

Seasonal storage of nutrients by perennial herbaceous species in undisturbed and disturbed deciduous hardwood forests

Mabry, Cathy M.^{1*}; Gerken, Michaelleen E.^{1,2} & Thompson, Janette R.^{1,3}

¹Department of Natural Resource Ecology and Management, Iowa State University, 339 Science II, Ames, IA 50011, USA;

²E-mail mgerken@iastate.edu; ³E-mail jrtr@iastate.edu;

*Corresponding author; Fax +1 5152942995; E-mail mabry@iastate.edu

Abstract

Question: Pollution and eutrophication of surface water is increasingly a problem in agricultural landscapes. Do intact (relatively undisturbed) and degraded forests differ in seasonal nutrient storage and therefore potential to ameliorate nutrient pollution?

Location: United States, Midwestern region.

Methods: We used three sets of paired plots, where intact plots were located close to disturbed woodlands. Herbaceous perennials located in eight 0.25 m² quadrats in the plots were harvested (in spring and mid-summer), dried, separated into above- and below-ground plant parts, and weighed to determine biomass. Nitrogen, phosphorus and potassium content of the plant tissues were then determined, and these data combined with biomass to estimate nutrient storage.

Results: In spring, intact sites had 62% greater above-ground biomass than disturbed sites and 75% greater below-ground biomass. In summer, below-ground biomass of intact plots was still much greater than that of disturbed plots (73 percent), but above-ground biomass was similar. Nutrient tissue concentration generally did not differ, nor did soil nutrient levels. The disturbed sites were largely missing one group of species, the spring ephemerals, and this accounted for the difference in biomass and nutrient storage between sites.

Conclusions: Relatively undisturbed woodlands in our study had a much greater capacity to store nutrients, and therefore ameliorate nutrient pollution, in early spring. This is significant because spring is also the time of highest potential leaching of nutrients into surface water.

Keywords: Above-ground biomass; Agricultural landscape; Below-ground biomass; Ephemeral; Pollution; Surface water.

Nomenclature: Anon. (1993+, 2005).

Introduction

The ecological consequences of nutrient over-enrichment of land and water is increasingly a global concern (Vitousek et al. 1997; Bennett et al. 2001). Pollution and eutrophication of water resulting from concentrated agricultural activities is one of the most serious ecological consequences (Vitousek et al. 1997; Carpenter et al. 1998). The Midwestern region of North America exemplifies these water nutrient pollution problems. There has been widespread loss of native perennial plant communities since European settlement, and agriculture has become more intensive, e.g. row cropping of corn and soy beans and large-scale animal confinement operations (Isenhardt et al. 1997). As a result, the number of impaired waterways is high and expected to rise. This is also a critical issue beyond the region because the nutrient pollution from the Midwest contributes directly to the hypoxic zone in the Gulf of Mexico (Mitsch et al. 2001).

One current focus of research aimed at addressing nutrient pollution is to establish or restore perennial plant communities, including forests, in critical landscape positions because these plant communities act as sinks for excess nutrients (Carpenter et al. 1998; Bennett et al. 2001; Mitsch et al. 2001). Investigators have found significant retention of nutrients and sediment by forests embedded in agricultural landscapes across North America, including Georgia (Lowrance et al. 1984), Maryland (Peterjohn & Correll 1984; Jordan et al. 1993), Delaware (Phillips et al. 1993), and Iowa (Isenhardt et al. 1997; Schultz et al. 2004).

Research dating back at least to the classic Hubbard Brook ecosystem studies in New Hampshire suggests that herbaceous species are critical to forest nutrient retention. These studies documented loss of nutrients following clear cutting and herbicide application (Bormann et al. 1968), and pointed to a spring ephemeral species, *Erythronium americanum*, as a critical component of this system (Muller & Bormann 1976). They proposed that *Erythronium* acts as a 'vernal dam' for nutrients, holding on to nutrients at a time of high potential leaching

loss and releasing them in time for uptake by aestival species (Muller & Bormann 1976). This idea has been supported by studies of *Claytonia virginica*, another spring ephemeral (Anderson & Eikmeier 2000), and for more diverse spring ephemeral communities (Blank et al. 1980; Peterson & Rolfe 1982). However, questions remain about the vernal dam concept. Not all spring ephemerals have rapid spring nitrogen uptake (Rothstein & Zak 2001), microbes may also play a significant role in nutrient retention spring (Groffman et al. 1993).

Beyond the vernal dam questions, there are other gaps in our knowledge. The studies cited above have clearly showed that forests can intercept significant amounts of nutrients, but do not provide insight into the functional capacity of the herbaceous community as a whole to retain nutrients (Muller & Bormann 1976; Blank et al. 1980; Peterson & Rolfe 1982; Anderson & Eikmeier 2000), including summer species (Peterson & Rolfe 1982; Tessier & Raynal 2003). In addition, most newly established riparian forests (e.g. riparian buffers) in the midwest do not include a perennial herbaceous layer, and many remnant natural riparian forests have lost much of this layer, primarily due to overgrazing by cattle (Whitney 1994; Mabry 2002), and there are no data to show how this might correspond to loss of function.

Iowa, as part of the intensively agricultural upper Midwest of the United States, is particularly well suited for studying the nutrient dynamics of forests in landscapes dominated by agriculture. Extensive conversion of land to agricultural uses, including grazing and row-cropping, has reduced forested area in the state by two-thirds (Jungst et al. 1998). Forested remnants tend to be concentrated in the uplands of eastern and southern Iowa, and riparian gallery forests throughout the state (Thompson 1992), with most remnants disturbed by human activities (Whitney 1994; Mabry 2002).

Because of the gaps in our understanding of the role herbaceous species play in nutrient retention, we conducted a study to (1) estimate the nutrient storage capacity of an entire herbaceous community across the growing season; (2) examine the role spring ephemeral species play in early-season nutrient storage; and (3) compare the nutrient storage capacity of woodlands with a diverse, native herbaceous layer to that of low diversity or degraded woodlands dominated by generalist forest species.

Material and Methods

Study area

The study was conducted in central Iowa, USA, (41°41'-41°57' N, 92°50'-93°32' W). Remnant central hardwood forests are concentrated along riparian areas and associated slopes and uplands, with oak-hickory and maple-basswood communities most common (Van der Linden & Farrar 1984). We identified three forested areas where intact and disturbed forests occur in close proximity. Each area had riparian forest located along higher-order streams, was about 20-40 ha in size, and was embedded in a landscape largely devoted to intensive row crop production of corn and soybeans.

No forests in our region have been entirely free of the influence of human activities (Whitney 1994). Thus, our intact forests were chosen because they were under permanent protection (two sites) or had been the subject of active understory restoration (one site), and had not been grazed by cattle. Because one of our research questions focused on the role of spring ephemerals in nutrient retention, we also chose sites that, upon visual inspection, had a dense cover of spring ephemeral species (e.g. species that complete their entire life cycle before canopy closure). These intact sites were chosen for maximal contrast with nearby areas that had been degraded by a known history of heavy cattle grazing, had no history of restoration, and had few spring ephemerals evident. Within each site, the intact and grazed areas were separated by no more than 0.5 km. The intact and disturbed sites at each study area shared similar overstory canopy dominants: *Quercus alba*, and *Q. rubra* (the two protected sites), and *Celtis occidentalis*, *Juglans nigra* and *Prunus serotina* (the restored site).

Plot selection and variables measured

In 2004 we located one 20 m² plot in each of the intact and disturbed sections, for a total of six plots. Within each plot we placed eight 0.25 m² quadrats at 3-m intervals along a single diagonal in both spring (between April 15-25) and summer (between June 22-July 6) for a total of 16 quadrats per plot. In spring, quadrats were randomly assigned to either the right or left side of the transect line. Summer quadrats were harvested from the opposite side. Harvest dates were timed to coincide with peak biomass production.

In order to quantify differences among intact and disturbed sites, we compared them for species richness, and mean frequency of occurrence of spring ephemerals (complete life occurs in spring) and spring herbaceous species (flowering occurs in spring), with frequency based on percent occurrence in quadrats. We also com-

pared sites for the frequency of occurrence of generalist species using a method developed by Swink & Wilhelm (1994) as adapted for the Iowa Flora (Iowa State University Ada Hayden Herbarium 2004). Species that occur in a wide range of sites, including those disturbed by humans, are assigned low values on a scale of habitat conservatism that runs from 0-10. We grouped species in our data set that were assigned values of 0-2 into a combined group of generalist species.

We identified species present and harvested all above- and below-ground herbaceous plant material in each quadrat. Harvested plants were stored in a cooler, rinsed thoroughly with water, separated into roots and stems, and oven-dried at 65 °C for 48 h. Dried samples were weighed to estimate biomass. After weighing, the plant tissue concentration of nitrogen, phosphorus, and potassium (N, P, and K, respectively) was determined (digestion and analyses followed Anderson & Henderson 1986). Some quadrats had insufficient herbaceous material present to perform digestion of the plant material. Our spring harvest included data from 20-24 quadrats across the three sites, but the summer harvest included only 18-20 quadrats from three sites for the above-ground data and 12-16 quadrats from two sites for the below-ground data.

To examine whether differences in plant tissue nutrient concentration or plant biomass could be attributed to soil nutrient levels, we collected soil samples from the first and last quadrat along the transect in each plot. Soil was cold-stored and then allowed to air-dry for one week. Soil N was extracted by the Dumas method of dry combustion (Bremner 1996). Soil P and K were extracted using the Mehlich-3 method (Mehlich 1978). All plant and soil nutrient analyses were done at the Iowa State University Soil and Plant Analysis Laboratory, Ames, Iowa.

Data analyses

Nutrient storage, the amount of nutrients retained by our study sites seasonally, was determined using the biomass and leaf tissue nutrient concentrations. We multiplied the biomass by the plant tissue nutrient

concentration measured for each quadrat. This was then converted to kg/ha and an average value was calculated for each plot. Two-way analysis of variance was used to compare sites. The independent variables were treatment (intact versus disturbed sites) and each pair of plots was grouped by site and treated as block factors. The dependent variables were plant biomass, tissue and soil nutrient concentration, estimated nutrient storage and floristic quality metrics. Factors were fixed, and biomass and nutrient storage values were square root transformed to improve normality. The possibility that biomass and richness were related was tested using Pearson Product Moment correlation between these factors at the quadrat level. All analyses were conducted using DataDesk® Version 6 software (1997). We declared statistical significance at $p \leq 0.05$.

Results

Differences in floristic quality metrics between the sites confirmed that we effectively captured site differences. The undisturbed sites had 92% more occurrences of spring ephemerals in the quadrats, and 23% more occurrences of spring ephemerals combined with spring growing species. Intact sites also had 36% fewer occurrences of generalist compared to disturbed sites. Each of the intact sites had at least one spring ephemeral or spring growing species that was absent from the corresponding disturbed site. The most common spring species at the intact sites included *Claytonia virginica*, *Dicentra cucullaria*, *Enemion biternatum*, *Erythronium albidum*, *Hydrophyllum virginianum*, *Phlox divaricata*, and *Sanguinaria canadense* (App. 1).

In spring, intact sites had 62% more above-ground biomass than disturbed sites and 75% greater below-ground biomass (Table 1). In summer, below-ground biomass of intact plots was still much greater than that of disturbed plots (73%), but above-ground biomass was similar (Table 1). The greater spring above-ground biomass was highly statistically significant. Although not detectable statistically, the other biomass differences all showed consistent trends, with the intact sites far

Table 1. Mean biomass (g) in 0.25-m² quadrats and ANOVA results for forest herbaceous plants for three intact versus three disturbed forests in central Iowa, USA. Numbers in parentheses \pm 1 SD.

	Intact	Disturbed	df	MS error	F-ratio	P
Spring						
above-ground	14.99 (8.8)	5.72 (4.9)	1,2	0.045	46.22	0.021
below-ground	24.53 (19.7)	6.03 (2.1)	1,2	1.100	7.10	0.117
Summer						
above-ground	11.61 (4.9)	10.92 (6.4)	1,2	0.079	0.59	0.523
below-ground	23.62 (19.3)	6.29 (4.5)	1,2	1.911	3.92	0.186

Table 2. Mean estimated nutrient storage ($\text{kg} \cdot \text{ha}^{-1}$) and ANOVA results for herbaceous plants for three intact versus three disturbed forests in central Iowa, USA. Numbers in parentheses are ± 1 SD. $N = 3$ for all means except summer below-ground with $N = 2$.

	Intact	Disturbed	df	MS error	F-ratio	P
Nitrogen						
Spring						
above-ground	19.4 (9.54)	7.8 (6.76)	1,2	0.008	533.5	0.002
below-ground	15.5 (9.31)	4.4 (0.13)	1,2	0.349	13.02	0.069
Summer						
above-ground	10.0 (3.64)	9.7 (4.35)	1,2	0.161	0.03	0.884
below-ground	14.2 (11.53)	4.1 (0.73)	1,1	1.02	2.41	0.364
Potassium						
Spring						
above-ground	21.7 (12.63)	8.9 (6.43)	1,2	0.045	93.27	0.011
below-ground	19.2 (16.3)	5.7 (2.21)	1,2	0.9	5.33	0.147
Summer						
above-ground	19.6 (13.84)	19.4 (9.99)	1,2	0.316	0.02	0.909
below-ground	19.4 (11.50)	7.6 (0.61)	1,1	0.75	3.23	0.323
Phosphorus						
Spring						
above-ground	1.5 (0.80)	0.4 (0.24)	1,2	0.009	51.84	0.019
below-ground	1.4 (1.09)	0.5 (0.19)	1,2	0.047	5.99	0.134
Summer						
above-ground	2.0 (1.16)	1.7 (0.82)	1,2	0.17	0.88	0.447
below-ground	2.6 (0.97)	1.0 (0.12)	1,1	0.65	5.95	0.248

outperforming the disturbed sites in biomass accumulation (Table 1).

In spring, estimated storage of the three nutrients was from 59 to 73% greater in intact versus disturbed sites (Table 2). In summer estimated above-ground nutrient storage was similar between sites, but below-ground nutrient storage in the intact sites remained from 61 to 71% greater (Table 2). These differences were detectable statistically at the $p \leq 0.05$ level for above-ground storage in spring for all three nutrients.

There were few differences in plant tissue nutrient concentration between the disturbed and intact sites and there were no patterns between sites to suggest that plant tissue concentration was driving the nutrient storage differences we observed (Table 3). Thus, differences in plant tissue nutrient concentration could

not explain the differences observed between sites. Soil nutrient concentration also did not differ between intact and disturbed sites for nitrogen, phosphorus or potassium (data not presented, minimum $p \geq 0.369$).

The sites did not differ in species richness in spring. Disturbed sites had greater summer richness and greater overall richness, the reverse of what would be expected if richness helped explain differences in nutrient storage (Table 4). There was a very high correlation between biomass and species richness at the quadrat level in spring at the disturbed sites and summer at both the intact and disturbed sites; however, there was no evidence of a correlation between these factors for the intact sites in spring (Table 4).

Table 3. Mean percent plant tissue concentrations of forest herbaceous plant tissue for intact versus disturbed forests in the Midwest, USA. Numbers in parentheses are ± 1 SD. $N = 3$ for all means except summer below-ground with $N = 2$.

	Nitrogen		Potassium		Phosphorus	
	Intact	Disturbed	Intact	Disturbed	Intact	Disturbed
Spring						
above-ground	3.51 (0.48)	3.49 (0.13)	3.71 (0.97)	3.78 (0.36)	0.25 (0.03)	0.18 (0.03)
below-ground	1.76 (0.36)	1.88 (0.23)	1.91 (0.12)	2.1 (0.37)	0.15 (0.02)	0.19 (0.02)
Summer						
above ground	1.86 (0.35)	1.94 (0.71)	3.76 (1.51)	3.7 (1.17)	.38 (0.14)	0.32 (0.10)
below ground	1.19 (0.05)	1.39 (0.77)	1.85 (0.51)	2.55 (1.19)	0.28 (0.14)	0.31 (0.09)

Table 4. Mean species richness per plot and ANOVA results for three intact and disturbed sites in the midwest, USA. Numbers adjacent to means are ± 1 SD; numbers below the means are correlation coefficients between quadrat level richness and biomass, followed by *P*-values.

	Intact	Disturbed	df	MS error	<i>F</i> -ratio	<i>P</i>
Spring	6.8 (1.01) -0.147 (0.4923)	6.3 (0.82) 0.616 (0.0013)	1,2	2.28	0.112	0.769
Summer	4.9 (1.01) 0.719 (< 0.0001)	6.8 (1.11) 0.690 (0.0002)	1,2	1.99	2.542	0.252

Discussion

Our study is novel in that we examined the entire forest herbaceous layer rather than a single or small subset of species and we examined the loss of function associated with degraded sites. Our intact forested sites had a much greater storage capacity of nitrogen, potassium and phosphorus compared to our disturbed sites in both above- and below-ground plant tissue in spring, and in below-ground plant tissue in summer. We could attribute this to the much greater plant biomass in spring for intact compared to the disturbed sites, which could, in turn, be attributed to the presence of spring ephemerals and other spring growing species in intact sites and their absence in the disturbed sites. In fact, it appears that the strong correlation between biomass and richness observed for disturbed sites in spring and summer and the intact sites in summer was overwhelmed by the very high biomass of intact sites in spring.

Our results excluded a number of alternative explanations for the differences between sites in nutrient storage. There were few differences in soil nutrient content or plant tissue nutrient concentration between the disturbed and intact sites and there were no patterns between sites to suggest that plant tissue concentration was driving the nutrient storage differences we observed. Thus, we could conclude that the greater plant biomass in intact sites was not due to more robust growth resulting from more nutrient rich soils. We could also exclude differences in species richness between intact and disturbed sites as an explanation for the differences in nutrient storage capacity in spring, e.g. that intact sites had greater biomass simply because they had greater species per unit sample areas.

Not all the differences we observed were detectable statistically at the $p \leq 0.05$ level; however, this was due only to the very high biomass accumulation at our restored intact site. This site had mean below-ground biomass that was six times greater than the other intact sites in spring and seven times greater in the summer, a pattern reflected in the large standard deviation of the mean. Because in this study nutrient storage differences were due to biomass differences, this site also had nutrient storage of a similar

greater magnitude. Had this intact site been more similar to the other sites, the spring and summer below-ground biomass differences would also have been detected statistically. Thus, while there was variation among intact sites in nutrient storage, the three intact sites all had greater biomass and nutrient storage than their paired disturbed site. In addition, the very high biomass at the restored site is an encouraging result, as it reinforces the potential for restoration of ecosystem function.

Other studies have pointed to a significant capacity of forest perennial herbaceous species to store nutrients; however, ours is the first to quantify this capacity for the entire suite of species found at a site, for both spring and aestival species, and the first to compare this capacity between largely intact sites and those that had been degraded. This study also provides support for the hypothesis that spring ephemerals are especially important for nutrient retention in forests, as our site differences were driven by biomass differences that could be attributed to spring ephemerals and spring growing species. Most important, our study provided support for the idea that forest herbaceous layers act as nutrient sinks in forests, and therefore may help ameliorate nutrient pollution of surface waters by storing nutrients at a time when they are particularly prone to leaching.

Our estimated nutrient storage for the entire spring community of 35 kg.ha⁻¹ of nitrogen is greater than the maximum uptake measured for individual species or small groups of species, reinforcing the importance of measuring the whole community. For example, uptake of nitrogen by the spring ephemeral *Claytonia virginica* was estimated as 18 kg.ha⁻¹ in Tennessee (Anderson & Eickmeier 2000), and 5.6 kg.ha⁻¹ in Indiana (Peterson & Rolfe 1982). In Indiana, uptake of *Erythronium albidum* was 1.0 kg.ha⁻¹ (Peterson & Rolfe 1982), while the closely related *E. americanum* uptake was 1.5 kg.ha⁻¹ (Blank et al. 1980). Comparative uptake for the other nutrients in these studies was similar. Uptake was 5.5 kg.ha⁻¹ recorded for a suite of six species in Indiana (Blank et al. 1980), and 10.6 kg.ha⁻¹ for a suite of four species, also in Indiana (Peterson & Rolfe 1982). Again, patterns for the other nutrients were similar.

Our results point to additional areas of research

needed to more completely understand the role herbaceous perennials play in nutrient cycling, to make broader generalizations about their function in deciduous forest systems, and to make recommendations for their restoration to degraded forests and addition to newly constructed riparian forest buffers.

There is evidence that seasonal nutrient storage varies both locally and regionally. For example, as we noted in a previous paragraph there is evidence for regional differences in nutrient uptake by *Claytonia virginica*. In a field trial this species changed both biomass and leaf tissue concentration in response to fertilization, especially under high light levels (Eickmeier & Schussler 1993), suggesting fertility is one mechanism for this regional difference. In addition, small-scale variation in plant tissue concentrations (due to resorption) has been tied to soil fertility and moisture levels (Boerner 1986; DeMars & Boerner 1997), although direct relationships between nutrients and resorption were complicated by mycorrhizal infection and possibly light levels (Boerner 1986). Additional research on these factors is needed to clarify the interactions and to understand how to achieve the greatest functional capacity in application.

The relative importance of plants versus the microbial community in storing nutrients in spring also needs greater resolution. Several studies have suggested that microbes can immobilize up to an order of magnitude more nitrogen than spring ephemerals (Vitousek & Matson 1984; Zak et al. 1986; Groffman et al. 1993). However, the capacity of microbes to store nutrients may vary seasonally and with soil drainage (Groffman et al. 1993), and may not exceed that of plants when the entire vegetation community is measured rather than a single plant species and when uptake is used as the metric rather than total nutrients stored in biomass (Tessier & Raynal 2003). The relative importance of plants and microbes in spring nutrient uptake may also vary with plant species. For example, Rothstein (2000) studied a site dominated by *Allium tricoccum*, which compared unfavorably to microbes in spring nutrient uptake; however, *Allium* has low nutrient uptake rates compared other spring ephemeral species (Rothstein & Zak 2001). Another possibility is that herbaceous species and microbes are competing for nitrogen (Muller 2003 and references therein). Clearly, much remains to be uncovered concerning the relative function of spring herbaceous species and the microbial community.

There are also more applied questions to be addressed: What species would be best to add to degraded forests and new riparian forests buffers, and how many species are needed in order to approach the functional capacity of intact forests? Our study and the literature suggests that groups can have far greater nutrient uptake capacity compared to a single species (Muller & Bormann 1976),

although not always (Anderson & Eickmeier 2000).

One spring growing species in our region, *Hydrophyllum virginianum*, produces tremendous biomass in spring, retains very high biomass below-ground biomass in summer, and produces additional vegetative growth in the fall (C. Mabry pers. obs.). Our intact restored site was dominated by *Hydrophyllum* and had a nutrient storage capacity that far exceeded the storage of other intact sites with a more diverse spring ephemeral community because of this tremendous biomass accumulation (hence the high variation observed in spring biomass, Table 2). Thus, the possibility that the functional capacity of an intact forest can be reached with a single or a small group of spring growing species rather than a rich array of spring ephemerals should be investigated. The answer has important practical implications because *Hydrophyllum* is much easier to propagate, and grows and matures quickly compared to true spring ephemerals, most of which have somewhat exacting germination requirements, and very slow growth to maturity (Cullina 2000).

Conclusions

Results from the forests we studied support the idea that the spring ephemeral and spring herbaceous plant community are important for nutrient retention, as nutrient storage was greatly reduced in sites where these species were sparse or absent. However, the broader functional implication of this work will not be clear until we have a better understanding of how plants, nutrients, light, fungi and microbes interact. Spring ephemeral communities are difficult and time consuming to establish, thus it would be fruitful to discover whether there are key functional species in this system that, if introduced alone, can functionally mimic the intact community.

Acknowledgements. This work was supported in part by McIntire-Stennis funds, State of Iowa funds, the Leopold Center for Sustainable Agriculture, and Pioneer Foundation. We thank Larissa Mottl, Steve Lekwa, and Don Farrar for permission to use their study sites, and Nettie Spitz, Troy Bowman and Adam Puderbaugh for assistance in collecting and processing samples. We also thank Lars Brudvig, Jennifer Fraterrigo, and two anonymous reviewers for their comments on the manuscript.

References

- Anon. 1993+. *Flora of North America North of Mexico*. 7 Vols. Flora of North America Editorial Committee, New York, NY, US.
- Anon. 1997. *DataDesk® Version 6*. Data Description, Inc. Ithaca, NY, US.
- Anon. 2004. *Coefficients of conservatism for Iowa plants*. URL: <http://www.public.iastate.edu/~herbarium>. Iowa State University- Ada Hayden Herbarium.
- Anon. 2005. *Plants database, Version 3.5*. URL: <http://plants.usda.gov>. Data compiled from various sources by Mark W. Skinner. USDA National Plant Data Center, Baton Rouge, LA 70874-4490 US.
- Anderson, D.L. & Henderson, L.J. 1986. Sealed chamber digestion for plant nutrient analyses. *Agronomy Journal* 78: 937-939.
- Anderson, W.B. & Eickmeier, W.G. 2000. Nutrient resorption in *Claytonia virginica* L.: implications for deciduous forest nutrient cycling. *Canadian Journal of Botany* 78: 832-839.
- Bennett, E., Carpenter, S.R. & Caraco, N.F. 2001. Human impact on erodable phosphorus and eutrophication: A global perspective. *BioScience* 51: 227-234.
- Blank, J., Olson, R. & Vitousek, P. 1980. Nutrient uptake by a diverse spring ephemeral community. *Oecologia* 47: 96-98.
- Boerner, R.E.J. 1986. Seasonal nutrient dynamics, nutrient resorption, and mycorrhizal infection intensity of two perennial forest herbs. *American Journal of Botany* 73: 1249-1257.
- Bormann, F.H., Likens, G.E., Fisher, D.W. & Pierce, R.S. 1968. Nutrient loss accelerated by clear-cutting a forest ecosystem. *Science* 159: 882-884.
- Bremner, J.M. 1996. Nitrogen – total. In: Sparks, D.L. et al. (eds). *Methods of soil analysis. Part 3. Chemical methods*, pp. 1085-1121. The Soil Science Society of America Book Series 5. Soil Science Society of America and American Society of Agronomy, Madison, WI, US.
- Carpenter, S., Caraco, D., Correll, D., Howarth, R., Sharpley, A. & Smith, V. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8: 559-568.
- Cullina, W. 2000. *Guide to growing and propagating wildflowers*. New England Wild Flower Society, Houghton Mifflin Co., Boston, MA, US.
- DeMars, B.G. & Boerner, R.E.J. 1997. Foliar phosphorus and nitrogen resorption in three woodland herbs of contrasting phenology. *Castanea* 62: 43-54.
- Eickmeier, W. & Schussler, E. 1993. Responses of spring ephemeral *Claytonia virginica* L. to light and nutrient manipulations and implications for the 'vernal dam' hypothesis. *Bulletin of the Torrey Botanical Club* 120: 157-165.
- Groffman, P.M., Zak, D.R., Christensen, S., Mosier, A. & Tiedje, J.M. 1993. Early spring nitrogen dynamics in a temperate forest landscape. *Ecology* 74: 1579-1585.
- Isenhardt, T., Schultz, R. & Colletti, J. 1997. Watershed restoration and agricultural practices in the midwest: Bear Creek of Iowa. In: Williams, J., Wood, C. & Dombeck, M. (eds.) *Watershed restoration: Principles and practices*, pp. 318-334. American Fisheries Society, Bethesda, MD, US.
- Jordan, T., Correll, D. & Weller, D. 1993. Nutrient interception by a riparian forest receiving inputs from adjacent cropland. *Journal of Environmental Quality* 22: 467-473.
- Jungst, S.E., Farrar, D.R. & Brandrup, M. 1998. The forest resources of Iowa in 1980. *Journal of the Iowa Academy of Science* 105: 61-66.
- Kucera, C.L. 1952. An ecological study of a hardwood forest area in central Iowa. *Ecology Monographs* 22: 283-299.
- Lowrance, R., Todd, R., Fail, J., Hendrickson, O., Leonard, R. & Asmussen, L. 1984. Riparian forests as filters in agricultural watersheds. *Bioscience* 34: 374-377.
- Mabry, C. 2002. Effect of cattle grazing on woodlands in central Iowa. *Journal of the Iowa Academy of Science* 109: 53-60.
- Mehlich, A. 1978. New extractant for soil test evaluation of phosphorus, potassium, magnesium, calcium, sodium, manganese, and zinc. *Communications in Soil Science and Plant Analysis* 9: 477-492.
- Mitsch, W., Day, J., Gilliam, J., Groffman, P., Hey, D., Randall, G. & Wang, N. 2001. Reducing nitrogen loading to the Gulf of Mexico from the Mississippi River Basin: Strategies to counter a persistent ecological problem. *Bioscience* 51: 373-388.
- Muller, R. 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In: Gilliam, F., & Roberts, M. (eds.) *The herbaceous layer in forests of Eastern North America*, pp. 15-37, Oxford University Press, Oxford, UK.
- Muller, R. & Bormann, F. 1976. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest system. *Science* 193: 1126-1128.
- Peterjohn, W. & Correll, D. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian buffer. *Ecology* 65: 1466-1475.
- Peterson, D. & Rolfe, G. 1982. Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. *American Midland Naturalist* 107: 325-329.
- Phillips, P., Denver, J., Shedlock, R. & Hamilton, P. 1993. Effect of forested wetlands on nitrate concentrations in ground water and surface water on the Delmarva peninsula. *Wetlands* 13: 75-83.
- Rothstein, D. 2000. Spring ephemeral herbs and nitrogen cycling in a northern hardwood forest: An experimental test of the vernal dam hypothesis. *Oecologia* 124: 446-453.
- Rothstein, D.E. & Zak, D.R. 2001. Relationships between plant nitrogen economy and life history in three deciduous-forest herbs. *Journal of Ecology* 89: 385-394.
- Schultz, R., Isenhardt, T., Simpkins, W. & Colletti, J. 2004. Riparian forest buffers in agroecosystems – lessons learned from the Bear Creek watershed, central Iowa, USA. *Agroforestry Systems* 61: 35-50.
- Swink, F. & Wilhelm, G. 1994. *Plants of the Chicago region*, 4th ed. Indiana Academy of Science, Indianapolis, IN, US.
- Tessier, J. & Raynal, D. 2003. Vernal nitrogen and phosphorus retention by forest understory vegetation and soil microbes. *Plant and Soil* 256: 443-453.
- Thompson, J.R. 1992. *Prairies, forests, and wetlands: the*

- Restoration of natural landscapes in Iowa*. University of Iowa Press, Iowa City, IA, US.
- Van der Linden, P.J. & Farrar, D.R. 1984. *Forest and shade trees of Iowa*. Iowa State University Press, Ames, IA, US.
- Vitousek, P.M. & Matson, P.A. 1984. Mechanisms of nitrogen retention in forest ecosystems: a field experiment. *Science* 225: 51-52.
- Vitousek, P.M., Aber, J., Howarth, R.W., Likens, G.E., Matson, P.W., Schindler, D.W., Schlesinger, W.H. & Tilman, D.G. 1997. Human alteration of the global nitrogen cycle: causes and consequences. *Issues in Ecology No. 1*. Ecological Society of America. Washington, DC, US.
- Whitney, G.G. 1994. *From coastal wilderness to fruited plain*. Cambridge University Press, Cambridge, UK.
- Zak, D.R., Pregitzer, K.S. & Host, G.E. 1986. Landscape variation in nitrogen mineralization and nitrification. *Canadian Journal of Forest Research* 16: 1258-1263.

Received 12 June 2006;

Accepted 22 March 2007;

Co-ordinating Editor: A. Acosta.

*For Apps. 1-3, see JVS/AVS Electronic Archives;
www.opuluspress.se/*

App. 1. Species occurring in at least 50 percent of quadrats in intact and disturbed plots in three central Iowa sites, USA. Species in bold only are true spring ephemerals; species in bold with an asterisk are those that reach peak growth in early spring with the ephemerals, but persist vegetatively or reappear in summer/fall. Numbers in parentheses are frequency of occurrence (number of quadrats/plot). Sites 1-2 are under permanent protection; site 3 is restored.

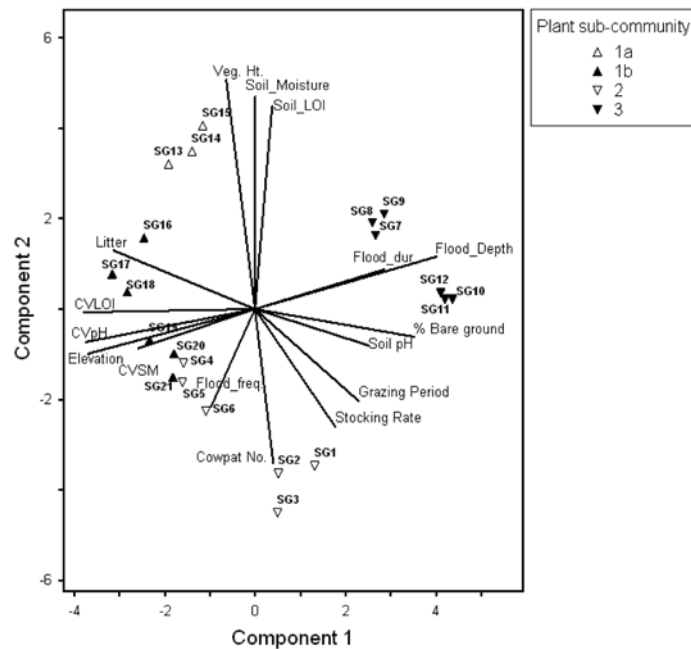
	Intact	Disturbed
Site 1	<i>Circaea lutetiana</i> (5) <i>Claytonia virginica</i> (8) <i>Osmorhiza longistylis</i> (5) <i>Sanicula odorata</i> (8) <i>Viola</i> spp. (5)	<i>Circaea lutetiana</i> (5) <i>Cryptotaenia canadensis</i> (4) <i>Ellisia nyctelea</i> (5) <i>Festuca subverticillata</i> (7) <i>Galium aparine</i> (6) <i>Osmorhiza longistylis</i> (6) <i>Sanicula odorata</i> (8)
Site 2	<i>Claytonia virginica</i> (8) <i>Dicentra cucullaria</i> (5) <i>Erythronium albidum</i> (8) *<i>Hydrophyllum virginianum</i> (7) <i>Enemion biternatum</i> *<i>Sanguinaria canadense</i> (8)	<i>Hydrophyllum virginianum</i> (4) <i>Osmorhiza</i> spp (4) <i>Viola</i> spp. (7)
Site 3	*<i>Hydrophyllum virginianum</i> (8) <i>Osmorhiza longistylis</i> (5) *<i>Phlox divaricata</i> (6) *<i>Viola</i> spp. (4)	<i>Carex blanda</i> (7) <i>Ellisia nyctelea</i> (7) <i>Galium aparine</i> (6) <i>Hydrophyllum virginianum</i> (5) <i>Osmorhiza longistylis</i> (8) <i>Ranunculus abortivus</i> (5) <i>Sanicula odorata</i> (8) <i>Teucrium canadense</i> (4) <i>Viola</i> spp. (4)

App. 2. Spearmann rank correlations of untransformed environmental variables used in PCA analysis. Soil LOI = soil loss-on-ignition. CV = Coefficient of variation.

	Elev- ation (m)	Flood Duration (%)	Flood Depth (m)	Flood Fre- quency	Soil LOI (%)	Soil Moisture (%)	Soil pH	Litter (%)	Cow- pats	Bare- ground (%)	Veg. ht. (cm)	Stocking Rate (LU/ha)	Grazing period (days)	Soil LOI CV	Soil Moist- ure CV	Soil pH CV
Elevation (m)	1															
Flood Duration (%)	-0.998 **	1														
Flood Depth (m)	-0.939 **	0.928 **	1													
Flood Frequency	0.671 **	-0.672 **	-0.672 **	1												
Soil LOI (%)	-0.517 *	0.511 *	0.525 *	-0.543 *	1											
Soil Moisture (%)	-0.264	0.249	0.366	-0.391	0.879 **	1										
Soil pH	-0.558 **	0.557 **	0.535 *	-0.354	-0.031	-0.250	1									
Litter (%)	0.340	-0.356	-0.271	0.122	0.220	0.529 *	-0.763 **	1								
Cowpats	-0.018	0.019	0.030	0.212	-0.472 *	-0.511 *	0.205	-0.190	1							
Bare Ground (%)	-0.406	0.415	0.379	-0.080	-0.003	-0.279	0.610 **	-0.709 **	0.411	1						
Veg. ht. (cm)	-0.125	0.113	0.218	-0.378	0.665 **	0.848 **	-0.415	0.614 **	-0.666 **	-0.595 **	1					
Stocking Rate (LU/ha)	-0.164	0.168	0.105	0.189	-0.484 *	-0.648 **	0.451 *	-0.502 *	0.905 **	0.651 **	-0.858 **	1				
Grazing period (days)	-0.135	0.144	0.073	0.206	-0.488 *	-0.670 **	0.452 *	-0.572 **	0.866 **	0.714 **	-0.890 **	0.986 **	1			
Soil LOI CV	0.332	-0.347	-0.346	0.304	-0.375	-0.122	-0.408	0.548 *	0.092	-0.632 **	0.145	-0.117	-0.195	1		
Soil Moisture CV	0.325	-0.335	-0.389	0.376	-0.467 *	-0.293	-0.491 *	0.500 *	0.238	-0.552 **	-0.058	0.065	-0.010	0.892 **	1	
Soil pH CV	0.643 **	-0.665 **	-0.548 *	0.528 *	-0.607 **	-0.287	-0.470 *	0.520 *	0.264	-0.530 *	-0.049	0.048	-0.026	0.710 **	0.712 **	1

**Correlation significant at 1% level (2-tailed)

*Correlation significant at 5% level (2-tailed)



App. 3. PCA of environmental variables showing ordination graph of samples scores for first two principal components, with vector overlays illustrating the correlation the principal components with the original environmental variables. Sampling grids are denoted SG, and the cluster analysis groupings (plant sub-communities) are overlain on the graph.