determine differences among community types, including the vegetation-free (''bare'') mesocosms. In all cases, significant differences were accepted at $P \leq 0.05$.

We were interested in nonadditive interactions between and among factors or contextual interactions. Therefore, we specifically investigated interactions, such as whether soil substrates or the four plant communities influenced nutrient export differently in the two locations (for example, location × soil, location × community). In the models that included year, we investigated how year influenced the factors (for example, year × location) and the interactions (for example, year × location × community). Expected mean squares were calculated to determine appropriate error terms for specific factors and interactions. Because we were interested in the relative contribution of each source of variation in determining nutrient export from each mesocosm, we used variance components to estimate the percent variation attributable to main effects and interactions (Steel and others 1997).

Results

Control of Hydrologic Export

Leachate output in the 1st year was not strongly influence by any factor, with 87% of the variance attributable to random factors (Table 2). In the following 3 years, location differences in output emerged, and then declined in importance (Table 2). Soil became increasingly important, rising to explain 33% of the total variance by year 4. In all years, mesocosms containing the Milton soil leached 20–50 L m^{-2} y^{-1} or about 5% more water than the Kullman soil (Table 3). The bare mesocosms typically exported more water than the plant communities (Table 4). Plant communities with

Table 2. Percent Variance in Total Annual Export of Nutrients (g m^{-2}) and Volume Output (L m^{-2})

	Calcium				Magnesium				Potassium				Water			
Source	97–98	98–99	99–00	00–01	97–98	98–99	99–00	00–01	97–98	98–99	99–00	00–01	97–98	98–99	99–00	00–01
Location	0.0	20.9[b]	3.2[a]	11.3[c]	11.7[a]	73.0[b]	3.1	57.8[c]	36.1[a]	0.0	35.2[a]	4.8	7.0	76.5[a]	67.5[b]	37.3[a]
Soil	94.0[c]	63.4[c]	88.6[c]	78.5[c]	35.6[b]	0.2	49.3[a]	3.4[a]	39.6[b]	49.8[c]	37.3[c]	59.4[b]	5.9	7.7[b]	9.6[b]	33.5[b]
Summed Abiotic Factors	94	84.3	91.8	89.8	47.3	73.2	52.4	61.2	75.7	49.8	72.5	64.2	12.9	84.2	77.1	70.8
Community	2.4[c]	3.3[b]	5.1[c]	5.9[c]	8.9[b]	3.3[c]	15.2[b]	2.9[c]	1.9	7.9[a]	3.6[a]	5.7[a]	0.0	0.5	0.0	4.3
Location × soil	0.8	7.8[a]	0.3	1.4	26.4[a]	16.0[b]	13.3[a]	32.6[b]	0.0	5.8[a]	0.0	0.0	0.0	0.0	5.6[a]	0.0
Location × community	0.0	0.2	0.8[a]	0.0	0.0	0.2[a]	5.0[a]	0.0	0.0	1.8	2.6	0.0	0.0	0.3	7.7[b]	3.9
Soil × community	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.4[a]	5.4	2.2	6.2[a]	0.0	0.3	1.8	3.4
Location × soil × community	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	1.2	3.2	0.0	0.7	0.0	0.9
Summed Interactions	1.1	8	1.1	1.4	26.4	16.2	18.3	32.6	8.1	13	6	9.4	0	1.3	15.1	8.2
Blk + error	2.8	4.4	1.9	2.8	17.3	7.3	14.1	3.4	16.4	29.3	19	23.9	87.0	14.7	7.5	16.5

[a] *Factor significant at* $P \leq 0.05$.
[b] *Factor significant at* $P \leq 0.01$.
[c] *Factor significant at* $P < 0.001$.

greater biomass did not reduce leachate volume until the final year of the study (Table 4), although this effect did begin at a plant-to-soil mass ratio of only 1:4,000. Hydrologic input varied between locations and among years and likely contributed to the significant differences in leachate output among years (Table 5).

Abiotic Control of Nutrient Export

Abiotic factors (location and soil) accounted for a large percentage (47%–94%) of the total variation in nutrient export (summing the main effects, location and soil). The range in values represents the range in variation attributed to factors across years (Table 2). The effects of location on the amount of nutrients leached were difficult to generalize because the patterns were not consistent over time (as shown for Ca in Figure 1A). Soil effects were easier to generalize. Mesocosms containing the Kullman soil consistently leached more nutrients than those containing the Milton soil (Figure 1B), with the exception of Mg at SB (Table 3).

The year × location interaction clearly shows the significant temporal inconsistencies in nutrient export patterns between the two locations (Table 5). The amount of nutrients exported from SB declined monotonically over the 4 years whereas the amount exported from Wolcott did not (Figure 1A and Table 3); this pattern follows the pattern of precipitation in the two locations. The year × soil interaction significantly influenced nutrient export for all three cations (Table 5). When averaged across both locations, the amount of cations leached from the Milton soil generally declined monotonically over the 4 years, but the amount leached from the Kullman soil varied (as shown for Ca in Figure 1B).

Biotic Control of Nutrient Export

Plant community accounted for a much smaller percentage of the total variation in nutrients exported than either location or soil; it was responsible for 2%–6%, 3%–15%, and 2%–8% of the variation in Ca, Mg, and K exported, respectively (Table 2). Again, the range in values represents the range in variation attributable across years. Each plant community exported a distinct amount of Ca and Mg every year (Table 4). Generally, mesocosms containing no vegetation and the community type with the least amount of biomass (WP & RM) exported less Ca and Mg than the other community types (Figure 2). The amount of K leached from the four communities differed in the

Table 3. Mean Annual Loss of Nutrients and Leachate Volume (±SE) by Location and Soil Type

Element	Site	Soil	Water Year 97–98	98–99	99–00	00–01	Total Exported	% Exported[a]
Ca (g m^{-2})	SB	Kullman	28.6 (0.6) a, A[b,c]	24.5 (0.6) b, A	22.3 (0.6) c, B	17.9 (0.5) d, A	93.3 (1.9)	2.1
		Milton	1.34 (0.7) a, B	12.7 (0.6) a, C	9.8 (0.5) b, C	9.7 (2.5) b, C	45.5 (2.1)	36.6
	WC	Kullman	29.4 (0.8) a, A	16.5 (0.7) c, B	25.4 (1.2) b, A	14.3 (0.6) c, B	85.7 (3.1)	2.0
		Milton	11.8 (0.9) a, B	9.4 (0.6)a b, D	11.9 (0.9) a, C	7.4 (0.4) b, D	40.5 (2.5)	32.6
Mg (g m^{-2})	SB	Kullman	4.18 (0.1) a, A	3.54 (0.1) b, B	3.03 (0.00) c, B	2.39 (0.04) d, B	13.2 (0.2)	19.0
		Milton	3.72 (0.2) a, A	4.07(0.1) a, A	2.53 (0.01) b, C	2.62 (0.06) b, A	13.0 (0.5)	26.3
	WC	Kullman	4.19 (0.1) a, A	2.42 (0.1) b, C	3.58 (0.02) c, A	1.98 (0.06) d, C	12.2 (0.4)	17.6
		Milton	2.40 (0.2) a, B	1.87 (0.1) b, D	2.51 (0.22) a, C	1.27 (0.06) c, D	8.06 (0.6)	16.3
K (g m^{-2})	SB	Kullman	1.59 (0.04) a, B	0.84 (0.02) b, A	0.72 (0.02) c, B	0.48 (0.01) d, A	3.63 (0.1)	58.5
		Milton	1.00 (0.02) a, C	0.56 (0.02) b, B	0.42 (0.02) c, C	0.31 (0.01) d, C	2.39 (0.1)	34.6
	WC	Kullman	2.17 (0.15) a, A	0.74 (0.04) bc, A	1.00 (0.01) b, A	0.53 (0.04) c, A	4.44 (0.4)	71.6
		Milton	1.58 (0.11) a, B	0.60 (0.04) b, B	0.72 (0.01) b, B	0.38 (0.03) c, B	3.38 (0.2)	49.0
Water (L × 10^3 m^{-2})	SB	Kullman	0.96 (0.01) a, B	0.68 (0.01) c, B	0.72 (0.01) b, C	0.46 (0.00) d, B	2.82 (0.02)	NA
		Milton	0.98 (0.02) a, AB	0.73 (0.02) b, A	0.74 (0.01) b, C	0.50 (0.01) c, A	3.06 (0.05)	NA
	WC	Kullman	1.01 (0.02) a, AB	0.52 (0.01) c, D	0.82 (0.02) b, B	0.42 (0.01) d, C	2.88 (0.05)	NA
		Milton	1.03 (0.01) a, A	0.57 (0.01) c, C	0.90 (0.01) b, A	0.46 (0.01) d, B	3.06 (0.03)	NA

Ca, calcium; Mg, magnesium; K, potassium; SB, South Burlington; WC, Wolcott.
Significant differences calculated by the Student-Newman-Keuls test at: $P < 0.05$.
[a]*Percent of initially available nutrients exported.*
[b]*Within each element, mean values followed by the same lower-case letters are not significantly different from one another when comparing within a particular location–soil combination across water years.*
[c]*Within each element, mean values followed by the same upper-case letters are not significantly different from one another when comparing within a water year across a location–soil combination.*

Table 4. Mean Annual Loss of Nutrients and Leachate Volume (±SE) by Plant Community

Community	Calcium Leached ($g\ m^{-2}$) 97–98[a,b]	98–99	99–00	00–01	Magnesium Leached ($g\ m^{-2}$) 97–98	98–99	99–00	00–01
RP & GB	22.5(2.9) a, A	17.4(1.9) ab, A	18.8(2.4) ab, A	13.7(1.4) b, A	4.1(0.3) a,A	3.3(0.3) b, A	3.1(0.2) b, A	2.2(0.2) c, A
RP & RM	21.3(2.9) a, A	16.9(2.3) a, A	18.2(2.3) a, A	13.4(1.4) a, A	3.9(0.3) a, A	3.3(0.4) a, A	3.1(0.1) a, AB	2.3(0.2) b, A
WP & GB	21.3(2.4) a, A	17.0(1.7) ab, A	17.3(2.2) ab, A	13.0(1.4) b, A	3.7(0.2) a, A	3.1(0.3) ab, A	2.8(0.2) b, B	2.1(0.2) c, A
WP & RM	18.3(2.8) a, B	14.1(2.0) a, B	14.0(2.1) a, B	10.4(1.3) a, B	3.2(0.3) a, B	2.8(0.3) a, B	2.5(0.2) ab, C	1.9(0.2) b, B
Bare	18.7(3.5) a, B	14.0(2.1) a, B	14.4(2.7) a, B	10.2(1.5) a, B	3.0(0.4) a, B	2.6(0.3) ab, C	2.4(0.2) ab, C	1.8(0.2) b, B
	Potassium Leached ($g\ m^{-2}$)				Water Leached ($L \times 10^3\ m^{-2}$)			
	97–98	98–99	99–00	00–01	97–98	98–99	99–00	00–01
RP & GB	1.55(0.18) a, A	0.69(0.07) b, A	0.71(0.11) b, A	0.42(0.04) b, A	1.00(0.02) a, AB	0.62(0.02) c, A	0.77(0.02) b, A	0.46(0.01) d, A
RP & RM	1.61(0.18) a, A	0.71(0.07) b, A	0.71(0.09) b, A	0.44(0.04) b,A	1.02(0.02) a, AB	0.64(0.02) c, A	0.77(0.02) b, A	0.46(0.01) d, A
WP & GB	1.60(0.15) a, A	0.75(0.04) b, A	0.71(0.07) b, A	0.44(0.02) b, A	0.97(0.02) a, A	0.64(0.04) d, A	0.80(0.02) b, A	0.49(0.02) d, B
WP & RM	1.36(0.11) a, A	0.62(0.02) b, A	0.60(0.04) b, A	0.38(0.02) c, A	1.00(0.02) a, AB	0.64(0.04) c, A	0.80(0.02) b, A	0.46(0.02) d, AB
Bare	1.71(0.33) a, A	0.75(0.09) b, A	0.75(0.11) b, A	0.46(0.07) b, A	1.02(0.01) a, B	0.66(0.04) c, A	0.84(0.01) b, B	0.49(0.02) d, B

GB, gray birch; RM, red maple; RP, red pine; WP, white pine.
Significant differences are SNK test: $P < 0.05$.
[a]*Within each element, values followed by the same lower-case letters are not significantly different from one another when comparing within a particular plant community across water years.*
[b]*Within each element, values followed by the same upper-case letters are not significantly different from one another when comparing within a water year across plant community types.*

Table 5. Significance Levels of Year and Factor Interactions from 1997 to 2001

Source	Ca	Mg	K	Water vol
Year	c	c	c	c
Location	a	a	NS	NS
Soil	c	b	b	b
Community	c	c	a	NS
Location × soil	b	b	NS	NS
Location × community	NS	NS	NS	a
Soil × community	NS	NS	a	a
Site × soil × community	NS	NS	NS	NS
Year × location	c	c	c	c
Year × soil	c	c	c	NS
Year × community	NS	b	a	a
Year × location × soil	b	b	NS	NS
Year × location × community	NS	NS	NS	NS
Year × soil × community	NS	NS	a	NS
Year × location × soil × community	NS	NS	a	NS

Ca, calcium; Mg, magnesium; K, potassium.
[a]*Factor significant at* $P \leq 0.05$.
[b]*Factor significant at* $P \leq 0.01$.
[c]*Factor significant at* $P \leq 0.001$.

last 3 years; generally the communities with the least amount of biomass exported less K (Table 2). However, differences among communities in the amount of K leached were small and not significant when the bare mesocosms were added to the analysis (Table 4). Unlike the results for Ca and Mg, the bare mesocosms exported more K than any of the plant communities (Figures 2 and 3), although not significantly so.

Based on estimates of annual biomass accumulation and biomass nutrient concentrations, the average amount of nutrients taken up by plant communities varied for Ca between 0.067–0.18 g m^{-2} y^{-1}, for Mg between 0.01 and 0.04 g m^{-2} y^{-1}, and for K between 0.03 and 0.12 g m^{-2} y^{-1} (Figure 3). The range represents differences across years. By year 4, plant biomass was substantially greater at SB than at Wolcott for each plant community type ($P \leq 0.001$), (Figure 4). Soil pH was also lower at SB than at Wolcott, at 6.8 and 7.2, respectively ($P \leq 0.05$). At both sites, average soil pH was lower in the mesocosms with the community types of greatest biomass, 6.8 and 6.9, than in the bare mesocosms, which had a pH of 7.3 ($P \leq 0.05$).

The percent variation attributable to community was variable across years; only for Ca did community type differences appear to account for an increasing proportion of the variation in nutrient export over the course of the experiment

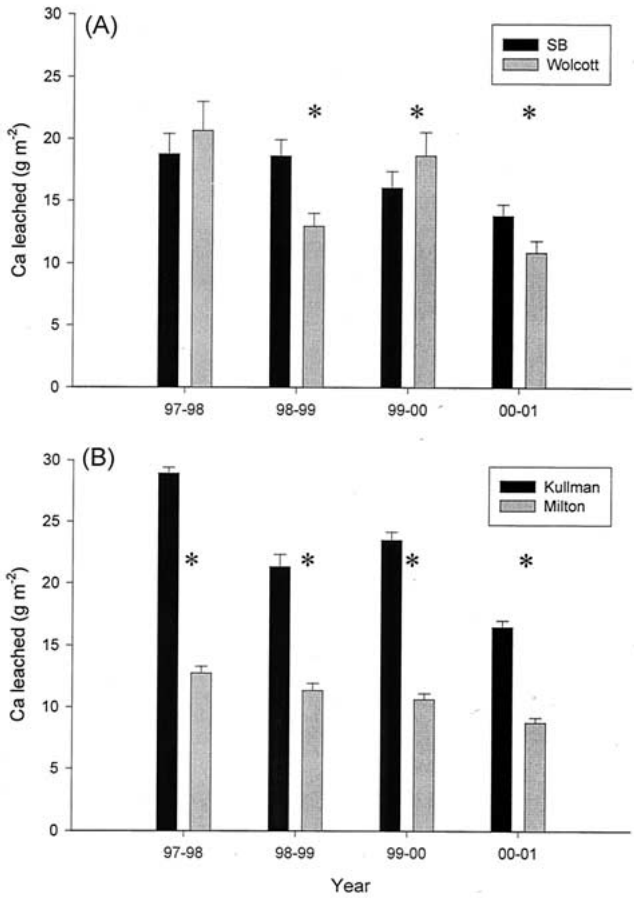

Figure 1. Mean annual calcium (Ca) export (g m^{-2} ± SE) by water year from mesocosms **A** at two locations, South Burlington (SB) and Wolcott, Vermont, and **B** containing two soil types, Kullman and Milton. (* Tests between treatments in that year are significant at $P < 0.05$.)

(Table 2). Moreover, differences among communities for Ca were relatively consistent across years, but the year × community interaction was significant for Mg and K, suggesting that the relative amount of nutrients exported from each community did vary across year (Table 5). As with the location and soil factors, developmental year in this 4-year study was not the most important component describing the role of the plant communities in controlling nutrient export.

Role of Contextual Interactions

Throughout the experiment, the sum of the main effects was more important (56%–97%) than the sum of the statistical interactions (1%–33%) in influencing annual nutrient export (Table 2). Interactions explained a small percentage of the

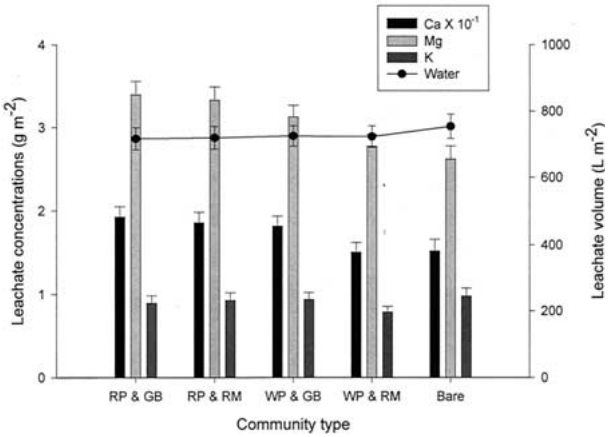

Figure 2. Mean annual nutrient (g m^{-2} ± SE) and water export (L m^{-2} ± SE) from mesocosms by plant community type. Ca, calcium; Mg, magnesium; K, potassium; SB, South Burlington; WC, Wolcott; RP & GB, red pine and gray birch; RP & RM, red pine and red maple; WP & GB, white pine and gray birch, WP & RM, white pine and red maple.

total variation in the amount of Ca and K exported (1%–8% and 6%–13% of the variation, respectively), but a substantially larger percent (16%–33%) of the variation in the amount of Mg exported (Table 2). Summed factor interactions explained 0%–15% of the variation in the volume of water exported.

Abiotic (location × soil) interactions were generally much stronger than abiotic–biotic (location × community, soil × community) interactions (Table 2). The location × soil interaction influenced the export of Mg in all years and accounted for more than 13% of the total variance in Mg export in every year (Table 2 and Figure 5). The mesocosms at Wolcott exported more Mg when filled with Kullman soil than Milton soil in all years. In contrast, the amount of Mg exported from mesocosms in SB, while dependent on soil, was inconsistent across years. The location × soil interaction was significant in only 1 year for Ca, K, and leachate volume, when it explained between 6%–8% of the total variation in the amount of each exported (Table 2).

Abiotic–biotic interactions (location × community and soil × community) were inconsistent and accounted for a small percent of the variation in Ca, Mg, and K export. The location × community interaction accounted for less than 1% and less than 1%–5% of the variation in Ca and Mg export, respectively (Table 2). The soil × community interaction explained 2%–6% of the total variance in K export.

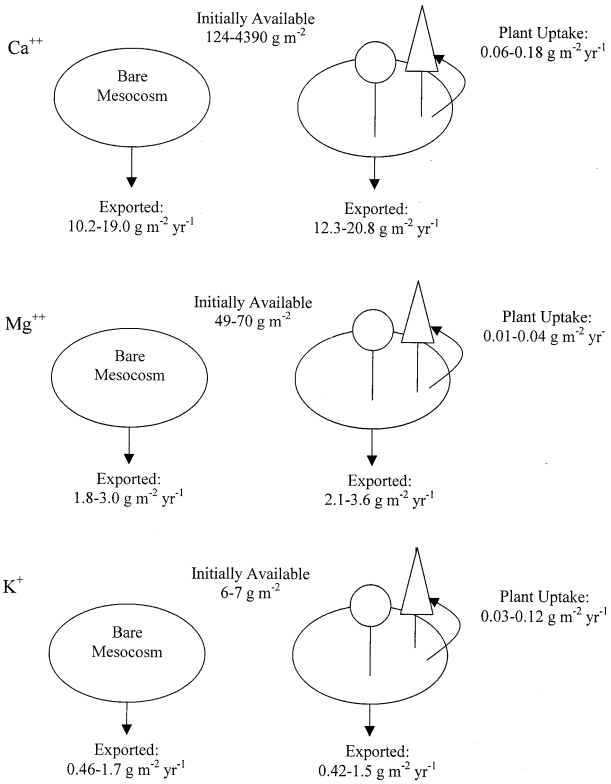

Figure 3. Initially available soil nutrients (g m^{-2}) and mean annual nutrient export and plant uptake (g m^{-2} y^{-1}) from bare and vegetated mesocosms. The vegetated mesocosms represent an average of the four plant community types. The range in initially available soil nutrients represents the difference between the soil types; the range in export and uptake represents variation across years. Ca, calcium; Mg, magnesium; K, potassium.

Discussion

Control of Nutrient Export

Our research provides a quantitative estimate of the magnitude and shifts in abiotic and biotic control of nutrient export during early primary succession in a simplified forest ecosystem. On average, nutrient losses over the 4-year mesocosm experiment approached 30% of the total available nutrients at the start of the experiment (Table 3). Our results show that variation in nutrient export was a function of leachate volumes (year and location), initial soil stocks (soil), and biological processes (plant community). The interplay of these factors, including some significant contextual interactions, proved to be fairly complex. However, there were some general trends.

Our results supported our prediction that the abiotic factors—soil (the amount of available nutrients) and location (the volume of input)—control

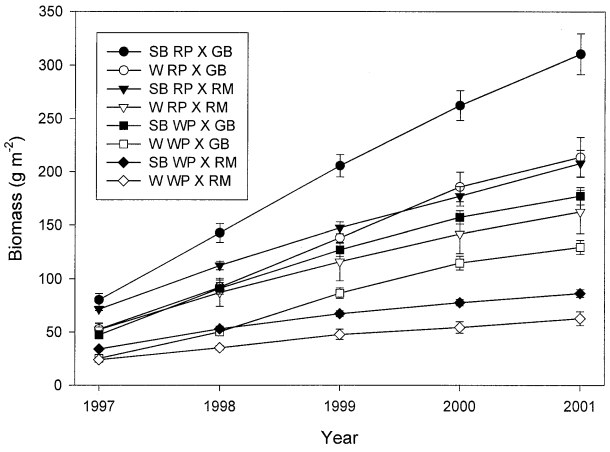

Figure 4. Average biomass of the plant communities (g m^{-2} ± SE) growing in mesocosms at two locations South Burlington (SB) and Wolcott (W) Vermont over 4 years. For plant community type, see Figure 2.

variation in nutrient export in the early stages of ecosystem development (Odum 1969). We were interested in learning how the relative importance of these factors in controlling nutrient export changed over time, including year into development. We expected the loss of labile cations in the newly exposed substrates to decline over time; the mesocosms demonstrated this trend well for all three cations—Ca (Table 3) and Mg and K (Tables 3 and 4). During the 1st year of the study, the amount of Ca leached from the Kullman soil and the amount of K leached from both soils were high compared to natural temperate, deciduous systems (Likens and Bormann 1995); during the subsequent 3 years, the export rates for all cations were in the range typical of temperate forests (Table 3).

Although there was a general decline in the amount of nutrients exported over time, significant year × location and year × soil interactions showed that the role of these factors in determining nutrient export changed over time (as shown for Ca in Figure 1). We did not expect this to occur because some location-associated factors (that is, length of growing season) and soil-associated factors (that is, soil texture) were consistent across years. This finding suggests that the overarching factors we used do not fully explain nutrient export; therefore factors associated with location and soil that change on a yearly basis need to be incorporated into models of nutrient export. For example, volume of input, which was associated with location and changed yearly, appeared to be important in the export process. To gain a better understanding of the processes controlling nutrient export, it would be useful to identify the factors that change with

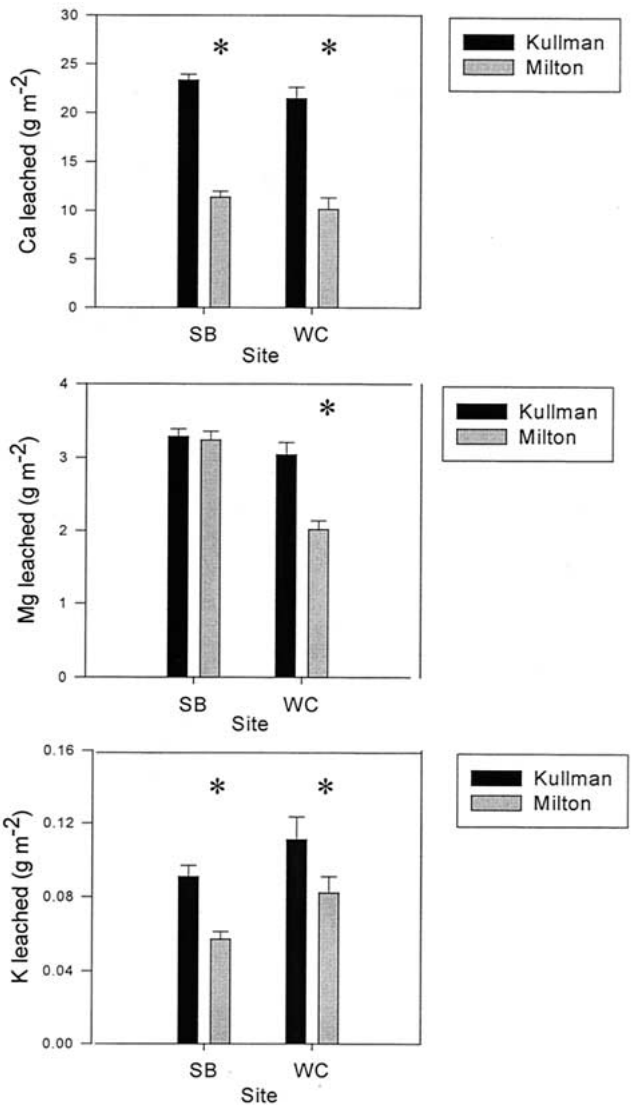

Figure 5. Mean annual nutrient export (g m^{-2} ± SE) from mesocosms containing two soil types, Kullman and Milton, at two locations, South Burlington (SB) and Wolcott (WC), VT, USA, for 4 years. * Tests between soils at one site are significant at $P < 0.05$. Ca, calcium; Mg, magnesium; K, potassium.

year and influence the role of the abiotic factors in controlling leachate chemistry. It would also be useful to determine how the annual variation we found affects general patterns at longer time scales.

To test our second prediction, we needed to evaluate the emergence of the plant communities as a controlling variable of nutrient export. Despite low productivity throughout the experiment (on average, 0.2 kg m^{-2} after 4 years), plant communities consistently and significantly affected leachate chemistry. Plant community processes (that is, plant-induced weathering), measured as the difference between bare and vegetated mesocosms,

resulted in greater loss of Ca and Mg (Figure 3). In all cases, the release of both Ca and Mg was significantly greater from than mesocosms containing the plant community with the largest biomass than from the bare mesocosms (Table 4). However, even though the mesocosms with greater biomass leached significantly more K than those with less biomass (Table 2), the amount of K leached from the bare mesocosms was greater than that from the vegetated mesocosms (Figures 2 and 3), although not significantly so. This finding suggests that plant-induced leaching is important for K, but it is masked to some extent by plant uptake and rapid weathering rates. It appears that the plants were depleting the available (ammonium acetate–extractable) nutrient pools of Ca and Mg, as supported by the changes in soil pH, to make available and use limiting K, despite the possible detrimental effects of enhancing the loss of other nutrients.

The patterns that emerged when we investigated the movement of nutrients into the biota further suggest that K was the least available and most mobile of the three nutrients. During the 4-year experiment, we found that the strictly abiotic release of nutrients, measured as the amount exported from the bare mesocosms, exceeded estimates of the amounts moving into plants on a yearly basis. The percentage taken up by plants was approximately 0.5%–1.0% for Ca, 0.7%–1.5% for Mg, and 6.7%–8.2% for K of that released from the bare mesocosms, with the range representing variation in years (Figure 3). Plant nutrient uptake also represented a much greater proportion of the initially available nutrients for K (4.58%) than it did for either Ca (0.02%) or Mg (0.19%). A clear limitation of our investigation of movement into the ''biota'' is that it included plants only. Over the 4 years this research was conducted, it is likely that a belowground food web developed that influenced rock weathering and took up at least some nutrients (Jongmans and others 1997; Landeweert and others 2001; Blum and others 2002).

Because our research was controled usms replicated experimental ecosystems over short a 4-year period, it is difficult to extrapolate the results and test hypotheses regarding how the control of nutrient export shifts with ecosystem development (for example, Odum 1969; Vitousek and Reiners 1975). However, our findings differ somewhat from the ''nutrient retention hypothesis,'' which suggests that as the amount of nutrients tied up in the biomass increases, the amount that is exported decreases (Vitousek and Reiners 1975). However, the results do support the following exception to that hypothesis: during primary succession, element input from plant-induced weathering should complicate the interpretation of nutrient retention (Vitousek 1977; Bormann and others 1998)—in this case, by taking up limiting nutrients (K) and exporting large amounts of the nutrients that are not limiting (Ca and Mg). In addition, our results did not confirm our prediction that as biomass increased, the biota would play an increasingly important role in regulating nutrient export (Odum 1969; Vitousek and Reiners 1975). Instead, we found that the role of the biota in controlling nutrient export remained relatively constant over the 4 years (Table 4).

The timing of biotic control over nutrient fluxes and pools is not as well documented in the literature as the importance of biotic control (Schwartzman and Volk 1989). In the 1st year of the study, when biomass was minimal (0.02–1.0 kg plant biomass per m^{-2} soil, or a plant-to–soil mass ratio of about 1:25,000), the plant biota (comparing vegetated versus bare mesocosms), as well as each plant community type, significantly influenced the export of Ca and Mg from the mesocosms (Tables 2 and 4). By the 2nd year, plant community types had significant effects on the amount of all nutrients leaving the mesocosms (Table 2). One surprising finding of this study is that even a small amount of living biomass has the ability to rapidly exert biogeochemical controls over ecosystem processes. However, because this experiment was conducted in an artificial system, it cannot be established whether this effect is typical of developing ecosystems.

Emergence of Interactions

A primary goal of ecological research is to develop more predictive models of ecological systems; however, interactive effects pose a major hindrance to this goal (Mooney and others 1991; Bazzaz and Fajer 1992; Kareiva 1994). Experimental and theoretical research at the organism, population, and community levels has demonstrated the impivtance of interactions in understanding ecological relationships (Tilman 1988, 1990; Kelty 1992; Tilman and others 1997; Finzi and Canham 1998; Loreau 1998). Although some researchers have suggested that they play an important role in ecosystem homeostasis and recovery (DeAngelis and Post 1991; Chapin and others 1996), specific projections of the relative magnitude of interactive effects between and among the factors that influence ecosystem development have not been well established. To

our knowledge, this is the first ecosystem study explicitly designed to test for and quantify interactions among multiple factors.

Although main effects (location, soil, and plant community) accounted for most of the variation in nutrient export in this study, the interactions between these factors were measurable, and in some cases significant, even though the percentage of variation attributable to interactions was generally small (Table 2). The most consistent interaction that did not involve year was the location × soil influence on Mg loss. Based on our definition of contextual interaction, this finding suggests that controls on Mg export associated with soils behave differently in different locations; however, this observation does not explain the ecological mechanism that creates the interaction. The two soils had different properties (available nutrients, CEC, percent sand), and the two locations had different properties (climatic regimes, nutrient inputs, and seed rain [plants/microbes]). Potential explanations for this interaction range from the physical to the biological.

Based on our results, we can offer one possible explanation for the location × soil influence on Mg export. We postulate that at SB, where productivity was greater than at Wolcott, nutrient export was driven more strongly by the growing plant communities that require limiting K. Thus, the plants growing at SB in the Milton soil, which had less initially available Mg and a lower CEC (Table 1), mined more soil nutrients than those growing in Kullman, and as a result, the loss of Mg from the Milton soil equaled that lost from the Kullman soil (Figure 5). In Wolcott, where productivity was lower, nutrient export was driven primarily by the abiotic factors. As was observed, we would expect that in a lower-productivity environment less Mg would be exported from the Milton soil than the Kullman soil (Figure 5). This hypothesis is also supported by the observation that, despite higher productivity, less K was exported at SB than at Wolcott (Figure 5 and Tables 2 and 3).

The importance of the consistently observed Mg location × soil interaction is that the three factors we investigated—that is to say, the only three factors we manipulated—could not explain what was driving Mg export in the mesocosms. The mechanism that we propose is consistent with the data and shows how information bearing on the controls of nutrient export could be lost if studies were directed at understanding only main effects (climate, soil, or plant communities) and treated ecological processes associated with interactions as error variance or uninterpretable noise. In fact, if our hypothesis is correct, determination of the mechanism that creates the interaction also leads to a fuller understanding of the system—in this case, by establishing the existence of a shift from abiotic to biotic control along a productivity gradient. Although more studies are needed to determine what created the contextual interactions found in this study, providing hard evidence of their existence by quantifying their effects is a first step.

One might wonder why we observed a consistent interaction for Mg export but not for Ca export. We postulate that the differences—or lack of differences—among the factor levels chosen for this study determined the magnitude of factor & factor control over nutrient export interval. There was a 30-fold difference between the two soils in the availability of Ca (Table 1). This initial condition—the differences between soil levels—accounted for most of the variation in Ca export, and the presence of such a dominant factor prevented interactions from developing. By contrast, there was a much smaller difference between the two soil types in the amounts of Mg initially available; and we found that all three of the main factors (location, soil, and plant community accounted more equal- for export and significant interactions emerged (Table 2). Thus, it can be difficult to quantify the importance of factors and their interactions because their control over a process depends, in part, on the a priori selection of both the factors and their levels.

Because the location and soil factors chosen for this study exerted strong controls on nutrient export, our experimental design may have tested conservatively for plant community controls over nutrient export and the strengths of the interactions. In addition, the study system had low productivity. We are not convinced that we could predict the results if the systems were highly productive. On one hand, a more productive system might exhibit greater differences between community types and therefore lead to greater interactions with the other factors. On the other hand, a more productive system might have a single dominant spaces and fewer interactions.

Many studies on ecosystem development involve successional changes in communities plant (Odum 1969; Vitousek and Reiners 1975; Gorham and others 1979). Because of the nature of our research, interactions resulting from successional changes could not be studied. Although the limitations of our experimental design prevent us from being able to extrapolate the results to ecosystems with different starting conditions (for example early colonists or understory plants) or longer-term

processes, it was out intention to show what is possible, not necessarily what is typical.

Although our measurements revealed that there were significant interactions among the factors we studied, our third prediction—that contextual interactions are an increasingly important driving force influencing nutrient export—was not strongly supported by the data. This relationship will be investigated as the experimental mesocosms continue to mature and we collect more data. The data we have collected to date do support research suggesting that there are interactions among the broad factors (climate, soil, and plant community) often used in studies of ecosystem development over longer time scale (Ford 1990; Hotchkiss and others 2000; Ewing 2002). Moreover, our study shows that these interactions are possible not only after the long time periods addressed by paleoecological studies, but also early in ecosystem development.

The contextual interactions found in this study show that the process of ecosystem development is much more complex than can be explained solely by the three factors we investigated. What is most interesting and unique about our study is its experimental design. We did not choose to look at these particular factors because we thought they were the most important ecosystem drivers. Instead, at the start of this experiment, they were chosen because they could be easily incorporated into the experimental design to create differences among the mesocosms. But ultimately our study revealed how complex ecosystem development can become even when starting from this simple state. In addition, we showed that attempts to identify the mechanisms underlying significant interactions can yield useful hypotheses about the functioning of an ecosystem.

Our simple interpretation of one such interactions underscores the difficulty posed by attempts to explain contextual interactions. If interactions truly originate from ''contextual'' factors that may change depending on species, location, soil, topography and rather than reflecting our lack of knowledge of some other mechanism or process that could be generalized, then they present real challenge to ecologists. The existence of contextual interactions, by definition, indicates that the context in which an ecological process occurs is important; thus, different interactions, and hence new hypotheses that attempt to explain these interactions, may result in different contexts. That is to say, although more factors could be included in an analysis aimed at explaining an interaction, their conclusion could lead to even more multiway interactions, especially in new contexts. Thus, the problem for ecologists is that attempts to understand a specific contextual interaction may not lead to greater general understanding of an ecosystem process.

Ecologists working in the field are attempting to study real ecosystems that are potentially embedded within a complex of contextual interactions that are not addressed explicitly. Our research does not provide a solution to this quandry. However, it does provide evidence that contextual interactions are measurable and important in a simplified experimental ecosystem. We think that the next challenge is to figure out how to apply these insights to the study of real ecosystems. Is there a way to deconstruct contextual interactions in field studies that do not have the advantages of a replicated, controlled experimental design? We need to devise a new approach to field work that will incorporate the analysis of contextual interactions and thereby improve our understanding of how real ecosystems function.

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