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Nutrient Uptake by a Diverse Spring Ephemeral Community

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Summary. Net production by the six most abundant species in a diverse spring ephemeral community was 66.8 g/m^2, and net uptake of nitrogen and potassium were 5.5 and 4.5 kg/ha respectively. These uptake rates are relatively large compared to those reported previously and to other fluxes of these nutrients in the site.

Introduction

Muller (1978, Muller and Bormann 1976) suggested that the spring ephemeral herb *Erythronium americanum* could significantly affect losses of nitrogen and potassium from a forested watershed at the Hubbard Brook Experimental Forest, New Hampshire. *E. americanum* grows during the brief period between snowmelt and the leafing-out of the deciduous canopy. The growth of *E. americanum* occurs as nutrient outputs from the watershed decline from their early spring maximum, and the magnitude of nitrogen and potassium uptake is similar to that of total system losses during that period. Little other above-ground biological activity is evident at this time. Accordingly, Muller and Bormann (1976) suggested that growth of *E. americanum* could act as a "vernal dam", retaining nutrients that might otherwise be lost from the ecosystem. Once the canopy has closed, the ephemerals senesce and release nitrogen and potassium at a time when trees are clearly active in growth and nutrient uptake. Thus, although the annual production and nutrient uptake by *E. americanum* is small in comparison to the production and nutrient uptake of trees, the timing of its activity could have a significant effect on nutrient losses from the system as a whole.

We examined the potential significance of nutrient uptake by the spring ephemeral community in a mesic hardwoods forest in south-central Indiana. In this area spring ephemerals are most abundant on rich north-facing slopes. Within such sites the spring-flowering herb community is diverse and appears to be highly productive. Visual comparisons of these areas with the Hubbard Brook forest suggested that the spring ephemerals are more abundant in suitable sites in Indiana (R.N. Muller, personal communication). Hubbard Brook occupies a position at the oligotrophic end of an eutrophic-oligotrophic spectrum of northern hardwood herbaceous communities (Siccama et al. 1970), while our study site is influenced by a calcareous substrate and has a higher pH and base saturation (5.8 and 47% respectively – Vitousek, unpublished data). Bard (1949) showed that more base-rich sites have the best developed spring ephemeral communities. Thus, the potential significance of the "vernal dam" effect on ecosystem nutrient dynamics might be even greater in richer communities. Information on vegetation, soils, litterfall and litterfall nutrient content, and nutrient concentrations in soil solution below the tree rooting zone were available for our site as a result of a comparative study of nitrate losses from disturbed ecosystems (Vitousek et al. 1979). We decided to measure productivity and nutrient uptake by spring ephemerals in this site and to compare our results with the magnitude of the major fluxes of nutrients in this system and with production and uptake by spring ephemerals at Hubbard Brook.

Methods

The study site was located on Indiana University property adjoining Lake Monroe in south-central Indiana. The 0.7 ha site is dominated by *Acer saccharum* (55% relative basal area) and *Fagus grandifolia* (17%), with 9 other tree species over 10 cm dbh. Spring flowering plants were censused and collected from plots located on two 80 m transects within the site. The 1 m^2 plots were located on each transect by a stratified random design. Each plot was censused in mid-February before above-ground growth had begun and twice weekly thereafter until the beginning of plant senescence.

The six most abundant species *(Dicentra canadensis*[1], *Erythronium americanum, Dentaria laciniata, Claytonia virginica, Arisaema triphyllum,* and *Podophyllum peltatum)* were selected for analysis of production and nutrient content. Five plants of each species were randomly selected near each of the twenty plots. These plants were washed in distilled water to remove attached soil particles and dried at 80 C in an oven to constant weight. Samples of each species were composited from each plot to yield 20 samples per species at each time. The samples were ground with a mortar and pestle and stored in glass vials in a dessicator until they could be analyzed.

Plant samples were digested using a persulfate wet oxidation procedure for total Kjeldahl nitrogen and phosphorus (Technicon Instrument Systems 1976), and nitrogen and phosphorus concentrations were determined colorimetrically on a Technicon Autoanalyzer II. Samples for cation analysis were digested using a dry-

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[1] Nomenclature following Gleason and Cronquist (1963).

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ashing procedure (Reiners and Reiners 1970) and analyzed using atomic absorption spectrophotometry. Net nutrient uptake was determined for each species by subtracting mid-February nutrient contents (tissue nutrient concentrations X biomass/unit area) from the nutrient contents at peak biomass.

Results and Discussion

An inventory of the spring herb flora of the site found 26 species growing and flowering in March and April (Table 1). Many of these species are not true ephemerals; they persist and grow through much of the summer (Sparling 1967). Of the six dominants studied, all but *P. peltatum* and *A. triphyllum* senesce soon after canopy development. *D. canadensis* was the most abundant species on the site. On the date of peak biomass for *D. canadensis*, the species contributed 55% of the total number of stems per m^2 of the six species studied in detail (Table 1).

The net uptake of nitrogen, phosphorus, calcium, magnesium, potassium, and sodium for each of the six species is reported in Table 2. Nitrogen and potassium uptake were much greater than the uptake of other ions studied. *D. canadensis* strongly dominated the site in terms of both production and nutrient uptake. For all species except *P. peltatum,* the relative magnitude of nitrogen uptake by each species paralleled its relative contribution to production. The negative value for *P. peltatum* suggests that this species makes most of its early growth through the translocation of nutrients from its very large rhizomes (Sohn and Policansky 1977).

Net uptake of these nutrients by spring ephemerals is compared with other major pools and fluxes of nutrients within this site in Table 3. Uptake of calcium, magnesium, and sodium are very small relative to the flux of these elements out of the system on an annual basis. However, net uptake of nitrogen and potassium are nearly equal to annual losses. Nitrogen uptake by ephemerals is 12% of the N in annual tree litterfall (a minimum estimate of tree uptake and translocation to above-ground parts) in this site, which is remarkable considering the restricted growth period of the spring flora.

Most strikingly, nitrogen uptake by the spring herb community is greater than the pool size of available nitrogen in the forest floor and upper mineral soil in late March (Table 3). Nitrogen

Table 1. Species inventory for study site (spring, 1979–1980). Mean number of stems/m^2 and the range (in 20 plots) are included for the six most abundant species

	Stems/m^2
Most abundant species	
Arisaema triphyllum	13/m^2 (4–34)
Claytonia virginica	112/m^2 (12–218)
Dentaria laciniata	45/m^2 (10–108)
Dicentra canadensis	217/m^2 (65–585)
Erythronium americanum	50/m^2 (2–128)
Podophyllum peltatum	9/m^2 (6–14)
Additional species	
Actaea alba	
Anemonella thalictroides	
Asarum canadense	
Caulophyllum thalictroides	
Dicentra cucullaria	
Erigenia bulbosa	
Hydrophyllum appendiculatum	
Hydrophyllum macrophyllum	
Jeffersonia diphylla	
Phlox divaricata	
Polemonium reptans	
Polygonatum pubescens	
Sanguinaria canadensis	
Stellaria pubera	
Stylophorum diphyllum	
Trillium gleasoni	
Trillium recurvatum	
Uvularia grandiflora	
Viola eriocarpa	
Viola sororia	
Species in the immediate vicinity	
Cardamine douglassii	
Delphinium tricorne	
Geranium maculatum	
Hepatica acutiloba	
Isopyrum biternatum	
Mertensia virginica	
Trillium sessile	

Table 2. Biomass in February, total net production (peaking standing crop minus February standing crop), and net uptake (see text) for the six abundant species of the spring ephemeral community

	Dicentra canadensis	*Erythronium americanum*	*Dentaria laciniata*	*Claytonia virginica*	*Arisaema triphyllum*	*Podophyllum peltatum*	Total
February biomass[a]	30.4 (8.6)[b]	1.5 (0.4)	5.5 (2.7)	4.0 (0.8)	1.2 (0.4)	9.7 (2.7)	52.3
Total net production	37.0 (11.4)	12.7 (2.2)	6.5 (3.2)	5.3 (1.4)	2.8 (0.4)	2.5 (0.6)	66.8
Net uptake[c]							
N	2.42	1.51	0.76	0.58	0.57	−0.31	5.53
P	0.02	0.07	0.01	0.02	0.02	−0.04	0.10
K	1.16	0.51	1.10	0.79	0.58	0.40	4.54
Ca	0.85	0.21	0.70	0.15	0.10	−0.23	1.78
Mg	0.30	0.08	0.05	0.14	0.03	0.02	0.62
Na	0.10	0.05	0.02	0.04	0.01	0.01	0.23

[a] g/m^2
[b] One standard error of the mean
[c] kg/ha

Table 3. Comparison of net nutrient uptake (February through April) of the spring herb community with estimated annual leaching losses, tree litterfall nutrient content, and soil nutrient pool sizes (forest floor plus the mineral soil to 15 cm depth). Annual losses were calculated by multiplying estimated hydrologic losses by element concentrations in samples collected by 10 porous cup lysimeters at 60 cm depth. Lysimeter samples were collected weekly for 14 months. The estimates of annual losses are likely to be rather rough approximations. Annual litterfall values were derived from two years of collections from fifteen 1.0 × 0.5 m littertraps within the site. Nutrient pool sizes reported are the extractable nutrient pool (extracted in 2 M KCl for nitrogen, ammonium acetate for cations, and acid fluoride for phosphorus). All units are kg/ha

Element	Net uptake	Annual loss	Tree litterfall	Available pool in soil
N	5.5	6[a]	48	4.5[a]
P	0.1	ND[b]	2.7	53
K	4.5	5	36	118
Ca	1.8	28	88	1,306
Mg	0.6	9	10	99
Na	0.2	6	4	40

[a] Ammonium-N plus nitrate-N. The available nitrate-N pool in late March was 1.8 kg/ha

[b] Not determined

uptake could significantly reduce this available nitrogen pool and thus reduce nitrogen losses, especially if nitrate (a very mobile anion) is utilized preferentially. Uptake by spring herbs could not significantly affect the availability of any of the other ions studied (at least within one season). Consequently, losses of the cations could be reduced only if the spring herbs significantly reduce the production or mobility of an anion such as nitrate (Johnson and Cole, in press).

These results suggest that the magnitude of nutrient uptake by spring ephemerals is sufficient to affect system-level fluxes of nitrogen. However, they do not address the most critical assumption of the vernal dam hypothesis, that the nutrients taken up by ephemerals would otherwise be lost from the system. A number of other processes could reduce or prevent such losses. Ammonium not taken up by plants could be retained within the soils by cation exchange. Additionally, a developed leaf canopy is not necessary for active uptake by tree roots. Edwards and Harris (1977) found that maximum fine root production and biomass in a Tennessee *Liriodendron* forest occurred before the trees leafed out in the spring. Maximum nutrient uptake need not coincide with peak root biomass, but the absence of above-ground activity is clearly insufficient to rule out nutrient uptake by trees as an important process.

Our results do show that uptake by spring ephemerals can be of a much larger magnitude than hitherto reported. Net nitrogen and potassium uptake exceeded the uptake observed by Muller between 5- and 6-fold. Indeed, the contribution of *E. americanum* alone was close to that observed by Muller, but *E. americanum* was the only important species at Hubbard Brook while it was not even the most important species in our site. The values presented here are somewhat conservative as only six of 26 species were included in our analysis. The importance of the spring herb component of deciduous forest ecosystems is worth experimental study.

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