The effects of varying levels of nitrogen on the relative growth rate and foliar nitrogen concentration of *Nasturtium officinale* and *Cardamine pensylvanica.*

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Abstract

Over the past century, anthropogenic activities have nearly doubled the amount of nitrogen entering the terrestrial nitrogen cycle. Due to this increase in a previously limiting nutrient, invasive nitrophilous species have become more dominant in wetland ecosystems, altering the species composition and diversity (Vitousek *et al.* 1997). To determine the effect of species type and increased nitrogen deposition on plant growth, forty-eight non-native *Nasturtium officinale* plants and forty-eight native *Cardamine pensylvanica* plants were subjected to an additional 0, 0.0184, 0.0368, 0.0736 millimoles of nitrogen per week for a duration of twenty-eight days. The interaction of species and nitrogen level had no significant effect on the plants relative growth rate. The relative growth rate of the plants did depend on species. The interaction of species and nitrogen level had a significant effect on the plants foliar nitrogen concentration ($F=136.2554$, $p<0.0001$). The foliar nitrogen concentration of *N. officinale* remained high across all treatment groups, while the foliar nitrogen concentration of *C. pensylvanica* increased with increasing nitrogen levels. These results suggest that *N. officinale* may have a competitive advantage over *C. pensylvanica* regardless of nitrogen levels.

Introduction

Nitrogen is the most abundant element in the atmosphere as molecular nitrogen (N_2). However, it is only available to support the growth of plants and microbes after it is converted into reactive forms such as ammonium (NH_4^+) and nitrate (NO_3^-) (Galloway *et al.* 2003). Previously, nitrogen fixation by several specialized bacteria accounted for the major inputs of biologically available nitrogen in the biosphere (Galloway *et al.* 2003). Over the past century, anthropogenic activities such as the cultivation of legumes, the combustion of fossil fuels, and the production of nitrogen fertilizers have approximately doubled the rate of nitrogen input into the terrestrial nitrogen cycle (Vitousek *et al.* 1997), with this rate increasing at roughly 0.3% per year (Olsen *et al.* 2001).

Nitrogen is the mineral nutrient needed in the largest amounts by plants, and therefore it is usually also the limiting factor for plant growth in terrestrial ecosystems, particularly in temperate and boreal regions (Vitousek and Howarth 1991). These areas are also the regions experiencing extensive increases in biologically accessible nitrogen due to nitrogen deposition (Vitousek *et al.* 1997). As long as other nutrients or resources are not secondarily limiting, most plant species respond to an increase in nitrogen availability with an increase in growth (Morecroft *et al.* 1994). However, the extent of plant growth response to nitrogen is species specific (Bradshaw *et al.* 1964). In habitats which are nitrogen limited under pristine conditions, native plants are often adapted to function optimally under this limitation and, in some cases, higher levels of nitrogen can prove detrimental to their growth (Press *et al.* 1986). As a result, nitrophilous species have increased in dominance in a variety of ecosystems, suppressing other plant species and reducing species diversity (Vitousek *et al.* 1997).

Changes in species composition, loss of overall plant diversity, conversion of a unique flora to one dominated by a few common species, and replacement of native species by exotics have been reported in connection with nitrogen deposition in several types of wetlands (Aerts and Berendse 1988; Ehrenfeld and Schneider 1991; Kooijman 1992). The most severe consequences have occurred in the wetlands of northern Europe where levels of nitrogen deposition, that range from 30-170 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$(Berendse *et al.* 1993) has converted many species-rich wetlands to virtually mono-specific stands of nitrophilous species (Verhoeven *et al.* 1996). While maximum deposition rates are lower in North America (Lovett 1994), nitrogen deposition is well above background levels, and outputs from agricultural watersheds and urban expansion can be substantial (Jordan *et al.* 1997). A number of wetlands in North America have already experienced losses of native plants (Ehrenfeld 1983).

Wetlands play a key role in global biogeochemical cycles. For example, wetlands function as net sinks for organic carbon because of the anaerobic nature of their soils (Morris 1991). Locally, wetlands serve as habitats for wildlife, as flood control systems, as stabilizers and sink for sediments, as reservoirs for water, and as natural water filters (Mitsch and Gosselink 1986; Peterjohn and Correll 1984). Changes in species composition due to increased nitrogen loading within wetlands threaten to alter the function of these ecosystems (Morris 1991).

The invasion of non-indigenous plants is considered one of the primary threats to rare and endangered species (Wilcove *et al.* 1998), and to the integrity and function of entire ecosystems (Williamson 1996). Species are termed invasive if they have characteristics that allow them to thrive after being introduced into a non-native habitat

(Merriam and Feil 2002). One of the factors that facilitate the competitive superiority of exotic invasives is their physiological plasticity, or ability to maximally utilize available resources, including nutrients (Hastwell and Panetta 2004). A variety of studies have documented the effect of nitrogen enrichment on the growth rate and competitive relationships between invasive and non-invasive wetland species (Svengsouk and Mitsch 2001; Wetzel and van der Valk 1998). For example, the results of nutrient additions to invasive species *Typha latifolia* and native species *Schoenoplectus tabernaemontani* showed that *T. latifolia* responded to an increase in the nutrients nitrogen and phosphorous at a greater rate than *S. Tabernaemontani* (Svengsouk and Mitsch 2001).

One notable invasive species that encroaches on the integrity of wetlands throughout North America is the perennial herb, *Nasturtium officinale* R. Br., commonly known as watercress (Les and Mehrhoff 1999). Introduced to North America from Britain in the 1800s (Les and Mehrhoff 1999), *N. officinale* is currently listed as an invasive species throughout much of the United States (Holm *et al.* 1997). *N. officinale* occurs at the edges of rivers, streams, ditches, springs and marshes, either just below or just above water level (Howard and Lyon 1952). Once established this species grows quickly and can baffle the flow of water, causing flooding and changing the hydrologic cycles of wetland ecosystems (Les and Mehrhoff 1999).

In this study we investigated the effect of increased levels of nitrogen deposition on the growth of *N. officinale* and compared its response to that of *Cardamine pensylvanica* (Muhl.) (Pennsylvania bittercress), an annual native species that grows in springs and wet grounds throughout the United States (Petersen and McKenny 1968). Unfortunately, little material is available about the life history and ecological importance of this species. However, *C. pensylvanica* and *N. officinale* are both low-growing forbs from the Brassicaceae family, and therefore, for the purposes of our study, *C. pensylvanica* serves as a model of a comparable native species, rather than for any ecologically important role it may have.

We proposed that that because of its invasiveness, *N. officinale* would demonstrate a greater physiological plasticity than the non-invasive species *C. Pensylvanica*, showing a larger growth response at higher levels of nitrogen, measured by both relative growth rate, and foliar nitrogen concentration. We hypothesized that as the available nitrogen increased, *N. officinale* would show a greater increase in relative growth rate than *C. Pensylvanica*. In addition, we hypothesized that an increase in nitrogen would increase the foliar nitrogen concentration of *N. officinale* more than that of *C. pensylvanica.* Extrapolating these hypotheses, we speculated that an increase in available nitrogen may change the dynamics of the competitive relationship between these two species, causing wetlands to become more vulnerable to invasion by *N. officinale*.

Methods

In order to determine whether *N. officinale* and *C. pensylvanica* differ in their growth response to increased levels of nitrogen, we used a 2 x 4, 2-way factorial experiment (Table 1). Experimental species *N. officinale* and *C. pensylvanica* were dug up from the Spring Valley Marsh located in Farmington, Pennsylvania. A 1:1 mixture of potting soil and vermiculite was prepared and 24 11.35-liter aquariums were filled half full with the mixture. This soil mixture was chosen because it was consistent with the choice of growth medium used in a study conducted by Weihe and Neely (1997) on an invasive and native wetland species. The soil was then saturated with distilled water, to avoid introducing additional nutrients found in tap water.

To obtain a measure of the plants growth prior to the beginning of our study, the plants were removed from their original soil, the roots were rinsed in distilled water, and the plant blotted on absorbent paper to remove as much water as possible. The plants were then weighed on an electronic balance prior to transplanting in the aquariums (McGraw and Garbutt 1990).

Three levels of nitrogen and a control group were used for each species. Three aquariums containing 4 plants of a single species were placed under each treatment (Table 1). Plants were randomly assigned to each treatment group. All treatment groups received 50 mL each of two stock solutions adapted from Lee and Weber (1979) that are designed to jointly mimic the nutrient content of the precipitation that the plants would be receiving in their natural habitats. The first solution contained 12.0 µmol NH_4Cl, 5.0 µmol $NaNO_3$, and 5.5µmol $CaSO_4$. The second solution contained 2.0 µmol KNO_3, 2.5 µmol $Mg(NO_3)_2 \cdot 6 H_2O$, and 2.5 µmol KH_2PO_4. The control group received no additional nitrogen besides the “natural” baseline level present in the simulated rain solution. The intermediate level treatment received an additional 0.0139 mmol/week of NH_4^+ and 0.0229 mmol/week of NO_3^- (0.0368 mmol nitrogen total) to represent the current level of nitrogen deposition in Parsons, West Virginia (National Atmospheric Deposition Program 2004) using a solution made from NH_4NO_3 and HNO_3. Levels of nitrogen deposition at Parsons, West Virginia appear to be declining (National Atmospheric Deposition Program 2004). Therefore, the lowest level treatment was half the intermediate level to represent the levels of nitrogen deposition in West Virginia should the current trend continue. However, global levels of nitrogen deposition are increasing (Vitousek *et al.* 1997), and therefore the highest level of treatment was double the intermediate level of treatment.

Treatments began the day after transplanting. The treatments and artificial rain solutions were applied once a week. In order to mimic the water level observed in the natural environment in which the plants were found, distilled water was added to the aquariums to maintain the water level at approximately 1 cm above the soil. The plants were grown under normal greenhouse conditions with an average daily temperature of 27° Celsius. In order to control for other factors such as shade and temperature, the aquariums were randomly rotated on the greenhouse bench each week.

At the end of the fourth week, the plants were removed from the aquariums and their roots rinsed with water to remove adhering growth medium. The plants were then blotted on absorbent paper to remove as much water as possible, and then each plant was weighed on an electronic balance. The initial (W_1) and final weight (W_2) of each plant was used to determine the relative growth rate (g/g*day) (RGR) of each plant for the 28 day (Δt) duration of the experiment using the following equation taken from McGraw and Garbutt (1990):

$$RGR = (\ln W_2 - \ln W_1)/ \Delta t$$

As another, indirect measure of growth, a Minolta SPAD-502 meter was used to estimate the final foliar nitrogen content of each plant. Using this non-destructive measurement, a numerical SPAD value can be generated by the meter that is proportional to the amount of chlorophyll present within the leaf on an area basis (Richardson *et al.*

2002). This value is based on leaf absorbency in red and near-infrared regions of the visible light spectrum (Richardson *et al.* 2002). Chlorophyll concentrations are proportional to nitrogen concentrations of leaves and therefore, the equation for converting SPAD measurements to foliar nitrogen concentrations was taken from correlation graphs (Richardson *et al.* 2002):

Nitrogen concentration (%) = (0.079* SPAD) - 0.154

The data collected was analyzed using a 2-way ANOVA to test for the significance of interactions and the main effects for the measured dependant variables. The significance threshold was $\alpha = 0.05$. The computer software that was used for this analysis was SAS JMP version 5.1.

Results

The relative growth rate of both species did not change significantly with increased levels of nitrogen (F=1.7066, p=0.1749). In general, *N. officinale* had a higher growth rate than *C. pensylvanica*, independent from nitrogen levels (F=26.6642, p<0.0001; Fig. 1; Table 2). Specifically, the mean relative growth rate of *N. officinale* for all treatment groups was 54.5% greater than the mean relative growth rate of *C. pensylvanica* for all groups (Table 2). The effect of varying levels of nitrogen deposition on relative growth rate did not depend on the species (F=0.9015, p=0.4456).

The effect of increased levels of nitrogen deposition on foliar nitrogen concentration depended on the species (F=4.881, p=0.0041). The foliar nitrogen concentration of *N. officinale* remained high across all levels of nitrogen treatments, whereas the foliar nitrogen concentration of *C. pensylvanica* increased as the levels of nitrogen increased (Fig. 2). The effect of increased levels of nitrogen on foliar nitrogen was significant for both species (F=3.6492, p=0.0172). However, while there was a significant effect of treatment for both species, the foliar nitrogen levels of *N. officinale* remained nearly constant across all levels of nitrogen treatments (Fig. 2). Therefore, nitrogen treatments appear to have the greater significance for the foliar nitrogen concentration of *C. pensylvanica,* which increased with increased levels of nitrogen (Fig. 2). The greatest increase in foliar nitrogen concentration for *C. pensylvanica* was observed between the 0.0184 mmol nitrogen/week and the 0.0368 mmol nitrogen/week treatments (Fig. 2). A much lower increase in foliar nitrogen concentration was observed between the 0.0368 mmol nitrogen/week and the 0.0756 mmol nitrogen/week treatments (Fig. 2). Overall, the foliar nitrogen concentration of *N. officinale* was significantly higher than that of *C. pensylvanica* apart from increased levels of nitrogen (F=136.2554, p<0.0001; Fig. 2). In particular, the mean foliar nitrogen concentration of *N. officinale* for all treatments was 41.4% greater than the mean foliar nitrogen concentration of *C. pensylvanica* for all treatments (Table 3).

Discussion

This experiment was designed to study the possibility that the growth responses of the *N. officinale* and *C. pensylvanica* differed when exposed to increasing levels of nitrogen deposition. The hypothesis was that the invasive species, *N. officinale*, would show a greater growth response to higher levels of nitrogen than the non-invasive species, *C. pensylvanica*; this was not supported by the data.

Looking at the overall results of this experiment, it can be concluded that at the 5% confidence interval, the growth responses of both species did not differ significantly as the levels of nitrogen deposition increased. This supports the null hypothesis that, in fact, there were no true differences in the response of species to increased levels of nitrogen. The relative growth rate of both species appeared to increase slightly from that of the control with increased levels of nitrogen (Fig 1). However, there was no significant difference in relative growth rate of both species with increasing levels of nitrogen. There was a large difference in the relative growth rate between *N. officinale* and *C. pensylvanica* regardless of the nitrogen treatments. Overall, the relative growth rate of *N. officinale* was significantly higher than that of *C. pensylvanica* across all treatments. This discrepancy may be related to the invasive properties of *N. officinale*.

One characteristic of an invasive species is its plasticity to environmental conditions, allowing it to take advantage of a variety of habitats (Claridge and Franklin 2002). *N. officinale* has a high affinity for nitrate, and its ability to remove nitrate directly from the water via its adventitious roots (Howard and Lyon 1952), as well as utilizing soil nitrate reserves via its basal roots (Howard-Williams *et al.* 1982), could facilitate its ability to fully access and utilize limited supplies of nitrogen. In addition, *N. officinale* can spread laterally to utilize a greater volume for nutrient uptake (Howard-Williams *et al.* 1982). This adaptation might further enable this species to maximize its use of limited nutrients.

Exotic plants have been shown to modify resource allocations through changes in their morphology (Meekins and McCarthy 2001). In a nutrient limited environment, such plants may thrive by allocating a greater proportion of their total biomass to roots rather than to leaves and stems (Meekins and McCarthy 2001). Unfortunately, our study did not differentiate between root and shoot biomass, because the initial measure of biomass was made on already mature species. A further study might examine whether *N. officinale* adapts to nutrient limited environments through changes in resource allocation.

The relative growth rate of *C. pensylvanica* was significantly lower than that of *N. officinale* across all treatment groups. This may, in part, be due to the fact that the root system of *C. pensylvanica* was noticeably smaller than *N. officinale*, which may explain why it struggled to survive and thrive in transplanted conditions (Maas *personal observations*). Its lower overall growth rate may also be attributed to higher energy costs for biomass construction. In a study comparing the construction costs of invasive species, *Lythrum salicaria*, to co-occurring native species, Nagel and Griffin (2001) demonstrated that the invasive species required significantly less energy for leaf construction and nitrogen uptake than did the native species. This concept may apply to the discrepancy in relative growth rate between *N. officinale* and *C. pensylvanica*.

There was a significant difference in the changes in foliar nitrogen concentration of both species between treatment groups. Not unexpectedly, the leaf nitrogen concentration of *N. officinale* remained high across all treatment groups. There is a positive relationship between photosynthetic rate and leaf nitrogen concentration (Meekins and McCarthy 2001), and therefore, nitrogen concentration is an indirect measurement of the plants growth. These results indicate that an increase in available nitrogen is not followed by a significant increase in the photosynthetic rate and hence growth of *N. officinale*. This corresponds to the relatively constant relative growth rate of this species across all the levels of treatment. In other words, the growth of *N. officinale* is not limited by the amount of nitrogen available. This may be due to its ability to fully access all accessible nitrogen via its large root system (Howard-Williams *et al.* 1982). Therefore, its growth may rather be limited by innate physiological processes that limit the rate it can utilize the nitrogen available.

In contrast, the foliar nitrogen concentration of *C. pensylvanica* increased significantly with increasing levels of nitrogen. Interestingly, the results from the nitrogen concentration analyses do not correspond with an increase in the relative growth rate of *C. pensylvanica*. However, this data corresponds with the results from a study by Saulnier and Reekie (1995) which found that the photosynthetic rate of the wetland species *Oenothera biennis* was lower under low nutrient availability, than high nutrient availability.

According to our results, the overall foliar nitrogen concentration of *N. officinale* was significantly higher than that of *C. pensylvanica*, regardless of treatments. This corresponds to our data showing that *N. officinale* has a significantly higher relative growth rate than *C. pensylvanica* across all treatment groups. These results imply that even if nitrogen additions increase the nitrogen uptake and photosynthetic rate of the native species, the invasive species may still have a competitive advantage.

If this experiment were to be repeated, it is very likely that the species main effect on both relative growth rate and foliar nitrogen concentration would remain the same. However, certain changes in the experimental design might yield significant results for both the effect of treatment and the effect of the interaction between species and treatment. Due to time constraints and seed availability, plants were brought in from the field rather than grown from seed. Each plant entered the experiment at a certain level of fitness due to intraspecific competition within the field. Moreover, the two species showed a differential response to transplantation: while the large root system allowed *N. officinale* to thrive, almost half of the *C. pensylvanica* died in all treatment groups, perhaps due to its smaller root system. To remedy this, it would be advantageous to start the plants from seed. In addition, extending the duration of the experiment from 4 weeks to perhaps half a year would allow further differentiation in the plant growth to occur in response to treatments and would thus give a more accurate set of data. Perhaps most importantly, each replicate should be planted in a separate pot. The intraspecific competition that occurred within the aquariums, particularly in the case of *N. officinale* may have produced results far different from those that would be obtained without this competition.

Although our data did not support our hypothesis that *N. officinale* would show greater growth response to increased levels of nitrogen than *C. pensylvanica*, it provides support of the invasive properties of *N. officinale.* While the foliar nitrogen concentrations of *C. pensylvanica* indicate that its photosynthetic rate increases with increased levels of nitrogen, the lack of significance in the effect of treatment on the relative growth rate contradicts these results. However, even if this study were repeated giving data that indicates that the growth of *C. pensylvanica* increases with increased levels of nitrogen, it is unlikely that it would ever match the growth rates of the invasive species, *N. officinale*. Thus even at high rates of nitrogen deposition, *N. officinale* may be able to out compete the native species *C. pensylvanica* through overshadowing and resource competition (Weihe and Neely 1997). For this reason, it is important that this species be kept under control so that it does not continue to cause damage to the wetland ecosystems that it has invaded.

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Table 1. Experimental design showing species versus nitrogen level and number of replicates per combination

		Nitrogen Level			
		Control	0.0184 mmol/week	0.0368 mmol/week	0.0736 mmol/week
Species	*Nasturtium officinale*	N=12	N=12	N=12	N=12
	Cardamine pensylvanica	N=12	N=12	N=12	N=12

Table 2. Replicate N and mean relative growth rate (g/g*day) (+/- standard errors) for *Nasturtium officinale* and *Cardamine pensylvanica* at varying nitrogen levels.

Species	Nitrogen Level (mmol/wk)	N	Mean Relative Growth Rate (g/g*day) (+/- s.e.)
Nasturtium Officinale	Control	12	0.0591 (+/- 0.0039)
	0.0184	12	0.0540 (+/- 0.0034)
	0.0368	12	0.0566 (+/- 0.0059)
	0.0736	12	0.0633 (+/- 0.0042)
Cardamine pensylvanica	Control	6	0.0325 (+/- 0.0109)
	0.0184	6	0.0169 (+/- 0.0084)
	0.0368	5	0.0431 (+/- 0.0153)
	0.0736	5	0.0346 (+/- 0.0133)

Table 3. Replicate N and mean foliar nitrogen concentration (%) (+/- standard errors) for *Nasturtium officinale* and *Cardamine pensylvanica* at varying nitrogen levels.

Species	Nitrogen Level (mmol/wk)	N	Mean Nitrogen Concentration (%) (+/- s.e.)
Nasturtium Officinale	Control	12	2.1429 (+/- 0.1036)
	0.0184	12	2.3799 (+/- 0.1131)
	0.0368	12	2.0982 (+/- 0.1449)
	0.0736	12	2.2193 (+/- 0.0823)
Cardamine pensylvanica	Control	6	0.4490 (+/- 0.1252)
	0.0184	6	0.6373 (+/- 0.1828)
	0.0368	5	1.2253 (+/- 0.3173)
	0.0736	5	1.3517 (+/- 0.2422)

Table 4. Results of ANOVA showing effects of species and nitrogen treatments on the relative growth rate (g/g*day) of *Nasturtium officinale* and *Cardamine pensylvanica.*

Source	df	ss	F	p
Species	1	0.0105	26.6642	<0.0001
Treatment	3	0.0020	1.7066	0.1749
Species x Treatment	3	0.0011	0.9015	0.4456
Error	62	0.0245		

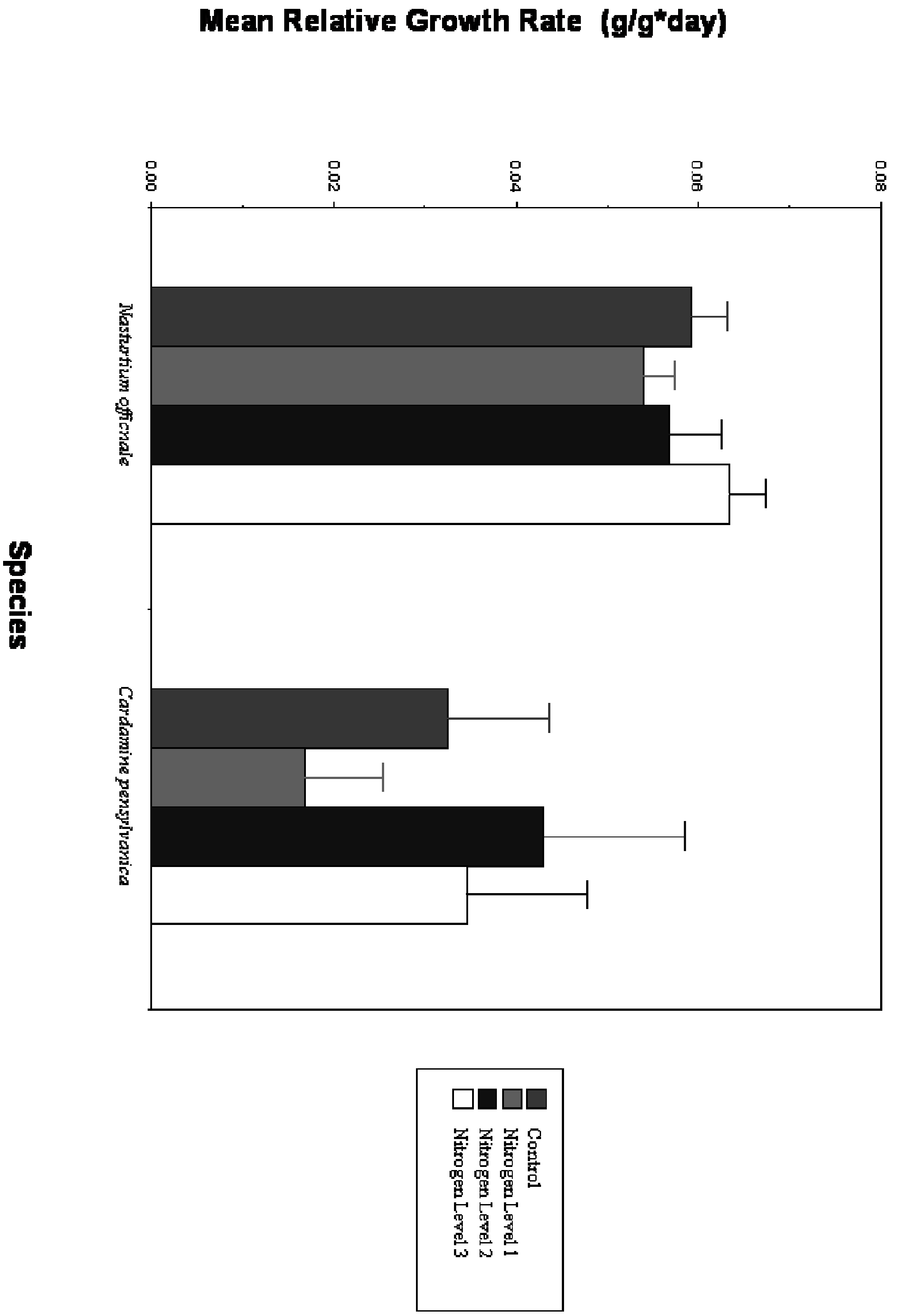
Table 5. Results of ANOVA showing effects of species and nitrogen treatments on the foliar nitrogen concentration (%) of *Nasturtium officinale* and *Cardamine pensylvanica.*

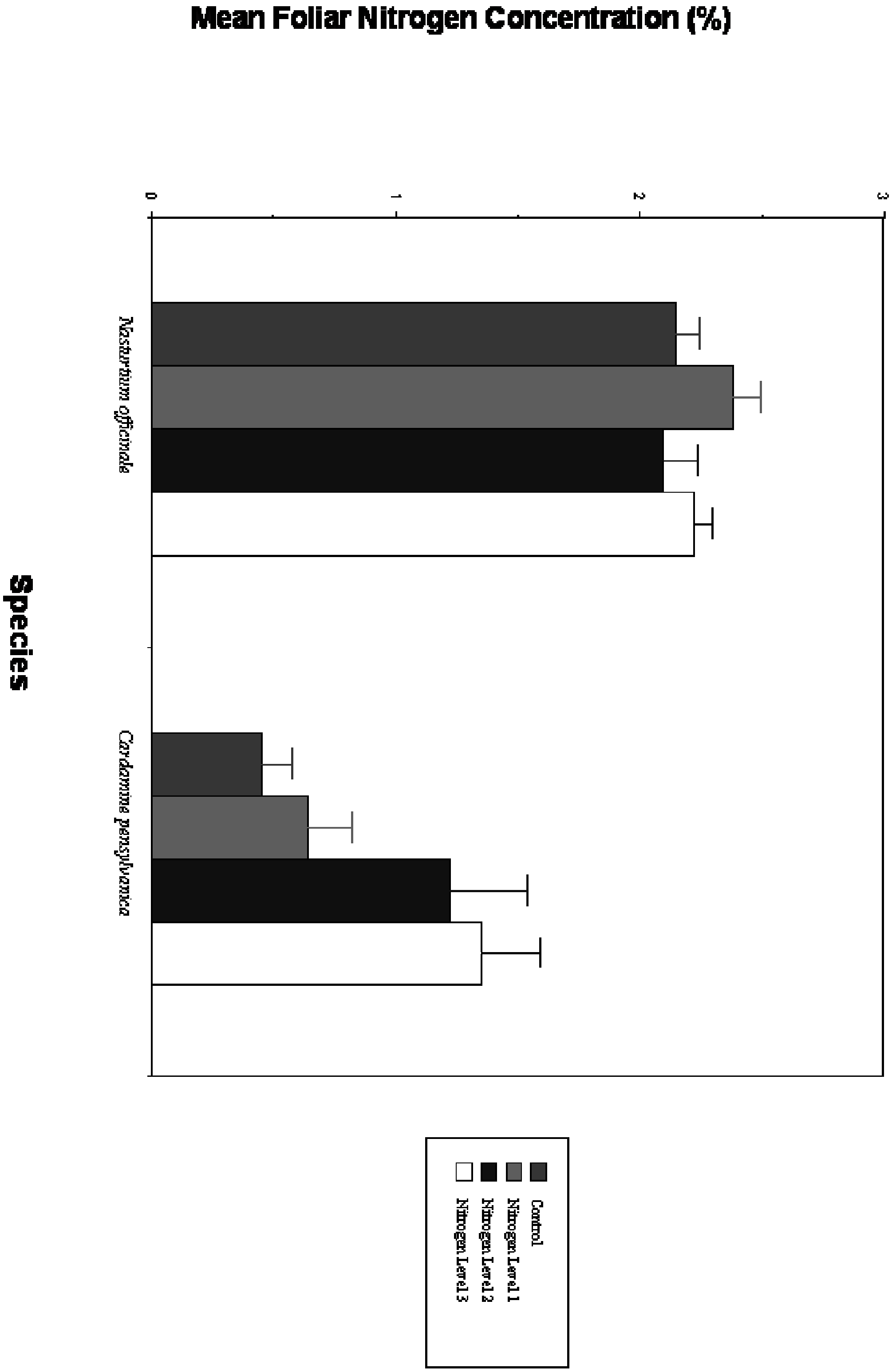
Source	df	ss	F	p
Species	1	25.1249	136.2554	<0.0001
Treatment	3	2.0187	3.6492	0.0172
Species x Treatment	3	2.7018	4.8841	0.0041
Error	62	11.4325		

Figure Legend

Figure 1. Mean relative growth rate (g/g*day) (+/- standard errors) of *Nasturtium officinale* and *Cardamine pensylvanica* grown under 0, 0.0184, 0.0368, 0.0736 mmol nitrogen/week.

Figure 2. Mean foliar nitrogen concentration (%) (+/- standard errors) of *Nasturtium officinale* and *Cardamine pensylvanica* grown under 0, 0.0184, 0.0368, 0.0736 mmol nitrogen/week.


Mean Relative Growth Rate (g/g*day)
0.00
0.02
0.04
0.06
0.08
Species
Nasturtium officinale
Cardamine pensylvanica
Control
Nitrogen Level 1
Nitrogen Level 2
Nitrogen Level 3


Mean Foliar Nitrogen Concentration (%)
0
1
2
3
Species
Nasturtium officinale
Cardamine pensylvanica
Control
Nitrogen Level 1
Nitrogen Level 2
Nitrogen Level 3