

# Spatial variability in soil nutrient availability in an oak–pine forest: potential effects of tree species

C.S.M. Washburn and M.A. Arthur

**Abstract:** Established species have been shown to affect soil nutrient availability, but the effects of “native invasive” species on soil nutrient availability are relatively unknown. Oak-dominated forests in the eastern deciduous forest are dynamic in their species composition, with increasing dominance of red maple (*Acer rubrum* L.) in the midstory and overstory. We hypothesized that higher quality red maple litter within a litter matrix dominated by oaks would accelerate N turnover, increase nutrient availability in the soil, and result in a thinner and less massive O horizon. We examined nutrient availability in soils under three overstory tree species (*Quercus prinus* L., *A. rubrum*, and *Pinus echinata* Mill. or *Pinus rigida* Mill.), under a shrub (*Vaccinium* spp.), and in locations without tree stems (“no tree”). Extractable nutrients (P, K, Mg, Ca) and total and available N were quantified in the O horizon and upper mineral soil at 0.5 m and 1.0 m from the base of individual trees or from the center of *Vaccinium* and no-tree locations. Despite low lignin concentration in red maple litter and low lignin/N ratio, the lowest N mineralization rates were found in red maple microsites; the highest N mineralization rates were found under oak. Extractable cations were generally highest under red maple and lowest under pines, and red maple had the highest levels of total N (but not NO<sub>3</sub> or NH<sub>4</sub>) in the upper mineral soil. Shifting species composition towards red maple and away from pines in these forests may alter nutrient cycling by increasing surface soil cation availability, but reducing soil N mineralization.

**Résumé :** Il a été démontré que les espèces déjà établies affectent la disponibilité des nutriments dans le sol mais on connaît peu d'effets similaires dus aux espèces indigènes envahissantes. Les forêts dominées par le chêne dans la forêt feuillue de l'Est sont dynamiques dans leur composition en espèces, avec une dominance croissante de l'érable rouge (*Acer rubrum* L.) dans les étages dominant et intermédiaire. Nous avons émis l'hypothèse que la litière d'érable rouge qui est de meilleure qualité, mélangée à la litière dominée par les chênes, devrait accélérer le recyclage de N, augmenter la disponibilité des nutriments dans le sol et entraîner la formation d'un horizon O plus mince et moins massif. Nous avons étudié la disponibilité des nutriments dans le sol sous le couvert de trois espèces d'arbres (*Quercus prinus* L., *A. rubrum* et *Pinus echinata* Mill. ou *Pinus rigida* Mill.), d'un arbuste (*Vaccinium* spp.) et à des endroits où il n'y avait pas d'arbre (« sans arbre »). Les nutriments extractibles (P, K, Mg, Ca) ainsi que N disponible et total ont été quantifiés dans l'horizon O et la couche supérieure du sol minéral à 0,5 et 1,0 m de la base d'arbres individuels ou du centre des tiges de *Vaccinium* ou des endroits sans arbre. Malgré la faible concentration en lignine dans la litière d'érable rouge et le faible rapport lignine : N, les plus faibles taux de minéralisation de N ont été observés dans les microsites occupés par l'érable rouge; les taux les plus élevés de minéralisation de N ont été observés sous le chêne. La quantité de cations extractibles était généralement la plus élevée sous l'érable rouge et la plus faible sous le pin. De plus, les plus grandes quantités de N total (mais pas de NO<sub>3</sub> ou de NH<sub>4</sub>) dans la partie supérieure du sol minéral ont été mesurées sous l'érable rouge. L'évolution de la composition en espèces dans ces forêts, du pin vers l'érable rouge, pourrait modifier le recyclage des nutriments en augmentant la disponibilité des cations à la surface du sol mais en réduisant la minéralisation de N dans le sol.

[Traduit par la Rédaction]

## Introduction

The effects of individual tree species on soil chemistry have been examined since the early 20th century (Gast 1937; Zinke 1962; Mina 1967; Gersper and Holowaychuk 1971; Boerner 1984; Miles 1985; France et al. 1989; Boettcher and

Kalisz 1990; Binkley and Valentine 1991; Finzi et al. 1998a, 1998b, among many others). Two recent reviews have summarized the evidence for effects of different trees species on soils (Binkley 1995) and the possible mechanisms leading to these effects (Binkley and Giardina 1998). For example, nutrients may be differentially accessed at depth and redeposited on the soil surface via litterfall (Zinke and Crocker 1962; Binkley 1995). Exudates produced by vegetation and their associated microbes can affect the rate of mineral dissolution (Tan 1986), and the types and quantities of exudates can differ among plant species (Smith 1976), thereby influencing the amount of nutrients available for uptake (Quideau et al. 1996). There may also be differences in the chemistry and quantity of throughfall and stemflow (Zinke 1962; Zinke and Crocker 1962; Mina 1967; Gersper and Holowaychuk 1971; Binkley and Valentine 1991; Moffet et al.

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1994; Rhoades 1997) influencing nutrient return and availability in the soil. Species may differ in fine root proliferation in deep soil, permitting some species to access greater stores of cations (Dijkstra and Smits 2002), or possibly increasing cation supplies from weathering (Binkley and Giardina 1998). Perhaps the most prevalent effect of tree species on soils is the strong negative correlation between the lignin/N ratio of leaf litter and N mineralization noted in many (Binkley and Giardina 1998; Ferrari 1999; Scott and Binkley 1997), but not all (Thomas and Prescott 2000), studies of this sort.

Studies examining single-species effects on soil nutrients have often focused on sites or mesocosms in which a suite of species was established simultaneously in separate plots or containers, and often in sites in which all the species have been established for very long periods (Zinke 1962; Zinke and Crocker 1962; Alban 1969; Turner and Franz 1985; Boettcher and Kalisz 1990). Throughout the eastern deciduous forest, the species composition of oak forest regeneration is shifting in the absence of fire, leading to communities with increasing dominance of red maple (*Acer rubrum* L.) or sugar maple (*Acer saccharum* Marsh.) (Lorimer 1984; McCune and Cottam 1985; Pallardy et al. 1998; Abrams and Downs 1990; Nowacki et al. 1990; Abrams 1998; Arthur et al. 1998). Research addressing the vegetation dynamics of this shift has focused on the mechanisms by which red maple has proliferated in oak-dominated forest stands (Abrams and Downs 1990; Lorimer 1993; Abrams 1998), the implications for future forest stand structure and composition (Abrams 1992; Pallardy et al. 1998), and the potential role of prescribed fire in maintaining oak dominance (Brose and Van Lear 1998; Loftis 1990). Equally important, however, is understanding the implications of shifting species composition for ecosystem-level processes such as nutrient cycling. If red maple has an effect on soils beneath its canopy that is different from the effects of the oak and pine species it may replace, then changes in species composition in this forest could have ecosystem-level consequences through changes in soil nutrient availability.

The objective of this study was to examine whether the effects of individual tree species on soil chemistry could be detected within a forest matrix dominated by oak overstory trees and litter. The relatively recent increase in the importance of red maple on the oak-dominated ridgetop in our study site provides the ideal community dynamic for testing the influence of red maple on soil nutrient availability. We hypothesized that higher-quality red maple litter within a litter matrix dominated by oaks would accelerate N turnover, increase nutrient availability in the soil, and result in a thinner and less massive O horizon.

## Materials and methods

### Study site

The study was located in the Cliff Section of the Cumberland Plateau in eastern Kentucky (Braun 1950), in the Red River gorge in the Daniel Boone National Forest. The study site was an oak–pine dominated forest community found on Koomer Ridge, a 42-ha ridgetop with a geologic substrate of sandstone with minor components of siltstone and shale.

Soils were classified as fine-loamy, mixed, mesic Typic Hapludults, formed mainly from weathered sandstone or loamy colluvium, deep to moderately deep, and well to excessively drained (Hayes 1993). The climate in this region is considered temperate, humid, and continental, with a mean temperature range of  $-6^{\circ}\text{C}$  to  $6^{\circ}\text{C}$  in January and  $17^{\circ}\text{C}$  to  $30^{\circ}\text{C}$  in July, and an annual mean temperature of  $12^{\circ}\text{C}$  (Hill 1976). Mean annual precipitation is 1170 mm, with typically more precipitation in the spring than in the fall.

Forest composition was dominated by oak species (chestnut oak (*Quercus prinus* L.), white oak (*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.)) in the overstory, while the regeneration pool was dominated by red maple (Fig. 1). Oaks accounted for 53% of the density of stems  $>10$  cm DBH and 68% of the basal area (Table 1). Pines (shortleaf and pitch pine combined (*Pinus echinata* Mill. and *Pinus rigida* Mill.)) contributed the second largest amount of basal area of any genus (10%). There were more red maple  $>10$  cm DBH per hectare than any other species (135 stems/ha or 25% of total), which contributed relatively little to the basal area (9%).

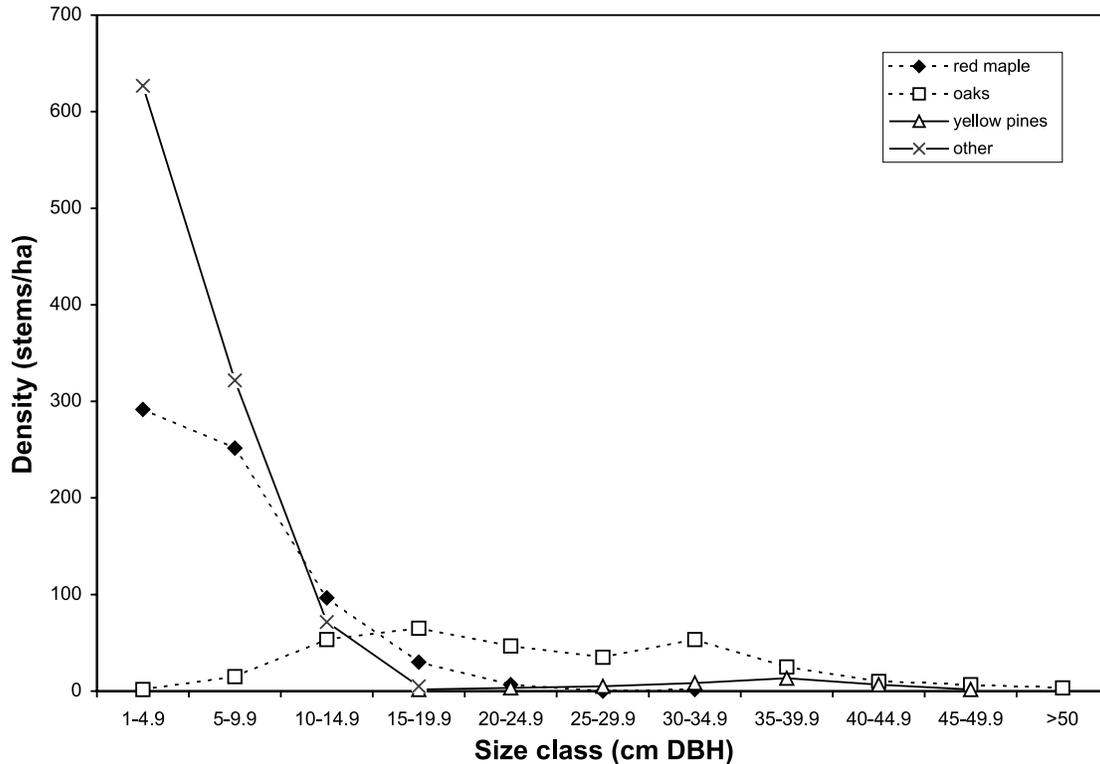
Other important species included eastern white pine (*Pinus strobus* L.) in the overstory and bigleaf magnolia (*Magnolia macrophylla* Michx.), black gum (*Nyssa sylvatica* Marsh.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), hickory (*Carya* spp.), sassafras (*Sassafras albidum* (Nutt.) Nees), and sourwood (*Oxydendrum arboreum* (L.) DC.) in the midstory stratum (stems 2–20 cm DBH). Blueberry shrubs (*Vaccinium* spp.) were common in the understorey, along with scattered mountain laurel (*Kalmia latifolia* L.) and greebrier (*Smilax* spp.).

### Experimental design

The experimental design consisted of five 0.12-ha blocks located at random points along the ridgetop. In June 1997, we inventoried all trees within the blocks with a DBH greater than 10 cm. Based on these results, three target tree species were chosen: chestnut oak, pines (either *P. echinata* or *P. rigida*), and red maple. Chestnut oak was selected from among the oak species present because it had the highest relative density (Table 1). Limited occurrence of overstory pines required us to combine them into a single “pine” group. The red maple trees in the study were smaller (15.7 cm DBH) and younger (52 years), on average, than the chestnut oak (26.8 cm DBH; 70 years) and pines (35.0 cm DBH; 70 years). We defined two additional microsite types, *Vaccinium* and “no-tree” microsites. No-tree microsites were areas with a 4-m diameter that were devoid of large shrubs and stems  $\geq 10$  cm DBH, but still within the closed canopy forest. *Vaccinium* microsites contained dense clusters of *Vaccinium pallidum* Aiton or *Vaccinium stamineum* L. and were defined as clumps with several stems, covering at least  $0.75\text{ m}^2$  of the ground surface. Each microsite type was replicated three times in each block, except in three blocks that contained only two no-tree sites that met the predetermined criteria, for a total of 72 microsites.

Since our experimental design unavoidably confounds microsite and species, we examined mineral soil texture and cation exchange capacity (CEC) to assess evidence that differences among microsites could pre-date the establishment

**Fig. 1.** Stem density by size class of all stems >1 cm DBH on Koomer Ridge in the Daniel Boone National Forest, Kentucky. Stems are divided into four categories: red maple, oak species (*Quercus alba*, *Quercus coccinea*, *Quercus prinus*, and *Quercus velutina*), pines (*Pinus echinata* and *Pinus rigida*), and all other species.



**Table 1.** Relative density (%) and basal area (%) of stems >10 cm DBH on Koomer Ridge, Daniel Boone National Forest, Kentucky.

Species	Relative density (%)	Relative basal area (%)
Red maple	25	9
Chestnut oak	19	14
White oak	18	19
Scarlet oak	16	35
Sourwood	7	2
Pitch pine	2	4
Shortleaf pine	3	6
Other*	8	4

**Note:** Total density was 550 stems/ha, and total basal area was 24 m<sup>2</sup>/ha.

\*Other species included *Pinus strobus*, *Nyssa sylvatica*, *Quercus velutina*, *Tsuga canadensis*, *Magnolia macrophylla*, *Carya tomentosa*, and *Sassafras albidum*. Only target species and those contributing at least 5% of the relative density or relative basal area were included in this table.

of different species. Soil texture was silt loam in all microsites, and there were no statistically significant differences in the percent sand, silt, or clay among microsites (Table 2). Mineral soil CEC also did not differ significantly among microsites, with a mean of 11.2 cmol<sub>c</sub>·kg<sup>-1</sup> (SE = 0.54) and a range of 10.4 to 12.3 cmol<sub>c</sub>·kg<sup>-1</sup>. Similar soil texture and CEC among microsites strongly suggests that the soil substrate was similar throughout the study site and that differences in nutrient concentrations among these microsites

were not due to soil mineralogy, an important underlying assumption of this study. Furthermore, red maple stem distribution was ubiquitous and showed no recognizable pattern in relation to landscape features, suggesting a priori similarity in inherent soil characteristics among microsites.

**Field sampling**

Soil samples were collected at a distance of 0.5 m from the bole of the tree or 0.5 m from the center of no-tree microsites, and one cardinal direction was randomly selected for each of the four sample dates (June 1997, and February, April, and June 1998) to avoid resampling any point.

In June 1997, cores were collected with a 2-cm soil probe and separated into organic horizon (Oe and Oa) and upper mineral soil (0–5 cm) in the field. Samples were composited for each individual microsite, placed on ice, and returned to the laboratory for analysis. Fresh litter samples were collected from mid-October through November 1998 from a subset of locations using 1-m<sup>2</sup> mesh screens. Samples were collected frequently to protect litter from precipitation. Litter was analyzed for Ca, Mg, K, N, and lignin (n = 4 to 5 samples per species for chestnut oak, scarlet oak, red maple, and pine).

In June 1997, we measured N mineralization in situ (Eno 1960) by compositing approximately one-fourth of the samples collected from a given microsite type for each block into one sample. Five microsites in each of five blocks gave a total of 25 composite samples. Each composite was divided in half and placed in Whirlpack® bags. One bag was returned to the laboratory for initial analysis, and the other

**Table 2.** Soil physical characteristics for no-tree, *Vaccinium*, pine, chestnut oak, and red maple microsites in the Daniel Boone National Forest, Kentucky.

	Microsite type					<i>F</i>	<i>p</i>
	No-tree	<i>Vaccinium</i>	Pines	Chestnut oak	Red maple		
<b>Mineral soil</b>							
Sand (%)*	20 (1.1)	22 (1.4)	20 (1.6)	22 (1.2)	21 (1.1)	2.21	0.07
Silt (%)*	63 (1.2)	62 (1.1)	62 (1.8)	60 (1.0)	62 (1.2)	2.15	0.08
Clay (%)*	16 (0.9)	16 (0.9)	19 (1.1)	18 (0.9)	17 (1.0)	0.87	0.48
Soil moisture (%) <sup>†</sup>	26.4ab (0.5)	25.5b (0.7)	27.6ab (0.7)	26.4ab (0.5)	28.6a (0.7)	3.06	0.02
<b>O horizon</b>							
Mass (kg/m <sup>2</sup> ) <sup>‡</sup>	2.5b (0.3)	3.4b (0.3)	10.1a (0.8)	4.0b (0.4)	3.5b (0.4)	19.84	0.0001
Depth (cm) <sup>‡</sup>	1.7b (0.3)	2.5b (0.2)	8.0a (0.8)	2.9b (0.3)	2.7b (0.2)	48.92	0.0001
Soil moisture (%) <sup>†</sup>	61.2c (1.1)	61.5c (1.3)	68.0a (0.9)	62.8bc (1.0)	64.5b (1.0)	7.48	0.0001

**Note:** Values are means with standard errors in parentheses. Within a row, different letters indicate statistically significant differences between microsite types at  $p < 0.05$  using pairwise comparison.

\*Particle size distribution in upper 5.0 cm of mineral soil for June 1997 samples.

<sup>†</sup>Soil moisture expressed as a percentage of total soil mass. Data are means of February, April, and June 1998 sampling dates.

<sup>‡</sup>Data pooled across February and April 1998 sampling dates.

was buried in the appropriate microsite. The O horizon samples were buried in the middle of the O horizon, and the mineral soil samples were buried at a depth of 5 cm. The in situ samples were removed from the field after 30 days and returned to the laboratory for analysis.

After the June 1997 sampling period, we refined the soil sampling methods as follows: (i) sample cores were taken with a 6.0-cm bulb planter for all remaining dates; (ii) in situ N mineralization was measured again only in June 1998, for mineral soil only, and sample size was increased by collecting soils separately by individual microsite location instead of being composited within a block; (iii) the mineral soil was sampled to a depth of 2.5 cm, restricting soil samples to the depth most likely affected by surface processes; and (iv) in June 1998, a sampling distance of 1.0 m was added to evaluate the radial extent of the zone of influence.

In February and April 1998, one 14.6 cm × 14.6 cm block of forest litter and forest floor was collected from each microsite at a distance of 0.5 m from the bole of the tree or the center of no-tree microsites. O horizon depth (O<sub>iea</sub>) was measured in situ at 0.5 m from the tree after the block was removed. The litter (O<sub>i</sub>) was returned to the laboratory, separated by species, and oven-dried at 60 °C to quantify litter mass and species composition. O horizon mass (O<sub>e</sub> and O<sub>a</sub>; grams per square metre) was determined after oven-drying at 60 °C and added to the mass of the O<sub>i</sub> layer to determine the total O horizon (O<sub>iea</sub>) mass.

### Laboratory analyses

Soil samples were refrigerated in the laboratory at 4.0 °C until processed, within 2 days of collection. Mineral soils were sieved through a 2-mm mesh. Large roots, stones, and debris were removed from O horizon soils by hand. Available N (NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N) in O horizon and upper mineral soils was extracted from 10 g of fresh, sieved soils using 50 mL of 1 mol/L KCl shaken for 1 h, filtered through No. 40 Whatman paper, and analyzed with a Technicon AutoAnalyzer II (Technicon Industrial Systems, Tarrytown, N.Y.). Available N on the pre- and post-incubated samples

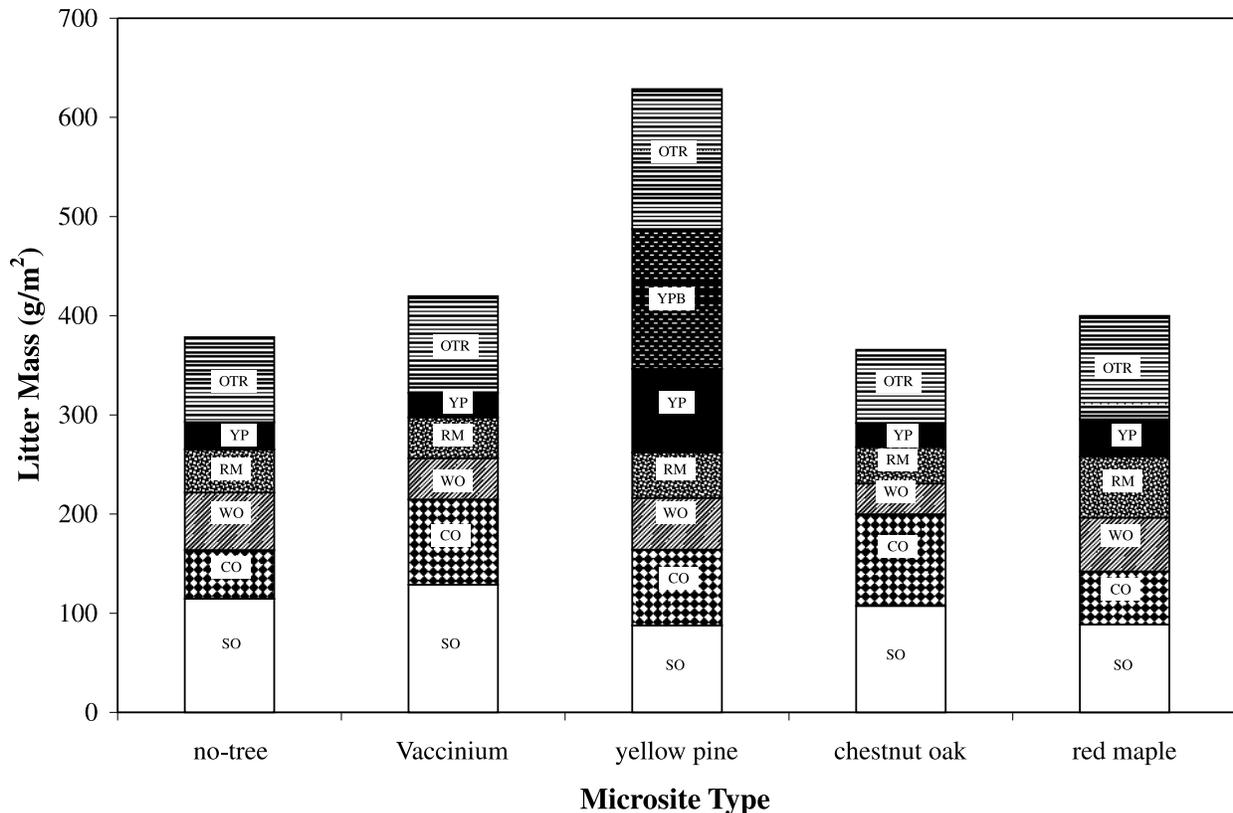
was used to calculate N mineralization (micrograms per gram dry mass per day).

Soil pH was determined using fresh sieved soil samples with a soil:water ratio of 1:10 for O horizon and of 1:2 for upper mineral soil (Hendershot et al. 1993). Gravimetric soil moisture was determined after oven-drying soil at 60 °C for 72 h on soils collected in February, April, and June 1998.

O horizon samples were dried and ground before completing the remaining analyses. Total N was extracted from O horizon samples using block digestion (McGill and Figueiredo 1993) and analyzed with a Technicon AutoAnalyzer II. Mineral soils were air dried, ground with a mortar and pestle, and analyzed for CEC using the ammonium acetate method (Rhoades 1982) and for soil texture using the pipette method (Gee and Bauder 1986). O horizon and upper mineral soils were oven-dried at 60 °C for 72 h and analyzed for Mehlich III extractable P, K, Ca, and Mg (Tran and Simard 1993). Oven-dried mineral soils were analyzed for total N and C using a LECO CN 2000 (LECO Corporation, St. Joseph, Mich.).

Oven-dried litter samples were block digested with concentrated (18 mol/L) H<sub>2</sub>SO<sub>4</sub> using a microKjeldahl technique (Wilde et al. 1979). Foliar N was analyzed on a Technicon II AutoAnalyzer, and foliar K, Mg, and Ca were analyzed on a Perkin-Elmer Atomic Absorption Spectrophotometer 4000 (Perkin-Elmer, Wellesley, Mass.). For lignin analysis, duplicate 0.5-g samples of ground litter were placed into filter bags (ANKOM No. F39, ANKOM Technology, Fairport, N.Y.) and agitated with acid detergent solution (Van Soest et al. 1991) for 60 min using an ANKOM 200 Fiber Analyzer. Samples were washed eight times with hot (90–100 °C) water to achieve a neutral pH, followed by an acetone rinse. Air-dried bags were oven-dried at 105 °C for a minimum of 2 h, cooled to ambient temperature, and weighed to determine fiber residue. Bags were then immersed in 72% H<sub>2</sub>SO<sub>4</sub> for 3 h. Samples were washed in hot water 14 times to reach neutral pH, rinsed in acetone, and dried as above, then weighed to determine lignin residue. Finally, bags were ashed in a muffle furnace at 525 °C for 3 h, and residual ash mass was determined. Lignin concentrations were calculated

**Fig. 2.** Litter composition at the 0.5-m distance in each microsite type. Data are presented for the top five species of litter, by mass. The remaining litter mass is represented as other. Species abbreviations: SO, scarlet oak; CO, chestnut oak; WO, white oak; RM, red maple; YP, pine; YPB, pine bark; OTR, other. "Other" includes *Pinus strobus*, *Quercus velutina*, *Amelanchier arborea*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Kalmia latifolia*, *Smilax* sp., *Vaccinium* sp., *Carya* sp., *Oxydendrum arboreum*, *Magnolia macrophylla*, *Sassafras albidum*, *Cornus florida*, *Fagus grandifolia*, woody debris, and unidentifiable litter fragments.



as the difference between the lignin ash residue mass and the bag ash residue mass divided by the original sample mass.

### Statistical analysis

Data were initially analyzed as a repeated measures randomized block design with five microsite types, five blocks, and four sampling dates. No seasonal effects were detected; hence data were pooled across all sample dates, and all further analyses were conducted on the pooled data. Only pooled data are reported. Statistical significance was evaluated at  $\alpha = 0.05$ , and means were compared with Tukey pairwise comparison (equal sample size) or least-square means (unequal sample size). Soil nutrient relationships to litter lignin concentration were analyzed using linear regression (PROC REG in SAS). All statistical analyses were conducted with the SAS statistical package (SAS Institute Inc., Cary, N.C.).

## Results

### Litterfall composition and chemistry

Oak litter dominated the Oi horizon in all microsites (Fig. 2). Scarlet oak was the most common species of litter collected in all microsite types except pine. For microsites with trees, the litter of the defining species was always the first or second largest component of litter. The litter under

pinus contained large amounts of sloughed bark, elevating the contribution of pine litter relative to that of other species within this microsite type

Litter chemistry differed significantly among species (Table 3). Scarlet and chestnut oak had similar N concentrations, which were significantly greater than N in pine and red maple. Red maple and chestnut oak had higher Ca and Mg concentrations than scarlet oak and pine. Potassium concentrations in litter were similar among the deciduous species, all of which were higher than the concentrations in pine litter. The lignin concentration of red maple litter was significantly lower than that of the other dominant tree species; the lignin concentration of scarlet oak litter, the dominant litter on the site, was lower than that of chestnut oak and pine litters, but higher than that of red maple litter.

### Soil physical and chemical characteristics

There were significant differences in O horizon mass, depth, and soil moisture among sites, indicating an important influence of tree species on soil physical characteristics (Table 2). Pine sites had significantly greater O horizon mass, depth, and soil moisture than all other microsites. Red maple microsites had higher soil moisture than *Vaccinium* microsites for both O horizon and mineral soils.

Soil nutrient availability varied among species, with pines having more acidic soils and lower nutrient availability compared with oaks, which in turn were generally lower in soil

**Table 3.** Nutrient concentrations (N, Ca, Mg, and K) and lignin (organic matter basis) in litter of dominant species.

	Litter type				F	p
	Pines	Scarlet oak	Chestnut oak	Red maple		
N (mg·g <sup>-1</sup> )	4.99b (0.16)	8.98a (0.17)	7.23a (0.17)	5.02b (0.16)	134.4	<0.0001
Ca (mg·g <sup>-1</sup> )	3.99d (0.14)	5.47c (0.15)	7.71b (0.15)	8.70a (0.14)	198.0	<0.0001
Mg (mg·g <sup>-1</sup> )	0.82c (0.02)	0.98b (0.02)	1.39a (0.02)	1.43a (0.02)	204.4	<0.0001
K (mg·g <sup>-1</sup> )	1.67c (0.56)	6.09b (0.63)	10.20a (0.63)	5.66b (0.56)	930.4	<0.0001
Lignin (%)	25.5a (0.83)	18.7b (0.66)	25.1a (1.18)	13.2c (0.32)	102.3	<0.0001

**Note:** Values are mean with standard errors in parentheses. Within a row, different letters indicate statistically significant differences between litter types at  $p < 0.05$  using pairwise comparison.

**Table 4.** Soil pH, extractable Ca, Mg, K, and P, NO<sub>3</sub>-N, NH<sub>4</sub>-N, and N mineralization in O horizon (Oea) at 0.5 m in no-tree, *Vaccinium*, pine, chestnut oak, and red maple microsites in the Daniel Boone National Forest, Kentucky.

Soil parameter	Microsite type					F	p
	No-tree	<i>Vaccinium</i>	Pines	Chestnut oak	Red maple		
pH	4.05a (0.04)	4.05a (0.04)	3.83b (0.03)	4.06a (0.03)	4.12a (0.04)	17.10	0.0001
Ca (µg·g <sup>-1</sup> )	1175b (86)	1325b (111)	1086b (72)	1120b (78)	1592a (109)	4.18	0.005
Mg (µg·g <sup>-1</sup> )	126 (7.6)	140 (9.0)	134 (5.7)	133 (8.6)	145 (9.4)	0.99	0.42
K (µg·g <sup>-1</sup> )	295b (18)	368a (28)	306ab (16)	343ab (25)	348a (23)	2.11	0.08
P (µg·g <sup>-1</sup> )	52.7 (3.2)	60.7 (3.9)	54.4 (2.7)	57.2 (3.5)	62.5 (4.1)	1.28	0.29
NO <sub>3</sub> -N (µg·g <sup>-1</sup> )	0.03 (0.02)	0.07 (0.05)	0.21 (0.01)	0.03 (0.02)	0.02 (0.02)	0.56	0.69
NH <sub>4</sub> -N (µg·g <sup>-1</sup> )	19.34 (6.84)	18.23 (6.18)	3.75 (0.63)	13.66 (2.40)	11.79 (2.23)	1.05	0.39
N mineralization (µg·g <sup>-1</sup> ·day <sup>-1</sup> )*	3.27ab (0.95)	2.21bc (1.45)	3.02abc (0.21)	4.76a (1.68)	1.07c (1.35)	3.93	0.04
Total N (%)	1.69ab (0.08)	1.80a (0.09)	1.49c (0.06)	1.55bc (0.06)	1.75a (0.06)	6.16	0.0003

**Note:** Values are means with standard errors in parentheses. Data are pooled across all four sampling dates (June 1997 and February, April, June 1998). Different letters within a row indicate statistically significant differences between microsites at  $p < 0.05$  using pairwise comparison.

\*N-mineralization data are from June 1997.

nutrients than red maple (Tables 4 and 5). Differences in soil nutrient availability among microsites were generally more apparent at the 0.5-m sampling distance than at 1.0 m; thus, only the data from the 0.5-m distance are shown in Tables 4 and 5.

Pine microsites had significantly lower pH than all other microsites in the O horizon and mineral soil at 0.5 m, and these differences in pH were maintained at the 1.0-m sampling distance. In addition, mineral soil pH was significantly higher under red maple (3.93) than under chestnut oak (3.81) at the 1.0-m distance. For all microsites, soil pH was slightly lower in the mineral horizon than in the organic horizon ( $3.83 \pm 0.10$  vs.  $4.02 \pm 0.11$  at the 0.5-m distance and  $3.82 \pm 0.11$  vs.  $3.94 \pm 0.14$  at the 1.0-m distance).

Extractable cation concentrations were generally highest in red maple microsites; the lowest concentrations were found under pines (Tables 4 and 5). At 0.5 m, red maple microsites had significantly higher Ca than all other microsite types in both O horizon and upper mineral soil. These differences were present at 1.0 m as well, but were less pronounced. Magnesium concentrations in the O horizon were not significantly different among microsites at either sampling distance. In the mineral soil, red maple sites had significantly higher Mg than all other microsites at 0.5 m (Table 5) and 1.0 m, with the exception of chestnut oak at

1.0 m. Red maple and *Vaccinium* microsites had significantly higher K than no-tree microsites in the O horizon at 0.5 m (Table 4); these differences among microsites for K in O horizon disappeared at 1.0 m. In the mineral soil, red maple and chestnut oak had significantly higher K than pines and *Vaccinium* at 0.5 m (Table 5); at 1.0 m this difference was no longer significant for chestnut oak.

Pine microsites had significantly lower total N in the O horizon at 0.5 m compared with all other microsites, whereas *Vaccinium* microsites had higher total N compared with red maple microsites (Table 4). There were no differences in total N among microsites in the O horizon at 1.0 m. Red maple had the highest levels of total N in the mineral soil at both distances (Table 5), and these differences were significant compared with all microsites except chestnut oak. Within a microsite type, total N concentrations in the O horizon were significantly lower at the 0.5-m distance than at the 1.0-m distance ( $1.65\% \pm 0.03\%$  vs.  $2.22\% \pm 0.04\%$ ), but they did not vary with distance in the mineral soil ( $0.20\% \pm 0.09\%$  vs.  $0.17\% \pm 0.05\%$ ). Available N (NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N) did not differ among microsites in either O horizon or upper mineral soil at the 0.5-m distance (Tables 4 and 5). In contrast, in O horizons at the 1.0-m distance, no-tree microsites had significantly higher NH<sub>4</sub><sup>+</sup>-N than all others, but there were no differences among microsites for NO<sub>3</sub><sup>-</sup>-N. In the

**Table 5.** Soil pH, extractable Ca, Mg, K, and P, NO<sub>3</sub>-N, NH<sub>4</sub>-N, N mineralization, total N, total C, and C/N in upper mineral soil at 0.5 m in no-tree, *Vaccinium*, pine, chestnut oak, and red maple microsites in the Daniel Boone National Forest, Kentucky.

Soil parameter	Microsite type					F	p
	No-tree	<i>Vaccinium</i>	Pines	Chestnut oak	Red maple		
pH	3.87a (0.02)	3.89a (0.02)	3.65b (0.02)	3.87a (0.02)	3.88a (0.03)	12.59	0.0001
Ca (µg·g <sup>-1</sup> )	100b (6.8)	89b (5.4)	92b (8.1)	97b (6.8)	143a (13)	5.41	0.0008
Mg (µg·g <sup>-1</sup> )	21.8b (1.0)	20b (0.8)	19.4b (1.1)	21.1b (0.9)	25.2a (1.3)	3.68	0.009
K (µg·g <sup>-1</sup> )	63.5ab (3.3)	55.6b (2.6)	53.1b (3.1)	60.7a (2.7)	66.8a (3.7)	3.89	0.007
P (µg·g <sup>-1</sup> )	12.1ab (0.6)	10.9b (0.5)	13.0a (0.9)	12.6a (0.6)	12.9a (0.6)	2.73	0.04
NO <sub>3</sub> -N (µg·g <sup>-1</sup> )	0.03 (0.01)	0.02 (0.01)	0.02 (0.01)	0.03 (0.02)	0.00 (0)	0.73	0.57
NH <sub>4</sub> -N (µg·g <sup>-1</sup> )	2.25 (0.28)	2.83 (0.36)	2.47 (0.37)	2.62 (0.45)	2.38 (0.41)	0.11	0.98
N mineralization (µg·g <sup>-1</sup> ·day <sup>-1</sup> )*	0.10a (0.04)	0.05a (0.04)	0.05a (0.04)	0.21a (0.06)	0.11a (0.03)	0.09	0.99
Total N (%)	0.16bc (0.01)	0.15c (0.01)	0.16bc (0.01)	0.17ab (0.01)	0.20a (0.01)	5.77	0.0005
Total C (%)	3.9b (0.1)	3.8b (0.2)	4.6a (0.3)	4.0ab (0.2)	4.6a (0.2)	2.84	0.03
C/N	24.5bc (0.6)	26.0b (0.7)	28.1a (0.5)	24.5c (0.5)	23.8c (0.5)	9.42	0.0001

**Note:** Values are means with standard errors in parentheses. Data are pooled across all four sampling dates (June 1997 and February, April, June 1998). Different letters within a row indicate statistically significant differences between microsites at  $p < 0.05$  using pairwise comparison.

\*N-mineralization data are from June 1997 and 1998.

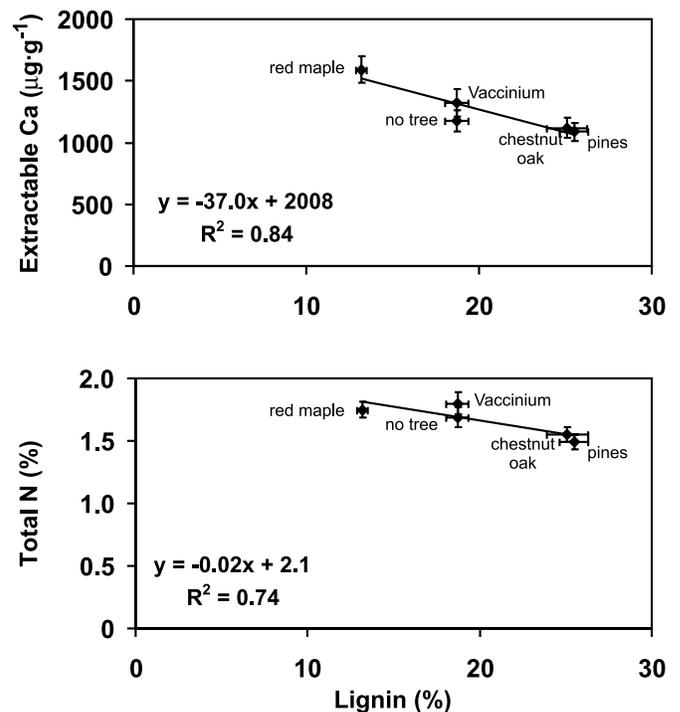
mineral soil at 1.0 m, there were no differences among microsites for NH<sub>4</sub><sup>+</sup>-N, but NO<sub>3</sub><sup>-</sup>-N was significantly higher under chestnut oak than under red maple. Rates of N mineralization in O horizons were highest in chestnut oak microsites (measured at the 0.5-m distance only), with significantly higher rates than those measured in *Vaccinium* and red maple microsites (Table 4). There were no differences among microsites for N mineralization rates in the mineral soil (Table 5).

Phosphorus concentrations did not differ among microsites in the O horizon, but there were differences in the mineral soil (Tables 4 and 5). Extractable P in the mineral soil was lowest in *Vaccinium* sites at 0.5 m, significantly lower than in chestnut oak, red maple, and pine microsites. At 1.0 m, extractable P in the mineral soil was significantly lower in *Vaccinium* microsites than in red maple and chestnut oak microsites. Phosphorus was the only nutrient in the mineral soil that was not significantly lower under pines compared with the other tree species.

Pine and red maple microsites had significantly higher total C in mineral soil than *Vaccinium* and no-tree sites at 0.5 m (Table 5); there were no differences in total C at 1.0 m. Pine microsites had significantly higher C/N ratios in the mineral soil than all other microsites at the 0.5-m distance, and the C/N ratio under *Vaccinium* was significantly greater than that of chestnut oak and red maple microsites (Table 5). At 1.0 m, C/N ratio in the mineral soil was higher under pine microsites than under red maple microsites. Total C was not measured in the O horizon.

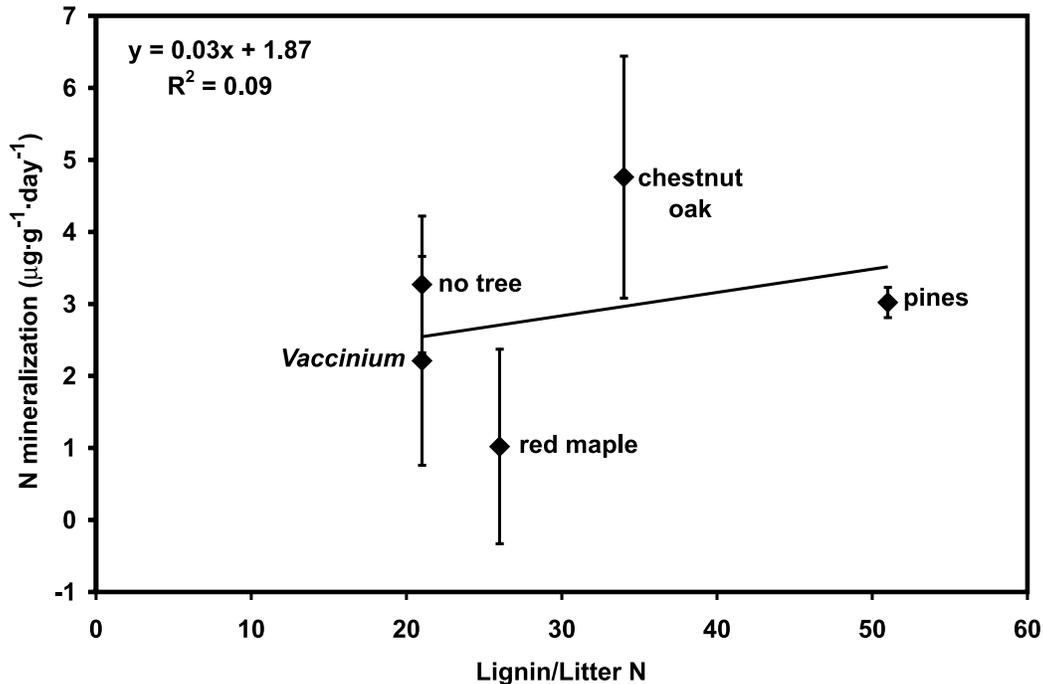
We examined soil properties in relation to litter quality; for no-tree and *Vaccinium* sites we used the lignin and N concentrations of scarlet oak, the dominant litter. The concentration of lignin in litter was negatively correlated with extractable Ca ( $p = 0.03$ ) and marginally significantly correlated with total N ( $p = 0.06$ ) in the O horizon (Fig. 3), but not significantly correlated with any of the other measured soil properties. The lignin/N ratio in litter was not correlated with N mineralization ( $p = 0.6$ , Fig. 4), despite large differ-

**Fig. 3.** Relationship between extractable Ca and total N in the O horizon and leaf litter lignin concentration. Labels indicate microsite type and corresponding leaf litter. Scarlet oak was used as the corresponding leaf litter for *Vaccinium* and no-tree microsites, since this was the dominant litter type for these microsites. Vertical and horizontal error bars indicate the standard error for O horizon soil nutrient and litter lignin concentration, respectively. Regression models yielded  $p$  values of 0.03 for extractable Ca and 0.06 for total N.



ences in lignin/N. The highest litter lignin/N ratio was found for pines (51), which had an N mineralization rate intermediate between those of chestnut oak and red maple micro-

**Fig. 4.** Relationship between lignin/N ratio in leaf litter and N mineralization in O horizon. Labels indicate microsite type and corresponding leaf litter. Scarlet oak was used as the corresponding leaf litter for lignin analysis in *Vaccinium* and no-tree microsites, since this was the dominant litter type for these microsites. Vertical error bars indicate the standard error for N mineralization.



sites. Red maple litter had the lowest lignin/N and the lowest N mineralization among microsites, contrary to our expectations or the prevailing paradigm of strong negative correlation between litter lignin/N and N mineralization.

## Discussion

One of the prevailing themes in studies of tree species effects on soils is a strong and inverse relationship between lignin/N ratio in litter and N mineralization (Binkley and Giardina 1998). In this study, red maple had the lowest lignin concentration, which we expected (Carreiro et al. 2000; Melillo et al. 1982), and which led to our hypothesis that red maple microsites would have high rates of N mineralization, as found previously (Finzi et al. 1998a). However, we measured the lowest rates of N mineralization in red maple microsites, which resulted in lignin/N in litter being a poor predictor of N mineralization. A study of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), and paper birch (*Betula papyrifera* Marsh.) litters also documented a poor relationship between lignin/N and N mineralization and found instead that the best predictor of forest floor N mineralization rate was N concentration in the forest floor (Thomas and Prescott 2000). In our study, red maple had relatively high forest floor and soil total N concentrations (despite low litter N concentrations), yet the lowest rate of N mineralization. We hypothesize that higher rates of N mineralization in oak microsites (despite relatively high lignin/N in litter) are related to decomposer specificity, such that decomposers with a greater efficiency for consuming oak litter dominate the soil biotic community (Mergen and Malcolm 1955; Nys et al. 1987).

*Vaccinium* microsites also had relatively low rates of N mineralization, especially compared with oak microsites. Gilliam et al. (2001) found a relationship between the presence of *Vaccinium vacillans* (Aiton) in the understory and low soil water  $\text{NO}_3$  in an Appalachian hardwood forest and attributed this, in part, to the role of associated ericoid mycorrhizae. Our five microsites potentially include three types of mycorrhizal associations, ectomycorrhizal (oaks and pines), endomycorrhizal (red maple), and ericoid mycorrhizal (*Vaccinium*). The ericoid mycorrhizae supported by ericaceous species such as *Vaccinium* spp. can limit N mineralization by secreting organic acids that are inhibitory to N-mineralizing microbes (Straker 1996). Although much remains to be learned about the functional differences within and among mycorrhizal groups, the presence of three different types of mycorrhizal associations could partially explain differences in nutrient cycling (Straker 1996; Smith and Read 1997), such as those found in this study.

Paradoxically, low litter lignin concentrations in red maple do not contribute to high rates of N mineralization or N availability, yet low lignin and high Ca concentrations in red maple litter do appear to contribute to greater availability of Ca in surface horizons compared with the other microsites (Fig. 3). Red maple microsites had higher extractable Ca in O horizon and mineral soils, as well as significantly higher Ca in litter, which relates to another theme common to studies of species effects on soils. Numerous studies have demonstrated that some species have a greater capacity than others to access soil cations, from an early paper on "calcium pumping" by dogwood trees (Thomas 1969) to more recent studies (Dijkstra and Smits 2002; Finzi et al. 1998b). Several mechanisms for enhanced cation access have been described, including differential uptake of exchangeable cations among tree species (Alban 1969; Dijkstra and Smits

2002), interspecific differences in fine root or mycorrhizal activity and their effects on the rate of organic acid release and stimulation of mineral dissolution (Tan 1986; Jongmans et al. 1997), and different mycorrhizal associations among species resulting in differential rates of nutrient acquisition (Read 1984). Since O horizons in this forest type are thin, we suggest that higher Ca in surface horizons is the result of greater acquisition of Ca by red maple fine roots or mycorrhizae and higher Ca return to the surface via litterfall. Distinguishing among the three potential mechanisms by which red maple accesses greater amounts of Ca will require additional research on fine root and mycorrhizal extent and activity.

A recent devastating pine bark beetle infestation in the region will likely hasten the demise of shortleaf and pitch pine, while continued fire suppression will enhance conditions for the proliferation of the fire-sensitive red maple (Abrams 1992). To the extent that surface soil chemistry is indeed caused by differences among species in nutrient uptake, nutrient return via litter, and differences in rates of N mineralization, changes in tree species composition will drive decadal-scale changes in surface soil acidity, Ca cycling, and possibly N cycling. Such shifts in nutrient cycling, although somewhat different from those we hypothesized, may have ecological consequences for the continued dominance of oak species in this forest system, whose numbers in the regeneration pool are already low (Arthur et al. 1998). To improve our understanding of the potential effects of shifts in species composition on nutrient cycling, further research should focus on differences in the soil biotic communities among these species. A classic litter decomposition study could also improve our understanding of how differences in the rates and end products of decomposition of the different litters influence how differences in nutrient cycling among the microsites are developed and maintained.

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