Diversity and Plant Species Cover After Long-Term Fertilization In Three Bogs

BIOS 569 – Practicum in Field Biology

Andrew Murray

1660 W Turtle Creek Dr.

Advisor: Dr. Scott Bridgham

Summer of 2002

Abstract. Low-nutrient ecosystems, such as peatlands, are limited in production by nutrients, generally nitrogen and phosphorous in wetlands. Plant species in infertile sites such as peatlands have developed many adaptations for survival. The nutrient levels in a particular site play an important part in determining the characteristics of the plant community that inhabit it. Sites with higher diversity levels may be able to resist change. This project investigated plant community response to a consistent disturbance regime in the form of nitrogen and phosphorous fertilization over a five-year period. The experiment took place on three bogs at UNDERC. Percent cover of individual plant species was measured at the end of the five-year project. Nitrogen fertilization resulted in nearly complete elimination of *Sphagnum*, although phosphorous fertilization along with nitrogen had a mediating effect. *Chamaedaphne calyculata* increased cover in response to nitrogen fertilization. Most other changes were variable. Diversity level did not seem to have an effect on the response of the bogs. The widely varying responses of individual plant species and the bogs to fertilization suggest that many more factors than nutrients are involved in determining the plant community and diversity of low-nutrient sites.

Introduction

Peatlands are an important type of nutrient-poor ecosystem. Peatlands contain nearly one-third of the world's global soil carbon pool (Bridgham et al 1998), and as such could have large impacts on global climate change (Bridgham et al 1995). Nutrient inputs to peatlands are increasing, not unlike other global ecosystems, as a result of increased industry and agriculture driven by rapid population growth (Vitousek 1994). Increased nutrient inputs can lead to important changes in the mechanisms at work in the effected ecosystems. The loss of diversity in European peatlands has been a cause for great concern (Bridgham et al 1996). However, these effects are neither as widely reported nor as well studied in North America (Bedford 1999).

Plants living infertile environments have to find ways to survive under constant low levels of nutrients. The limiting nutrient is that which, when added will bring about increased growth (Chapin et al 1996). In bogs, nitrogen has been found to be the most common limiting nutrient, however, phosphorous can also be limiting. In many cases, both nutrients can be limiting, although one nutrient can usually be considered primarily limiting (Güsewell et al 1998). Many adaptations and strategies have evolved in these plants to make the best use of the nutrients available. These adaptations include but are not limited to preferential allocation of resources to roots, mychorrhizal associations, evergreen leaves, luxury consumption, and low tissue nutrient requirements, (Chapin 1980) While no one species combines all these adaptations, all are frequently used, and some are commonly found in combination. In general, these plant species also show growth rates (Chapin 1988).

In addition to having to survive in a low-nutrient environment, these plants also have to deal with interspecific competition. Competition in low-nutrient sites is, predictably, over nutrients. The debate over interspecific competition, commonly known as the 'Grime-Tilman' debate, centers over the importance and mechanisms of interspecific competition in infertile environments (Aerts 1999). However, this debate continues as data showing conclusive evidence has not yet been presented.

After adapting to the low-nutrient levels, as well as other factors like pH, hydrology, and local flora, the resulting plant community displays a certain level of diversity. Diversity is a combination of the number of species present, and the relative proportions of each species. Low-nutrient levels are often associated with high diversity levels, although the relationship between the two has not been determined (Bedford 1999). It has also been argued that high diversity has important effects on ecosystem processes, and in particular can increase a system's resistance (Chapin et al 1997).

The goal of this project was to determine the response of three unaltered, Northern, ombrotrophic bogs to consistent, increased nutrient input of nitrogen and phosphorous over a period of five years. The levels of nitrogen and phosphorous added were to be comparable to those found in areas of moderate deposition, to illustrate the effects of even small changes in nutrient availability. In particular, the effects of increased nutrients on plant community diversity and individual plant species were emphasized.

Materials and Methods

The study was conducted on three bogs (pH=3.8) at the University of Notre Dame Environmental Research Center near Land O'Lakes, Wisconsin. The bogs consist mainly of a *Sphagnum spp.* carpet, ericaceous shrubs, and a few *Carex spp.* Donut was the smallest bog and had the least tree cover of the three. South Gate was the most heavily treed, mostly *Picea mariana* with a few *Larix laricina*, and in the middle in terms of area. County Road B had similar tree cover to South Gate, although not quite as dense, and had the largest area. The bogs displayed both intrasite and intersite heterogeneity.

Fertilization of the bogs began in 1998. In each bog, four 32 x 32 ha treatment plots were marked out for the control plot as well as nitrogen (N), phosphorous (P), and nitrogen and phosphorous (N+P) additions. Within each treatment plot, five $1 m^2$ plots were randomly selected as permanent plots, to be measured for percent cover. Nitrogen fertilization was undertaken, in both N and N+P plots, through additions of urea ($Co(NH_2)_2$) in 6 g N/m^2 concentration. For phosphorous fertilization, superphosphate ($Ca(H_2PO_4)_2$) was added in a 2 g P/m^2 concentration. The control plots received no fertilization throughout the duration of the experiment. All fertilizer was added as a solid with hand spreaders. Beginning in 1998, fertilizer was spread twice during the growing season, with half of the total added per application. For 2001 and 2002, the full annual treatment was added at the beginning of the growing season.

Percent cover was taken for each of the $1 m^2$ permanent plots using the point-intercept method. The data was gathered between the 7th and 10th of July, 2002, during peak growing season. The data was broken down per species for the tree saplings, shrubs, forbs, and grasses, although all *Sphagnum spp.* were treated as one value. Only trees <1m in height were counted in the percent cover values, since taller trees were present before the treatments began. Tree cover, for trees taller than 1m, cover was measured with a visual estimate in each of the treatments. Percent cover values for *Sphagnum* have a maximum value of 100%, since *Sphagnum* cover was measured as a monolayer, with 100% indicating complete groundcover. However, percent cover for the shrubs and grasses could exceed 100%, as they exist in a multidimensional space, and thus have no theoretical maximum.

Percent cover data was also used to calculate evenness, richness, and diversity. Diversity was calculated using the Shannon-Weiner Diversity Index. A two-way analysis of variance (ANOVA) was used to determine the effects of site, treatment, and interaction on diversity. Tukey Post-Hoc Comparison Tests were used to make pairwise comparisons between the treatments and the control. The data was transformed using the natural log function in order to normalize the data. For all statistical analysis, a p value of 0.05 was used to determine significance.

Percent cover data was also analyzed using ANOVAs to determine cover differences for species between site and treatment. This analysis was undertaken only for species averaging >5.00% cover in any individual treatment plot. Fifteen species of shrub, graminoid, tree, and moss met this qualification. Five species were present >5% in at all three site, while 3 more were >5% in two sites. Seven more species were present >5% in only one site. After determining the species to be analyzed, the data was transformed using the square root function in an attempt to normalize the data. While the attempt did not succeed, the transformed data was more normal than the original data. Species that were >5% in a treatment in either two or all three of the sites were analyzed with two-way ANOVAs to determine the effect of site and treatment on percent cover. Tukey Post-Hoc Comparison Tests were used to show pairwise comparisons between the sites and treatments.

. Species with >5% cover in only one site were submitted to one-way ANOVAs to determine differences in treatment. Tukey Post-Hoc Comparison Tests were again used to show pairwise comparisons between the treatments. The species analyzed in only one site were also analyzed using Kruskal-Wallis Non-Parametric Tests to supplement any differences indicated by the ANOVAs.

Results

The changes in diversity and percent cover for individual species differed depending on the site. In order to adequately address all the factors, each one will be presented separately.

The Shannon-Weiner values for diversity differed with site. In general, Donut was the least diverse bog, while County Road B and South Gate displayed similar diversity levels. In County Road B Bog, the N (1.96±0.07) and N+P (2.00±0.14) treatments were greater than the C (1.60±0.25) plot, but P (1.76±0.23) did not differ from anything (Table 1). In Donut, the N treatment (1.47±0.23) showed greater diversity than all of the other treatments (Table 1). In South Gate, the P (1.47±0.15) plot exhibited greatly decreased diversity in comparison to all the other plots (Table 1). Evenness and richness for the sites were also calculated, and both indicators behaved similarly to diversity (data not shown). The diversity values from 1998 (data not shown) differ, but not in a similar fashion to the 2002 data.

For seven of the fifteen tested individual species, although percent cover was widely variable between sites, it did not change within sites. Two species which were present in all three bogs showed the same behavior in all three sites. *Carex oligosperma* was present at >5% in all three sites, but did not exhibit changes in cover in any treatment. *Sphagnum spp.* cover, which existed as a solid carpet in both the C and P plots, was greatly reduced in both the N and N+P plots, although consistently higher in the N+P plots than in the N plots (Figure 1). The other species present at >5% in all bogs, differed between the sites. *Chamaedaphne calyculata* showed higher percent cover in the N+P plot than in the C and P in County Road B, increased percent cover versus C and P in both N and N+P in Donut, but in South Gate, no differences were found (Figure 2, Table 2). *Kalmia polifolia* showed thicker cover in the N+P plot in County Road B, no differences in Donut, and was not present in the P plot in South Gate (Figure 2, Table 2). *Vaccinium oxycoccos* had higher cover in both the N and N+P plots. In County Road B, the cover in both the N and N+P plots was greater than C, but N+P was also greater than the P plot cover. In Donut, both N and N+P were greater than both C and P. In South Gate, only the N plot differed, but in this case was greater than C, N+P, and P (Figure 2, Table 2). For species present in two of the sites, only *Scheuchzeria palustris* in Donut showed any difference in treatment effect, where the percent cover of *S. palustris* was greater in the N plots than in any of the others (Table 2). *Ledum groenlandicum* and *Picea mariana*, both present in both County Road B and South Gate, showed no treatment effect.

For the species present in only one site, the Kruskal-Wallis tests supported the results of the ANOVAs in six of the seven cases. The exception was for *Carex* *paupercula*, which went from p=0.048 in the ANOVA to p=0.082 in the Kruskal-Wallis test. *Carex trisperma*, in South Gate, exhibited higher percent cover in the N+P plots versus all other treatments (Table 2). In the N plot of South Gate, *Liparis loeselii* had a higher percent cover than in both N+P and P plots. *Andromeda glaucophylla, Carex lasiocarpa, Carex paupercula, Eriophorum spissum,* and *Vaccinium myrtiloides* showed no response to the treatment.

Discussion

The response of both diversity and most plant species differed in each site. This suggests that even similar bog communities may have variable responses to nutrient enrichment depending on the individual characteristics of the particular bog.

Most of the changes in individual plant species cover can be attributed to competitive interactions in the peatlands. Most species in nutrient-poor systems like bogs are adapted for slow-growth and show low rates of nutrient uptake even when nutrient inputs in the soil increase (Chapin 1980). In such an environment, species with the ability to survive in low nutrient conditions and also increase growth in response to an increase in nutrients will exploit species with less plastic growth regimes.

Furthermore, the majority of the changes in plant cover occurred in N and N+P treatments. Very little response was seen in the P plots in comparison to the C plots. This may indicate the bogs are generally N limited. However, the fact that most plants living in infertile environments have a low capacity to take up phosphate (Chapin 1988) may have limited the response generated by the phosphorous fertilization.

C. calyculata appears to have this type of capability, as it made up the largest percentage of plants in the N and N+P plots, suggesting N limitation. The low levels of

C. calyculata in the N+P plot in South Gate bog were influenced by a large increase in tree cover in that plot, and particularly a large number of downed trees. The response of *C. calyculata* to increased nutrients has been documented by Bartsch (1994), who described increasing biomass production; higher shoot density and increased leaf-area. These results indicate a competitive advantage of *C. calyculata* over most bog species. Furthermore, the increased biomass could also confer an advantage to *C. calyculata* in competition for light, especially over plant species with creeping or extremely short growth forms. *C. calyculata*'s evergreen character also most likely gives it added advantages (Chapin 1980).

V. oxycoccos is another species that seemed to be able to respond to N addition. The particularly strong response of *V. oxycoccos* in County Road B bog appeared to be due to the large number of *Sphagnum* hummocks present in that bog. The creeping growth form of *V. oxycoccos* allowed it to grow on the sides of the hummocks, where other species were less successful.

However, the most interesting response was the change in cover of *Sphagnum*. Furthermore, unlike all the other species that exhibited a response to the fertilization, *Sphagnum* had a similar response in all the bogs, regardless of the intersite heterogeneity *Sphagnum*, the primary mat forming species, and most integral part of the bog community, showed drastic decreases when supplied with increased nitrogen. However, the *Sphagnum* made a recovery, although limited, in the N+P treatments. The decrease of *Sphagnum* cover in the N plots suggests a toxic effect of nitrogen levels. Interestingly, the same levels of N in the N+P plot did not induce the same response. This may indicate the ability of P to balance out the excess levels of N, which seems to inhibit *Sphagnum*. Another factor that seemed to have an effect on *Sphagnum* levels was the increased shading in the N and N+P plots. As discussed above, the thick growth of *C. calyculata* in the N and N+P plots allowed less light to reach species close to the mat, like *Sphagnum*. However, since light limitation does not account for the recovery of *Sphagnum* in the N+P sites, both factors probably contributed to the eventual result.

In two of the three sites, County Road B and Donut, increased N levels led to increased diversity. In the third, South Gate, P enrichment led to a drastic drop in diversity. It seems unusual that the two more diverse bogs, County Road B and South Gate, would show such different effects. However, Bedford (1999) warns that nutrients are not the only determinant of richness, particularly in undisturbed sites like those in this study. Furthermore, problems exist in comparing responses within community types.

Even in this small number of similar bogs with similar pH, hydrology, and plant communities, a wide array of results were found, with *Sphagnum* being the only consistent change. Overall, the results suggest that different species have different nutrient requirements, and particular species' response to nutrient additions varies depending on the particular combination of competitors, as well as the various chemical and geological factors at work at its site. The integration of all these specific species responses over the wetland would then result in changes in diversity. The variable results of both diversity and plant species cover between the bogs emphasize how much work still needs to be done to understand the interactions between low-nutrient systems and the plant communities inhabiting them.

Acknowledgements

I would like, first and foremost, to thank the Bernard J. Hank Family Endowment for the funds that allowed me to participate in this project. I would also like to thank Scott Bridgham and Colleen Iversen for their help in organizing the paper and processing the data, Laurie Kellogg for her help and guidance during the field work on this project, and James Philson for his invaluable assistance in the field

Table 1. Shannon-Weiner diversity index results for each plot. In County Road B, both the N and N+P plots were different from the C plots (N v. C:p=0.034, N+P v. C:p=0.017). In Donut, the N treatment differed from the C and P plots (N v. C:p=0.05, N v. p=0.05).

	C	**N**	**N+P**	**P**
County Road B	1.5988±0.2531	1.9617±0.0719[a]	2.0008±0.1402[a]	1.7554±0.2258
Donut	1.1621±0.1613	1.4743±0.2344[ad]	1.2546±0.1041	1.1642±0.1757
South Gate	1.7706±0.1501	1.8387±0.1654	1.7515±0.1903	1.4715±0.1497[abc]

a- different than C
b- different than N
c- different than N+P
d- different than P

Table 2. Percent cover (±SE) of species found at greater than 5% cover in a treatment in a site. Significant increases in percent cover were seen for *C. trisperma* in the N+P plot of South Gate bog over all other plots(N+P v. C: p=0.027, N+P v. N:p=0.034, N+P v. P:p=0.006). *L. loeselii* showed significant increases in the N plot versus the N+P and P plots (N v. N+P:p=0.011, N v. P:p=0.001). *S. palustris* showed significant increases in the N plot over all other plots (N v. C:p=0.001, N v. N+P:p=0.011, N v. P:p=0.002).

Species	Site	C	N	N+P	P
A. glaucophylla	County Rd B	3.00±3.26	13.00±12.42	17.50±15.81	8.00±3.71
C. lasiocarpa	County Rd B	2.00±2.09	6.50±10.84	4.00±2.24	12.00±7.37
C. paupercula	South Gate	6.50±4.54	32.00±35.15	0.00	2.50±4.33
C. trisperma	South Gate	3.00±4.11	10.50±23.48	56.00±39.83^{abd}	0.00
E. spissum	Donut	4.00±6.27	0.00	0.00	30.00+47.47
L. groenlandicum	County Rd B	6.00±9.78	5.00±11.18	34.00±21.84	3.00±3.26
	South Gate	35.50±11.37	45.50±27.92	46.50±17.46	39.50±22.87
L. loeselii	South Gate	31.50±10.84	68.50±12.94^{cd}	23.50±17.19	12.50±10.00
P. mariana	County Rd B	7.50±7.91	11.00±9.94	13.00±9.25	5.50±6.71
	South Gate	1.00±2.24	11.50±11.12	21.00±45.57	6.00±8.94
S. palustris	County Rd B	8.00±4.11	13.50±13.42	16.00±3.35	9.00±10.98
	Donut	1.50±3.35	24.50±14.40^{acd}	4.50±4.47	2.00±3.26
V. myrtiloides	South Gate	2.50±5.59	23.50±52.55	0.00	0.00

a- different than C
b- different than N
c- different than N+P
d- different than P

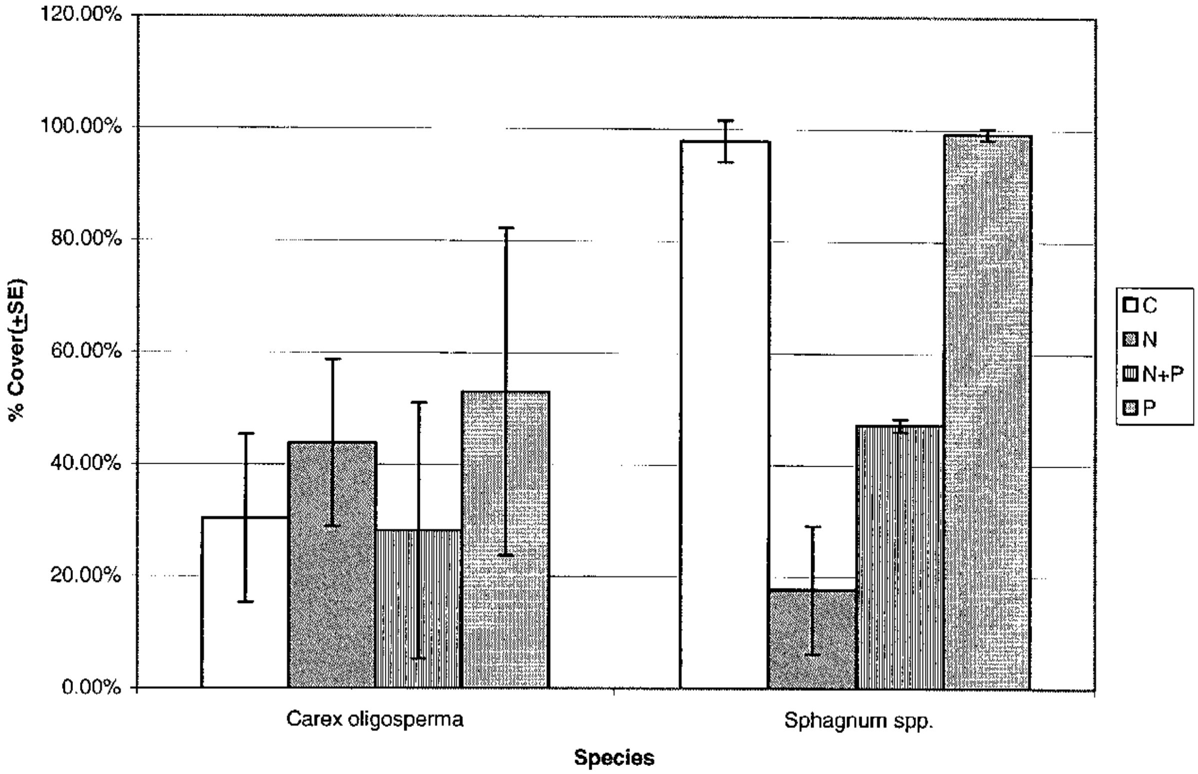
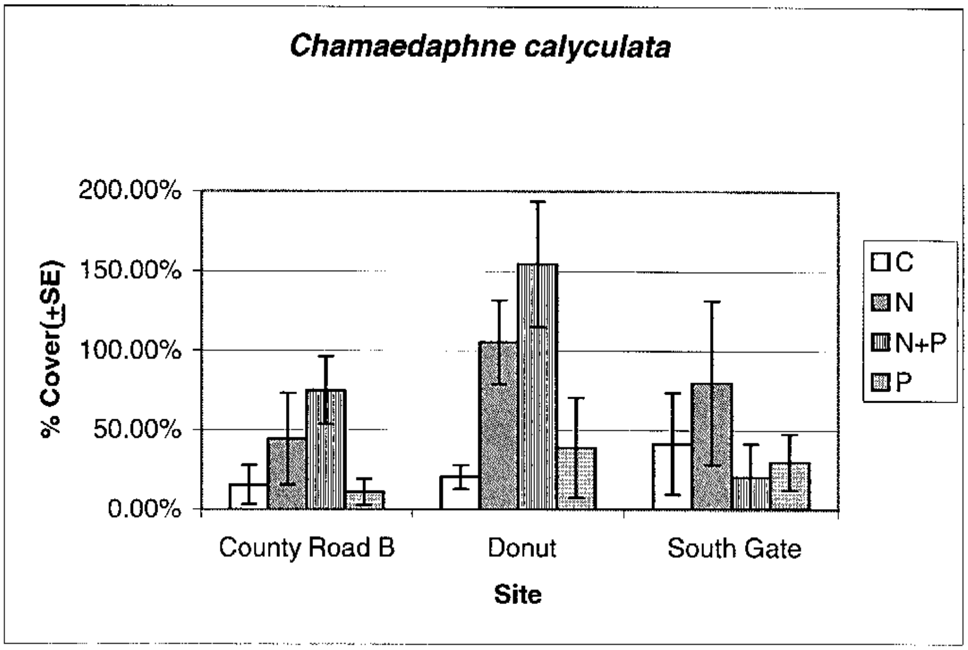
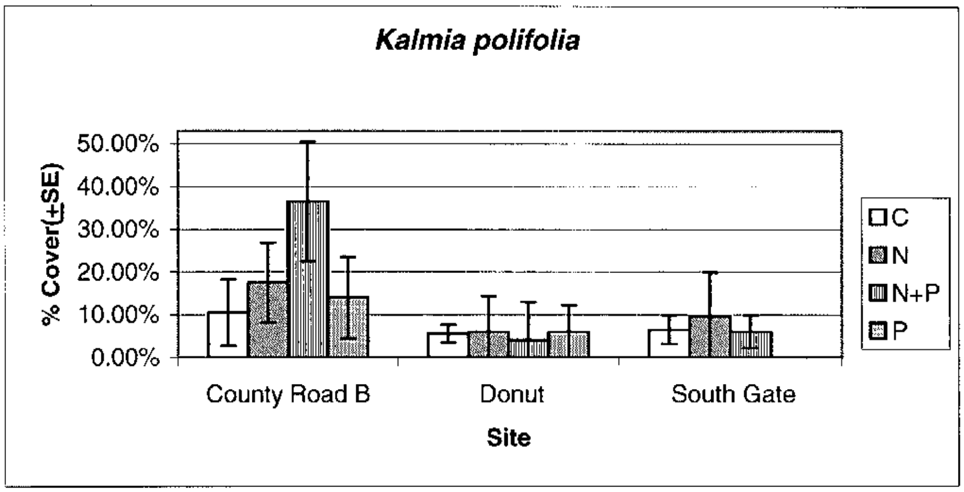


Figure 1. Percent cover of *C. oligosperma* and *Sphagnum*. Cover of *C. oligosperma* did not differ between treatments. *Sphagnum* showed significant decreases in both N and N+P in comparison to C and P (N v. C:p=0.00, N v. P:p=0.00, N+P v. C:p=0.00, N+P v. P:p=0.00), and N was even significantly depressed in comparison to N+P(N v. N+P:p=0.00)


Chamaedaphne calyculata
% Cover(±SE)
200.00%
150.00%
100.00%
50.00%
0.00%
County Road B
Donut
South Gate
Site
C
N
N+P
P


Kalmia polifolia
% Cover(±SE)
50.00%
40.00%
30.00%
20.00%
10.00%
0.00%
County Road B
Donut
South Gate
Site
C
N
N+P
P

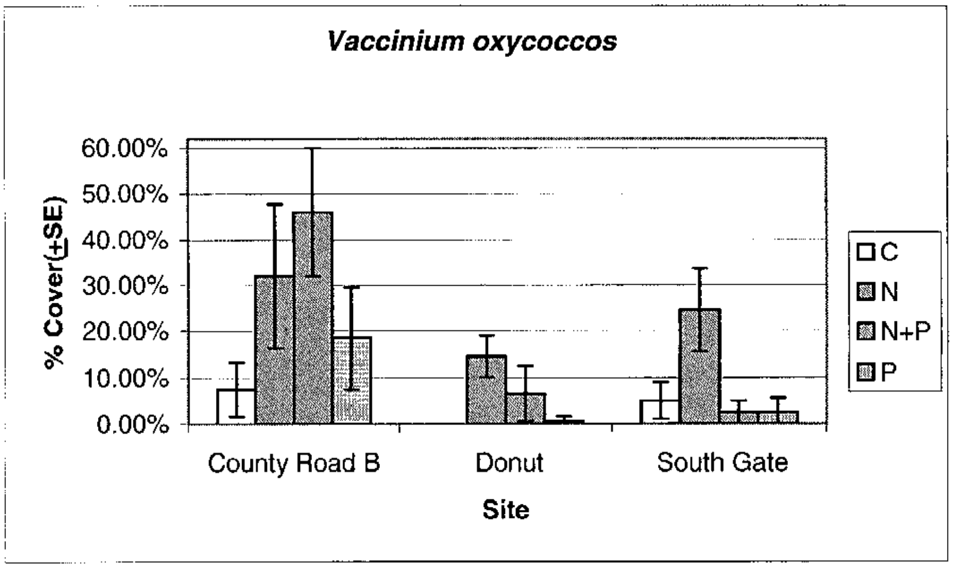

Vaccinium oxycoccos
% Cover(±SE)
60.00%
50.00%
40.00%
30.00%
20.00%
10.00%
0.00%
County Road B
Donut
South Gate
Site
C
N
N+P
P

Figure 2. Percent cover of *C. calyculata*, *K. polifolia*, and *V. oxycoccos*. *C. calyculata* showed significant increases of cover in County Road B in the N+P plots versus the C and P plots (N+P v. C:p=0.002, N+P v. P:p=0.001), in Donut in the N and N+P plots over C and P(N v. C:p=0.00, N v. P:p=0.004, N+P v. C:p=0.00, N+P v. P:p=0.00). *K. polifolia* in County Road B showed significant increases in cover over the C and P plots (N+P v. C:p=0.011, N+P v. P:p=0.033). *V. oxycoccos* showed significant increases of cover in County Road B in the N plot versus the C plot (N v. C:p=0.01) and in the N+P plot over the C and the P plots (N+P v. C:p=0.00, N+P v. P:p=0.020). In Donut, *V. oxycoccos*, both the N and N+P plots had significant cover increases over the C and P plots (N v. C:p=0.00, N v. P:p=0.00, N+P v. C:p=0.007, N+P v. P:p=0.021), while in South Gate, the N plot showed a significant increase over all other plots (N v. C:p=0.005, N v. N+P:p=0.001, N v. P:p=0.001).

Works Cited

1. Aerts, R. 1999. Interspecific competition in natural-plant communities: mechanisms, trade-offs and plant soil feedbacks. Journal of Experimental Botany. 50:29-37.
2. Bartsch, I. 1994. Effects of fertilization on growth and nutrient use by *Chamaedaphne calyculata* in a raised bog. Canadian Journal of Botany. 72:323-329
3. Bedford, B.L., M.R. Walbridge, A. Aldous. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology. 80:2151-2169.
4. Bridgham, S.D., C.A. Johnston, J. Pastor, K. Updegraff. 1995. Potential feedbacks of northern wetlands on climate change. BioScience. 45:262-274.
5. Bridgham, S.D., J. Pastor, J.A. Janssens, C. Chapin. 1996. Multiple limiting gradients in peatlands: a call for a new paradigm. Wetlands. 16:45-65.
6. Bridgham, S.D., K. Updegraff, J. Pastor. 1998. Carbon, nitrogen, and phosphorous mineralization in northern wetlands. Ecology. 79:1545-1561.
7. Chapin III, F.S. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-60.
8. Chapin III, F.S. 1988. Ecological aspects of plant mineral nutrition. Advances in Plant Nutrition. 3:161-191.

9. Chapin III, F.S., P.M. Vitousek, K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. Am. Nat. 127:48-58.

10. Chapin III, F.S., B.H. Walker, R.J. Hobbs, D.U. Hooper, J.H. Lawton, O.E. Sala, D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science. 277:500-504.

11. Güsewell, S., W. Koerselman, J.T.A. Verhoeven. 1998. The n:p ratio and the nutrient limitation of wetland plants. Bulletin of the Geobotanical Institute. 63:77-90.

12. Vitousek, P.M. 1994. Beyond global warming: ecology and global change. Ecology. 75:1861-1876.