

EFFECTS OF HERBIVORY, COMPETITION, AND DISTURBANCE ON A
WETLAND PLANT COMMUNITY WITH EMPHASIS ON THE
DOMINANT AQUATIC MACROPHYTE,
NYMPHAEA ODORATA AITON

by

JULIA ADELAIDE CHERRY

A DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy
in the Department of Biological Sciences
in the Graduate School of
The University of Alabama

TUSCALOOSA, ALABAMA

2005

COLL.
QH
91.5
.C54
2005

Submitted by Julia Adelaide Cherry in partial fulfillment of the requirements for the degree of Doctor of Philosophy specializing in Aquatic Biology.

Accepted on behalf of the Faculty of the Graduate School by the dissertation committee:

[Redacted]

D. Albrex Arington, Ph.D.

[Redacted]

Arthur C. Benke, Ph.D.

[Redacted]

Robert R. Haynes, Ph.D.

[Redacted]

Timothy K. Lowrey, Ph.D.
University of New Mexico

[Redacted]

Laura Gough, Ph.D.
Chairperson

[Redacted]

Martha Powell, Ph.D.
Department Head

[Redacted]

Ronald W. Rogers, Ph.D.
Dean of the Graduate School

Dec. 17, 2004
Date

1/10/05
Date

(F)

LIST OF ABBREVIATIONS AND SYMBOLS

$A = \pi r^2$	Formula for calculating the area of a circle where A is the surface area, π is a constant (3.1416) and r is the radius
$A = \frac{1}{2} W * L$	Formula for calculating the area of a triangle where A is the surface area, W is the width, or base, and L is the length, or height
AC	Aboveground competition only treatment
ACI	Absolute competition intensity
AG	Aboveground
ANOVA	Analysis of variance
ANCOVA	Analysis of covariance
ANOSIM	Analysis of similarities
ANPP	Aboveground net primary production
BC	Belowground competition only treatment
BG	Belowground
BG:AG	Ratio of belowground biomass to aboveground biomass
C	Carbon
°C	Degrees Celsius
%C	Percent carbon
CI	Competition intensity
cm	Centimeter
cm ²	Square centimeter
C:N	Ratio of carbon to nitrogen

cont.	Continued
C-S-R	Competitor – shade-tolerator – ruderal primary plant strategies
DD	Drawdown water level treatment
df	Degrees of freedom
e.g.	Exempli gratia (for example)
et al.	Et alii (and others)
F	F ratio statistic
Fig.	Figure
FL	Flooded water level treatment
g	Gram
g m^{-2}	Grams per square meter
$\text{g m}^{-2} \text{mo}^{-1}$	Grams per square meter per month
$\text{g m}^{-2} \text{y}^{-1}$	Grams per square meter per year
GOH	Grazing optimization hypothesis
ha	Hectare
HSS	H Hairston, Smith and Slobodkin
i.e.	Id est (that is)
km	Kilometer
m	Meter
m^2	Square meter
MANOVA	Multivariate analysis of variance
MDS	Multidimensional scaling
mg	Milligram

mm	Millimeter
mo ⁻¹	Per month
MS	Mean squares term
n	Sample size
N	Nitrogen
%N	Percent nitrogen
NC	No competition treatment
no.	Number
no. m ⁻²	Number per square meter
no. plant ⁻¹	Number per plant
no. plot-1	Number per plot
<i>P</i>	Probability
<i>P</i> _{alone}	Plant performance when growing alone
<i>P</i> _{mixture}	Plant performance when growing in a mixture
PVC	Polyvinyl chloride
<i>R</i> ²	Coefficient of determination
<i>R</i> [*]	Equilibril resource concentration
RCI	Relative competition intensity
REI	Relative efficiency index
Rhiz.	Rhizome
SA	Saturated water level treatment
SIMPER	Similarity percentage analysis
sp.	Species, singular

spp.	Species, plural
SW	Switched water level treatment
TC	Total competition treatment
Tukey's HSD	Tukey's honestly significant differenced multiple comparison test
var.	Variety, nomenclature of intraspecific taxa
Wilks' λ	Wilks' lambda statistic for within-subject comparisons
$\mu\text{mol m}^{-2} \text{s}^{-1}$	Micromoles per square meter per second
<	Less than
=	Equal to
+	Plus
\pm	Plus or minus
%	Percent
x	By, when describing statistical interactions
®	Registered trademark

ACKNOWLEDGMENTS

I would like to thank my parents for teaching me the value of education, and my husband, John Miller, for his undying support and encouragement. I owe Dr. David Kesler at Rhodes College a great deal of thanks for introducing me to the wonders of ecology, and my advisor, Dr. Laura Gough for helping me, in every way, grow as a scientist. I would also like to thank my committee members, Drs. D. A. Arrington, A. Benke, R. Haynes, T. Lowrey, and R. Wetzel for their numerous contributions and constructive comments. Thank you especially to Dr. R. Wetzel, who was unable to participate in my final defense, but contributed in every other way to my progress while at Alabama. Many others have assisted me with their encouragement and support, especially Drs. A. Ward, M. Ward, A. Arrington, and M. Powell.

This research would not have been possible had Mr. and Mrs. Willie Williams not opened their front yard to me; Lake Ponderosa is a beautiful place to call home. In addition, I am indebted to many colleagues, undergraduate students, and technicians for their help. Thanks especially to N. Wellendorf, J. Pollock, A. Hunter, and F. Fontanella for their friendship, assistance in the field, and hours shared discussing science. I would like to acknowledge the NSF-IGERT Program, the SWS Student Research Grant Program, and the Department of Biological Sciences at the University of Alabama for funding this research.

In addition to the research presented here, I also had the great opportunity, as part of the NSF-IGERT Program, to conduct research with students and faculty at the University of New Mexico and with scientists at the U.S.D.A. Invasive Plant Research Lab. As part of my exchange research at the University of New Mexico, I collaborated with Jenn Follstad-Shah and Dr. Tim Lowrey on a project investigating the role of flooding for successful restoration of native vegetation on sand bars of the Rio Grande. In particular, I determined the number of individuals, species richness, and native:non-native ratio of plants germinating from the seed bank when exposed to different water level treatments. During my IGERT externship, I collaborated with Dr. Ted Center and others on a project related to the biological control of waterhyacinth. More specifically, we characterized the development of two weevil populations when growing and feeding on plants exposed to different fertilization levels. I plan to continue collaborating with J. Follstad-Shah and T. Center on the exchange and externship projects, respectively, and hope to submit results of these projects for publication in the near future.

CONTENTS

LIST OF ABBREVIATIONS AND SYMBOLS.....	iii
ACKNOWLEDGMENTS.....	vii
LIST OF TABLES.....	xi
LIST OF FIGURES.....	xii
ABSTRACT.....	xvi
CHAPTER ONE: HERBIVORY, COMPETITION, AND DISTURBANCE IN PLANT COMMUNITIES	
INTRODUCTION.....	1
LITERATURE CITED.....	7
CHAPTER TWO: EFFECTS OF HERBIVORY ON GROWTH, PRODUCTION, AND ALLOCATION OF BIOMASS AND RESOURCES IN <i>NYMPHAEA ODORATA</i>	
ABSTRACT.....	11
INTRODUCTION.....	13
RESEARCH OBJECTIVES.....	27
FIELD AND GREENHOUSE METHODS.....	29
RESULTS.....	41
DISCUSSION.....	66
LITERATURE CITED.....	76
CHAPTER THREE: GROWTH AND PRODUCTION DYNAMICS OF <i>NYMPHAEA ODORATA</i> IN THE PRESENCE OF ABOVEGROUND AND BELOWGROUND COMPETITION FROM A SIMILAR SPECIES, <i>NUPHAR ADVENA</i>	
ABSTRACT.....	84

INTRODUCTION.....	86
RESEARCH OBJECTIVES.....	103
METHODS.....	105
RESULTS.....	113
DISCUSSION.....	129
LITERATURE CITED.....	136

CHAPTER FOUR: CONTRIBUTION OF SEED BANK TO VASCULAR PLANT
RICHNESS ON TEMPORARY FLOATING ISLANDS

ABSTRACT.....	143
INTRODUCTION.....	145
METHODS.....	148
RESULTS.....	156
DISCUSSION.....	168
LITERATURE CITED.....	174

LIST OF TABLES

Table 2-1. Mean pH \pm 1 SE, water temperature ($^{\circ}$ C) \pm 1 SE, water depth (m) \pm 1 SE, ambient light intensity (μ mol m ⁻² s ⁻¹) \pm 1 SE, and percent difference in light intensity above and below experimental frames \pm 1 SE for each herbivory treatment at Lake Ponderosa over the 2001 and 2002 experimental period. Minimum and maximum values are shown in parentheses.....	44
Table 2-2. Multivariate analysis of split-strip plot repeated measures models for leaf density, leaf biomass, and ANPP at Lake Ponderosa during the 2001–2002 experimental period. For Wilks' λ tests, error df are shown in parentheses.....	52
Table 2-3. Multivariate analysis of split-strip plot repeated measures models for leaf turnover time and leaf turnover rate at Lake Ponderosa during the 2001–2002 experimental period. For Wilks' λ tests, error df are shown in parentheses. Analysis of turnover time included control plots.....	55
Table 3-1. Mean pH \pm 1 SE, water temperature ($^{\circ}$ C) \pm 1 SE, water depth (m) \pm 1 SE, ambient light intensity (μ mol m ⁻² s ⁻¹) \pm 1 SE, and percent difference in light intensity above and below experimental frames \pm 1 SE for each competition treatment at Lake Ponderosa during 2002. Minimum and maximum values are shown in parentheses. Treatment abbreviations: NC = no competition, AC = aboveground competition only, BC = belowground competition only, and TC = total competition.....	114
Table 3-2. Multivariate analysis of two-way split plot repeated measures models for RCI calculated using leaf density, leaf biomass, and ANPP at Lake Ponderosa in 2002. For Wilks' λ tests, error df are shown in parentheses. Between-subject factor abbreviations: AG = aboveground competition, BG = belowground competition.....	125
Table 3-3. Multivariate analysis of two-way split plot repeated measures models for ACI calculated using leaf density, leaf biomass, and ANPP at Lake Ponderosa in 2002. For Wilks' λ tests, error df are shown in parentheses. Between-subject factor abbreviations as in Table 3-2.....	126
Table 4-1. Species list and corresponding plant habit for plants identified in field surveys and in the greenhouse seed bank experiment. Mean aerial percent cover of adults in the field and the mean percentage of total individuals in each water level treatment are presented for every species.....	157

LIST OF FIGURES

Figure 2-1. Conceptual model of grazing optimization with corresponding compensatory responses. Redrawn from McNaughton 1983 and as recreated in Belsky 1986.....	24
Figure 2-2. Mean percentage of biomass removed by grazers ± 1 SE between treatments at Lake Ponderosa for 2001 and 2002. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons.....	42
Figure 2-3. Mean water depth (m) ± 1 SE among herbivory treatments at Lake Ponderosa. Arrows reference precipitation events during the experimental period (see text for description).....	45
Figure 2-4. Linear regression models relating A) estimated leaf surface area (cm^2) to actual leaf surface area (cm^2), and B) actual leaf surface area (cm^2) to leaf biomass (g) for <i>N. odorata</i>	47
Figure 2-5. Mean leaf A) density (no. m^{-2}) ± 1 SE, B) biomass (g m^{-2}) ± 1 SE, and C) annual ANPP ($\text{g m}^{-2} \text{y}^{-1}$) ± 1 SE between herbivory treatments at Lake Ponderosa for 2001 and 2002. Means and standard errors are reverse square-root transformed values for density and reverse log-transformed values for biomass and ANPP. Letters denote significant differences at the $\alpha = 0.05$ level for all pairwise comparisons.....	48
Figure 2-6. Mean leaf turnover time (days) ± 1 SE between herbivory treatments at Lake Ponderosa for 2001 and 2002.	50
Figure 2-7. Total number of flowers produced (no. plot^{-1}) ± 1 SE between herbivory treatments at Lake Ponderosa for 2001 and 2002. Letters denote significant differences at the $\alpha = 0.05$ level for all pairwise comparisons.....	51
Figure 2-8. Mean monthly leaf A) density (no. m^{-2}) ± 1 SE, B) biomass (g m^{-2}) ± 1 SE, and C) ANPP ($\text{g m}^{-2} \text{mo}^{-1}$) ± 1 SE between herbivory treatments at Lake Ponderosa during the 2001–2002 experimental period.....	53
Figure 2-9. Mean monthly A) turnover time (days) ± 1 SE and B) turnover rate (mo^{-1}) ± 1 SE between herbivory treatments at Lake Ponderosa during the 2001–2002 experimental period.....	56

Figure 2-10. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean A) percent change in wet weight ± 1 SE, B) percent change in rhizome size ± 1 SE, and C) leaf density (no. plant ⁻¹) ± 1 SE for mature plants harvested from the greenhouse experiment. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons.....	57
Figure 2-11. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean A) aboveground biomass (g plant ⁻¹) ± 1 SE, B) belowground biomass (g plant ⁻¹) ± 1 SE, C) total biomass (g plant ⁻¹) ± 1 SE, and D) BG:AG ± 1 SE for mature plants harvested from the greenhouse experiment. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons.....	59
Figure 2-12. Total number of flowers produced (no. plant ⁻¹) ± 1 SE by mature plants in the greenhouse experiment for year 1 and year 2. Means and standard errors are reverse log-transformed values. Letters denote significant differences at the $\alpha = 0.05$ level for all pairwise comparisons.....	60
Figure 2-13. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean A) %N ± 1 SE, and B) total N (g) ± 1 SE among treatments and tissue types for mature plants harvested from the greenhouse experiment. Means and standard errors for total N are reverse log-transformed values. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons. Plant tissue abbreviations: AG = aboveground, Rhiz = rhizome, Roots = roots.....	61
Figure 2-14. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean A) %C ± 1 SE, and B) total C (g) ± 1 SE among treatments and tissue types for mature plants harvested from the greenhouse experiment. Means and standard errors for total C are reverse log-transformed values. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons. Plant tissue abbreviations as in Figure 2-13.....	64
Figure 2-15. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean C:N ± 1 SE among treatments and tissue types for mature plants harvested from the greenhouse experiment. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons. Plant tissue abbreviations as in Figure 2-13.....	65
Figure 3-1. Conceptual representation of the C-S-R model of primary plant strategies. Redrawn from Grime 2001.....	95
Figure 3-2. Conceptual representation of the resource-based model of competition for two species (A and B) competing for two resources. Numbered regions represent initial resource supply rates corresponding to specific outcomes of competition including 1) both species going extinct, 2) species B cannot exist, 3) species A out competing species B, 4) both species coexisting, 5) species B out competing species A, and 6) species A cannot exist. Adapted from Tilman 1982.....	96

Figure 3-3. Mean water depth (m) \pm 1 SE among competition treatments at Lake Ponderosa. Treatment abbreviations as in Table 3-1.....	115
Figure 3-4. Linear regression models relating A) estimated leaf surface area (cm ²) to actual leaf surface area (cm ²), and B) actual leaf surface area (cm ²) to leaf biomass (g) for <i>N. odorata</i>	117
Figure 3-5. Linear regression models relating A) estimated leaf surface area (cm ²) to actual leaf surface area (cm ²), and B) actual leaf surface area (cm ²) to leaf biomass (g) for <i>N. advena</i>	118
Figure 3-6. Mean leaf A) density (no. m ⁻²) \pm 1 SE, B) biomass (g m ⁻²) \pm 1 SE, and C) annual ANPP (g m ⁻² y ⁻¹) \pm 1 SE for <i>N. odorata</i> among competition treatments at Lake Ponderosa for 2002. Means and standard errors are reverse square-root transformed values for density and reverse log-transformed values for biomass and ANPP. Treatment abbreviations as in Table 3-1.....	120
Figure 3-7. Mean leaf turnover time (days) \pm 1 SE for <i>N. odorata</i> among competition treatments at Lake Ponderosa for 2002. Treatment abbreviations as in Table 3-1.....	121
Figure 3-8. Mean monthly leaf A) density (no. m ⁻²) \pm 1 SE, B) biomass (g m ⁻²) \pm 1 SE, and C) ANPP (g m ⁻² mo ⁻¹) \pm 1 SE for <i>N. odorata</i> among competition treatments at Lake Ponderosa during 2002. Means and standard errors are reverse square-root transformed values for density and reverse log-transformed values for biomass and ANPP. Treatment abbreviations as in Table 3-1.....	122
Figure 3-9. Mean monthly A) turnover time (days) \pm 1 SE and B) turnover rate (mo ⁻¹) \pm 1 SE for <i>N. odorata</i> among competition treatments at Lake Ponderosa during 2002. Treatment abbreviations as in Table 3-1.....	123
Figure 3-10. Relationship between plot productivity (total g m ⁻²) and two competition intensity indices [ACI (---) and RCI (—)] for <i>N. odorata</i> leaf A) density, B) biomass, and C) ANPP.....	127
Figure 4-1. MDS ordination of plant assemblages on and off of floating islands in the field for both years. Ordination is based on percent cover of plants in each plot. Circles distinguish assemblage types [floating islands (---) and no floating islands (—)]......	160
Figure 4-2. The relationship between water depth and the number of species in each field plot in 2001 (—) and 2002 (---).....	161
Figure 4-3. MDS ordination of plant assemblages in each of the four seed bank water level treatments. Ordination is based on species' abundances in seed bank samples for each treatment. Shapes distinguish assemblage types [flooded (—), saturated (---), and drawdown (---)]. Switched assemblages are not delineated.....	163

Figure 4-4. Changes in total number of species per sample (98.53 cm^{-2} per container) present as seedlings in each of the four seed bank water level treatments ($n = 15$ per point; error bars are ± 1 SE). Means and standard errors are reverse log-transformed values.....164

Figure 4-5. Mean number of seedlings per m^2 in different seed bank water level treatments for each plant habit group (error bars ± 1 SE). Letters denote significant differences within groups at the $\alpha = 0.05$ level. Means and standard errors are reverse log-transformed values.....165

Figure 4-6. MDS ordination of plant assemblages on and off of floating islands in the field and in each of the four seed bank water level treatments. Ordination is based on presence/absence of species. Shapes distinguish assemblage types [flooded (—, ○), switched (---, ○), drawdown (---, ○), floating island (—, □), and no floating island (---, □)]. Saturated assemblages are not delineated.....167

ABSTRACT

The importance of herbivory, competition, and disturbance may differ within and between terrestrial and wetland ecosystems. Separate field and greenhouse experiments were performed to determine how these biotic interactions influenced the performance of a dominant macrophyte, *Nymphaea odorata*, and how the deep-water marsh community in which it occurs responded to physical disturbance.

During a two-year exclosure study in the field and a two-year greenhouse experiment, the effects of grazing on *N. odorata* growth and production were quantified to determine if moderate grazing affected plant performance as predicted by the grazing optimization hypothesis. Results tended to support the grazing optimization hypothesis, although increased aboveground growth in response to herbivory may have been at the expense of belowground growth.

During another experiment, *N. odorata* performance was quantified when growing alone and in mixture with a similar species, *Nuphar advena*. Interspecific competition between these two species was negligible, suggesting that other factors were more important for regulating *N. odorata*. Despite the lack of competition as a main effect, competition intensity tended to decline with increasing productivity, which is different from patterns frequently documented in terrestrial ecosystems.

To examine the contribution of seed banks to the formation of distinct plant assemblages after a physical disturbance, plant percent cover on and off floating islands was assessed in the field. A controlled greenhouse seed bank experiment in which water

levels were manipulated was also conducted. Emergent plants dominated floating islands, which were characterized by localized declines in inundation, whereas *N. odorata* dominated undisturbed sites. Assemblages in the greenhouse experiment differed among water level treatments in a manner consistent with differences observed in the field. This suggests that floating island formation temporarily altered inundation favoring the germination of a more species-rich, emergent plant assemblage, and may be one mechanism maintaining otherwise rare plant populations. These experiments suggest that herbivory and disturbance are more important than competition for regulating *N. odorata* and for influencing the surrounding deep-water marsh community at this site.

CHAPTER ONE: HERBIVORY, COMPETITION, AND DISTURBANCE IN PLANT COMMUNITIES

INTRODUCTION

A primary goal of ecology is to detect and test general patterns that explain how populations are regulated and communities are structured. Ecologists have long been interested in how biotic interactions, including herbivory and competition, and abiotic factors, such as physical disturbance, shape communities, regulate populations, and potentially maintain diversity by permitting coexistence among species (Diamond 1975, Keddy 1992, Wilson 1999). Discovering general patterns across ecosystems and within and among trophic levels has proven difficult, although many theories and models have been developed to describe how various environmental factors determine the structure and function of natural plant communities.

Plants have evolved in communities experiencing different intensities and frequencies of herbivory, competition and disturbance. As a result, plants often experience trade-offs in their abilities to tolerate each, such as trade-offs between competitive ability and secondary defense against herbivores (Grime 1979, Bazzaz 1987, van der Meijden et al. 1988, Herms and Mattson 1992). In his triangular model of plant strategies, Grime proposed that trade-offs exist among competitive ability, toleration of

stress, and toleration of disturbance, such that communities prone to frequent disturbances, for example, should be dominated by short-lived, rapidly growing ruderal species that produce a large number of seeds (1979, 2001). Thus, the relative effects of competition, herbivory, and disturbance can influence community composition, as well as ecosystem function.

Early generalizations concerning the relative importance of these factors for plant population control and community structure have stimulated a great deal of discussion and research. For example, based on a series of observations, Hairston et al. (1960) generalized that primary producers are limited by competition for resources, not by herbivory or physical disturbances. Subsequent discussion and research questioned that assumption by demonstrating that herbivores may exert control on plant populations, can reduce the effects of competition by selectively grazing on competitive dominants, can maintain species richness, and can potentially alter nutrient cycling within an ecosystem (Erlich and Birch 1967, Menge and Sutherland 1976, Connell and Slatyer 1977, Huston 1979, Huntly 1991, Grover 1994, de Mazancourt et al. 1998, de Mazancourt and Loreau 2000, Belovsky and Slade 2002). Disturbances can also reduce the effect of negative interactions among species and, ultimately, promote long-term coexistence by affecting the strength of competitive interactions, altering community composition, creating new habitat for species, and influencing succession (van der Valk and Davis 1976, 1978, Keddy and Reznicek 1982, Turkington et al. 1993, Wilson and Tilman 1995, Grime 2001, Rees et al. 2001, Engelhardt and Ritchie 2002).

Many of the predictions concerning the relative importance of herbivory, competition and disturbance at population and community levels have been developed for

terrestrial systems (e.g., Hairston et al. 1960, Menge and Sutherland 1976, Grime 1979, Huston 1979, Tilman 1982, 1988). However, they are important in other ecosystems as well, including wetlands. For example, herbivory in aquatic systems has been shown to occur at levels similar to or higher than those in terrestrial ecosystems (Lodge 1991, Newman 1991, Cyr and Pace 1993, Cebrian 2004, Cebrian and Lartigue 2004).

Moreover, competition among wetland plants is often intense, asymmetrical, and hierarchical, and can vary along environmental gradients (e.g., Catling et al. 1988, Moen and Cohen 1989, Johansson and Keddy 1991, McCreary 1991, Twolan-Strutt and Keddy 1996, Keddy et al. 1997, Van et al. 1999). Such interactions are thought to cause the development of distinct vegetation zones dominated by one to two species typical of many wetlands (Spence 1982, McCreary 1991). Disturbances, particularly involving water level fluctuations, have also been shown to enhance wetland species richness, replenish genetic stocks within seed banks, and mediate the effects of biotic interactions (van der Valk and Davis 1976, 1978, Keddy and Reznicek 1982, Gerritsen and Greening 1989, Leck and Simpson 1995, Brock and Rogers 1998, Nicol et al. 2003).

Ecological patterns of herbivory, competition and disturbance may differ among terrestrial and aquatic ecosystems because wetlands are characterized by a number of unique properties. For instance, aquatic ecosystems present constraints on plant growth, primarily due to saturation or flooding of sediments resulting in oxygen depletion, reducing conditions, and metal and toxic gas accumulation (Keddy 2000, Mitsch and Gosselink 2000). Aquatic plants are uniquely adapted to life in these otherwise stressful environments (Grace 1993, Keddy 2000, Wetzel 2001), but amelioration of these conditions may be at the expense of growth or reproduction (Keddy 2000, Engelhardt and

Ritchie 2002). Despite these constraints, wetlands are among the most highly productive ecosystems in the world, and are characterized by a mixture of emergent, floating, and submerged plant species (Wetzel 1999, 2001).

Field experiments can test the effects of biotic and abiotic factors on plant performance in wetlands and provide comparisons with patterns in terrestrial ecosystems. Separate field experiments, as well as complementary greenhouse experiments, were performed in this research to investigate the effects of herbivory, interspecific competition, and physical disturbance within a deep-water marsh. All field experiments were conducted during 2001 and 2002 at Lake Ponderosa, a small (12 ha), privately owned freshwater reservoir located within the Oakmulgee District of the Talladega National Forest, Bibb County, Alabama (N 32° 55', W 87° 19'). Lake Ponderosa lies within the Fall Line Hills of the Coastal Plain physiographic province, and is part of the Cahaba River watershed. The lake drains two unnamed intermittent first-order streams, one of which flows through an extensive emergent wetland at the north end of the lake.

The majority of the watershed surrounding Lake Ponderosa is mixed coniferous - deciduous forest that extends to the shores of the northern half of the lake. The land along the southern half of the lake has been cleared for farming and for the owners' residences. Access to the lake by the general public is restricted, and because the experiments were limited to a shallow (< 1.1 m), densely vegetated zone, study sites were not physically disturbed by human activity.

The flora of Lake Ponderosa and the surrounding wetlands is diverse. Within the deep-water marsh, there is an extensive population of *Nymphaea odorata*, one of three rooted floating-leaved perennial macrophytes present at the lake. The other two, *Nuphar*

advena and *Brasenia schreberi*, are less abundant. Also present in the deep-water marsh are the aquatic plants *Juncus repens*, *Utricularia gibba* var. *biflora*, and *Mayaca fluviatilis*. The formation of temporary floating islands within the deep-water marsh creates different habitat that is colonized by several otherwise uncommon sedges and forbs present in the seed bank. These include *Cyperus albomarginatus*, *C. erythrorhizos*, *Eleocharis baldwinii*, *E. olivacea*, *Fimbristylis autumnalis*, and *Ludwigia decurrens*. Shoreline vegetation consists primarily of large graminoids and rushes, such as *Panicum* spp., *Leersia virginica*, *L. oryzoides*, and *Juncus effusus*. Many other less abundant species, including *Dulichium arundinaceum*, *Sagittaria latifolia*, *Xyris* spp., and *Typha latifolia*, also occur along the lakeshore and within the adjacent emergent marsh. At higher elevations within the emergent marsh, there are dense stands of *Alnus serrulata* and *Myrica cerifera*.

In the following chapters, results from field and greenhouse experiments designed to elucidate the effects of biotic interactions and disturbance on plants at Lake Ponderosa are presented. The objective of these studies was to determine how biotic interactions influenced the performance of the dominant aquatic macrophyte, and how the deep-water marsh community responded to physical disturbance. Specifically, in Chapter Two, the effects of herbivory on plant growth, production, and resource allocation are investigated. In Chapter Three, results of a one-year manipulative competition experiment between two similar aquatic macrophytes are presented, and in the final chapter, seed bank responses to temporary changes in inundation level are discussed. The results of this research suggest that herbivory and disturbance are more important than competition

within the deep-water marsh of Lake Ponderosa because they can affect the dominant macrophyte and lead to short-term changes in community structure.

LITERATURE CITED

- Bazzaz, F. A., N. R. Chiariello, P. D. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. *BioScience* **37**:58-67.
- Belovsky, G. E., and J. B. Slade. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Science* **97**:14412-14417.
- Brock, M. A., and K. H. Rogers. 1998. The regeneration potential of the seed bank of an ephemeral floodplain in South Africa. *Aquatic Botany* **61**:123-135.
- Catling, P. M., K. W. Spicer, and L. P. Lefkovitch. 1988. Effects of the introduced floating vascular aquatic, *Hydrocharis morsus-ranae* (Hydrocharitaceae), on some North American aquatic macrophytes. *Naturaliste Canadien* **115**:131-137.
- Cebrian, J. 2004. Role of first-order consumers in ecosystem carbon flow. *Ecology Letters* **7**:232-240.
- Cebrian, J., and J. Lartigue. 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecological Monographs* **74**:237-259.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Cyr, H., and M. L. Pace. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* **361**:148-150.
- de Mazancourt, C., and M. Loreau. 2000. Grazing optimization, nutrient cycling, and spatial heterogeneity of plant-herbivore interactions: Should a palatable plant evolve? *Evolution* **54**:81-92.
- de Mazancourt, C., M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* **79**:2242-2252.

- Diamond, J. M. 1975. Assembly of species communities. Pages 342-444 in M. L. Cody and J. M. Diamond, editors. *Ecology and Evolution of Communities*. Belknap Press of Harvard University Press, Cambridge, Mass.
- Ehrlich, P. R., and L. C. Birch. 1967. The "Balance of Nature" and "Population Control". *American Naturalist* **101**:97-107.
- Engelhardt, K. A. M., and M. E. Ritchie. 2002. The effect of aquatic plant species richness on wetland ecosystem processes. *Ecology* **83**:2911-2924.
- Gerritsen, J., and H. S. Greening. 1989. Marsh seed banks of the Okefenokee Swamp: effects of hydrologic regime and nutrients. *Ecology* **70**:750-763.
- Grace, J. B. 1993. The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. *Aquatic Botany* **44**:159-180.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester.
- Grime, J. P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*, 2nd edition. John Wiley & Sons, Ltd, New York, NY, USA.
- Grover, J. P. 1994. Assembly rules for communities of nutrient-limited plants and specialist herbivores. *American Naturalist* **143**:258-252.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:357-361.
- Herns, D. A., and W. J. Mattson. 1992. The dilemma of plants - to grow or defend. *Quarterly Review of Biology* **67**:283-335.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* **22**:477-503.
- Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81-101.
- Johansson, M. E., and P. A. Keddy. 1991. Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. *Oikos* **60**:27-34.
- Keddy, P. A. 1992. Assembly and response rules - two goals for predictive community ecology. *Journal of Vegetation Science* **3**:157-164.
- Keddy, P. A. 2000. *Wetland Ecology: Principles and Conservation*. Cambridge University Press, Cambridge, UK.

- Keddy, P. A., and A. A. Reznicek. 1982. The role of seed banks in the persistence of Ontario's coastal plain flora. *American Journal of Botany* **69**:13-22.
- Keddy, P. A., L. Twolan-Strutt, and B. Shipley. 1997. Experimental evidence that interspecific competitive asymmetry increases with soil productivity. *Oikos* **80**:253-256.
- Leck, M. A., and R. D. Simpson. 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. *American Journal of Botany* **82**:1547-1557.
- Lodge, D. M. 1991. Herbivory on freshwater macrophytes. *Aquatic Botany* **41**:195-224.
- McCreary, N. J. 1991. Competition as a mechanism of submersed macrophyte community structure. *Aquatic Botany* **41**:177-193.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **110**:351-369.
- Mitsch, W. J., and J. G. Gosselink. 2000. *Wetlands*, 3rd edition. John Wiley & Sons, Inc., New York.
- Moen, R. A., and Y. Cohen. 1989. Growth and competition between *Potamogeton pectinatus* L. and *Myriophyllum exalbescens* Fern. in experimental ecosystems. *Aquatic Botany* **33**:257-270.
- Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *Journal of the North American Benthological Society* **10**:89-114.
- Nicol, J. M., G. G. Ganf, and G. A. Pelton. 2003. Seed banks of a southern Australian wetland: the influence of water regime on the final floristic composition. *Plant Ecology* **168**:191-205.
- Rees, M., R. Condit, M. J. Crawley, S. W. Pacala, and D. Tilman. 2001. Long-term studies of vegetation dynamics. *Science* **293**:650-655.
- Spence, D. H. N. 1982. The zonation of plants in freshwater lakes. *Advances in Ecological Research* **12**:37-126.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey.

- Turkington, R., E. Klein, and C. P. Chanway. 1993. Interactive effects of nutrients and disturbance: an experimental test of plant strategy theory. *Ecology* **74**:863-878.
- Twolan-Strutt, L., and P. A. Keddy. 1996. Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology* **77**:259-270.
- van der Meijden, E., M. Wijn, and H. J. Verkaar. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* **51**:355-363.
- van der Valk, A. G., and C. B. Davis. 1976. The seed banks of prairie glacial marshes. *Canadian Journal of Botany* **54**:1832-1838.
- van der Valk, A. G., and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**:322-335.
- Van, T. K., G. S. Wheeler, and T. D. Center. 1999. Competition between *Hydrilla verticillata* and *Vallisneria americana* as influenced by soil fertility. *Aquatic Botany* **62**:225-233.
- Wetzel, R. G. 1999. Plants and water in and adjacent to lakes. Pages 269-299 in A. J. Baird and R. L. Wilby, editors. *Eco-hydrology: Plants and Water in Terrestrial and Aquatic Environments*. Routledge Publishing, New York.
- Wetzel, R. G. 2001. *Limnology*, 3rd edition. Academic Press, San Diego.
- Wilson, J. B. 1999. Assembly rules in plant communities. Pages 130-164 in E. Weiher and P. A. Keddy, editors. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge, UK.
- Wilson, S. D., and D. Tilman. 1995. Competitive responses of 8 old-field plant species in 4 environments. *Ecology* **76**:1169-1180.

CHAPTER TWO: EFFECTS OF HERBIVORY ON GROWTH, PRODUCTION, AND ALLOCATION OF BIOMASS AND RESOURCES IN *NYMPHAEA ODORATA*

ABSTRACT

The general extent to which herbivores influence community composition and ecosystem processes is not well understood, except in specific, well-studied systems. The grazing optimization hypothesis predicts a unimodal pattern where primary production is enhanced at some intermediate level of herbivory resulting in overcompensation by plants, which is when grazed plants produce a greater amount of biomass than ungrazed plants. Existing evidence both supports and refutes grazing optimization, leading to debate concerning the roles of herbivory in nature. Moreover, the majority of research investigating compensation and grazing optimization has been conducted in terrestrial ecosystems, and, as a result, less is known about the effects of herbivory on aquatic macrophytes.

During a two-year enclosure study in the field, semi-aquatic insect herbivory on a dominant aquatic macrophyte, *Nymphaea odorata* Aiton, was controlled to ascertain if the plant compensates for the loss of biomass due to grazing. In general, leaf density, biomass, and annual aboveground net primary production were greater in plots in which

plants experienced ambient levels of grazing, suggesting that aboveground compensatory growth does occur for *N. odorata* in the field.

Additionally, a two-year simulated herbivory experiment in the greenhouse investigating resource and biomass allocation in plants experiencing different levels of grazing intensity was established to test the grazing optimization hypothesis. *Nymphaea odorata* was capable of exactly compensating for moderate levels of herbivory with respect to aboveground vegetative and reproductive response variables. However, at high levels of herbivory, *N. odorata* undercompensated for the loss of biomass due to grazing. Aboveground compensation may have been at the expense of belowground growth, as any level of damage resulted in undercompensation with respect to belowground biomass and carbon stores. Increased allocation of nitrogen to leaves to enhance photosynthesis is one possible mechanism by which *N. odorata* was capable of compensating aboveground.

Field and greenhouse results tended to support the grazing optimization hypothesis, particularly for aboveground vegetative and reproductive response variables. The potential for aboveground compensation has important community and ecosystem-level implications by potentially increasing the amount of organic matter available to decomposers, accelerating decomposition and nutrient recycling rates, and increasing herbivore consumption rates.

INTRODUCTION

Because of the complexity of interactions existing in nature between plants and their herbivores, controversy has emerged concerning the responses of plants to indirect and direct damage attributable to herbivory. Generally, opinions of plant-herbivore interactions are divided between those who contend that direct impacts on plants are negative (Crawley 1983, Belsky 1986) and those who argue that direct effects can be positive (McNaughton 1983, 1986, McNaughton et al. 1989, Paige and Whitman 1987). Regardless of the mechanisms and magnitude of responses, plant-herbivore interactions may be diverse, complex, and capable of dramatically influencing various processes at population, community, and/or ecosystem levels (Huntly 1991, Lodge 1991, Newman 1991). As such, additional studies addressing direct and indirect effects of grazing, especially within understudied aquatic ecosystems, are required in order to draw general conclusions concerning the impact of herbivory on vascular plants.

Historically, the majority of work in this field has focused on interactions in terrestrial ecosystems (Belsky 1986, Lodge 1991). In aquatic ecosystems, the literature is dominated primarily by studies of grazing on periphyton and phytoplankton (Gregory 1983, Cyr and Pace 1993). Herbivory on live freshwater plants has been assumed to be insignificant with less than 10% of total macrophyte production consumed (Wetzel 2001). These assumptions developed, in part, because many aquatic macrophytes exhibit

morphological and chemical defenses to grazing, and because they were thought to have lower nutritional value than algae (Lodge 1991, Wetzel 2001). Additionally, of the aquatic invertebrate fauna, only 9% are characterized as shredder-herbivores (Merritt and Cummins 1984) indicating that most aquatic invertebrate consumers are not herbivorous. However, several studies and reviews suggest that the level of herbivory of aquatic macrophytes might rival that of terrestrial vascular plants and is of significance to the dynamics of many aquatic ecosystems (Cahoon and Stevenson 1986, Sheldon 1987, Lodge 1991, Newman 1991, Cyr and Pace 1993, Wetzel 2001, Cebrian 2004, Cebrian and Lartigue 2004).

Effects of herbivory at population, community and ecosystem levels

Plants may respond to herbivory in various ways at population, community and ecosystem levels. The effects of herbivory on individual plant performance can vary depending on intensity and frequency of attacks, timing of attacks, developmental stage of the plant under attack, and the location and type of plant tissue attacked (Maschinski and Whitman 1989, Huntly 1991, Reichman and Smith 1991, Crawley 1997, Karban and Thaler 1999). Within populations, responses may include changes in plant biomass, abundance, longevity, seedling growth and survival, shoot and root growth, plant shape, flowering, seed production, productivity, and turnover rates (McNaughton 1983, Louda 1984, Huntly 1991, Hunter 1992, Crawley 1997). Density, biomass, production, and richness of plant species may affect the abundance, species richness and diversity of associated herbivores as well as other populations that use the plant for shelter or oviposition (Siemann 1998, Collier et al. 1999).

Changes within populations can lead to further changes within the surrounding community. For example, herbivory has been shown to increase the amount of detritus by increasing plant turnover rates (Setälä and Mäkelä 1991). Herbivory also has been demonstrated to increase species richness and diversity by controlling competitive dominants, augmenting the competitive ability of some plant species, and altering plant community composition (Huntly 1991, Grover 1994, Gough and Grace 1998*b*, Arrington et al. 1999, Callaway et al. 1999, Gross 2001). Additionally, herbivory can alter the habitat and food availability for other organisms, and influence rates of succession (Bertness 1984, Brown 1985, Arrington et al. 1999, Carson and Root 2000, Wardle et al. 2001). Effects of herbivory within communities may have impacts at the ecosystem level by affecting decomposition rates, nutrient cycling, and productivity.

Nutrient cycling rates and the extent of carbon storage in ecosystems may depend on the nutritional quality of plants and consumption rates of plant material (Cebrian 1999, 2004) because herbivore consumption rates are often positively correlated with plant palatability (e.g., Elger and Willby 2003). In many ecosystems, herbivory tends to accelerate nutrient cycling and ultimately increase net primary production (McNaughton 1979, de Angelis 1992, de Mazancourt et al. 1998, Belovsky and Slade 2000, de Mazancourt and Loreau 2000*a, b*). By increasing inputs of detritus into aquatic systems, herbivory increases the amount of fine particulate organic matter (FPOM) and dissolved organic matter (DOM) available for detrital production pathways (Cebrian 1999) or for transport via currents to the remainder of the system (Grubaugh et al. 1986, Webster et al. 1999). Removal of vegetation from either terrestrial or freshwater systems impacts the hydrology of the system, which can affect the entire watershed by altering sedimentation

rates, nutrient retention, peat formation and transpiration rates (Ward and Elliot 1995, Mitsch and Gosselink 2000).

Plant responses to herbivory that result in changes to the physical environment may cause feedback loops that indirectly influence plant-herbivore interactions. In aquatic ecosystems, plant responses to herbivory can affect the physical environment by influencing resource availability, hydrology, pH, oxygenation, and temperature (Huntly 1991). Any changes to the surrounding environment can result in changes to the function of the community and possibly the ecosystem as a whole, and more specifically, can influence plant-herbivore interactions. Nutrient, light and water availability, salinity, and competition can all influence the responses of plants to herbivores (Whitman et al. 1991). Furthermore, effects of herbivory on plants may be more severe when combined with the influence of environmental stresses such as flooding, increased salinity, nutrient imbalances, or water deficits (Whitman et al. 1991, Louda and Collinge 1992, Gough and Grace 1998*a, b*). Not only can herbivory affect processes at different ecological scales (i.e., population, community, ecosystem), it can also alter abiotic conditions, which influence plant-herbivore interactions indirectly.

Plant defenses against herbivores: chemical, morphological, and physiological

Plants have evolved a variety of defensive strategies, including chemical, morphological and physiological defenses, to protect against herbivores. Classical plant defense theory proposes a biochemical coevolution process between insects and plants, suggesting that plant species evolve secondary compounds called allelochemicals in response to insect attacks while insects evolve detoxification systems (discussed in Howe

and Westley 1988). Induction of increased levels of secondary compounds is one documented response to herbivory. An increase in the production of these secondary chemicals, an energetically costly process creating a trade-off between defense and plant growth and reproduction (McKey 1974, Bazzaz et al. 1987), usually results in a decline in grazing damage (e.g., Cronin and Hay 1996, Newman et al. 1996, Thaler 1999).

However, in most cases, plants will have at least one herbivore, usually an insect, that is specialized to feed on the plant despite its chemical defenses (Brattsen 1979). In addition, plants can have morphological adaptations such as spines, thorns, or tough, pubescent leaves that deter herbivores, or they may exhibit physiological adaptations, such as enhancement of primary production, to compensate for damage caused by herbivores.

One theory incorporating multiple mechanisms of plant responses to herbivory suggests that plants easily accessible to herbivores evolve different, more elaborate chemical defenses than plants that are more difficult for herbivores to locate (discussed in Howe and Westley 1988). Similarly, plants subjected to herbivory may experience trade-offs between regrowth capacity and allelochemical defense systems (Bazzaz et al. 1987, van der Meijden et al. 1988, Herms and Mattson 1992). Such an evolutionary trade-off does not exist for all plants (Almeida-Cortez et al. 1999), although van der Meijden et al. (1988) hypothesized that annuals would be more likely to have lower regrowth capacity and stronger chemical defense systems whereas perennials would be more likely to have higher regrowth capacity and weaker chemical defense systems.

Aquatic ecosystems are dominated by clonally reproducing perennials (Barrett et al. 1993, Grace 1993), so one might expect aquatic plant communities to be dominated by species with high regrowth capacities. Many plants exposed to aboveground herbivory

are capable of accumulating carbon in belowground tissue (Chapin et al. 1990, Holland et al. 1996, Mikola et al. 2000), and perennials with large belowground storage organs may be better adapted to capitalize on reserves for regrowth. Therefore, perennials may be able to overcome potential negative effects of herbivory if reserves of carbon or nutrients stored in belowground plant organs are accessible to the plant for regrowth in subsequent seasons (Chapin et al. 1990). Allocating biomass to belowground plant organs may be one mechanism promoting physiological defenses, especially if there is no significant negative relationship between long-term grazing and root mass, as has been demonstrated for some perennial grasses (Milchunas and Lauenroth 1993, McNaughton et al. 1998).

Physiological defenses against herbivores

Physiological defenses against herbivory are complicated and controversial, resulting in a set of three alternative hypotheses addressing different ways plants can respond to herbivory. The first assumes that because herbivory damages plant tissue, it must negatively affect the plant. Such negative effects result in undercompensation when “the cumulative dry weight of the treated plants is less than that of the controls” (Belsky 1986). The second hypothesis proposes that herbivory can have compensatory effects that may benefit the plant and serve to improve plant fitness (McNaughton 1983, Paige and Whitman 1987, Paige 1992, Huntly 1991, Whitman et al. 1991). In such instances, overcompensation occurs when “the cumulative total dry weight (including removed tissue) of the grazed or clipped plants is greater than the total dry weight of the control plants” (Belsky 1986). The third hypothesis, referred to as exact compensation, occurs

when “the cumulative dry weight of the treated plants equals that of the controls” (Belsky 1986).

Compensation hypotheses are defined strictly in terms of the accumulation of total plant biomass. However, a review of the literature reveals that a variety of response variables in addition to total plant biomass have been measured as indicators of plant performance, including leaf/shoot density, aboveground biomass, and flower production. Moreover, compensation has been observed when only measuring a subset of total plant performance. Such positive responses in a subset of total plant performance, such as aboveground biomass, can be significant at population and community levels even if herbivory is not directly resulting in positive, long-term changes in total plant fitness.

Evidence of undercompensation

In a review of compensation literature for grassland species, Belsky (1986) concluded that there was not substantial evidence to suggest that herbivory benefits plants in natural conditions. Instead, the majority of studies reviewed indicated that grassland species are more likely to undercompensate for damage attributable to herbivory. While the majority of compensation experiments have been performed in grasslands, experiments in other terrestrial ecosystems and in aquatic ecosystems have been conducted that support Belsky’s claim that compensation is rare in plant communities. Seven such studies are presented here.

While researching the effects of moose herbivory on balsam fir (*Abies balsamea*), Brandner et al. (1990) concluded that herbivory negatively affected plant performance. In the presence of intensive moose grazing, fir height, growth and recruitment were

suppressed, and in sites with sustained herbivory, the fir did not return to the canopy. Similarly, undercompensation was observed in a study of the effects of chrysomelid beetle grazing on a dominant plant species in an old field (Carson and Root 2000). During an outbreak, beetles reduced the biomass, density, height, survivorship and reproduction of goldenrod (*Solidago* spp.). Even at non-outbreak levels, the cumulative effects of sustained herbivory affected the dominance of goldenrod. Additionally, a study of the effects of severing lateral roots and rhizomes on herbivore impact indicated that insect herbivory on bittercress (*Cardamine cordifolia*) increased when plants were subjected to moderate levels of stress (Louda and Collinge 1992). The bittercress did not compensate for losses due to herbivory.

Evidence of undercompensation exists for aquatic and wetland plant species as well. For example, Sheldon (1987) found that herbivorous snails damaged up to 13% of leaf area and significantly decreased macrophyte species richness. The remaining macrophyte species were those least preferred by snails in laboratory feeding assays. Similarly, crayfish (*Procambarus clarkii*) that graze on submersed macrophytes have been shown to significantly reduce pondweed (*Potamogeton pectinatus*) biomass through direct herbivory; intense herbivory completely eliminated pondweed from the system (Feminella and Resh 1989).

In a study of grazing on leaf production and longevity, Kouki (1991) found that herbivory by a water-lily beetle decreased the lifespan of water lily (*Nuphar lutea*) leaves, but did not change the number of floating leaves produced. Rather, herbivory altered the timing of nutrient release by causing leaves to decompose earlier in the growing season. In an attempt to assess the potential for biocontrol, McGregor et al.

(1996) quantified the change in coverage, abundance and biomass of water primrose (*Ludwigia grandiflora*) in the presence and absence of an herbivorous flea beetle (*Lysathia ludoviciana*). They concluded that the beetle drastically reduced the biomass of the primrose and resulted in a shift in dominance from primrose to pickerelweed (*Pontederia cordata*). A year later, they found that the primrose had not recovered. Other studies addressing the effectiveness of biocontrol on freshwater plants have also demonstrated negative effects of specialist herbivores on various plant response variables (e.g., Center et al. 1999, Wheeler and Center 2001, Aguilar et al. 2003, but see Callaway et al. [1999]).

Evidence of exact- and overcompensation

In 1983, McNaughton reviewed the literature and argued that overcompensation of vegetative tissues and reproductive tissues can occur to combat moderate levels of herbivory. Several studies conducted since then in terrestrial and aquatic ecosystems also suggest herbivory may be beneficial by resulting in compensation, at least aboveground. Five studies are described here.

In a study of mammalian herbivory, Paige and Whitman (1987) concluded that scarlet gilia (*Ipomopsis aggregata*) benefited from grazing even when 95% or more of aboveground biomass was removed. Those plants exposed to herbivory flowered sooner and had more inflorescences. As a result, there were greater numbers of flowers and fruits on grazed plants. Even though there was no difference in total seed and fruit production, germination success, seed weight, and seed survival, the grazed plants still exhibited a 2.4 fold increase in fitness because they produced a greater number of flowers and fruits per

plant. Furthermore, aboveground vegetative compensation occurred in this population without a corresponding negative response belowground. Dyer et al. (1991) also observed compensation in a terrestrial community when carbon fixation rates, carbon storage and regrowth of grasses exposed to herbivory were examined. They found that regrowth compensated and possibly overcompensated for grazing losses. When grazing-adapted plants were grazed upon, they fixed more carbon, produced and stored more carbon in leaves, stored less in stems, and had more labile carbon in roots than plants protected from herbivory.

There is also evidence of compensation by aquatic and wetland plant species. Wallace and O'Hop (1985) assessed the impact of herbivore production on turnover and nutrient dynamics of water lily (*Nuphar luteum*) leaves. They found that chrysomelid beetles grazed between 7% and 27% of the leaf surface. The longevity of leaves exposed to grazing pressure was 17 days with an average of 5.1% of leaf surface remaining whereas ungrazed leaves lived for longer than 6 weeks. They concluded that herbivory hastened decomposition of leaves by making leaves vulnerable to microbial attack. However, estimates of turnover rates indicated that plants replaced their leaves as quickly as they were lost.

Another study of the effects of chrysomelid beetle grazing on water lily (*Nuphar luteum*) leaf production and nutrient dynamics indicated that grazing at moderate levels ranged from 3% to 6.1% of net primary production, but did not reduce biomass (Setälä and Makela 1991). Rather, leaves were replaced rapidly as there was an increase in leaf production rate and degradation rates. As a result, there were increased inputs of carbon and nitrogen into the detrital pool of the ponds. Similarly, Hik and Jeffries (1990), while

studying the effects of snow geese on a salt-marsh grass, *Puccinellia phryganodes*, found that net aboveground production increased in the presence of grazing. The ability of the plant to recover depended on the presence of goose feces, which resulted in rapid recycling of nutrients available to the plants.

Conflicting evidence concerning compensation in plant populations exists for both terrestrial and aquatic ecosystems. In some cases, contrasting conclusions have been reached for the same species (i.e., Wallace and O'Hop 1985, Kouki 1991, and Setälä and Mäkelä 1991). Because a variety of response variables were measured, general conclusions on the role of herbivory in aquatic ecosystems, and, therefore, comparisons between aquatic and terrestrial ecosystems, are difficult to make.

Evaluating compensation within the grazing optimization framework

The grazing optimization hypothesis (GOH) combines the three alternative compensatory hypotheses so that effects of herbivory on plant net primary production are evaluated along a gradient of increasing grazing intensity (Fig. 2-1). The GOH postulates that plant production will increase from low levels of herbivory to some moderate level when overcompensation occurs as plant primary production is enhanced by herbivores (McNaughton 1979, Hik and Jeffries 1990). Furthermore, at moderate levels of grazing intensity, biomass and nitrogen availability to grazers should also increase compared to protected plants. However, as grazing intensity continues to increase, plants are no longer capable of compensating, resulting in declines in primary production, biomass, and nitrogen availability for herbivores.

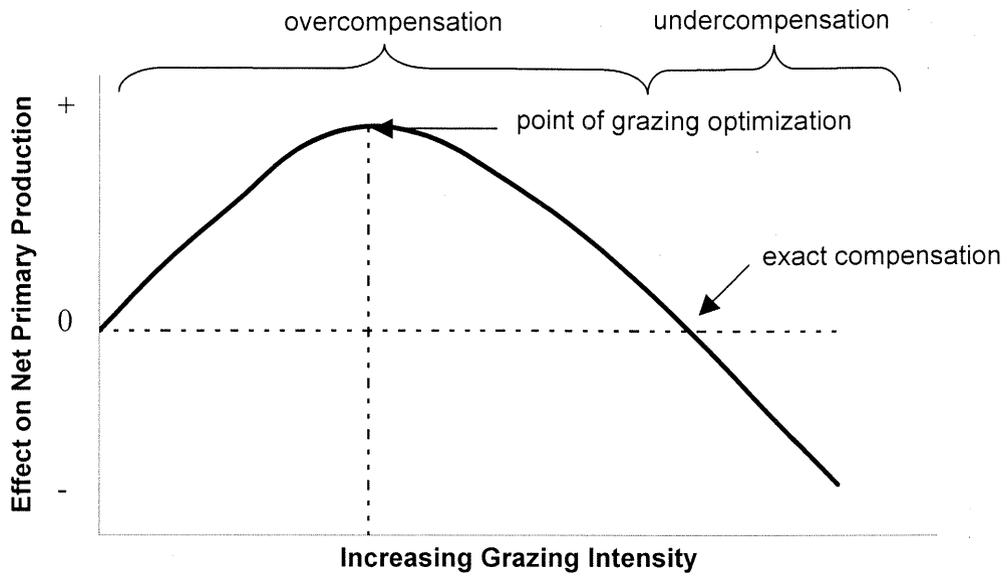


Figure 2-1. Conceptual model of grazing optimization with corresponding compensatory responses. Redrawn from McNaughton 1983 and as recreated in Belsky 1986.

Studies designed to model or directly test the GOH have attempted to answer general questions pertaining to compensation. In particular, questions regarding grazing optimization include whether or not plants are capable of overcompensating at moderate grazing intensities, and if so, whether overcompensation is indicative of a mutualistic relationship (Belsky 1986, McNaughton 1986, de Mazancourt et al. 1999, de Mazancourt and Loreau 2000*b*). Furthermore, if grazing optimization does occur, what factors limit or facilitate it (e.g., van der Meijden et al. 1988), and when might the evolution of optimization be favored (e.g., de Mazancourt and Loreau 2000*b*)? In an attempt to answer some of these questions, several models incorporating nutrient cycling have been proposed to suggest that herbivory can result in grazing optimization (de Angelis 1992, de Mazancourt et al. 1998, de Mazancourt et al. 1999, Belovsky and Slade 2000, de Mazancourt and Loreau 2000*a, b*). For example, de Mazancourt et al. (1998) constructed a model predicting grazing optimization when there are large losses of nutrients during recycling or when herbivores introduce a new source of limiting resources. There have also been field studies that have directly tested grazing optimization, suggesting that, in certain ecosystems, plants can overcompensate for moderate grazing (McNaughton 1979, Hik and Jeffries 1990, Leriche et al. 2003). Even so, generalizations about plant responses along a grazing intensity gradient, especially in aquatic ecosystems, are lacking, and more research is needed to understand if and how herbivory benefits plants.

Defining compensation when testing grazing optimization

Compensation and, more specifically, grazing optimization have been defined in terms of production of biomass and foliar nitrogen content. Belsky (1986) argued that

grazing optimization should be defined in terms of total plant responses if the contention is that herbivory benefits the plant or increases fitness. For example, if plants respond positively to herbivory aboveground but are negatively affected belowground, which has been demonstrated in some terrestrial systems (e.g., Crawley 1983, Ruess et al. 1998, van der Wal et al. 2000), the net effect of herbivory may be negative. In this scenario, aboveground compensation would be evidence of short-term enhancement of growth or production, not of an overall, long-term benefit to the plant population. However, as the literature review demonstrated, researchers often use a variety of response variables when testing compensation hypotheses, and these variables are not always measures of total plant performance.

One impediment to discovering broad patterns among ecosystems is the lack of uniform response variables as indices of plant fitness. Measurements of fitness require data concerning both sexual and asexual reproduction of a population, and must include data from germination through maturity (McNaughton 1983, Whitman et al. 1991). As a result, measures of growth, primary production and reproduction over limited temporal scales are typically used as indices of plant fitness (McNaughton 1983). Examination of some subset of performance can provide important population and community level information, even if observed compensatory responses do not affect fitness in the long-term. In this way, compensation and grazing optimization hypotheses have been modified in this study and others to evaluate multiple plant responses to herbivory, and have not been limited to measures of total plant production.

RESEARCH OBJECTIVES

As evidenced in this review of the literature, herbivory can significantly affect both plant and herbivore populations directly, and the structure and function of the community and ecosystem indirectly. However, because compensation has been evaluated using a suite of response variables, general conclusions concerning the impact of herbivory on plants are difficult to make. The goal of this research was to address the issue of compensatory responses within the framework of the GOH in an aquatic ecosystem. This was accomplished by quantifying aboveground effects of semi-terrestrial insects on an aquatic macrophyte in the field, and by examining aboveground and belowground changes in biomass and resource allocation in plants across an artificial grazing intensity gradient in the greenhouse.

Complementary field and greenhouse experiments were conducted to test a series of hypotheses related to the GOH. In particular, 1) the focal plant species, *Nymphaea odorata* Aiton (Nymphaeaceae), would overcompensate vegetatively at ambient grazing intensity in the field and at moderate grazing intensity in the greenhouse relative to ungrazed controls. Compensation was measured in terms of leaf density, biomass, and aboveground net primary production (ANPP). Furthermore, 2) leaf turnover times would be shorter with ambient grazing in the field than with no grazing, and therefore, turnover rates would be higher. Higher turnover rates would be indicative of enhanced production

as biomass accumulates at a faster rate. As evidence of a trade-off between sexual reproduction and growth, 3) *N. odorata* would undercompensate reproductively in terms of total number of flowers produced annually at ambient grazing intensity in the field and at moderate grazing intensity in the greenhouse. For *N. odorata* in the greenhouse experiment, 4) carbon and biomass would be allocated belowground at moderate grazing intensity while nitrogen would be allocated aboveground to leaves. Finally, 5) *N. odorata* subjected to moderate grazing intensity in the greenhouse would allocate a greater amount of carbon and biomass belowground in the first year resulting in greater aboveground biomass in the second year as plants compensated for the first year's damage.

The combination of field and greenhouse experiments permits investigation of the effects of herbivory on a range of plant population responses under both controlled and natural conditions. From both experiments, it was predicted that grazing optimization would occur at intermediate levels of herbivory corresponding to ambient levels in the field and moderate levels in the greenhouse. Optimization at ambient/moderate levels of herbivory would occur as plants quickly replaced leaves throughout the growing season, allocated biomass and carbon belowground, and allocated nitrogen aboveground as mechanisms to maximize regrowth capacity in subsequent years. Conversely, optimization would not occur at levels corresponding to low/no herbivory in the field and greenhouse, or at levels corresponding to heavy grazing in the greenhouse.

FIELD AND GREENHOUSE METHODS

Study site

This study was conducted in the deep-water marsh of Lake Ponderosa, a small (12 ha), privately owned reservoir located in the Fall Line Hills of the Coastal Plain in Bibb County, Alabama (N 32° 55', W 87° 19'). Lake Ponderosa drains two unnamed streams, one of which flows through an extensive emergent marsh at the north end of the lake. Adjacent to the emergent marsh, there is a deep-water marsh dominated by the rooted floating-leaved perennial, *Nymphaea odorata*. Fifteen experimental plots were established within the northern section of the lake in which *N. odorata* occurred.

Water depths ranged from 0.10 m to 0.82 m in the absence of temporary floating island formation. Floating islands form when live vegetation and associated sediments separate from the underlying substrate and float at or near the surface due to accumulation of gases in the sediment and aerenchyma tissue of existing vegetation (King et al. 1984, Hogg and Wein 1988, Clark 2000). At Lake Ponderosa, floating islands formed in late May 2001 and early June 2002 causing a localized decline in inundation to less than 0.10 m. Islands persisted until early October of both years, at which time they subsided and were completely inundated throughout winter and spring. This unexpectedly affected four of the 15 plots in 2001 and three in 2002.

Focal plant species

The focal plant species, *Nymphaea odorata*, is native to the United States, but found predominately in the eastern, central and midwestern states, including Alabama. It occurs in slow moving or still waters (e.g., lakes, ponds, marsh pools, ditches), and has been introduced into several western and northeastern states (Wiersema 1997). It is an aquatic perennial herb with long petiolate leaves arising directly from a horizontal rhizome. *Nymphaea odorata* can reproduce clonally by rhizome expansion and sexually by seed. Flowers are white and float on or just above the water's surface. After the flower's final closing, the peduncle coils so that the developing fruit is brought underwater to the substrate. Morphologically, the species is variable, exhibiting a diversity of leaf sizes and textures, petiole diameters, flower sizes and rhizome sizes depending on the environmental conditions in which it grows. Under adverse environmental conditions, the size of leaves and flowers is often diminished (Godfrey and Wooten 1981).

Several herbivores graze on *N. odorata* despite production of nitrogenous-based alkaloids for defense. Herbivores of *N. odorata* include leaf beetles (Coleoptera: Chrysomelidae) in the genera *Galerucella* and *Donacia*; pyralid moths (Lepidoptera: Pyralidae) in the genera *Synclita*, *Munroessa*, and *Parapoynx*; and leaf miners (Diptera: Chironomidae) such as *Hyporhygma* sp. (Merritt and Cummins 1984, Carter 1995, Cronin et al. 1998, Cronin et al. 1999, Dorn et al. 2001).

Field experimental design

Field research consisted of control, shade control, and a grazing manipulation treatments in a randomized design. Fifteen sampling frames, five for each treatment, delineating 0.25 m² of lake bottom each, were placed in the lake during January 2001 when leaf densities were low, thus preventing selection bias. Quadrats consisted of a 0.5 m x 0.5 m wooden frame attached at the corners to PVC legs, which were inserted into the substrate so that the wooden frame remained 15 cm above the water's surface allowing for changes in lake water level. The five control quadrats remained uncovered allowing for natural levels of herbivory. The second set of quadrats was covered by a 20 x 20 mesh per inch Lumite® screen (BioQuip, Gardena, CA). The screen extended across the top and 15 cm below the water's surface on each side. It excluded semi-terrestrial herbivores but not aquatic ones grazing on petioles, rhizomes, or undersides of leaves, and prevented leaves from floating outside of the 0.25 m² area. To control for the effects of shading by the Lumite® screen, the tops of the remaining five quadrats were covered leaving the sides exposed to aerial semi-terrestrial adults, and thus allowing herbivory to occur at the same levels as in the open, control plots. In order to eliminate cage effects and keep leaves within the delineated sampling areas of the control and shade-control plots, a 10 cm band of Lumite® screen was placed around each plot just below the water's surface in a manner consistent with enclosure plots. This did not exclude semi-terrestrial herbivores from these plots. All plots were placed at least seven meters apart to ensure that no individual plant was sampled in multiple plots due to horizontal rhizome connection.

Field measurements of environmental variables

The 15 plots were monitored weekly for water depth, monthly for pH and water temperature ($^{\circ}\text{C}$), and seasonally for light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) from January 2001 to December 2002. Water depth was measured with a meter stick from the water's surface to the top of the substrate at two points within each plot from which mean water depth per plot was calculated. Water pH and temperature at each plot were measured using an Orion Model 250A meter (Orion Research Group, Inc., Beverly, MA). Light intensity was measured with a point quantum sensor and light meter (Model LI-250, Li-Cor, Inc., Lincoln, NE) at sites throughout the experimental area to determine yearly minimums and maximums, and at three points above each frame and at three points at the water's surface (i.e., under the screen in shade-control and enclosure plots) to calculate the average light intensity above and below frames. These data were used to determine the average percentage of ambient light blocked by the frames in each of the three treatments. Daily precipitation amounts measured at a nearby (approximately 11.3 km away) weather station at the Talladega Wetland Ecosystem in Hale County, Alabama (N $32^{\circ} 52'$, W $87^{\circ} 26'$) were used to approximate annual rainfall patterns at Lake Ponderosa for 2001 and 2002.

Field measurements of plant response variables

All plants in the 15 plots were measured approximately weekly from January 2001 to December 2002 for leaf longevity, leaf density, leaf surface area, number of flowers and leaf damage. The petioles of each leaf emerging within a plot were tagged

with a labeled cork float when first observed, and the subsequent time of their senescence was recorded to determine leaf longevity in days. Leaf longevity, or turnover time, was equal to the difference between the time of senescence and the time of emergence. Time of emergence was calculated as the median between the previous sampling date and the sampling date on which the leaf was first tagged. Time of senescence was calculated as the median day between the date on which the leaf was last measured and the date on which the leaf was no longer present in the plot. From these data, leaf turnover rates were calculated as growth period divided by leaf longevity, as described by Setälä and Makela (1991). Growth period was defined as 365 days because leaves were continuously measured for two full calendar years and new leaves did emerge in the winters of both years. Leaf density was equivalent to the number of leaves present per 0.25 m² quadrat. Total number of flowers present per quadrat in each year was reconstructed from field notes by summing weekly counts of flowers. Double-counting of flowers in a given plot was unlikely because developmental stages of flowers (i.e., bud, bloom, fruit) were recorded and multiple flowers of the same stage were never present in the same plot at a given time.

Individual leaf length and width measurements were recorded weekly in order to calculate leaf surface area. Surface areas for the round *N. odorata* leaves were calculated using the formula $A = \pi r^2$, where r is half the average of the leaf's width and length and A is surface area. Surface area estimates were used to predict leaf biomass from an independently developed regression model relating leaf surface area (cm²) to leaf biomass (g). To develop the regression model, 55 leaves from Lake Ponderosa were collected on 25 April 2001 and transported back to the laboratory. Actual leaf surface

area was determined using a leaf area meter (Li-3000A Portable Area Meter console with Li-3050A Belt Conveyor, LiCor, Inc., Lincoln, NE). The leaves were dried at 60 °C for 48 hours and weighed (Mettler Toledo PB153-S, Columbus, OH) to obtain leaf biomass in grams \pm 0.001 g. The leaves used to develop the model ranged in size from 4.28 cm² to 582.89 cm², and 0.02 g to 4.99 g. To correct for potential shape variation among leaves, another regression relating estimated and actual surface areas was developed. From mean monthly biomass estimates and leaf turnover rates, ANPP was estimated in every plot. ANPP was expressed in units of mass per area per time and was calculated as mean monthly turnover rate multiplied by mean monthly biomass, as described by Setälä and Mäkelä (1991) and Carter (1995). Summation of production estimates over monthly intervals provided an annual estimate of ANPP. A direct method was also used to calculate annual ANPP for each year by summing the maximum biomass of every leaf tagged in a plot over the entire year.

Leaf damage was observed throughout the experiment to determine if the exclosure treatment successfully reduced grazing. Herbivores were manually removed when observed within exclosures. Damage was estimated qualitatively by ranking grazing damage on leaf surfaces on a scale of 1 to 5, where 1 was no grazing, 2 was very light grazing, 3 was light grazing, 4 was moderate grazing, and 5 was heavy grazing. In addition, leaves were photographed with either a 35 mm camera or a digital camera in the field over a contrasting background of a known surface area. From the photographs, the amount of leaf surface area removed by herbivores was quantified using a digital planimeter (Planix 7, Sokkia Corporation, Overland Park, KS), and the herbivore responsible for the grazing was classified based on damage patterns. When background

areas were compromised, as was the case with some of the 35 mm photographs, the proportion of area removed relative to the leaf's surface area in the photograph was determined and converted to an estimate of the actual amount removed based on surface area calculations for the leaf obtained in the field.

Greenhouse methods and experimental design

Sixty-two individuals of *N. odorata* were collected from Lake Ponderosa on 24 May 2001. Younger individuals with leaves 7.5 cm to 10 cm in width and minimal grazing were selected. Actively growing tips of rhizome were extracted, leaving as many of the roots intact as possible, and placed in quart-sized plastic bags filled with lake water. The bags remained open to permit air circulation and out of direct sunlight to prevent overheating. All of the bags were then placed within rigid containers for transport. In the lab, all the plants were rinsed with untreated groundwater to remove sediment and any associated invertebrates. The initial wet weight, initial rhizome size determined from measurements of rhizome length and width, and number of leaves per plant were recorded before transplanting each individual into a three gallon nursery bucket filled with a 50:50 mix of top soil and manure. The soil surface was covered with a layer of wet sand to prevent nutrient exchange into the water column. Nursery buckets were placed in Min-O-Cool Frigid Units (2.8 m x 0.55 m x 0.52 m; Frigid Units, Inc., Toledo, OH) in the greenhouse of the Experimental Mesocosm Facility at the University of Alabama on 25 May 2001 (treatments and statistical design described below). The units were filled with deionized water to a depth of 0.48 m. Water levels were maintained between 0.45 m and 0.48 m throughout the course of the experiment by manually

refilling tanks when necessary. The 48 experimental plants were allowed to acclimate for 68 days before receiving the first treatment on 1 August 2001. Eight extra plants were also in the tanks in case any of the original 48 died from the transplanting process. All transplants survived the acclimation period.

The greenhouse experiment was a 3 x 2 factorial design with three grazing treatments and two durations of time. The three treatments included a control (no grazing treatment), a moderate grazing treatment, and a heavy grazing treatment. Each treatment represented a different level of simulated herbivory such that plants in the no grazing treatment had 0% of their leaf surface area removed, those in the moderate grazing treatment had 5% of their leaf surface area removed, and those in the heavy grazing treatment had 15% of their leaf surface area removed. To simulate herbivory, a standard hole-punch was used to remove leaf surface area at the time of leaf emergence, restricting holes to the outer leaf margins to prevent puncturing major leaf veins. This mimics what occurs in the field when chrysomelid beetles and pyralid moths remove biomass in small circles or chunks, respectively, often from the periphery of leaves rarely injuring major veins. Leaf surface area was estimated using the $A = \pi r^2$ method as explained above. The 5% and 15% values for leaf area removal were selected because they fall within the range of those reported for other floating macrophytes (Lodge 1991). Plants were exposed to the grazing treatments for a duration of one or two years. Eight plants were assigned to each treatment combination and randomly placed in the Min-O-Cool Frigid Units.

The experiment was designed to have six treatment combinations with eight replicates in each, for a total of 48 plants. However, at the initiation of the experiment, one plant was exposed to the wrong grazing level such that 5%-year 1 had seven

replicates and 15%-year 1 had nine replicates. All other treatment combinations contained eight replicates.

Greenhouse measurements of plant response variables

The 48 plants were measured every two weeks from 1 August 2001 to 1 August 2003 for leaf longevity, leaf density per plant, and leaf surface area. Petioles of every leaf were tagged with a labeled plastic ribbon at the time of emergence, and the subsequent time of their senescence was recorded to determine leaf longevity in days. Turnover rates, leaf density per plant, and initial individual leaf lengths and widths were calculated as explained above for the field experiment. Leaf surface area estimates were used to determine how much of the leaf needed to be clipped to remove 5% or 15% of the leaf's total surface area, and to estimate initial leaf biomass using the same regression as explained above.

At the end of the first year on 1 August 2002 and again at the end of the second year on 1 August 2003, designated plants were harvested, rinsed to remove sediment, and final wet weights, final rhizome size, and number of leaves per plant were determined. Each plant was separated into its roots, rhizomes, aboveground chlorophyllous tissue, and aboveground reproductive tissue, and each tissue was dried separately in brown paper bags at 60 °C for 48 hours, or until the material broke easily. Following drying, each plant portion was weighed (Mettler Toledo PB153-S, Columbus, OH) to obtain dry weights to the nearest mg. After obtaining dry weights, plant portions were ground to pass through a 60 mm mesh screen on an Intermediate Thomas®-Wiley® Mill (Thomas Scientific, Swedesboro, NJ), producing a homogenized sample of plant material. Plant percent total

nitrogen (%N) and percent total carbon (%C) were analyzed by combustion on a Carlo-Erba CHNS-O analyzer (Model EA-1108, Thermo Electron Corporation, Milan, Italy). For each plant sample, three sub-samples were analyzed to ensure accuracy, and the average %N and %C values for each sample were used in statistical analyses. From the biomass and elemental analyses, belowground:aboveground (BG:AG) ratios, total carbon and nitrogen mass (g), and C:N ratios were determined for each plant.

Statistical analyses

Simple linear regression was used to develop models relating biomass and leaf surface area, and estimated and actual leaf surface areas. Differences in annual values for environmental variables among grazing treatments in the field were analyzed using ANOVAs. To compare mean leaf density, mean biomass, ANPP, turnover times, and leaf damage averaged over each year, and total flower number in each year, 3 x 2 ANOVAs were performed with grazing treatment and time (year) as fixed factors. Leaf density data were square-root transformed and leaf biomass and ANPP log transformed to meet distributional and variance assumptions.

To look at patterns over the duration of the experiment, separate Repeated Measures ANOVAs were performed to develop a split strip-plot model testing the main effects of treatment, year (2001 and 2002) and season nested within year (winter, spring, summer, fall, and winter) on seasonal leaf density, biomass, ANPP, turnover time, and turnover rate. Within each year, another set of separate Repeated Measures ANOVAs were performed to develop a split-plot model testing the main effects of treatment and month (March through November) on monthly leaf density, biomass, ANPP, turnover

time, and turnover rate. When the assumption of sphericity could not be met (Mauchly's criterion for orthogonal components > 0.05), multivariate tests of hypotheses for within-subject effects were used instead of univariate tests (Moser et al. 1990, von Ende 2001). For Repeated Measures analyses, leaf density data were square-root transformed and leaf biomass and ANPP log transformed to meet distributional and variance assumptions.

For the greenhouse experiment, a 3 x 2 MANOVA was performed with grazing treatment and time (year 1 and year 2) as fixed factors, and change in wet weight, change in rhizome size, leaf density per plant, aboveground biomass, belowground biomass, total biomass, BG:AG ratio, belowground allocation, and aboveground allocation simultaneously as dependent variables. Multiple comparisons within grazing treatments were made with a Bonferroni correction. Wet weights and rhizome sizes were standardized $[(\text{final} - \text{initial})/\text{final}]$ to account for initial size differences among transplants. Because of the potential for correlation among dependent variables, subsequent 3 x 2 univariate analyses were performed separately for each dependent variable to confirm the validity of the MANOVA test.

Additionally, a 3 x 2 ANOVA with grazing treatment and time (year 1 and year 2) as fixed factors was performed to compare the total number of flowers in each grazing treatment for each year. Flower number was log transformed to meet distributional and variance assumptions. Separate 3 x 2 x 3 ANOVAs were performed with grazing treatment, time, and tissue type (aboveground, rhizome and roots) as fixed factors to test for the effects of grazing treatment and duration on %N, %C, C:N, total N in grams, and total C in grams. Multiple comparisons within grazing treatment and tissue type were

made with Tukey's HSD. Total N, total C, and C:N were log transformed to meet distributional and variance assumptions.

When data were transformed, reverse transformed means and standard errors are presented as indicated in figure legends. All hypotheses were tested at the $\alpha = 0.05$ level. In the field, for all response variables except turnover time, control plots were omitted from multiple comparisons because they did not differ from shade-controls when analyzed independently; thus, differences reported are between shade-controls and exclosures only. Repeated Measures ANOVAs were performed in SAS (version 8.1e, SAS Institute, Inc., Cary, NC); all other statistical analyses were performed in SPSS (version 9.0, SPSS, Inc., Chicago, IL).

RESULTS

Leaf damage in the field

Exclosures were successful at reducing damage to leaves. Leaves exposed to ambient grazing in shade-control plots experienced a significantly greater loss of leaf biomass than those in exclosures, as determined from quantified estimates of damage ($F_{1,16} = 48.42$, $P < 0.0001$, Fig. 2-2). Exclosures did not completely exclude semi-terrestrial herbivores, which emerged within or gained other unknown access to plots. For both treatments, the amount of surface damaged did not differ between years, nor was there a significant treatment x time interaction. The majority of the damage was from chrysomelid beetles in the genus *Donacia*, and pyralid moth larvae. Very little grazing occurred on *N. odorata* by beetles in the genus *Galerucella*, although damage was observed on two other rooted, floating leaved macrophytes, *Brasenia schreberi* and *Nuphar advena*, present in low abundances at Lake Ponderosa (J. A. Cherry, personal observation). Similarly, based on mean qualitative ranking scores, leaves in shade-control plots were damaged significantly more than those in exclosures ($F_{1,16} = 93.52$, $P < 0.0001$), indicating that quantified estimates of damage were representative of damage and confirming that exclosures successfully reduced grazing.

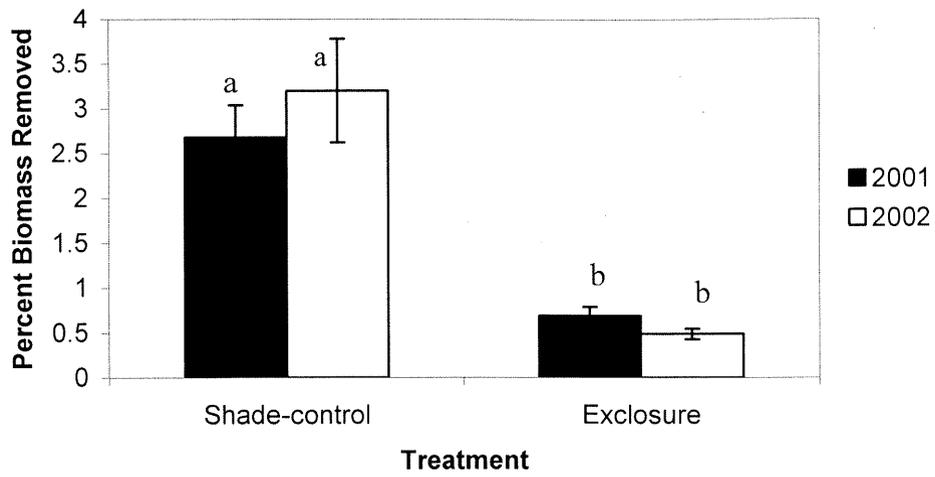


Figure 2-2. Mean percentage of biomass removed by grazers \pm 1 SE between treatments at Lake Ponderosa for 2001 and 2002. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons.

Field environmental variables

During the 2001–2002 experimental period, mean water pH at Lake Ponderosa was 5.33 ± 0.02 (± 1 SE), mean water temperature was $20.61 \text{ }^\circ\text{C} \pm 1.45$, and mean water depth was $0.38 \text{ m} \pm 0.01$. Water pH remained relatively constant over time, whereas water temperature, water depth, and light intensity changed seasonally. Water temperatures and light intensities were greatest in the summers and lowest in the winters, with mean monthly water temperatures ranging from $8.4 \text{ }^\circ\text{C} \pm 0.12$ to $32.0 \text{ }^\circ\text{C} \pm 1.41$ and mean seasonal light intensities ranging from $455.85 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1} \pm 79.50$ to $1969.94 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1} \pm 12.39$ during 2001 and 2002. Water depths were highest in the spring and lowest in late summer, ranging from a weekly mean of $0.12 \text{ m} \pm 0.02$ to $0.70 \text{ m} \pm 0.02$. Total annual precipitation was 889.38 mm in 2001 and 1025.38 mm in 2002.

The mean pH, water temperature, and water depth at Lake Ponderosa during 2001 and 2002 did not differ among grazing treatments (Table 2-1). Water depths did not differ significantly among grazing treatments during the periods of floating island formation in the summers of 2001 and 2002 (Fig. 2-3), even though shade-control plots tended to be deeper during the summers than control and exclosure plots. In 2001, floating islands formed in one control plot, one shade-control plot and two exclosure plots. In 2002, floating islands formed in one control plot and two exclosure plots. Floating islands resulted in localized decreases in inundation, contributing to the patterns of decreased water depths among treatments in the summers of 2001 and 2002. Storms in both years contributed to the variation in depth through time, which affected all plots equally (Fig. 2-3). In March and September of 2001 and January, March and November of 2002, flooding in the area resulted in peaks in water depth. In September 2002, heavy rains

Table 2-1: Mean pH \pm 1 SE, water temperature ($^{\circ}\text{C}$) \pm 1 SE, water depth (m) \pm 1 SE, ambient light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) \pm 1 SE, and percent difference in light intensity above and below experimental frames \pm 1 SE for each herbivory treatment at Lake Ponderosa over the 2001 and 2002 experimental period. Minimum and maximum values are shown in parentheses.

	Control	Shade	Exclosure
pH	5.33 \pm 0.05 (4.80 – 5.72)	5.31 \pm 0.05 (4.80 – 5.70)	5.30 \pm 5.86 (4.80 – 5.86)
Water temperature ($^{\circ}\text{C}$)	20.4 \pm 1.49 (8.40 – 31.6)	21.1 \pm 1.52 (8.42 – 32.0)	20.8 \pm 1.55 (8.42 – 32.8)
Water depth (m)	0.36 \pm 0.01 (0.09 – 0.71)	0.40 \pm 0.01 (0.14 – 0.68)	0.38 \pm 0.02 (0.13 – 0.71)
Light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1219 \pm 193 (441 – 1985)	1152 \pm 200 (538 – 1958)	1123 \pm 210 (389 – 1967)
% light blocked	7.97 \pm 2.91 (0 – 20.24)	37.2 \pm 2.73 (26.6 – 46.5)	44.3 \pm 2.29 (36.6 – 53.6)

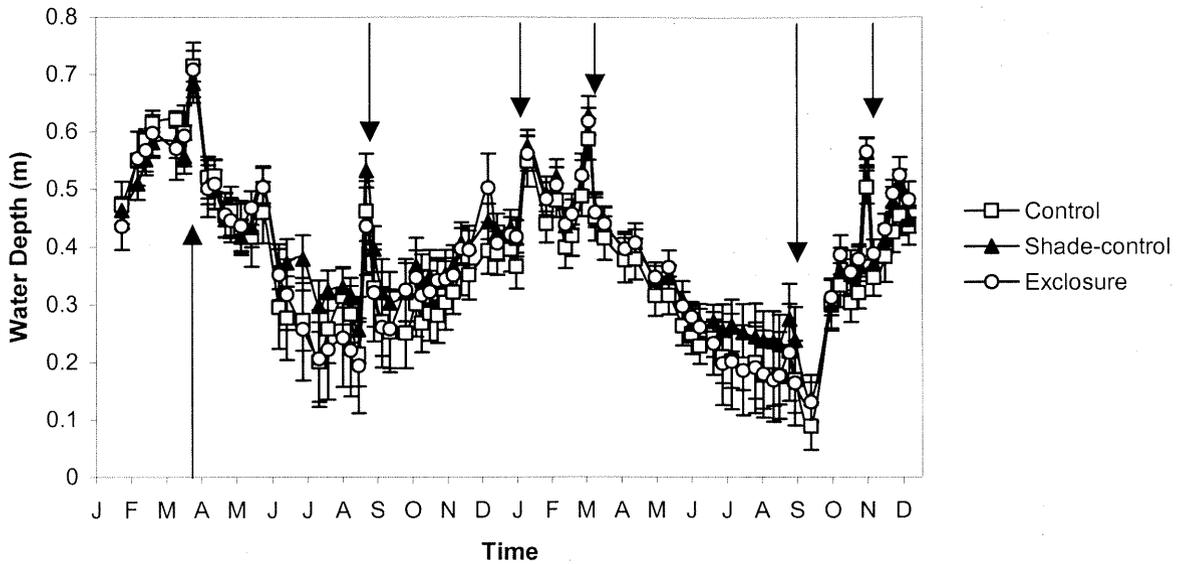


Figure 2-3. Mean water depth (m) \pm 1 SE among herbivory treatments at Lake Ponderosa. Arrows reference precipitation events during the experimental period (see text for description).

from tropical storm Isidore caused flash flooding at Lake Ponderosa and the owners activated the sump pump to drain excess water. However, expecting more rain than there was, they left the pump on for too long and the lake water level actually dropped, which explains the decline in water depth observed at the end of September. Approximately one week after each storm event, lake water level returned to levels similar to those observed the week prior to storms.

Leaf surface area and biomass regressions

Significant simple linear regressions were developed relating estimated leaf surface areas (cm^2) to actual leaf surface areas (cm^2), based on the πr^2 method described above, and predicting biomass (g) from actual surface area (cm^2) (Fig. 2-4). These regressions were used to non-destructively determine leaf biomass from estimates of leaf surface areas obtained in the field.

Plant responses to herbivory in the field

A total of 3,807 leaves (1,891 in 2001 and 1,916 in 2002) were tagged at Lake Ponderosa during this experiment. There were significantly fewer leaves in enclosure plots than in shade-control plots when averaged for 2001 and 2002 ($F_{1,16} = 8.52$, $P = 0.01$, Fig. 2-5A), and there was marginally less biomass on average in enclosure plots than in shade plots in both years ($F_{1,16} = 4.27$, $P = 0.055$, Fig. 2-5B). Additionally, annual ANPP as calculated from summing maximum biomass values was marginally greater in shade-control plots than in enclosures ($F_{1,16} = 4.20$, $P = 0.057$, Fig. 2-5C). Mean leaf density, mean biomass, and annual production did not differ between years and

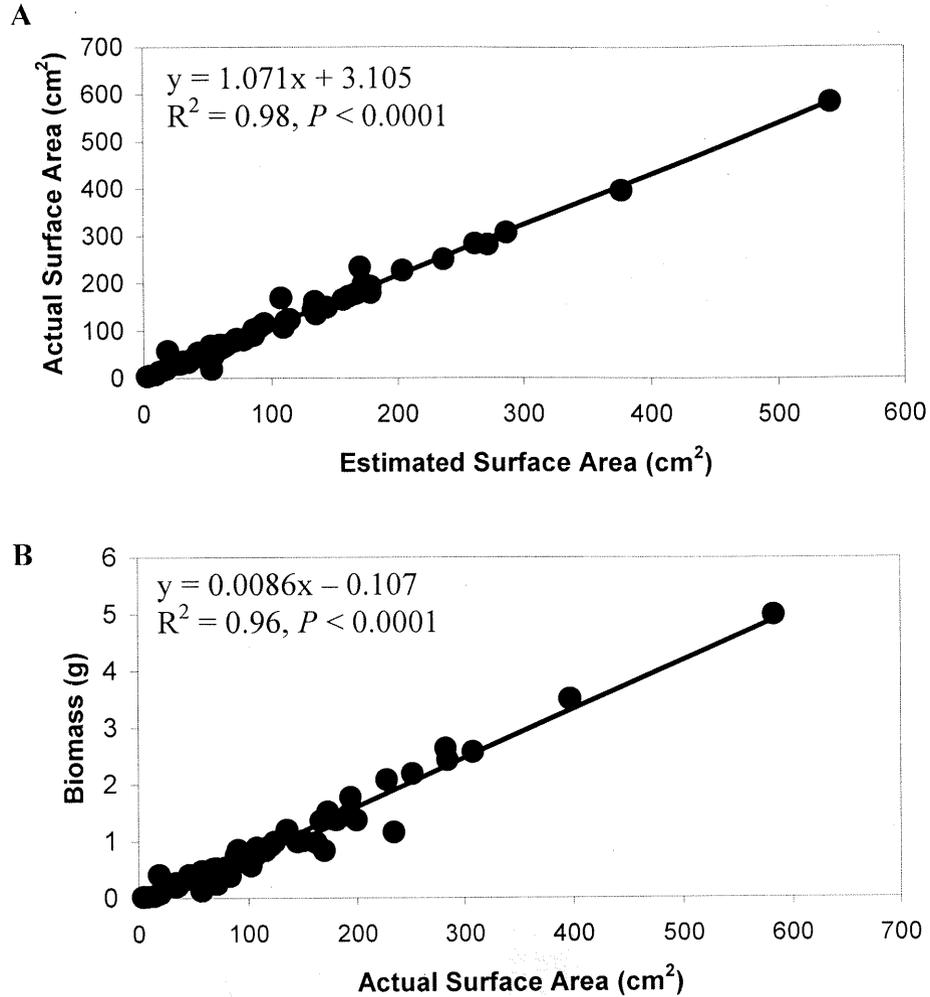


Figure 2-4. Linear regression models relating A) estimated leaf surface area (cm²) to actual leaf surface area (cm²), and B) actual leaf surface area (cm²) to leaf biomass (g) for *N. odorata*.

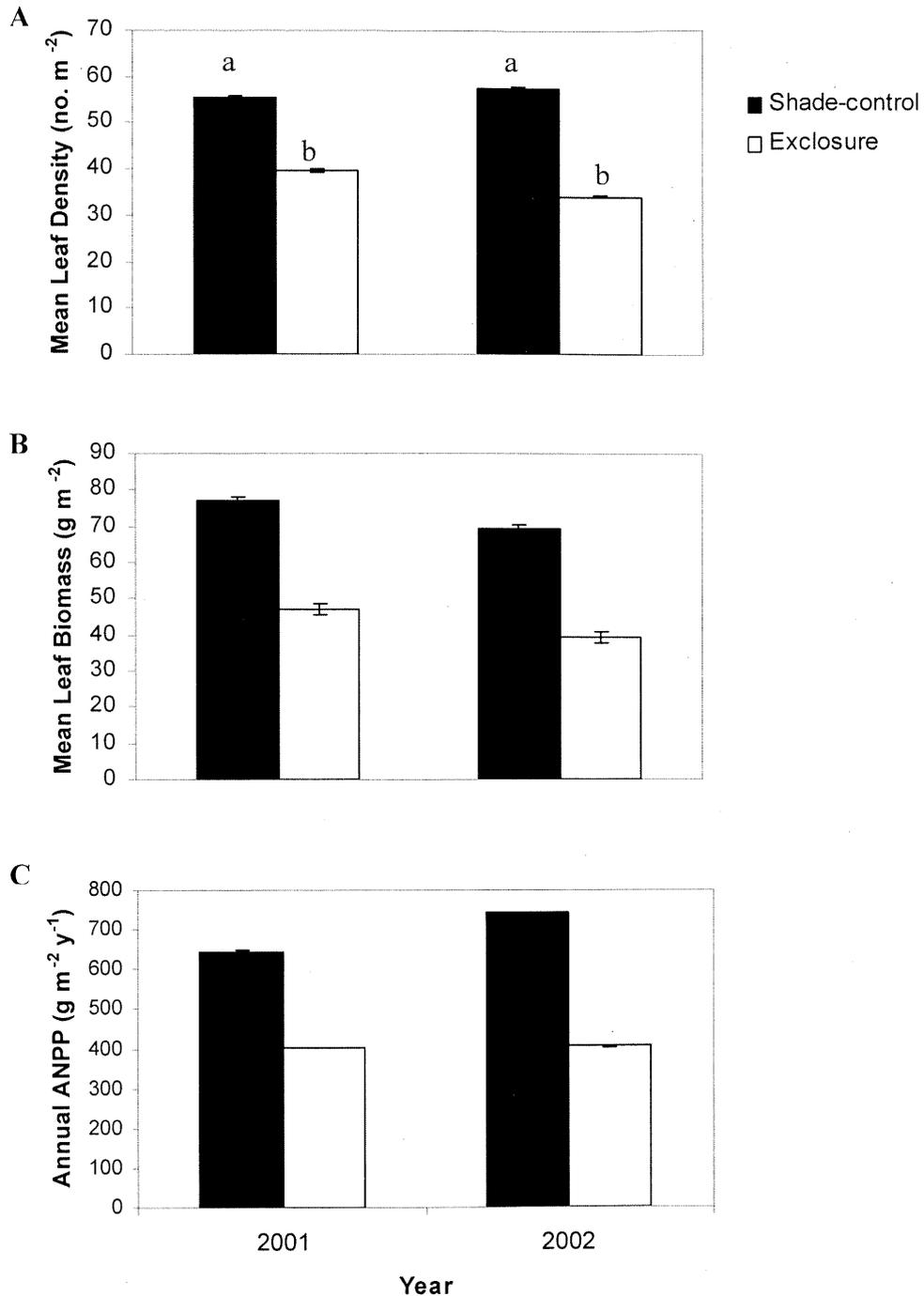


Figure 2-5. Mean leaf A) density (no. m⁻²) \pm 1 SE, B) biomass (g m⁻²) \pm 1 SE, and C) annual ANPP (g m⁻² y⁻¹) \pm 1 SE between herbivory treatments at Lake Ponderosa for 2001 and 2002. Means and standard errors are reverse square-root transformed values for density and reverse log-transformed values for biomass and ANPP. Letters denote significant differences at the $\alpha = 0.05$ level for all pairwise comparisons.

responded similarly between years regardless of treatment (i.e., no significant treatment x time interaction). Mean annual turnover times were similar among treatments and between years, and responded similarly over time regardless of treatment (Fig. 2-6). For this analysis, control plot turnover times were included in the 3 x 2 ANOVA because, when analyzed separately, leaves in control plots had shorter turnover times than those in shade-control plots ($F_{1,16} = 5.5$, $P = 0.03$). However, only shade-control and exclosures means are presented in Fig. 2-6. There were fewer flowers in exclosure plots than in shade-control plots in both years ($F_{1,16} = 17.46$, $P = 0.001$, Fig. 2-7), but no significant year or interaction effects.

Seasonal leaf density, biomass, and production were not significantly affected by grazing treatment in the field despite the tendency for shade-control plants to have more leaves, more biomass and greater production over time than plants in exclosure plots (Table 2-2 and Fig. 2-8). Leaf density, biomass and ANPP exhibited unimodal patterns in 2001 and 2002 regardless of treatment, with peaks occurring in summer (Figure 2-8). However, seasonal patterns were not consistent between years. Summer leaf density, biomass and ANPP were greater in 2001 while spring and fall leaf density, biomass and ANPP were greater in 2002. Within year analyses of monthly leaf density, biomass and ANPP confirmed the effects of grazing treatment presented above with one exception (Fig. 2-8). Grazing treatment did not affect leaf density in 2001, but in 2002, there were significantly more leaves in shade-control plots than in exclosures ($F_{8,1} = 9.12$, $P = 0.02$, Fig. 2-8A). Furthermore, both methods of calculating annual ANPP were consistent; summation of production in monthly intervals did not differ significantly from maximum biomass summation values (data not shown).

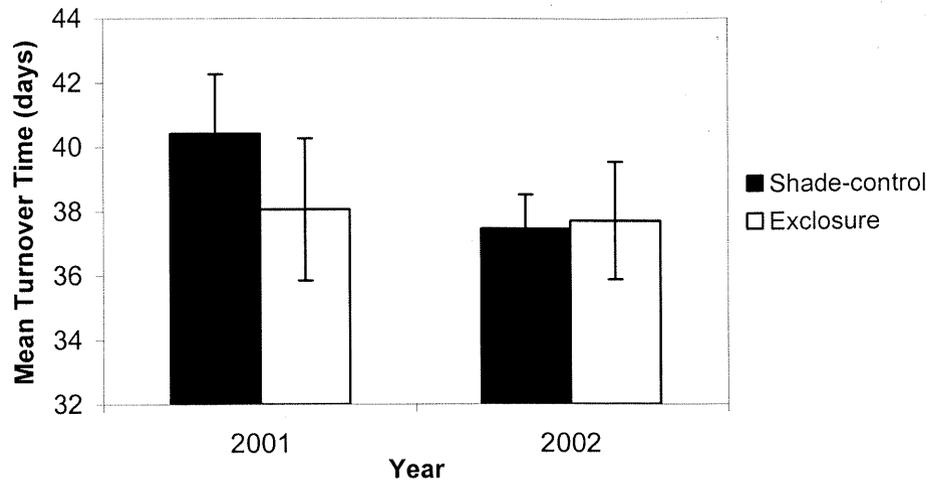


Figure 2-6. Mean leaf turnover time (days) \pm 1 SE between herbivory treatments at Lake Ponderosa for 2001 and 2002.

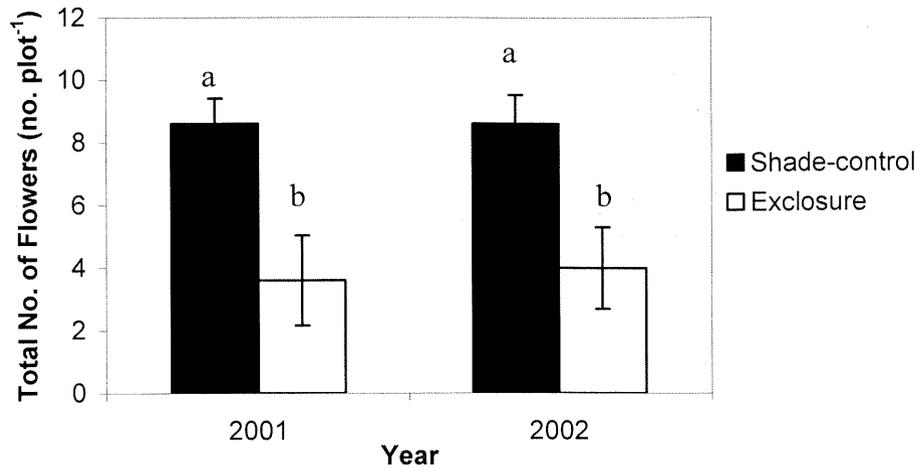


Figure 2-7. Total number of flowers produced (no. plot⁻¹) \pm 1 SE between herbivory treatments at Lake Ponderosa for 2001 and 2002. Letters denote significant differences at the $\alpha = 0.05$ level for all pairwise comparisons.

Table 2-2. Multivariate analysis of split-strip plot repeated measures models for leaf density, leaf biomass, and ANPP at Lake Ponderosa during the 2001–2002 experimental period. For Wilks' λ tests, error df are shown in parentheses.

Response Variable	Source	df	Wilks' λ	MS	F	<i>P</i> value
Leaf Density	Treatment	1		1.604	3.87	0.08
	Error	8		0.415		
	Year	1	0.371 (8)		13.58	0.01
	Year x treatment	1	0.994 (8)		0.05	0.83
	Season	4	0.002 (5)		579.91	<0.0001
	Season x treatment	4	0.754 (5)		0.41	0.8
	Year x season	4	0.094 (5)		11.99	0.01
	Year x season x treatment	4	0.493 (5)		1.29	0.39
Leaf Biomass	Treatment	1		1.782	1.78	0.22
	Error	8		1.001		
	Year	1	0.457 (8)		9.52	0.02
	Year x treatment	1	0.995 (8)		0.04	0.85
	Season	4	0.004 (5)		284.54	<0.0001
	Season x treatment	4	0.761 (5)		0.39	0.81
	Year x season	4	0.123 (5)		8.88	0.02
	Year x season x treatment	4	0.613 (5)		0.79	0.58
ANPP	Treatment	1		2.014	2.18	0.18
	Error	8		0.925		
	Year	1	0.947 (8)		0.45	0.53
	Year x treatment	1	0.879 (8)		1.11	0.33
	Season	4	0.002 (5)		702.99	<0.0001
	Season x treatment	4	0.814 (5)		0.29	0.88
	Year x season	4	0.055 (5)		21.37	0.002
	Year x season x treatment	4	0.382 (5)		2.02	0.23

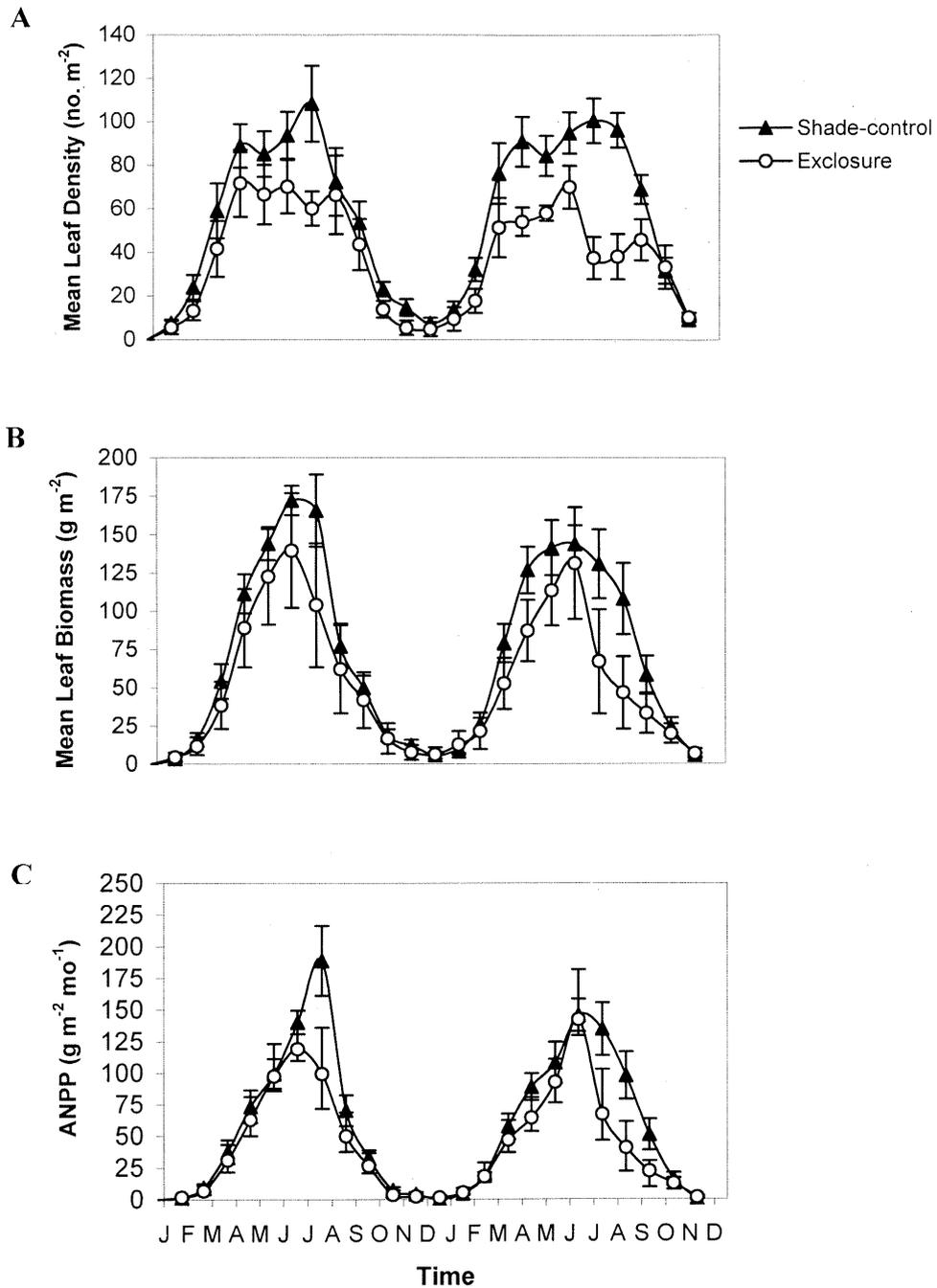


Figure 2-8. Mean monthly leaf A) density (no. m⁻²) ± 1 SE, B) biomass (g m⁻²) ± 1 SE, and C) ANPP (g m⁻² mo⁻¹) ± 1 SE between herbivory treatments at Lake Ponderosa during the 2001–2002 experimental period.

Grazing treatment did not affect seasonal turnover times or turnover rates of *N. odorata* in the field (Table 2-3 and Fig. 2-9). Turnover times were greatest in the winters and lowest in the summers in 2001 and 2002 regardless of treatment. As expected, turnover rates exhibited the inverse pattern, although seasonal turnover rates did not respond similarly in shade-control and exclosure plots as indicated by a significant season x treatment interaction ($F_{4,4} = 18.19, P = 0.01$; Fig. 2-9). As with leaf density, biomass and ANPP, these seasonal patterns were not consistent between years. Within year analyses of monthly values confirmed that grazing treatment did not affect turnover time or turnover rate (Fig. 2-9).

Plant responses to simulated herbivory in the greenhouse

A total of 3,787 leaves were tagged during the two-year greenhouse experiment. Plants grown in the greenhouse responded differently among treatments and between years ($P < 0.0001$ and $P = 0.002$, respectively). As expected, plants grown in the greenhouse for two years increased wet weight more than those harvested after only one year ($F_{1,42} = 5.34, P = 0.03$, Fig. 2-10A), although percent change in rhizome size and leaf density per plant did not differ between harvests. Grazing treatment significantly affected percent change in wet weight and rhizome size, and leaf density per plant ($F_{2,42} = 5.17, P = 0.01$; $F_{2,42} = 4.88, P = 0.01$; and $F_{2,42} = 6.74, P = 0.003$, respectively, Fig. 2-10). In all cases, highly clipped plants did not grow as much as those with no clipping, while those with moderate clipping did not differ from either of the other treatments.

Table 2-3. Multivariate analysis of split-strip plot repeated measures models for leaf turnover time and leaf turnover rate at Lake Ponderosa during the 2001–2002 experimental period. For Wilks' λ tests, error df are shown in parentheses. Analysis of turnover time included control plots.

Response Variable	Source	df	Wilks' λ	MS	F	<i>P</i> value
Turnover time	Treatment	2		498.85	1.3	0.31
	Error	12		383.42		
	Year	1	0.349 (12)		22.35	0.0005
	Year x treatment	2	0.851 (12)		1.05	0.38
	Season	4	0.078 (9)		26.73	<0.0001
	Season x treatment	8	0.357 (18)		1.51	0.22
	Year x season	4	0.088 (9)		23.40	<0.0001
	Year x season x treatment	8	0.604 (18)		0.65	0.73
Turnover rate	Treatment	1		3.72	1.64	0.24
	Error	7		2.27		
	Year	1	0.980 (7)		0.14	0.72
	Year x treatment	1	0.992 (7)		0.06	0.82
	Season	4	0.001 (4)		773.53	<0.0001
	Season x treatment	4	0.052 (4)		18.19	0.01
	Year x season	4	0.085 (4)		10.81	0.02
	Year x season x treatment	4	0.600 (4)		0.67	0.65

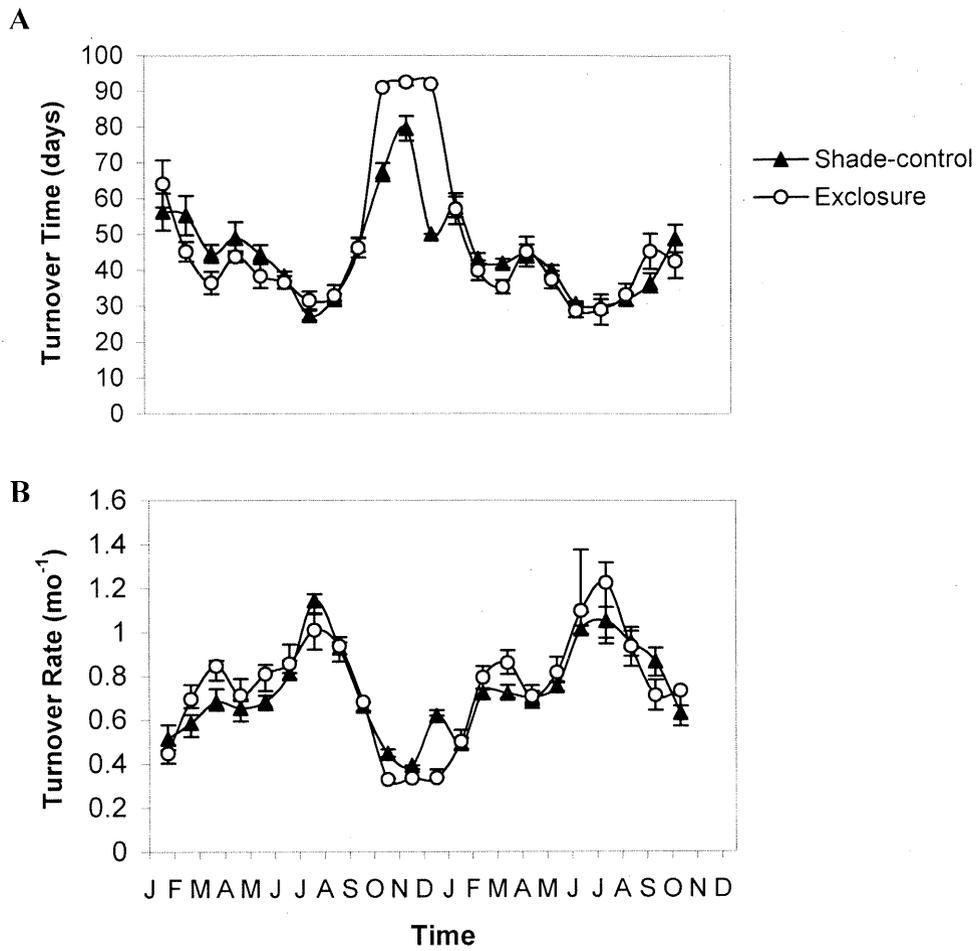


Figure 2-9. Mean monthly A) turnover time (days) \pm 1 SE and B) turnover rate (mo^{-1}) \pm 1 SE between herbivory treatments at Lake Ponderosa during the 2001–2002 experimental period.

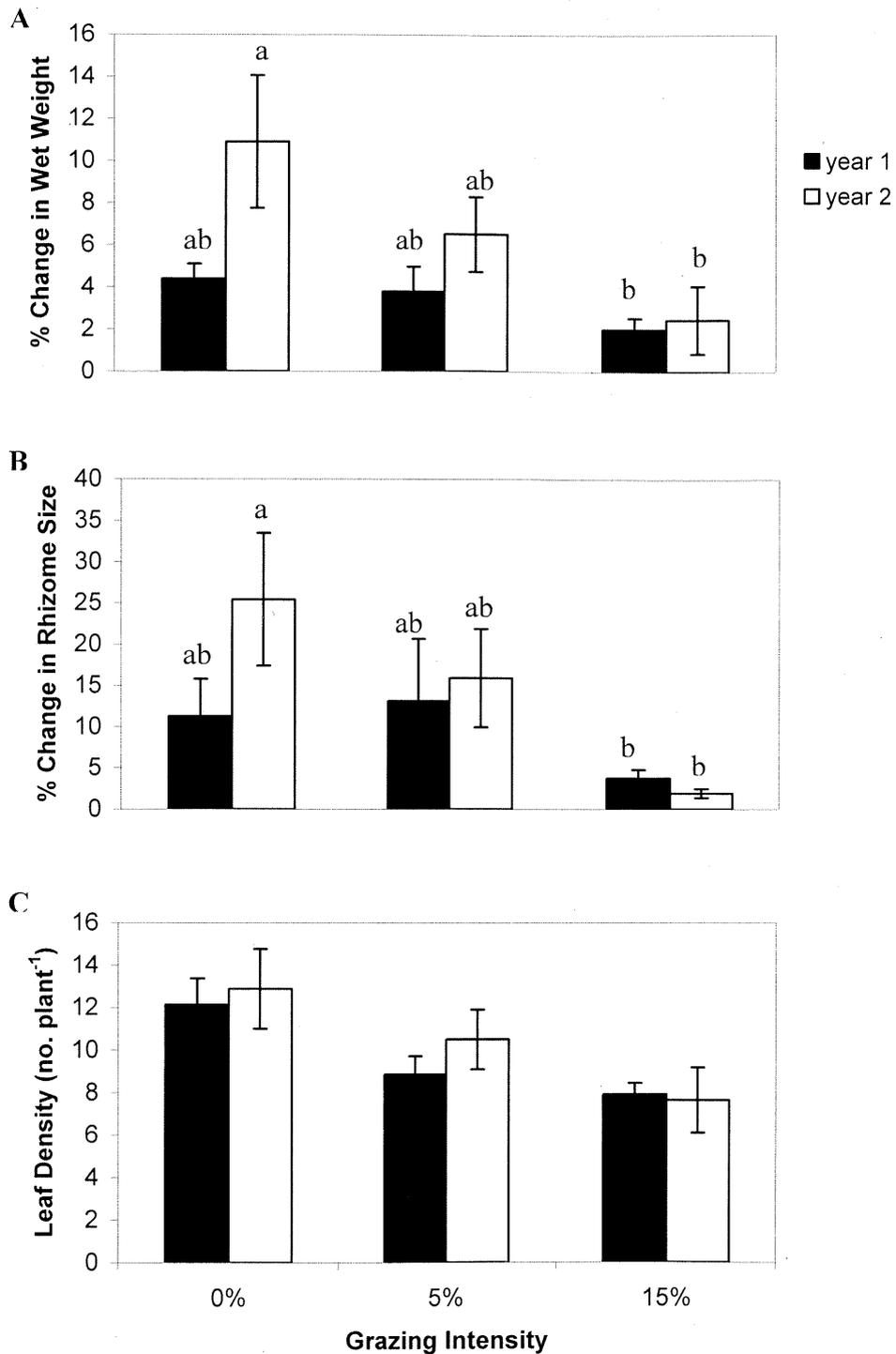


Figure 2-10. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean A) percent change in wet weight \pm 1 SE, B) percent change in rhizome size \pm 1 SE, and C) leaf density (no. plant⁻¹) \pm 1 SE for mature plants harvested from the greenhouse experiment. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons.

Plants grown in the greenhouse for two years had greater aboveground biomass, belowground biomass, and total plant biomass than those harvested after only one year ($F_{1,42} = 6.12, P = 0.02$; $F_{1,42} = 4.59, P = 0.04$; and $F_{1,42} = 5.31, P = 0.03$, respectively, Fig. 2-11), although BG:AG did not differ between years because of large variation in the second year. Amount of leaf surface area removed in grazing treatments significantly affected aboveground biomass, belowground biomass, and total biomass ($F_{2,42} = 9.93, P < 0.0001$; $F_{2,42} = 20.16, P < 0.0001$; and $F_{2,42} = 17.80, P < 0.0001$, respectively, Fig. 2-11), but not BG:AG. Belowground biomass differed among all treatment combinations such that plants that were not clipped had the most belowground biomass and plants with high levels of clipping had the least. Plants with no or moderate levels of clipping had greater aboveground biomass and total plant biomass than those with the high level of clipping. Grazing treatment and duration of the experiment did not affect the amount of total biomass allocated belowground or aboveground (data not shown). Separate univariate analyses for each of the dependent variables confirmed all of the treatment and time effects of multivariate analysis discussed above.

Grazing intensity also significantly affected reproductive output of *N. odorata* in the greenhouse experiment. Plants with no and moderate clipping produced more flowers each year than those highly clipped ($F_{2,66} = 14.35, P < 0.0001$, Fig. 2-12); duration of the experiment did not affect the number of flowers produced.

Percent nitrogen differed among grazing treatments and plant tissue type ($F_{2,126} = 8.29, P < 0.0001$ and $F_{2,126} = 39.86, P < 0.0001$, respectively, Fig. 2-13A). Plants with no or moderate levels of clipping had significantly lower %N than those with high levels of clipping, and aboveground tissue had significantly higher %N than rhizomes and roots.

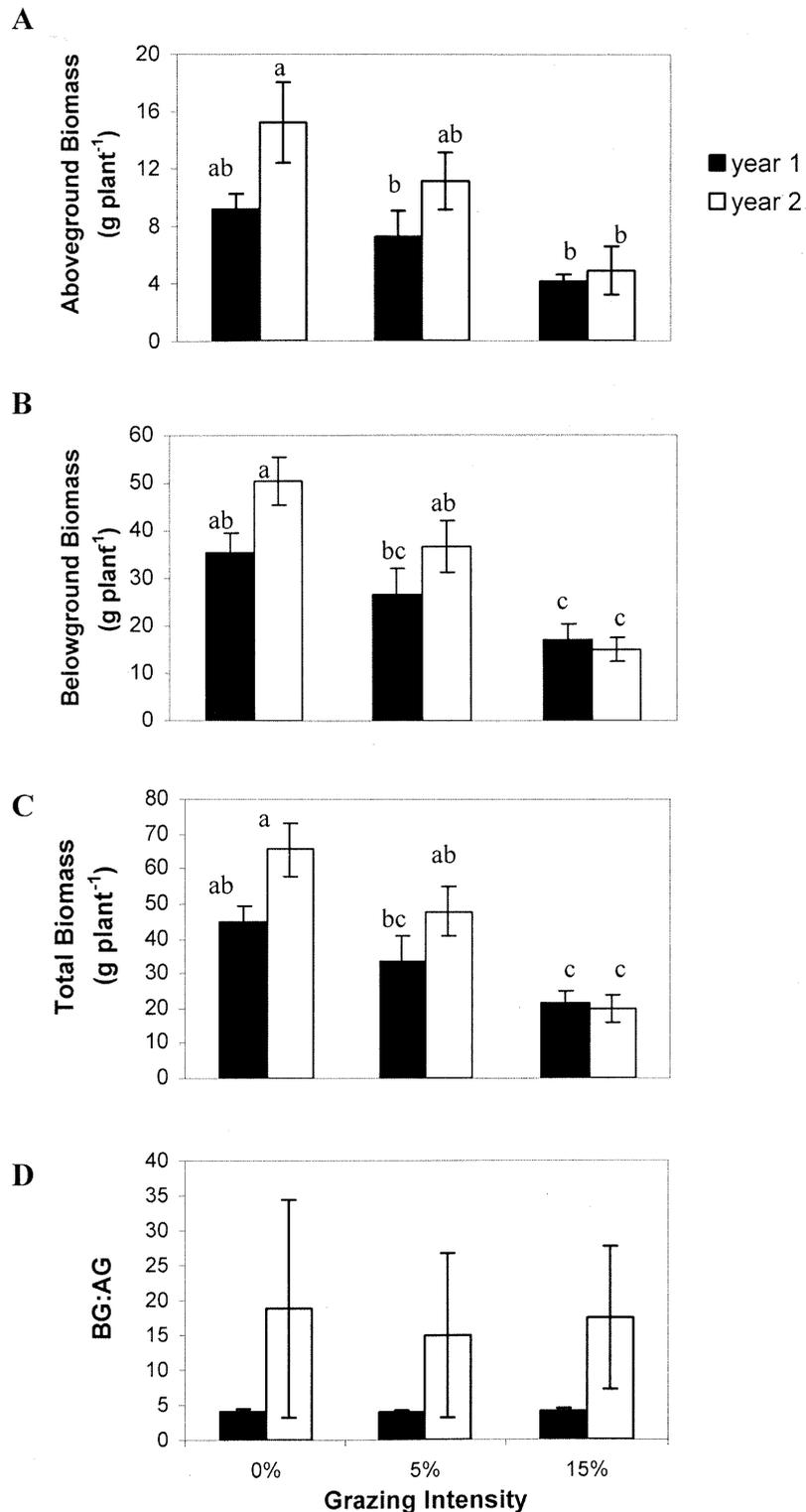


Figure 2-11. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean A) aboveground biomass (g plant^{-1}) ± 1 SE, B) belowground biomass (g plant^{-1}) ± 1 SE, C) total biomass (g plant^{-1}) ± 1 SE, and D) BG:AG ± 1 SE for mature plants harvested from the greenhouse experiment. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons.

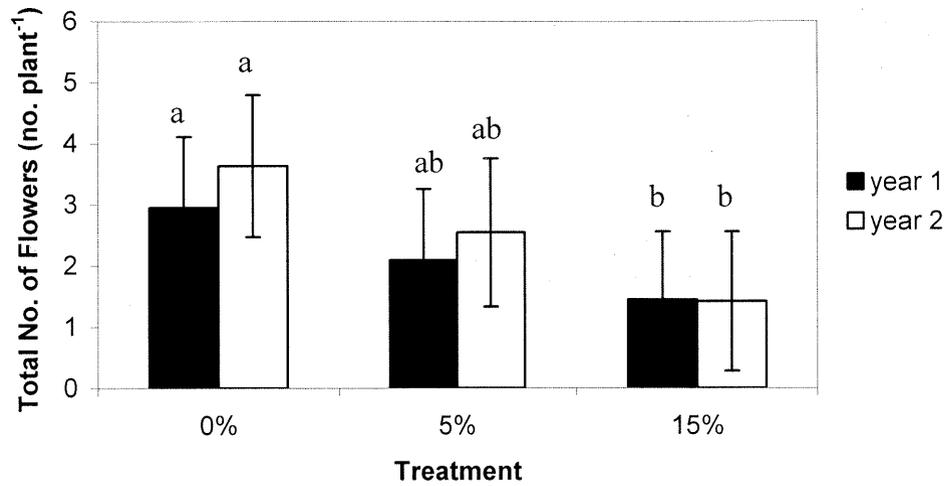


Figure 2-12. Total number of flowers produced (no. plant⁻¹) ± 1 SE by mature plants in the greenhouse experiment for year 1 and year 2. Means and standard errors are reverse log-transformed values. Letters denote significant differences at the $\alpha = 0.05$ level for all pairwise comparisons.

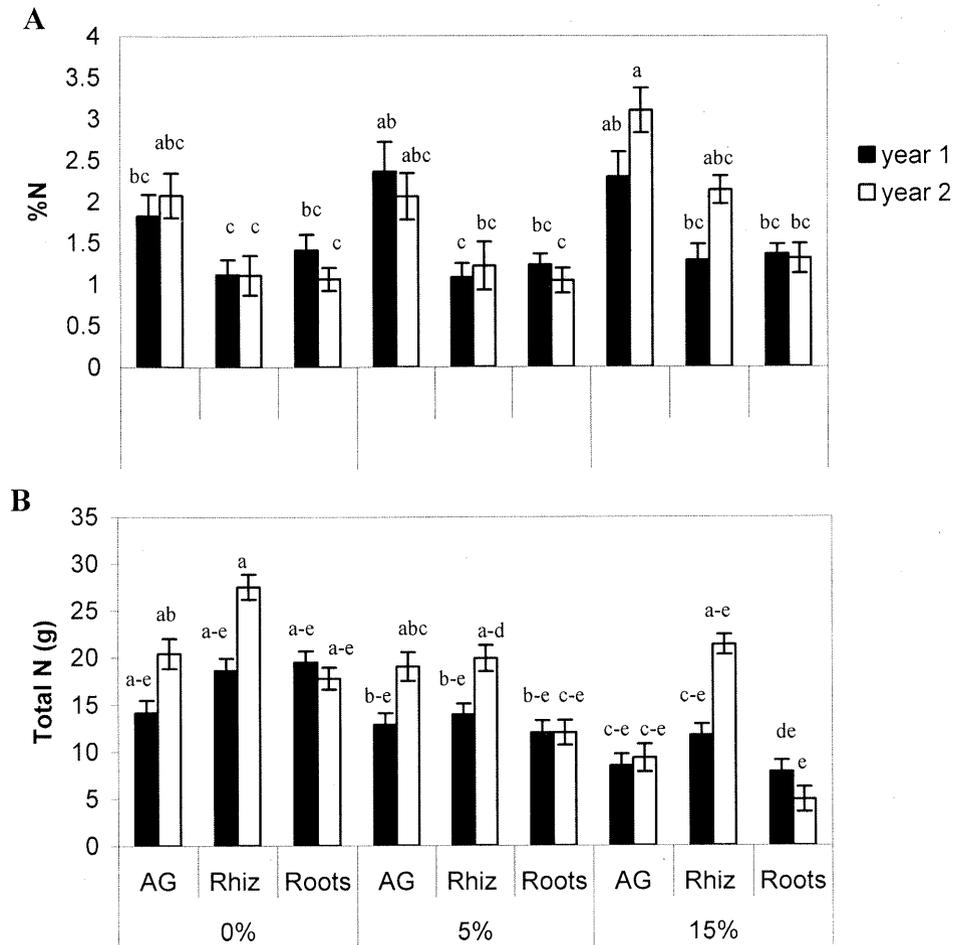


Figure 2-13. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean A) %N \pm 1 SE, and B) total N (g) \pm 1 SE among treatments and tissue types for mature plants harvested from the greenhouse experiment. Means and standard errors for total N are reverse log-transformed values. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons. Plant tissue abbreviations: AG = aboveground, Rhiz = rhizome, Roots = roots.

Percent nitrogen did not differ between years. However, plants of different treatments did not respond similarly between years (treatment x time interaction: $F_{2,126} = 3.79$, $P = 0.03$). Percent nitrogen in rhizomes tended to increase between years regardless of treatment, whereas it tended to decline between years in roots. Percent nitrogen in aboveground tissue tended to increase between years for plants with no or heavy clipping, but tended to decrease between years for plants with moderate clipping.

Furthermore, total N mass in each plant differed among grazing treatment and plant tissue type ($F_{2,126} = 10.13$, $P < 0.0001$ and $F_{2,126} = 4.86$, $P = 0.01$, respectively, Fig. 2-13B). Plants with no or moderate clipping had significantly more nitrogen than those with high clipping, and rhizomes had significantly more nitrogen than roots. Total N did not differ between years, although N content in roots tended to decrease between years, whereas it tended to be maintained or slightly increase in aboveground tissue and rhizomes.

Percent carbon in plants was not affected by grazing treatment, time of harvest, or tissue type (Fig. 2-14A). However, total C in plants was affected by grazing treatment and tissue type ($F_{2,126} = 22.98$, $P < 0.0001$ and $F_{2,126} = 19.65$, $P < 0.0001$, respectively, Fig. 2-14B). Plants with no or moderate clipping had significantly more carbon than those with high clipping. Rhizomes had significantly more carbon than both aboveground tissue and roots. In addition roots had more carbon than aboveground tissue, although this difference was marginally significant ($P = 0.052$). Total C did not differ between years, although resource content in roots tended to decrease between years, whereas it tended to be maintained or slightly increase in aboveground tissue and rhizomes. C:N differed with plant tissue type ($F_{2,126} = 8.62$, $P < 0.0001$, Fig. 2-15), but not with grazing treatment or

time of harvest. C:N was greater in rhizomes and roots than in aboveground chlorophyllous tissue.

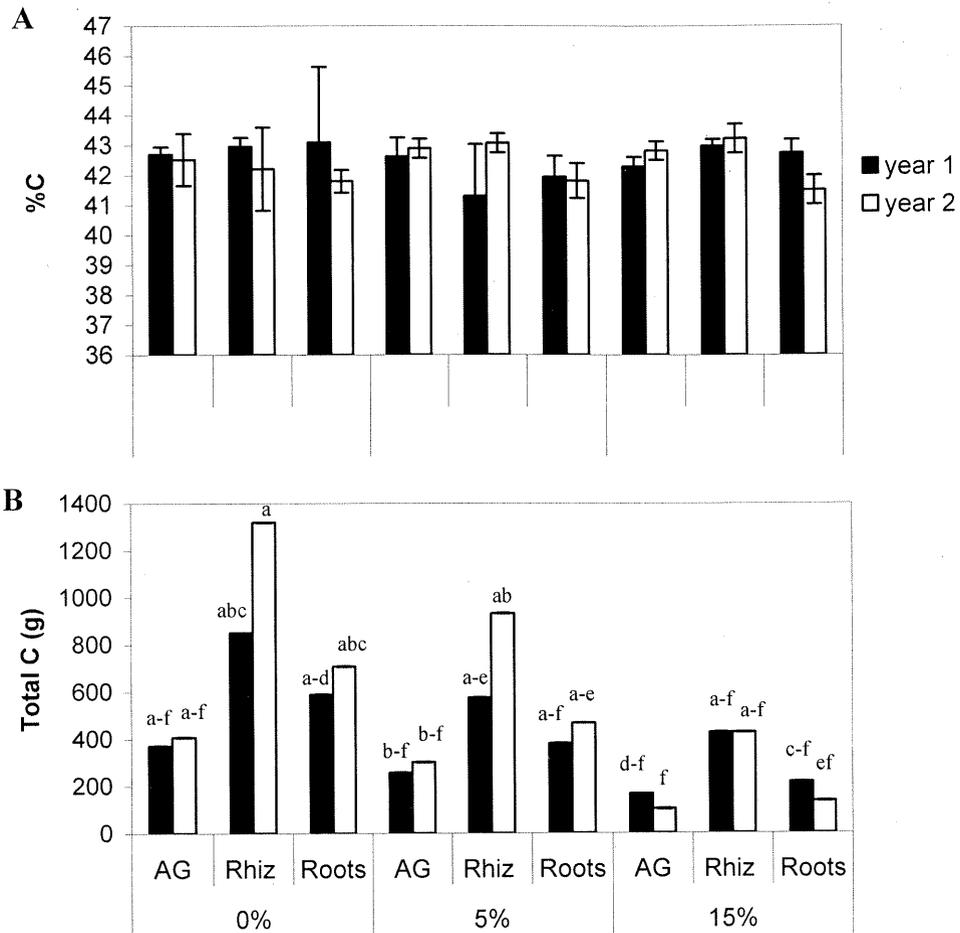


Figure 2-14. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean A) %C \pm 1 SE, and B) total C (g) \pm 1 SE among treatments and tissue types for mature plants harvested from the greenhouse experiment. Means and standard errors for total C are reverse log-transformed values. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons. Plant tissue abbreviations as in Figure 2-13.

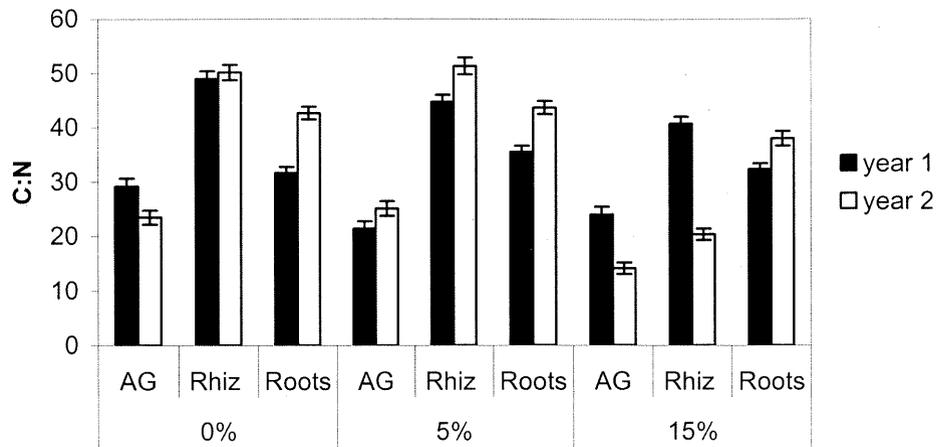


Figure 2-15. The effect of grazing intensity (0%, 5% and 15% surface area removed) and duration (year) on mean C:N \pm 1 SE among treatments and tissue types for mature plants harvested from the greenhouse experiment. Letters denote significant differences at the $\alpha = 0.05$ level among all pairwise comparisons. Plant tissue abbreviations as in Figure 2-13.

DISCUSSION

Variability in field response influenced temporal patterns

Nymphaea odorata exposed to ambient grazing in the field consistently had more leaves, greater biomass, and were more productive than those exposed to very low levels of grazing. However, these temporal patterns were rarely supported statistically, most likely because of high within-treatment variability resulting from differences in water depth among plots. At Lake Ponderosa, there was a natural water depth gradient over which *N. odorata* existed, as well as differences in water depth created by floating island formation. In shallower water, *N. odorata* leaves tend to be smaller than when in deeper water (data not shown). When subjected to adverse conditions, leaf size of this species is often diminished (Godfrey and Wooten 1981). The combination of differences in plant responses arising from natural variation in water depth and the disturbance of floating island formation likely contributed to the variation observed within treatments.

Alternatively, variability within plots could have been due to clonal integration among leaves of the same genet if some leaves were exposed to ambient grazing outside of enclosure plots. Effects of grazing can spread among leaves of the same individual, a strategy thought to minimize the risk of mortality for the plant by spreading the risk of damage among many leaves, or ramets (e.g., Piqueras 1999). At Lake Ponderosa, most plants were contained entirely within screened sampling plots and very few leaves

occurred on plot margins. Therefore, water depth variation, not clonal integration, was more likely responsible for high within-treatment variability and the lack of consistent statistical support for overcompensation by *N. odorata* in the field.

Potential vegetative and reproductive overcompensation by N. odorata

Plants exposed to ambient grazing in the field and moderate clipping in the greenhouse were capable of exactly compensated, and potentially overcompensating, for grazing with respect to vegetative responses, tending to support the first hypothesis. Mean leaf density, mean biomass, and annual ANPP averaged for 2001 and 2002 were greater under ambient grazing conditions than reduced grazing (marginally significant for biomass and production), suggesting that grazing enhanced aboveground performance by *N. odorata* in the field. Furthermore, plants exposed to ambient grazing tended to have consistently higher leaf densities, biomass and ANPP through time than those protected from herbivores. In the greenhouse, such grazing optimization or overcompensation did not occur at moderate grazing intensity as predicted. Rather, moderately clipped plants grew similarly to unclipped plants with respect to changes in wet weight and rhizome size, leaf density, and aboveground and total biomass, suggesting that *N. odorata* exactly compensated for moderate levels of herbivory. The only exception was for belowground biomass, which was negatively affected by both moderate and heavy clipping (discussed below).

In general, plants responded positively to ambient grazing in the field when compared to those exposed to reduced grazing. However, this pattern was not the result of enhanced leaf turnover rates, leading to the rejection of the second hypothesis.

Herbivory has been demonstrated to decrease leaf turnover times and increase leaf turnover rates, resulting in greater ANPP, for other water lilies in the same family as *N. odorata* (Wallace and O'Hop 1985, Setala and Makela 1991). This was not the case for *N. odorata* at Lake Ponderosa. *Nymphaea odorata* may differ from other water lilies in the mechanism by which production is enhanced such that grazed individuals simply produce more leaves per plant rather than rapidly replacing a smaller number of leaves through time. Additionally, turnover rates between treatments at Lake Ponderosa responded differently through time. In the spring of both years, turnover rates for plants exposed to ambient grazing rapidly increased before stabilizing more so than protected plants. This difference may have provided grazed plants an advantage before entering the summer growth period. As a result, *N. odorata* tended to respond positively to ambient grazing in this study.

The generally positive response of *N. odorata* to grazing at Lake Ponderosa differed from that observed for *N. odorata* in another Alabama wetland where leaf density, biomass and production were lower than in this study and were negatively affected by grazing (Carter 1995). This difference occurred despite the similarity of ambient grazing intensities to those reported for other aquatic macrophytes (Lodge 1991, Setala and Makela 1991, Carter 1995). Aboveground responses at Lake Ponderosa, as a relatively productive system, may have been enhanced by greater nutrient recycling allowing plants to regrow and compensate for herbivory (see McNaughton 1979, de Angelis 1992, de Mazancourt et al. 1998, Belovsky and Slade 2000, de Mazancourt and Loreau 2000a, b). Greater nutrient recycling would be possible if high foliar nutrient concentrations stimulated grazing (e.g., Elger and Willby 2003) and resulted in increased

decomposition rates of plant biomass (see Cebrian 1999, 2004, de Mazancourt and Loreau 2000b). Furthermore, intraspecific competition among dense stands of *N. odorata* may have positively influenced how the population responded to herbivory (e.g., Parmesan 2000, van der Wal et al. 2000). At greater densities, the effects of herbivory at Lake Ponderosa would have been spread among more leaves such that plants were less likely to be negatively affected by grazing (Piqueras 1999). All of these factors potentially contributed to the observed aboveground vegetative optimization by *N. odorata* at Lake Ponderosa.

The positive effects of herbivory, or neutral effects for greenhouse plants, were not limited to vegetative responses. *Nymphaea odorata* was also capable of exactly compensating, and potentially overcompensating, for grazing with respect to reproductive output, leading to the rejection of the third hypothesis. Generally, plants are thought to differentially allocate energy to one of three areas – growth, reproduction, and defense – creating trade-offs within plants (Bazzaz et al. 1987). Because vegetative responses related to growth and production were enhanced or maintained when exposed to ambient or moderate grazing, a corresponding negative effect of grazing on sexual reproductive output in *N. odorata* was expected. That was not the case in this study where plants exposed to ambient grazing in the field produced more flowers than those exposed to low levels of grazing, and, moderately clipped plants in the greenhouse produced a similar numbers of flowers as unclipped plants, but more than highly clipped plants. Reproductive optimization and vegetative optimization can occur simultaneously in ecosystems with high rates of nutrient recycling and resource competition among

individuals (Yamauchi and Yamamura 2004), conditions that may have been satisfied at Lake Ponderosa.

Despite positive or neutral responses of *N. odorata* sexually and vegetatively, there may have been trade-offs occurring between growth and clonal reproduction within grazed plants. Clonal reproduction was not directly measured in this study. However, rhizomes of moderately clipped and unclipped plants grew similarly throughout the greenhouse experiment, suggesting that grazing may not negatively affect clonal expansion. Regardless of the effects of herbivory on clonal reproduction, *N. odorata* compensated for ambient or moderate levels of herbivory both vegetatively and in terms of sexual reproduction. The absence of a trade-off between sexual reproduction and growth indicated that *N. odorata* was capable of compensation with respect to all aboveground response variables measured.

Differential above- and belowground responses of N. odorata to moderate damage

In the greenhouse, *N. odorata* responded differently above- and belowground to the level of simulated herbivory. Plants compensated for biomass removal for most vegetative response variables at moderate levels of grazing, while those heavily damaged were negatively affected. However, at moderate and heavy levels of grazing, belowground biomass and total carbon were negatively affected by clipping relative to unclipped plants, leading to the rejection of the fourth hypothesis as it pertains to biomass and carbon allocation. This may be evidence of a trade-off between aboveground and belowground responses, where the potential for aboveground compensation was at the expense of belowground biomass and carbon stores. Grazing in other systems has also

resulted in significant negative belowground effects on root biomass and production (Crawley 1983, Holland and Detling 1990, Ruess et al. 1998; van der Wal et al. 2000), even when aboveground responses were optimized.

Plants have been shown to allocate carbon and biomass to both shoots and roots in response to grazing, but the response may be largely species-specific. A perennial grass adapted to grazing exhibited increased carbon fixation and stored more carbon aboveground than below when damaged (Dyer et al. 1991), while no effects of defoliation on carbon allocation were observed in mountain beech (Mikola et al. 2000). Conversely, significant positive relationships between grazing and carbon allocation to roots were observed for maize (Holland et al. 1996). For *N. odorata*, there was more carbon in rhizomes than other tissues and more biomass belowground than aboveground.

Furthermore, there was less carbon and lower total biomass in heavily clipped plants than in plants of either other treatment. Declines in belowground biomass and carbon sources for sediment-based microbial processes in response to grazing may have ecosystem-level implications for nutrient cycling processes within the detrital food web (e.g., nitrogen cycling in grasslands [Holland and Detling 1990]). Inputs of aboveground biomass to the detrital pathway, especially if enhanced by herbivory, may represent the more significant source of organic matter within the deep-water marsh of Lake Ponderosa.

As with biomass and total C, nitrogen in *N. odorata* responded differently above- and belowground to differing levels of simulated herbivory. Total N declined with increased grazing, a pattern that mimicked the one observed for biomass and total C. However, %N increased with grazing intensity and was greatest in aboveground tissues.

There was a greater amount of nitrogen relative to carbon in aboveground tissue (i.e., lower C:N aboveground than belowground). This indicates that *N. odorata* allocated a greater proportion of nitrogen to its shoots as damage increased, and supports the fourth hypothesis with regards to nitrogen allocation. Leaf N is generally positively related to photosynthetic rate (reviewed in Peterson et al. 1999). Concentration of nitrogen in shoots with increased grazing intensity may be indicative of *N. odorata* compensating for the loss of photosynthetic area due to clipping. An alternative explanation is that increases in aboveground %N corresponded to increases in alkaloid production, a nitrogen-based secondary defense compound found in *N. odorata*. Production of secondary compounds, because it is energetically costly and can reduce growth and reproduction (McKey 1974, Bazzaz 1987), is often induced or accelerated only after damage occurs (Ohnmeiss and Baldwin 1994, Cronin and Hay 1996, Newman et al. 1996, Thaler 1999), and may require chemical cues present in the saliva of herbivores. Therefore, it was more likely that the increase in aboveground %N in this study was due to photosynthetic compensation in response to damage, not induction of secondary defenses.

Finally, plants harvested after two years tended to be larger and weigh more than those harvested after one year. However, this pattern was independent of treatment. This suggests that grazing did not result in greater regrowth capacity for moderately clipped plants in the second year, leading to the rejection of the fifth hypothesis. The effects of herbivory on plant size and biomass may not be evident in the short term; sustained herbivory for more than two years may be required to parse out differences along a grazing intensity gradient. In the short term, it may be better to look at allocation of

nitrogen because nitrogen was shown to accumulate in leaves with increased grazing after only one year.

Thresholds exist above which plants cannot compensate

The grazing optimization hypothesis describes a unimodal pattern where primary production is maximized at some moderate level of herbivory (McNaughton 1979). The greenhouse experiment did not support enhancement of plant responses at moderate grazing as predicted by the GOH. Instead, in the greenhouse, plants exposed to moderate levels of herbivory compensated exactly, while a high level of herbivory caused undercompensation. In the field, *N. odorata* tended to overcompensate at ambient levels of herbivory. The moderate grazing treatment in the greenhouse removed a greater percentage of leaf biomass than was removed naturally at Lake Ponderosa, and may have been too high to optimize plant responses aboveground as was observed in the field.

Additionally, herbivory indirectly contributes to grazing optimization when nutrient recycling rates are enhanced (Belovsky and Slade 2000, de Mazancourt and Loreau 2000*a, b*). Lake Ponderosa, as a more open system with greater allochthonous inputs of organic matter, greater autochthonous production, and a more complete assemblage of decomposers, likely had greater nutrient recycling rates than the closed tanks of the greenhouse experiment. Additionally, if *N. odorata* at Lake Ponderosa contained leaves with high nutrient concentrations, they likely would have decomposed more rapidly (see Cebrian 1999, 2004, de Mazancourt and Loreau 2000*b*) than those in the greenhouse. Therefore, there would have been greater nutrient recycling, allowing plants to regrow and compensate for ambient grazing (see Belovsky and Slade 2000, de

Mazancourt and Loreau 2000*a, b*). This feedback was likely limited in the absence of actual herbivores in the greenhouse, and may have contributed to the lack of grazing optimization at moderate grazing intensities there.

While grazing optimization was not observed in the greenhouse, overcompensation in the field suggests that optimization is possible for this plant species at low to moderate levels of herbivory. An increase in the concentration of nitrogen in aboveground tissue for the enhancement of photosynthetic rates is a possible mechanism explaining the observed compensatory responses in *N. odorata*. Enhanced photosynthetic rates in grazed plants would allow for greater carbon fixation and biomass production. Furthermore, greater foliar nitrogen content can stimulate herbivory, as consumption is usually positively related to palatability (Cebrian 1999, 2004, Elger and Willby 2003), which may, in turn, further enhance plant production. Therefore, there is the potential for grazing optimization by *N. odorata*, although high nutrient recycling rates and high foliar nutrient concentrations may be required.

Conclusions and implications

Nymphaea odorata was capable of exactly compensating or potentially overcompensating for low to moderate levels of herbivory with respect to aboveground vegetative and reproductive response variables. However, at high levels of simulated herbivory, *N. odorata* was negatively affected, resulting in undercompensation. Field and greenhouse results tended to support the GOH, which predicts plants will overcompensate at moderate grazing intensities, but undercompensate at high grazing intensities. Differences between field and greenhouse responses at ambient/moderate

grazing may have been due to slight differences in the level of biomass removal. Ambient grazing removed approximately three percent of leaf biomass and was associated with vegetative and reproductive overcompensation in the field. Slightly higher levels of artificial grazing in the greenhouse may have been too high to observe overcompensation, but low enough for plants to compensate relative to ungrazed plants.

Allocation of nitrogen to leaves to enhance photosynthesis was one possible mechanism by which *N. odorata* was able to compensate aboveground. Aboveground compensation may have been at the expense of belowground growth, as any removal of biomass in the greenhouse resulted in significant declines in belowground biomass and carbon stores. The differential above- and belowground responses in *N. odorata* underscore the importance of looking at whole plant responses when considering the potential benefits of herbivory to plants (sensu Belsky 1986). However, compensation, even when limited to aboveground plant responses, may have significant consequences at the population, community, and ecosystem levels by increasing the amount of organic matter available to decomposers, increasing decomposition rates, enhancing nutrient recycling rates and overall ecosystem productivity, and increasing herbivore consumption rates.

LITERATURE CITED

- Aguilar, J. A., O. M. Camarena, T. D. Center, and G. Bojorquez. 2003. Biological control of waterhyacinth in Sinaloa, Mexico with the weevils *Neochetina eichhorniae* and *N. bruchi*. *BioControl* **48**:595-608.
- Almeida-Cortez, J. S., B. Shipley, and J. T. Arnason. 1999. Do plant species with high relative growth rates have poorer chemical defences? *Functional Ecology* **13**:819-827.
- Arrington, D. A., L. A. Toth, and J. W. Koebel, Jr. 1999. Effects of rooting by feral hogs *Sus scrofa* L. on the structure of a floodplain vegetation assemblage. *Wetlands* **19**:535-544.
- Barrett, S. C. H., C. G. Eckert, and B. C. Husband. 1993. Evolutionary processes in aquatic plant populations. *Aquatic Botany* **44**:105-145.
- Bazzaz, F. A., N. R. Chiariello, P. D. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. *BioScience* **37**:58-67.
- Belovsky, G. E., and J. B. Slade. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Science* **97**:14412-14417.
- Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. *American Naturalist* **127**:870-892.
- Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology* **65**:370-381.
- Brandner, T. A., R. O. Peterson, and K. L. Risenhoover. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. *Ecology* **71**:155-164.
- Brattsen, L. B. 1979. Biochemical defense mechanisms in herbivores against plant allelochemicals. Pages 199-270 in G. A. Rosenthal and D. H. Janzen, editors. *Herbivores: Their interactions with secondary plant metabolites*. Academic Press, New York.

- Brown, V. K. 1985. Insect herbivores and plant succession. *Oikos* **44**:17-22.
- Cahoon, D. R., and J. C. Stevenson. 1986. Production, predation, and decomposition in a low-salinity *Hibiscus* marsh. *Ecology* **67**:1341-1350.
- Callaway, R. M., T. H. DeLuca, and W. M. Belliveau. 1999. Biological-herbivores may increase competitive ability of the noxious weed *Centaurea maculosa*. *Ecology* **80**:1196-1201.
- Carson, W. P., and R. B. Root. 2000. Herbivory and plant species coexistence: community regulation by and outbreaking phytophagous insect. *Ecological Monographs* **70**:73-99.
- Carter, S. 1995. Herbivory by *Donacia rufescens* Lacordaire and *Donacia cincticornis* Newman on the white water-lily, *Nymphaea odorata* Aiton. Dissertation. University of Alabama, Tuscaloosa.
- Cebrian, J. 1999. Patterns in the fate of production in plant communities. *American Naturalist* **154**:449-468.
- Cebrian, J. 2004. Role of first-order consumers in ecosystem carbon flow. *Ecology Letters* **7**:232-240.
- Cebrian, J., and J. Lartigue. 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecological Monographs* **74**:237-259.
- Center, T. D., F. A. Dray, Jr., G. P. Jubinsky, and A. J. Leslie. 1999. Waterhyacinth weevils (*Neochetina eichhorniae* and *N. bruchi*) inhibit waterhyacinth (*Eichhornia crassipes*) colony development. *Biological Control* **15**:39-50.
- Chapin, F. S., III, E. D. Schulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* **21**:423-447.
- Clark, M. W. 2000. Biophysical characterization of floating wetlands (flotant) and vegetative succession of a warm-temperate aquatic ecosystem. Dissertation. University of Florida, Gainesville.
- Collier, K. J., P. D. Champion, and G. F. Croker. 1999. Patch- and reach-scale dynamics of a macrophyte-invertebrate system in a New Zealand lowland stream. *Hydrobiologia* **392**:89-97.
- Crawley, M. J. 1983. *Herbivory: The dynamics of animal-plant interactions*. University of California Press, Los Angeles.
- Crawley, M. J. 1997. Plant-herbivore dynamics. Pages 401-474 in M. J. Crawley, editor. *Plant ecology*. Blackwell Press, Malden, Massachusetts.

- Cronin, G., and M. E. Hay. 1996. Induction of seaweed chemical defenses by amphipod grazing. *Ecology* **77**:2287-2301.
- Cronin, G., T. Schlacher, D. M. Lodge, and E. L. Siska. 1999. Intraspecific variation in feeding preference and performance of *Galerucella nymphaeae* (Chrysomelidae: Coleoptera) on aquatic macrophytes. *Journal of the North American Benthological Society* **18**:391-405.
- Cronin, G., C. D. Wissing, and D. M. Lodge. 1998. Comparative feeding selectivity of herbivorous insects on water lilies: aquatic vs. semi-terrestrial insects and submersed vs. floating leaves. *Freshwater Biology* **39**:243-257.
- Cyr, H., and M. L. Pace. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* **361**:148-150.
- de Angelis, D. L. 1992. Dynamics of nutrient cycling and food webs. Chapman and Hall, London.
- de Mazancourt, C., and M. Loreau. 2000a. Effect of herbivory and plant species replacement on primary production. *American Naturalist* **155**:735-754.
- de Mazancourt, C., and M. Loreau. 2000b. Grazing optimization, nutrient cycling, and spatial heterogeneity of plant-herbivore interactions: Should a palatable plant evolve? *Evolution* **54**:81-92.
- de Mazancourt, C., M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* **79**:2242-2252.
- de Mazancourt, C., M. Loreau, and L. Abbadie. 1999. Grazing optimization and nutrient cycle: potential impact of large herbivores in a savanna system. *Ecological Applications* **9**:784-797.
- Dorn, N. J., G. Cronin, and D. M. Lodge. 2001. Feeding preferences and performance of an aquatic lepidopteran on macrophytes: plant hosts as food and habitat. *Oecologia* **128**:406-415.
- Dyer, M. I., M. A. Acra, G. M. Wang, D. C. Coleman, D. W. Freckman, S. J. McNaughton, and B. R. Strain. 1991. Source-sink carbon relations in two *Panicum coloratum* ecotypes in response to herbivory. *Ecology* **72**:1472-1483.
- Elger, A., and N. J. Willby. 2003. Leaf dry matter content as an integrative expression of plant palatability: the case of freshwater macrophytes. *Functional Ecology* **17**:58-65.

- Feminella, J. W., and V. H. Resh. 1989. Submersed macrophytes and grazing crayfish: an experimental study of herbivory in a California freshwater marsh. *Holarctic Ecology* **12**:1-8.
- Godfrey, R. K., and J. W. Wooten. 1981. Aquatic and wetland plants of the southeastern United States: Dicotyledons. University of Georgia Press, Athens, GA.
- Gough, L., and J. B. Grace. 1998a. Effects of flooding, salinity and herbivory on coastal plant communities, Louisiana, United States. *Oecologia* **117**:527-535.
- Gough, L., and J. B. Grace. 1998b. Herbivore effects on plant species density at varying productivity levels. *Ecology* **79**:1586-1594.
- Grace, J. B. 1993. The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. *Aquatic Botany* **44**:159-180.
- Gregory, S. V. 1983. Plant-herbivore interactions in stream systems. Pages 157-189 in J. R. Barnes and G. W. Minshall, editors. *Stream ecology: Application and testing of general ecological theory*. Plenum Press, New York.
- Gross, E. M., R. L. Johnson, and N. G. Hairston, Jr. 2001. Experimental evidence for changes in submersed macrophyte species composition caused by the herbivore *Acentria ephemerella* (Lepidoptera). *Oecologia* **127**:105-114.
- Grover, J. P. 1994. Assembly rules for communities of nutrient-limited plants and specialist herbivores. *American Naturalist* **143**:258-252.
- Grubaugh, J. W., R. V. Anderson, D. M. Day, K. S. Lubinski, and R. E. Sparks. 1986. Production and fate of organic material from *Sagittaria latifolia* and *Nelumbo lutea* on Pool 19, Mississippi River. *Journal of Freshwater Ecology* **3**:477-484.
- Harms, D. A., and W. J. Mattson. 1992. The dilemma of plants - to grow or defend. *Quarterly Review of Biology* **67**:283-335.
- Hik, D. S., and R. L. Jefferies. 1990. Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *Journal of Ecology* **78**:180-195.
- Hogg, E. H., and R. W. Wein. 1988. The contribution of *Typha* components to floating mat buoyancy. *Ecology* **69**:1025-1031.
- Holland, E. A., and J. K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology* **71**:1040-1049.

- Holland, J. N., W. Cheng, and D. A. Crossley, Jr. 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. *Oecologia* **107**:87-94.
- Howe, H. F., and L. C. Westley. 1988. *Ecological Relationships of Plants and Animals*. Oxford University Press, New York.
- Hunter, M. D. 1992. Interactions within herbivore communities mediated by the host plant: The keystone herbivory concept. Pages 287-325 in M. D. Hunter, T. Ohgushi, and P. W. Price, editors. *Effects of Resource Distribution on Animal-Plant Interactions*. Academic Press, San Diego.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* **22**:477-503.
- Karban, R., and J. S. Thaler. 1999. Plant phase change and resistance to herbivory. *Ecology* **80**:510-517.
- King, G. M., T. Berman, and W. J. Wiebe. 1984. Methane formation in the acidic peats of Okefenokee Swamp. *American Midland Naturalist* **105**:386-389.
- Kouki, J. 1991. The effect of water-lily beetle, *Galerucella nymphaeae*, on leaf production and leaf longevity of the yellow water-lily, *Nuphar lutea*. *Freshwater Biology* **26**:347-353.
- Leriche, H., X. Le Roux, F. Desnoyers, D. Benest, G. Simioni, and L. Abbadie. 2003. Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. *Ecological Applications* **13**:1346-1354.
- Lodge, D. M. 1991. Herbivory on freshwater macrophytes. *Aquatic Botany* **41**:195-224.
- Louda, S. M. 1984. Herbivore effect on stature, fruiting, and leaf dynamics of a native crucifer. *Ecology* **65**:1379-1386.
- Louda, S. M., and S. K. Collinge. 1992. Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. *Ecology* **73**:153-169.
- Maschinski, J., and T. G. Whitman. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist* **134**:1-19.
- McGregor, M. A., D. R. Bayne, J. G. Steeger, E. C. Webber, and E. Reutebuch. 1996. The potential for biological control of water primrose (*Ludwigia grandiflora*) by the water primrose flea beetle (*Lysathia ludoviciana*) in the Southeastern United States. *Journal of Aquatic Plant Management* **34**:74-76.

- McKey, D. 1974. Adaptive patterns in alkaloid physiology. *American Naturalist* **108**:305-320.
- McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist* **113**:691-703.
- McNaughton, S. 1983. Compensatory plant growth as a response to herbivory. *Oikos* **40**:329-336.
- McNaughton, S. 1986. On plants and herbivores. *American Naturalist* **128**:765-770.
- McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. *Ecology* **79**:587-592.
- McNaughton, S. J., M. Oesterhek, D. A. Frank, and K. J. Williams. 1989. Ecosystem level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* **341**:142-144.
- Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America. Second edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.
- Mikola, J., G. M. Barker, and D. A. Wardle. 2000. Linking above-ground and below-ground effects in autotrophic microcosms: effects of shading and defoliation on plant and soil properties. *Oikos* **89**:577-587.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**:327-366.
- Mitsch, W. J., and J. G. Gosselink. 2000. *Wetlands*. Third edition. John Wiley & Sons, Inc., New York.
- Moser, E. B., A. M. Saxton, and S. R. Pezeshki. 1990. Repeated measures analysis of variance: application to tree research. *Canadian Journal of Forest Research*. **20**:524-535.
- Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *Journal of the North American Benthological Society* **10**:89-114.
- Newman, R. M., W. C. Kerfoot, and Z. Hanscom, III. 1996. Watercress allelochemical defends high-nitrogen foliage against consumption: effects on freshwater invertebrate herbivores. *Ecology* **77**:2312-2323.

- Ohnmeiss, T. E., and I. T. Baldwin. 1994. The allometry of nitrogen allocation to growth and an inducible defense under nitrogen-limited growth. *Ecology* **75**:995-1002.
- Paige, K. N. 1992. Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* **73**:2076-2085.
- Paige, K. N., and T. G. Whitman. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist* **129**:407-416.
- Parmesan, C. 2000. Unexpected density-dependent effects of herbivory in a wild population of the annual *Collinsia torreyi*. *Journal of Ecology* **88**:392-400.
- Peterson, A. G., J. T. Ball, Y. Q. Luo, C. B. Field, P. B. Reich, P. S. Curtis, K. L. Griffin, C. A. Gunderson, R. J. Norby, D. T. Tissue, M. Forstreuter, A. Rey, and C. S. Vogel. 1999. The photosynthesis leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis. *Global Change Biology* **5**:331-346.
- Piqueras, J. 1999. Herbivory and ramet performance in the clonal herb *Trientalis europaea* L. *Journal of Ecology* **87**:450-460.
- Reichman, O. J., and S. C. Smith. 1991. Responses to simulated leaf and root herbivory by a biennial, *Tragopogon dubius*. *Ecology* **72**:116-124.
- Ruess, R. W., R. L. Hendrick, and J. P. Bryant. 1998. Regulation of fine root dynamics by mammalian browsers in early successional Alaskan taiga forests. *Ecology* **79**:2706-2720.
- Setälä, H., and I. Makela. 1991. *Galerucella nymphaeae* (Col., Chrysomelidae) grazing increases *Nuphar* leaf production and affects carbon and nitrogen dynamics in ponds. *Oecologia* **86**:170-176.
- Sheldon, S. P. 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology* **68**:1920-1931.
- Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* **79**:2057-2070.
- Thaler, J. S. 1999. Induced resistance in agricultural crops: effects of jasmonic acid on herbivory in tomato plants. *Environmental Entomology* **28**:30-37.
- van der Meijden, E., M. Wijn, and H. J. Verkaar. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* **51**:355-363.

- van der Wal, R., M. Egas, A. van der Veen, and J. Bakker. 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* **88**:317-330.
- von Ende, C. N. 2001. Repeated-measures analysis: growth and other time-dependent measures. Pages 134-157 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Oxford University Press, Inc., New York.
- Wallace, J. B., and J. O'Hop. 1985. Life on a fast pad: waterlily leaf beetle impact on water lilies. *Ecology* **66**:1534-1544.
- Ward, A. D., and W. J. Elliott. 1995. *Environmental Hydrology*. CRC Press, New York.
- Wardle, D. A., G. M. Barker, G. W. Yeates, K. I. Bonner, and A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecological Monographs* **71**:587-614.
- Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens, and D. J. D'Angelo. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology* **41**:687-705.
- Wetzel, R. G. 2001. *Limnology*. Third edition. Academic Press, San Diego.
- Wheeler, G. S., and T. D. Center. 2001. Impact of the biological control agent *Hydrellia pakistanae* (Diptera: Ephydriidae) on the submersed aquatic weed *Hydrilla verticillata* (Hydrocharitaceae). *Biological Control* **21**:168-181.
- Whitman, T. G., J. Maschinski, K. C. Larson, and K. N. Paige. 1991. Plant responses to herbivory: The continuum from negative to positive and underlying physiological mechanisms. Pages 639 in P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley & Sons, Inc., New York.
- Wiersema, J. H. 1997. Nymphaeaceae Salisbury - Water-lily Family. Pages 66-77 in *Flora of North America*. Volume 3. Magnoliophyta: Magnoliidae and Hamamelidae. Oxford University Press, Inc., Oxford.
- Yamauchi, A., and N. Yamamura. 2004. Herbivory promotes plant production and reproduction in nutrient-poor conditions: effects of plant adaptive phenology. *American Naturalist* **163**:138-153.

CHAPTER THREE: GROWTH AND PRODUCTION DYNAMICS OF *NYMPHAEA ODORATA* IN THE PRESENCE OF ABOVEGROUND AND BELOWGROUND COMPETITION FROM A SIMILAR SPECIES, *NUPHAR ADVENA*

ABSTRACT

Interspecific competition has been shown to occur for a variety of interacting organisms in many different ecosystems. However, common patterns describing the role of competition in regulating populations and structuring communities is lacking. Within plant communities, different predictions exist to explain how plants compete, and how overall strength of competition, as well as above- and belowground components of competition, are likely to change along environmental gradients. To examine these patterns for plants in a freshwater marsh community, the performance of a dominant aquatic macrophyte, *Nymphaea odorata*, was quantified for a variety of population-level response variables when growing alone and in mixture with a similar aquatic macrophyte, *Nuphar advena*. Treatments included above- and belowground competition occurring separately as well as simultaneously.

Results of this one-year manipulative field experiment demonstrated that competition was negligible in this community; the presence of a similar plant species did not affect the leaf density, biomass or annual net primary production of *N. odorata*. These results suggest that other factors, such as physical disturbance, plant adaptations

permitting coexistence, intraspecific competition, or herbivory, were more important for regulating *N. odorata*, although the duration of this study may not have been long enough to detect interspecific competition. Despite the lack of competition as a main effect, there was a tendency for competition intensities to decline with increasing productivity, regardless of the index used to calculate intensity. Such a pattern is in contrast to predominant theories for terrestrial plants that suggest no or positive relationships between competition and productivity. These results suggest that competition may be less important for rooted, floating-leaved aquatic macrophytes than for terrestrial or emergent wetland plant species.

INTRODUCTION

Interspecific competition arguably plays an important role in nature by regulating populations and structuring communities (Hairston et al. 1960, Menge and Sutherland 1976, Connell and Slatyer 1977), and potentially maintaining diversity (Huston 1979, Connell 1980, Callaway and Pennings 2000). Furthermore, some scientists have invoked competition to explain current patterns of species distributions, niche differentiation, and resource partitioning (e.g. Connell 1961, Pacala and Roughgarden 1985) in a phenomenon referred to as “the ghost of competition past” (Connell 1980). Despite the importance attributed it, generalizations concerning the role of competition among ecosystems, within and among trophic levels, and between particular species combinations have been elusive, and ecologists continue to disagree on the prevalence and importance of competitive interactions in natural systems relative to other factors.

This lack of consensus is due in part to variations in how interspecific competition is defined (see Grace 1990), how frequent and how important competition is in nature (reviewed by Connell 1983 and Schoener 1983, Welden and Slauson 1986), how competition intensity (CI) is quantified (Grace 1995, Miller 1996), and contrasting predictions of how interactions change along environmental gradients (Grime 1979, 2001, Huston 1979, Keddy 1990 vs. Newman 1973, Tilman 1982, 1988, Taylor et al. 1990). In order to detect and refine general patterns pertaining to competition, additional

examination of the various aspects of this debate is necessary. Furthermore, experimentation that directly manipulates interactions between similar co-occurring species is needed to understand better the role of competitive interactions across ecosystem types.

Many of the examples of plant competition and the predictions pertaining to competitive interactions were formulated from research conducted in terrestrial ecosystems (e.g., Grime 1979, 2001, Tilman 1982, Gurevitch 1986, Goldberg 1987, Reader and Best 1989, Wilson and Tilman 1991, 1993, 1995, Campbell and Grime 1992, Turkington et al. 1993, Reader et al. 1994, Davis et al. 1998, Cahill 1999). Of the research conducted in wetlands, the majority has focused on interactions among emergent plant species (e.g., Johansson and Keddy 1991, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Gough and Grace 1997, Callaway and Pennings 2000, Keddy et al. 2000) or among submerged species (Moen and Cohen 1989, McCreary 1991, Engelhardt and Ritchie 2002), with relatively few investigating the effects of competition between rooted floating-leaved and other aquatic plants (e.g., Catling et al. 1988, Van et al. 1999). To my knowledge, there have not been any studies on the effects of competition between two similar rooted, floating-leaved aquatic plants.

In general, interactions among other types of wetland plants are thought to be strong and often asymmetrical (Catling et al. 1988, Moen and Cohen 1989, Johansson and Keddy 1991, McCreary 1991, Keddy et al. 1997, Van et al. 1999), resulting in the dominance of one or two species that create distinct vegetation zones within wetlands (Spence 1982, McCreary 1991). Researching competition between two similar rooted, floating-leaved macrophytes tests the general patterns of competition proposed for other

wetland plant species, and the applicability and robustness of predictions of competition based primarily on interactions in terrestrial ecosystems.

Defining interspecific competition and its mechanisms

Semantic differences in how interspecific competition is defined can result in conflicting predictions of how species compete (Grace 1990, 1993). While more specific, narrower definitions have been used, two of which will be discussed below, a broad definition from Begon et al. (1996), which includes all potential mechanisms of competition, is used here. Their definition states “competition is an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned (p 214).” In other words, competition is a mutually negative interaction for the individuals involved, and any mechanism of competition could be responsible for observed negative effects.

Traditionally, mechanisms of competition have been divided into two categories – exploitation and interference. Exploitative competition occurs through depletion of a shared resource while interference competition occurs through direct interaction between species (Morin 1999). Schoener (1983) expanded the two classes of competition to include six types of interspecific competition - consumptive, preemptive, overgrowth, chemical, territorial, and encounter – where the first two are best described as forms of exploitation and the remaining as forms of interference. Consumptive competition was proposed as the mechanism for the majority (38%) of experiments reviewed by Schoener, followed by encounter (14%), overgrowth (12%), and preemption (11%). More

specifically, for plants, exploitative mechanisms of competition were more likely than interference ones to explain the observed outcomes of competition (Schoener 1983), which is not surprising given that plants are sessile organisms and do not actively defend territories. Therefore, consumption of shared resources in limited supply and passive occupation of space are more common mechanisms of competition for plants.

Occurrence of interspecific competition in nature

Experimental evidence of interspecific competition has accumulated for a variety of organisms living in many different ecosystems. For example, competitive interactions have been demonstrated for algae (e.g., Tilman 1977), terrestrial and aquatic plants (e.g., Grace and Wetzel 1981, Gurevitch 1986, Goldberg 1987, Reader et al. 1994, Gough and Grace 1997, Keddy et al. 1997), protists (e.g., Gause 1934), sessile marine organisms (e.g., Connell 1961), and other animals, including lizards (e.g., Pacala and Roughgarden 1985), salamanders (e.g., Hairston 1980), and rodents (e.g., Munger and Brown 1981).

Reviews of field experiments have revealed that interspecific competition occurs frequently in nature. For example, Schoener (1983) reported that interspecific competition occurred in 90% of the studies reviewed regardless of the biome in which experiments were conducted. Of the 390 species examined, 57% competed under every experimental circumstance examined. Similarly, Connell (1983) reported that 93% of the studies he reviewed demonstrated interspecific competition in field experiments when only one species was studied. However, only 48% of these studies demonstrated competition when two or more species were studied concurrently. These reviews, as well as subsequent reviews of plant competition (Aarssen and Epp 1990, Goldberg and Barton

1992, Gurevitch et al. 1992), demonstrate that interspecific competition does occur frequently in nature. However, the knowledge that interspecific competition commonly occurs in nature is not necessarily indicative of its strength or importance for regulating populations and structuring communities.

Trophic level patterns of interspecific competition

Given that competition does occur in nature, how does its strength or intensity differ among trophic levels and ecosystem types? Several hypotheses addressing this question exist, and reviews and meta-analyses of competition experiments permit examination of these hypotheses. Hairston, Smith and Slobodkin (1960), or HSS, proposed that the strength of competition within trophic levels would be greater for producers and carnivores than for herbivores. Conversely, Menge and Sutherland (1976) predicted that producers would compete least, herbivores at an intermediate level, and carnivores the most. Reviews of the competition literature have been unable to conclusively confirm or refute either hypothesis.

More specifically, Schoener (1983) concluded that studies conducted in freshwater and terrestrial ecosystems tended to support HSS, while those in marine ecosystems did not. Conversely, Connell (1983) concluded that experimental evidence did not support HSS regardless of the biome considered. A meta-analysis of 46 competition studies detected yet another pattern where herbivores and filter-feeders competed most intensely, producers at an intermediate level, and carnivores and deposit feeders least intensely, regardless of ecosystem-type (Gurevitch et al. 1992). Clearly,

there is disagreement concerning patterns of competition across trophic levels despite a wealth of information collected through extensive experimentation.

Perhaps more consistent patterns exist within a more narrowly defined level of organization where the species included are more likely to function similarly, such as for plants. Within the field of plant ecology, there are conflicting theories of how plants compete, how competition is likely to change along environmental gradients, and how CI varies between above- and belowground plant components (Newman 1973, Grime 1979, Huston 1979, Tilman 1982, 1988, Keddy 1990, Taylor et al. 1990). A great number of plant competition studies have been conducted to address these conflicting predictions. A discussion of CI and predominant plant competition theory, as well as a review of the evidence, are presented to evaluate proposed patterns of plant competition.

Quantifying competition intensity

Over 25 indices have been used to quantify the intensity of competition (Weigelt and Jolliffe 2003), two of which, absolute competition intensity (ACI) and relative competition intensity (RCI), have been a source of debate with respect to patterns of competition among plant communities. If the goal of science is the “detection, testing, and refinement of general principles” (Keddy 1990, p. 266), then measures of ecological processes need to be quantified in such a way as to permit comparisons among different species, environmental conditions, and habitat types (Miller 1996). Therefore, indices that quantify the intensity of competition are useful when attempting to detect patterns of competition among different species, communities, and ecosystems.

CI is a measure of competition between interacting individuals that can be defined as the amount of strain competition induces in an organism (Welden and Slauson 1986). Measures of CI attempt to standardize performance of individuals exposed to competition from neighbors to account for environmental factors other than competition that may influence performance (Miller 1996). CI is most often calculated as absolute reductions (ACI) and proportional reductions (RCI) in performance. ACI is calculated as

$$ACI = P_{\text{alone}} - P_{\text{mixture}}$$

where P_{alone} is biomass or growth rates of individuals grown in monocultures, and P_{mixture} is biomass or growth rates of individuals grown with competitors (Grace 1995, Miller 1996). Negative values indicate facilitation, positive values competition, and zero indicates no competition. RCI is calculated as

$$RCI = (P_{\text{alone}} - P_{\text{mixture}}) / P_{\text{alone}}$$

(Grace 1995, Miller 1996). For RCI, values can range from negative infinity to one, where one is equivalent to complete competition (Miller 1996).

Intensity indices, such as ACI and RCI, describe the process of competition among individuals, but are not necessarily correlated with the importance of competition. Importance refers to the products of competition, including effects on individual plant fitness or community structure (Welden and Slauson 1986). More specifically, competition may be important when intensity is weak, if it is one of the few factors influencing plant performance. Conversely, intense competition may not be important in regulating populations or structuring communities relative to other processes influencing plant performance. Therefore, CI should be evaluated in conjunction with changes in overall plant performance to determine the importance of competitive interactions.

Predominant theories of plant strategy and competitive ability

Within the past 20 years, two theories of plant strategy and competitive ability have been at the forefront of debate among plant ecologists, and as a result, have stimulated a great deal of research aimed at testing their hypotheses. The two theories are the triangular model of plant strategies, or C-S-R model, (Grime 1979) and the resource-based mechanistic model of competition (Tilman 1982, 1988). Each offers different predictions concerning which plant characteristics contribute to competitive ability and how CI changes along environmental gradients (see Grace [1990] for a detailed discussion of both models). Because these theories have stimulated a great deal of debate and research, a brief overview of their fundamental components is needed before presenting research testing their predictions.

Grime (1979) expanded upon r- and K-selection theory (MacArthur and Wilson 1967) to formulate the C-S-R triangular model of plant strategies, which incorporates competitive ability. Grime (2001) defines competition as the “tendency of neighbouring plants to utilise the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space” (p 12), which, because it excludes interference mechanisms of interspecific competition, may be better defined as the tendency of neighboring plants to exploit a shared resource (Grace 1990). C-S-R theory proposes a trade-off among competitive ability, toleration of stress, and toleration of disturbance that is dependant on a plant’s life history characteristics. Briefly, plants adapted to low levels of stress and disturbance are “competitors” (C), those adapted to high levels of stress and low levels of disturbance are “stress-tolerant” (S), and those adapted to high levels of disturbance and

low stress levels are “ruderals” (R) (Fig. 3-1). According to this model, superior competitors are predicted to have high maximum relative growth rates indicative of an ability to exploit conditions of low stress and low disturbance.

Tilman (1977, 1982) expanded on the Monod model of competition (discussed in Morin 1999) to formulate a resource-based mechanistic model of competition that describes effects of competition on resource concentration and population size. Tilman’s model is defined in terms of population characteristics rather than individual traits, and requires knowledge of growth rates, average mortality rates, and resource supply rates of competing populations. As such, Tilman’s model suggests that good competitors are those that more efficiently utilize resources, experience lower mortality rates, and have higher growth rates than their competitors. More specifically, Tilman’s model demonstrates that when two or more species compete for a limited resource(s), the outcome of competition is determined by which species is able to reduce that resource to a lower equilibrium concentration. A species’ equilibrium resource level is referred to as its R^* , and superior competitors are those capable of depressing their own R^* to a level lower than that required by competing species (Fig. 3-2). Subsequent expansions in this model include adjustments to accommodate size-structured populations and incorporate colonization, longevity, and predation (Holt et al. 1994, Tilman 1988, 1994).

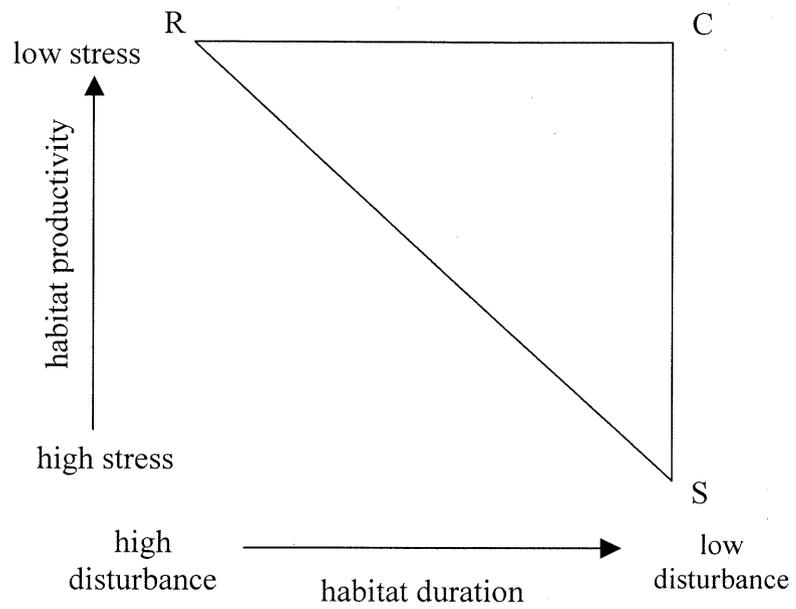


Figure 3-1. Conceptual representation of the C-S-R model of primary plant strategies. Redrawn from Grime 2001.

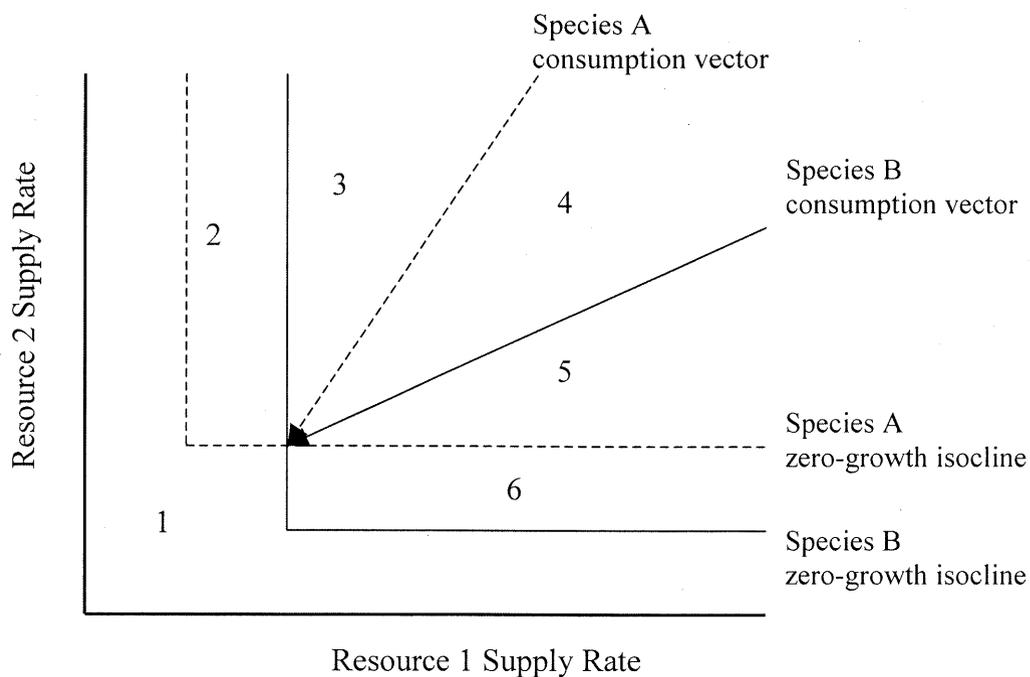


Figure 3-2. Conceptual representation of the resource-based model of competition for two species (A and B) competing for two resources. Numbered regions represent initial resource supply rates corresponding to specific outcomes of competition including 1) both species going extinct, 2) species B cannot exist, 3) species A out competing species B, 4) both species coexisting, 5) species B out competing species A, and 6) species A cannot exist. Adapted from Tilman 1982.

Competition intensity and productivity

Differences between Grime's and Tilman's models have led to other conflicting predictions of how CI changes along environmental gradients, specifically with increasing productivity. Productivity, in this case, refers to the amount of plant biomass that a given soil produces per unit time (Keddy et al. 1997). From Grime's C-S-R model, which includes disturbance and stress as factors influencing dominance, competition is predicted to increase with increasing productivity (Fig. 3-1), whereas in unproductive or heavily disturbed habitats, species better adapted to stress or disturbance are likely to dominate (Grime 1979). Other scientists have made similar predictions that intensity of competition is likely to increase with increasing productivity (e.g., Huston 1979, Keddy 1990, Campbell and Grime 1992), as well as with the degree of asymmetry among competitors (Keddy 1990, Keddy et al. 1997).

Conversely, Tilman, whose model does not incorporate stress and disturbance as factors influencing competitive success, predicts that in unproductive habitats, belowground competition for nutrients is more intense than aboveground competition. As productivity increases, competition for light becomes more intense as biomass accumulates aboveground (Tilman 1982, 1988). In this scenario, CI may remain constant along the productivity gradient (Newman 1973, Tilman 1982, 1988), or change relative to the ratio of resource supply and demand (Taylor et al. 1990).

Results of experiments assessing these models are often conflicting. Some support the prediction that CI increases with increasing productivity (e.g., Wilson and Keddy 1986, Reader and Best 1989, Campbell and Grime 1992, Turkington et al. 1993, Twolan-Strutt and Keddy 1996, Van et al. 1999, Keddy et al. 2000), while others suggest that CI

does not change with productivity (e.g., Wilson 1988, Wilson and Tilman 1991, 1993, Belcher et al. 1995). There is also evidence that CI decreases with increasing productivity for multiple response variables (e.g., Davis et al. 1998, Goldberg et al. 1999). Moreover, the relationship may vary depending on the community or species considered (Reader et al. 1994, Wilson and Tilman 1995, Cahill 2002).

Supporters of Grime's predictions have advocated the use of ACI over RCI, citing experimental results demonstrating a positive relationship between ACI and productivity. For example, greenhouse studies comparing the response of target species grown alone and in mixtures along soil fertility and disturbance gradients demonstrated that CI increased with productivity, but only when calculated as ACI (Campbell and Grime 1992). Similarly, experimentation in artificial communities of four species exposed to fertility and disturbance gradients revealed that, when calculated as ACI, intensity increased with productivity (Turkington et al. 1993). However, when calculated as RCI, intensity did not change. When the effects of competition on a grass, *Poa pratensis*, were examined among 12 communities on three continents, ACI increased nonlinearly with increasing neighbor biomass for all communities, while RCI increased with increasing neighbor biomass in only one of the 12 communities (Reader et al. 1994).

On the other hand, supporters of Tilman's predictions have advocated the use of RCI, citing experimental results demonstrating no change in RCI with increasing productivity. For instance, experimental evaluation of old-field grasses grown under different fertilization regimes demonstrated a lack of relationship between productivity and RCI (Wilson and Tilman 1991, 1993). In an old-field experiment, competitive responses of eight grasses varied with soil fertility such that RCI increased with neighbor

biomass for only three of the species, while no relationship was apparent for the remaining five species (Wilson and Tilman 1995).

In an attempt to reconcile differences among experiments investigating the relationship between competition and productivity, Goldberg et al. (1999) performed a meta-analysis of 296 cases in 14 studies and discovered that all response variables declined with increasing productivity. In fact, RCI for plant biomass and growth was negative in some unproductive treatments, indicating facilitation between neighboring species rather than competition. These results do not support either of the predominant models describing the relationship between CI and productivity, suggesting that strong differences exist between specific taxa and/or habitats.

With so many conflicting examples in the literature, the lack of general patterns of plant competition along productivity gradients is not surprising, but could this simply be due to differences in which competition intensity index was used? Plants free of competition are expected to perform better with increasing productivity than when grown in the presence of a competitor. Therefore, ACI is more likely to increase with productivity than RCI (Grace 1995), as demonstrated by the studies discussed above. In an attempt to ascertain which of the two indices is more appropriate, Grace (1995) asked the question “which measure is most useful in explaining patterns of species abundance and distribution in nature?” (p 305). Using the Relative Efficiency Index (REI) proposed by Connolly (1987) as an objective criterion, Grace evaluated ACI and RCI to determine which is more consistent with how species compete in mixtures, and concluded RCI is a better measure of intensity. Miller (1996) concurred that a relative index of competition is superior, but to quantify changes in the per-unit-biomass competitive effects of

neighbors, the index should be regressed against neighbor biomass in an approach advocated by Goldberg and Scheiner (2001). Doing both allows for an understanding of target plant performance and how it changes as competitor biomass increases.

Furthermore, many studies examining the intensity and importance of competition in plant communities along productivity gradients have quantified effects on individual fitness response variables for pairwise comparisons of species (Keddy 1990, Goldberg et al. 1999). This individual-level data must then be used to infer changes at population levels (Goldberg et al. 1999). In competition experiments, individual biomass is most often used as the response variable (Gurevitch et al. 1992), although other measures, including growth rates, stem or tiller densities, production, and survival, have been examined. The choice of response variable can potentially influence the patterns observed (Goldberg et al. 1999). Therefore, more studies testing competition-productivity hypotheses are needed that are designed to quantify intensity using several response variables at the population-level to determine which variables and indices are the best for examining competition between pairs of species and across ecosystems.

Above- and belowground components of competition

Recall that Grime's C-S-R theory predicts that total competition (i.e., both aboveground and belowground components of competition) increases in intensity as productivity increases, while Tilman's resource-based model predicts that total competition remains constant along productivity gradients. The relative importance of above- and belowground competition and how each changes with productivity is also of importance, and once again, there is debate between Grime and Tilman concerning

different components of competition along productivity gradients. Grime (1979, 2001) predicts that the relative importance of above- and belowground competition remains constant as productivity increases, while Tilman (1982, 1988) predicts that there is a shift in CI from belowground to aboveground as productivity increases. How is the relative importance of above- and belowground competition expected to change with increasing productivity, and what evidence is there to support each prediction?

In a review of competition among primarily agricultural and weedy species, Wilson (1988) concluded that belowground competition was more intense than aboveground in the majority of studies examined, but there was no conclusive evidence to support a trade-off between above- and belowground competition as resource supply increased. Subsequent experiments conducted in terrestrial ecosystems have tested for trade-offs between above- and belowground competition along productivity gradients, and have demonstrated differences in the strength of aboveground, belowground, and total competition (e.g., Wilson and Tilman 1991, 1993, 1995, Belcher et al. 1995). When differences were observed, aboveground competition tended to remain constant or increase with increasing productivity, while belowground competition tended to decrease with increasing productivity (e.g., Wilson and Tilman 1991, 1993, 1995, Belcher et al. 1995).

Results of a study conducted in Canadian wetlands were consistent with an increase in aboveground competition with productivity in the terrestrial ecosystems mentioned above, but the strength of belowground competition remained constant instead of declining along a natural productivity gradient (Twolan-Strutt and Keddy 1996). Furthermore, when examining the ratio of belowground to aboveground competition,

belowground competition was more intense relative to aboveground competition in unproductive conditions. In productive conditions, above- and belowground competition were equally intense, as has been demonstrated elsewhere (Wilson 1988, Wilson and Tilman 1991, 1993). From this wetland study of plant competition, the investigators proposed an alternative model of the predicted relationship between competition and productivity for wetlands that combines aspects of Grime (1979, 2001) and Tilman (1982, 1988). They propose that total competition increases with increasing productivity (sensu Grime 1979, 2001), while the ratio of belowground to aboveground CI decreases with increasing productivity (sensu Tilman 1982, 1988). In summary, the observed patterns may depend on ecosystem-type (Twolan-Strutt and Keddy 1996) and may vary among species pairs (Cahill 2002).

RESEARCH OBJECTIVES

As evidenced from this review of the literature, common patterns of competition within plant communities are lacking, and conflicting results exist that support different models of plant competition. The overall goal of this research was to determine the relative intensities of aboveground, belowground and total competition on a rooted, floating-leaved aquatic macrophyte occurring at natural densities with a similar species. Because there is some evidence that wetland plant species may exhibit patterns of competition different from those proposed for terrestrial plants (Keddy et al. 1994, Twolan-Strutt and Keddy 1996), this experiment allows for important comparisons of competition patterns for floating-leaved aquatic species with those documented for terrestrial and other wetland species.

To accomplish the objective, a field experiment was conducted in which plant performance was quantified using a variety of population-level response variables for plants growing alone, in mixture, and when above- and belowground competition were separated. This manipulative field experiment was conducted to test hypotheses related to the effects of competition on the growth and production of the target species in its natural environment. Specifically, 1) the presence of a neighbor would negatively affect target plant performance, and 2) the intensity of this interaction would be greater for plants competing fully than for those experiencing above- or belowground competition only.

Furthermore, for all variables, 3) RCI would remain constant, and ACI would be greatest, when productivity was high relative to other plots, and 4) during the summer when plant biomass and production were greater than in other times of the year. Testing of these hypotheses permitted investigation of the effects of various components of competition on multiple population-level response variables.

METHODS

Study site

This study was conducted in the deep-water marsh of Lake Ponderosa, a small (12 ha), privately owned reservoir located in the Fall Line Hills of the Coastal Plain in Bibb County, Alabama (N 32° 55', W 87° 19'). It drains two unnamed intermittent first-order streams, one of which flows through an extensive emergent marsh at the north end of the lake dominated by *Alder serrulata* and *Myrica cerifera* at higher elevations, and tall graminoid and rush species at lower elevations. Adjacent to the emergent marsh, there is a deep-water marsh dominated by the rooted, floating-leaved perennial, *Nymphaea odorata* Aiton (Nymphaeaceae), and the less abundant rooted, floating-leaved perennial, *Nuphar advena* (Aiton) W. T. Aiton (Nymphaeaceae). In addition to the low pH of water in Lake Ponderosa, the abundance of floating-leaved species may have excluded or prevented the establishment of submerged species, presumably by shading the underlying water and sediment.

Twenty experimental plots were established within the northern section of the lake at sites in which *N. odorata* and *N. advena* both existed. Plants occurred across a water depth gradient of 0.10 m to 1.30 m with patches of *N. advena* encroaching into *N. odorata* stands from either the shoreline in shallower water or the littoral-pelagic margin in deeper water. Water depths less than 0.10 m occurred in the presence of floating

islands. Floating islands form when live vegetation and associated sediments separate from the underlying substrate and float at or near the surface due to the accumulation of gases in the sediment and aerenchyma tissue of existing vegetation (King et al. 1984, Hogg and Wein 1988, Clark 2000). At Lake Ponderosa, floating islands formed in early June 2002 causing a localized decline in inundation and affecting four of 20 plots. Islands persisted until early October 2002, at which time they subsided and were completely inundated throughout the remainder of the experiment.

Species descriptions

The target plant species, *N. odorata*, and the competitor species, *N. advena*, are both rooted, floating-leaved aquatic macrophytes in the Nymphaeaceae family. Both are native to the eastern United States, including Alabama, and found in slow moving or still waters (e.g., lakes, ponds, marsh pools, ditches) (Wiersema 1997). They are rhizomatous, aquatic, perennial herbs with long petiolate leaves arising directly from horizontal rhizomes. Both can reproduce clonally by rhizome expansion and/or sexually by seed.

The flowers of *N. odorata* are white and float on or just above the water's surface. After the flower's final closing, the peduncle coils so that the developing fruit is brought underwater to the substrate. The flowers of *N. advena* are yellow, and float on or just above the water's surface. *N. advena* fruit mature above water, as the peduncle does not recoil to the substrate. *N. odorata*'s ovate leaves float on the water's surface and are rarely emersed, whereas *N. advena*'s oblong leaves are generally emersed or floating, and sometimes submersed (Godfrey and Wooten 1981, Wiersema 1997). When co-occurring at Lake Ponderosa, *N. odorata* leaves were always floating, while *N. advena* leaves were

often emerged and capable of shading the underlying water surface. Rhizomes of *N. odorata* tend to be smaller (< 5 cm in diameter) than those of *N. advena* (5 – 10 cm in diameter). The greater rhizome size potentially provides greater belowground storage, which may confer some competitive advantage to *N. advena* (Grime 2001).

Field experimental design

Field research consisted of a control (i.e., no competition), aboveground competition, belowground competition, and total competition treatments in a randomized block design. Twenty sampling frames, five for each treatment, delineating 0.25 m² of lake bottom each, were placed in the lake on 13 –14 November 2001 when leaf densities were low, thus preventing selection bias. Plots were not standardized for leaf densities of either species because areas in which *N. odorata* and *N. advena* co-occurred were limited. Quadrats consisted of a 0.5 m x 0.5 m wooden frame attached at the corners to PVC legs, which were inserted into the substrate so that the wooden frame remained 15 cm above the water's surface.

Treatments were randomly assigned to one of five experimental units located in one of two blocks. Two of the experimental units were located within the shallower, shoreline region (block 1) and three along the littoral-pelagic margin (block 2). No competition (NC) plots contained only the target species and remained uncovered throughout the experiment. Aboveground competition (AC) plots contained only the target species, but the tops of the frames were covered by Coolaroo® Outdoor Shade Fabric (Gale Pacific Pty. Ltd., Altamonte Springs, FL) to simulate shading from emerged *N. advena* leaves. Shade cloth was selected based on light intensity measurements taken

under emerged *N. advena* leaves in October 2001. These measurements indicated that emerged leaves blocked up to $85.19\% \pm 1.93$ (± 1 SE) of ambient light. Belowground competition (BC) plots contained both the target and competitor species. Leaves of the competitor were tied back outside the frame to prevent shading aboveground, while belowground competition between species was not manipulated. Total competition (TC) plots contained both the target and competitor species and remained unmanipulated so that above- and belowground interaction between species could occur naturally.

In order to prevent leaves of either species from floating outside the delineated sampling areas, string was placed around each plot just below the water's surface. All plots were placed at least seven meters apart to ensure that no individual plant was sampled in multiple plots due to horizontal rhizome connection.

Field measurements of environmental variables

The 20 plots were monitored every other week for water depth, every other month for pH and water temperature ($^{\circ}\text{C}$), and seasonally for light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) from January 2002 to December 2002. Water depth was measured with a meter stick from the water's surface to the top of the substrate at two points within each plot from which mean water depth per plot was calculated. Water pH and temperature at each plot were measured using an Orion Model 250A meter (Orion Research Group, Inc., Beverly, MA). Light intensity was measured with a point quantum sensor and light meter (Model LI-250, Li-Cor, Inc., Lincoln, NE) at sites throughout the experimental area to determine yearly minimums and maximums, and at three points above each frame and at three points below each frame (i.e., under the screen in AC plots) to calculate the average light

intensity above and below frames. These data were used to determine the average percentage of ambient light blocked by the frames in each treatment. Daily precipitation amounts measured at a nearby (approximately 11.3 km away) weather station at the Talladega Wetland Ecosystem in Hale County, Alabama (N 32° 52', W 87° 26') were used to characterize the annual rainfall pattern at Lake Ponderosa in 2002.

Field measurements of plant response variables

All leaves of both species in the 20 plots were measured fortnightly from January 2002 to December 2002 for leaf longevity, leaf density, and leaf surface area. The petioles of every leaf emerging within a plot were tagged with a labeled cork float at the time of emergence and species noted. The subsequent time of leaf senescence was recorded to determine leaf longevity in days. Leaf longevity, or turnover time, was equal to the difference between the time of senescence and the time of emergence. Time of emergence was calculated as the median between the previous sampling date and the sampling date on which the leaf was first tagged. Time of senescence was calculated as the median day between the date on which the leaf was last measured and the date on which the leaf was no longer present in the plot. From these data, leaf turnover rates were calculated as growth period divided by leaf longevity, as described by Setälä and Mäkelä (1991). Leaf density was equivalent to the number of leaves present per 0.25 m² plot.

Individual leaf length and width measurements were recorded every two weeks in order to calculate leaf surface area. Because the two species differed in leaf shape, different surface area equations were used to develop species-specific regression models. Surface areas for *N. odorata*'s ovate leaves were calculated using the formula $A = \pi r^2$,

where r is half the average of the leaf's width and length and A is surface area. Surface areas for *N. advena*'s oblong leaves were calculated using the formula $A = \frac{1}{2} W * L$, where W is leaf width, L is leaf length and A is surface area. Surface area estimates for both species were used to predict leaf biomass from independently developed regression models relating leaf surface area (cm^2) to leaf biomass (g).

To develop the regression models, 55 *N. odorata* and 55 *N. advena* leaves were collected on 25 April 2001 and 24 June 2002, respectively, and transported back to the laboratory. For both species, actual leaf surface area was determined using a leaf area meter (Li-3000A Portable Area Meter console with Li-3050A Belt Conveyor, LiCor, Inc., Lincoln, NE). The leaves were then dried at 60°C for 48 hours and weighed (Mettler Toledo PB153-S, Columbus, OH) to obtain leaf biomass in grams ± 0.001 g. The leaves used to develop the *N. odorata* model ranged in size from 4.28 cm^2 to 582.89 cm^2 , and 0.02 g to 4.99 g. *N. advena* leaves ranged in size from 13.57 cm^2 to 387.04 cm^2 , and 0.10 g to 3.64 g. To correct for potential shape variation among leaves, another regression relating estimated and actual surface areas was developed for both species.

From mean monthly biomass estimates and leaf turnover rates, ANPP for *N. odorata* and *N. advena* was estimated for every plot. ANPP was expressed in units of mass per area per time and was calculated as mean monthly turnover rate multiplied by mean monthly biomass, as described by Setälä and Makela (1991) and Carter (1995). Summation of production estimates over monthly intervals provided an annual estimate of ANPP. A direct method was also used to calculate annual ANPP for each species by summing the maximum biomass of every leaf tagged in a plot over the entire year.

Statistical analyses

Simple linear regression was used to develop models relating biomass and leaf surface area, and estimated and actual leaf surface areas for both plant species.

Differences for environmental variables among competition treatments in the field were analyzed using one-way ANOVAs.

To compare *N. odorata* mean leaf density, mean biomass, ANPP, and turnover times for the year, two-way ANOVAs were performed with presence/absence of aboveground competition (hereafter AG competition) and presence/absence of belowground competition (hereafter BG competition) as fixed factors. To look at patterns over the duration of the experiment, separate two-way Repeated Measures ANOVAs were performed to develop a split-plot model testing the main effects of AG competition, BG competition and month (March through November) on *N. odorata* monthly leaf density, biomass, ANPP, turnover time, and turnover rate. For ANOVAs and Repeated Measures ANOVAs, leaf density data were square-root transformed and leaf biomass and ANPP log transformed to meet distributional and variance assumptions.

Differences in competition indices (i.e., ACI and RCI), when calculated using leaf density, biomass, and ANPP for the entire year, were also analyzed as separate two-way ANOVAs with AG competition and BG competition as fixed factors. Separate Repeated Measures ANOVAs were performed to test the main effects of AG competition, BG competition and month on ACI and RCI when calculated using leaf density, biomass, and ANPP. To determine if productivity calculated as total plot biomass (i.e., *N. odorata* + *N.*

advena) influenced CI, an ANCOVA was performed to develop a model relating CI to index type (ACI and RCI) with plot productivity as a covariate.

When data were transformed for any test, reverse transformed means and standard errors are presented as indicated in figure legends. All hypotheses were tested at the $\alpha = 0.05$ level. For all Repeated Measures analyses, multivariate tests of hypotheses for within-subject effects were used instead of using univariate tests when the assumption of sphericity could not be met (Mauchly's criterion for orthogonal components > 0.05) (Moser et al. 1990, von Ende 2001). Repeated Measures ANOVAs and ANCOVA were performed in SAS (version 8.1e, SAS Institute, Inc., Cary, NC); all other statistical analyses were performed in SPSS (version 9.0, SPSS, Inc., Chicago, IL).

RESULTS

Field environmental variables

During 2002, mean water pH at Lake Ponderosa was 5.38 ± 0.12 , mean water temperature was $21.12 \text{ }^\circ\text{C} \pm 3.64$, and mean water depth was $0.52 \text{ m} \pm 0.02$. Water pH remained relatively constant over time, whereas water temperature, water depth, and light intensity changed seasonally. Water temperature and light intensity were greatest in the summer and lowest in spring, fall, and winter, with mean bimonthly water temperatures ranging from $8.07 \text{ }^\circ\text{C} \pm 0.14$ to $29.86 \text{ }^\circ\text{C} \pm 0.24$, and mean seasonal light intensities ranging from $1133.76 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1} \pm 145.92$ to $1866.10 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1} \pm 67.07$. Water depths were highest in the early spring and lowest in late summer, ranging from a bimonthly mean of $0.37 \text{ m} \pm 0.04$ to $0.68 \text{ m} \pm 0.06$. Total annual precipitation was 1025.38 mm in 2002.

The mean pH, water temperature and water depth at Lake Ponderosa during 2002 did not differ among competition treatments (Table 3-1), although plots located in the shoreline zone were shallower and had a lower pH than those along the littoral-pelagic margin (block effects: $P = 0.0001$ for both). Water depths did not differ significantly among treatments during the period of floating island formation in the summer (Fig. 3-3), even though AC plots tended to be shallower than NC, BC, and TC plots. In 2002, floating islands formed in one NC plot, three AC plots, and no BC and TC plots. Floating

Table 3-1: Mean pH \pm 1 SE, water temperature ($^{\circ}\text{C}$) \pm 1 SE, water depth (m) \pm 1 SE, ambient light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) \pm 1 SE, and percent difference in light intensity above and below experimental frames \pm 1 SE for each competition treatment at Lake Ponderosa during 2002. Minimum and maximum values are shown in parentheses. Treatment abbreviations: NC = no competition, AC = aboveground competition only, BC = belowground competition only, and TC = total competition.

	NC		AC		BC		TC	
pH	5.31 \pm 0.08	(4.85 – 5.64)	5.35 \pm 0.07	(4.73 – 5.59)	5.40 \pm 0.10	(4.81 – 5.66)	5.39 \pm 0.05	(4.89 – 5.84)
Water temperature ($^{\circ}\text{C}$)	20.7 \pm 0.39	(7.92 – 29.5)	20.4 \pm 0.55	(7.92 – 29.7)	20.4 \pm 0.42	(8.26 – 29.6)	20.5 \pm 0.20	(8.18 – 30.7)
Water depth (m)	0.50 \pm 0.08	(0.30 – 0.66)	0.41 \pm 0.10	(0.20 – 0.67)	0.56 \pm 0.13	(0.42 – 0.68)	0.61 \pm 0.16	(0.50 – 0.72)
Light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1505 \pm 107	(1154 – 1857)	1503 \pm 112	(1141 – 1865)	1437 \pm 133	(1048 – 1826)	1554 \pm 75.4	(1192 – 1916)
% light blocked	7.31 \pm 1.70	(1.92 – 12.7)	68.47 \pm 2.13	(67.2 – 69.7)	5.97 \pm 2.19	(3.46 – 8.48)	2.33 \pm 2.36	(2.01 – 2.66)

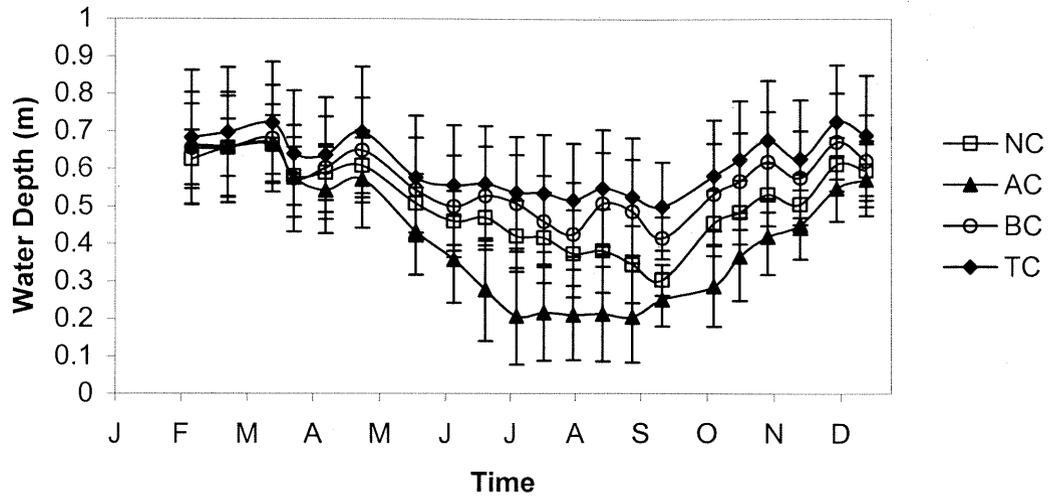


Figure 3-3. Mean water depth (m) \pm 1 SE among competition treatments at Lake Ponderosa. Treatment abbreviations as in Table 3-1.

islands resulted in temporary localized decreases in inundation, which contributed to the pattern of decreased water depths in AC plots in the summer of 2002

Leaf surface area and biomass regressions

Significant simple linear regressions were developed relating estimated leaf surface areas (cm^2) to actual leaf surface areas (cm^2) for *N. odorata* using πr^2 and for *N. advena* using $\frac{1}{2} W * L$, as described above (Fig. 3-4A and 3-5A, respectively). In addition, significant regressions predicting biomass (g) from actual surface area (cm^2) were developed for both species (Fig. 3-4B and 3-5B, respectively). These regressions were used to non-destructively determine leaf biomass from estimates of leaf surface areas obtained in the field.

Population growth patterns of N. odorata and N. advena

Leaves of *N. odorata* emerged in February, 38 days prior to the emergence of the first *N. advena* leaves, and leaves of both species were present through the end of December. A total of 1,814 *N. odorata* leaves in 20 plots, roughly 91 leaves per plot, were tagged during 2002, while 368 *N. advena* leaves in 10 plots, approximately 37 leaves per plot, were tagged. Mean leaf densities for *N. odorata* ranged from 23 leaves m^{-2} to 41 leaves m^{-2} while those for *N. advena* were lower and ranged from 14 leaves m^{-2} to 15 leaves m^{-2} . *Nuphar advena* leaves in total competition plots overlapped *N. odorata* leaves despite having lower leaf densities. This was possible because *N. advena* leaves were larger than *N. odorata* leaves ($166.00 \text{ cm}^2 \pm 0.10$ and $135.70 \text{ cm}^2 \pm 0.14$, respectively) and remained at the surface longer ($36.71 \text{ days} \pm 1.24$

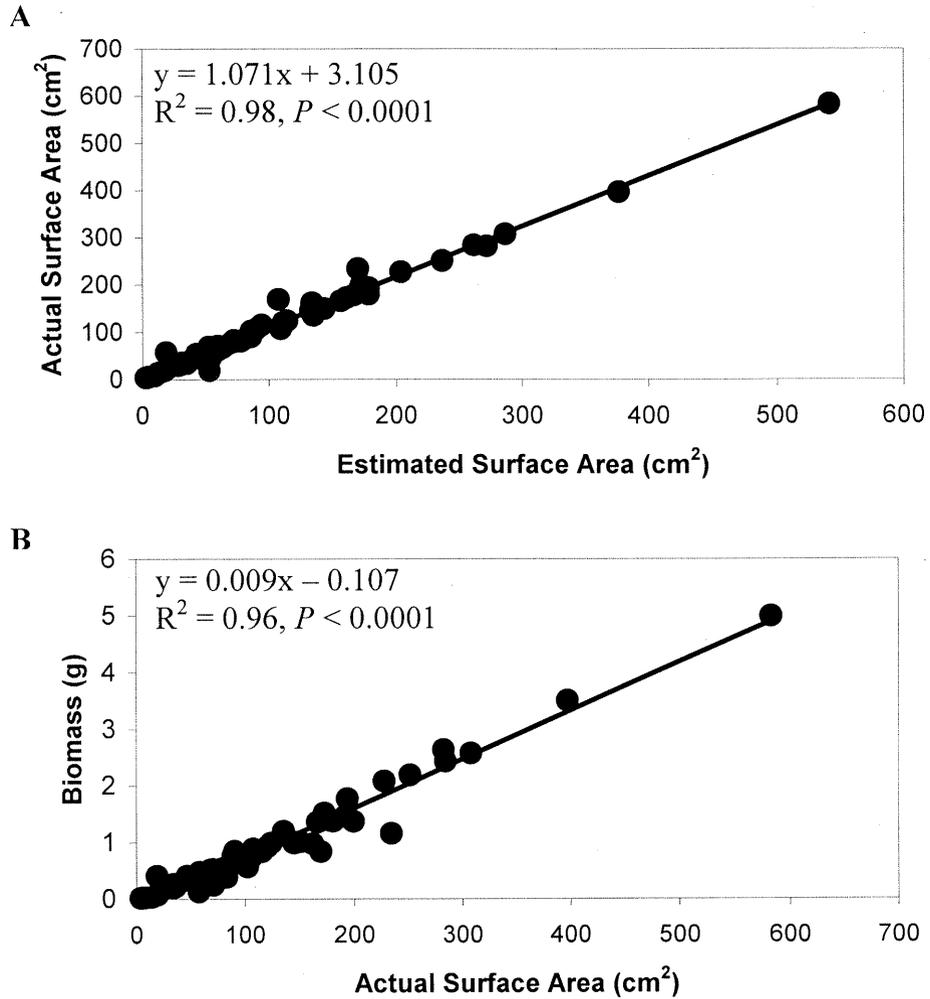


Figure 3-4. Linear regression models relating A) estimated leaf surface area (cm²) to actual leaf surface area (cm²), and B) actual leaf surface area (cm²) to leaf biomass (g) for *N. odorata*.

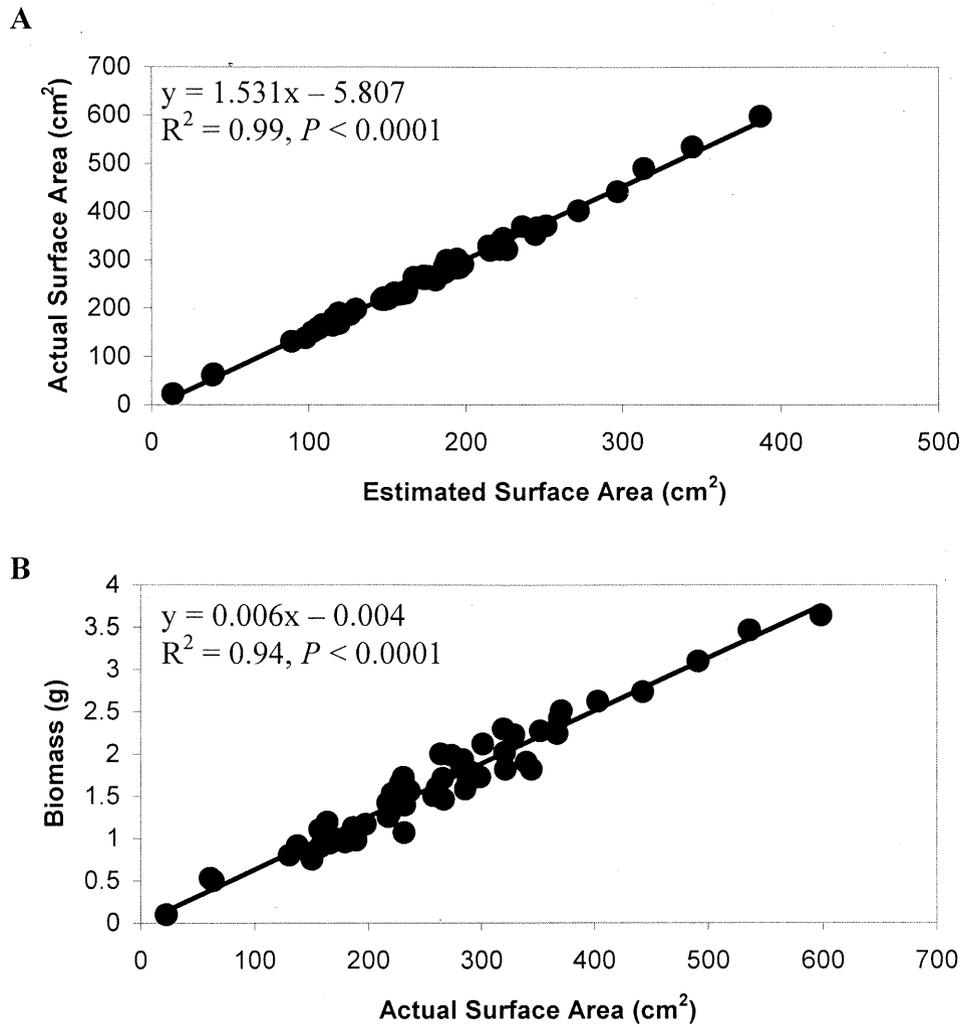


Figure 3-5. Linear regression models relating A) estimated leaf surface area (cm²) to actual leaf surface area (cm²), and B) actual leaf surface area (cm²) to leaf biomass (g) for *N. advena*.

and $33.47 \text{ days} \pm 0.49$, respectively). Generally, *N. odorata* was more productive than *N. advena*, accumulating between $338.11 \text{ g m}^{-2} \text{ y}^{-1} \pm 1.44$ and $450.58 \text{ g m}^{-2} \text{ y}^{-1} \pm 1.21$ during 2002 compared to $208.95 \text{ g m}^{-2} \text{ y}^{-1} \pm 1.32$ to $220.21 \text{ g m}^{-2} \text{ y}^{-1} \pm 1.30$ for *N. advena*. Both species experienced grazing damage, but it tended to be more severe for *N. odorata* than for *N. advena* (J. A. Cherry, personal observation). In addition, both species flowered during the summer of 2002.

Interaction of above- and belowground competition on performance of N. odorata

The presence of *N. advena* did not affect the performance of *N. odorata* when compared to its performance growing alone (Fig. 3-6 and 3-7). While a greater number of leaves were present in the shoreline region than along the littoral-pelagic margin (block effect: $F_{1,12} = 6.62$, $P = 0.02$), mean *N. odorata* leaf density, biomass, annual ANPP, and turnover time were similar for NC, AC, BC, and TC treatments ($P > 0.05$ for all), although ANPP tended to be lower in AC treatments than other treatments. Furthermore, competition treatments as main effects did not significantly affect leaf density, biomass, ANPP, or turnover times even after plots containing floating islands were excluded from analysis (data not shown). This pattern remained consistent for ANPP regardless of the method used to calculate annual production.

Nymphaea odorata monthly leaf density, biomass and ANPP were greater in summer months than any other time of the year (month effect: $P < 0.001$ for all), were similar for all types of competition (AG and BG effects: $P > 0.05$ for all), and responded similarly over time regardless of the component of competition examined (no AG x BG

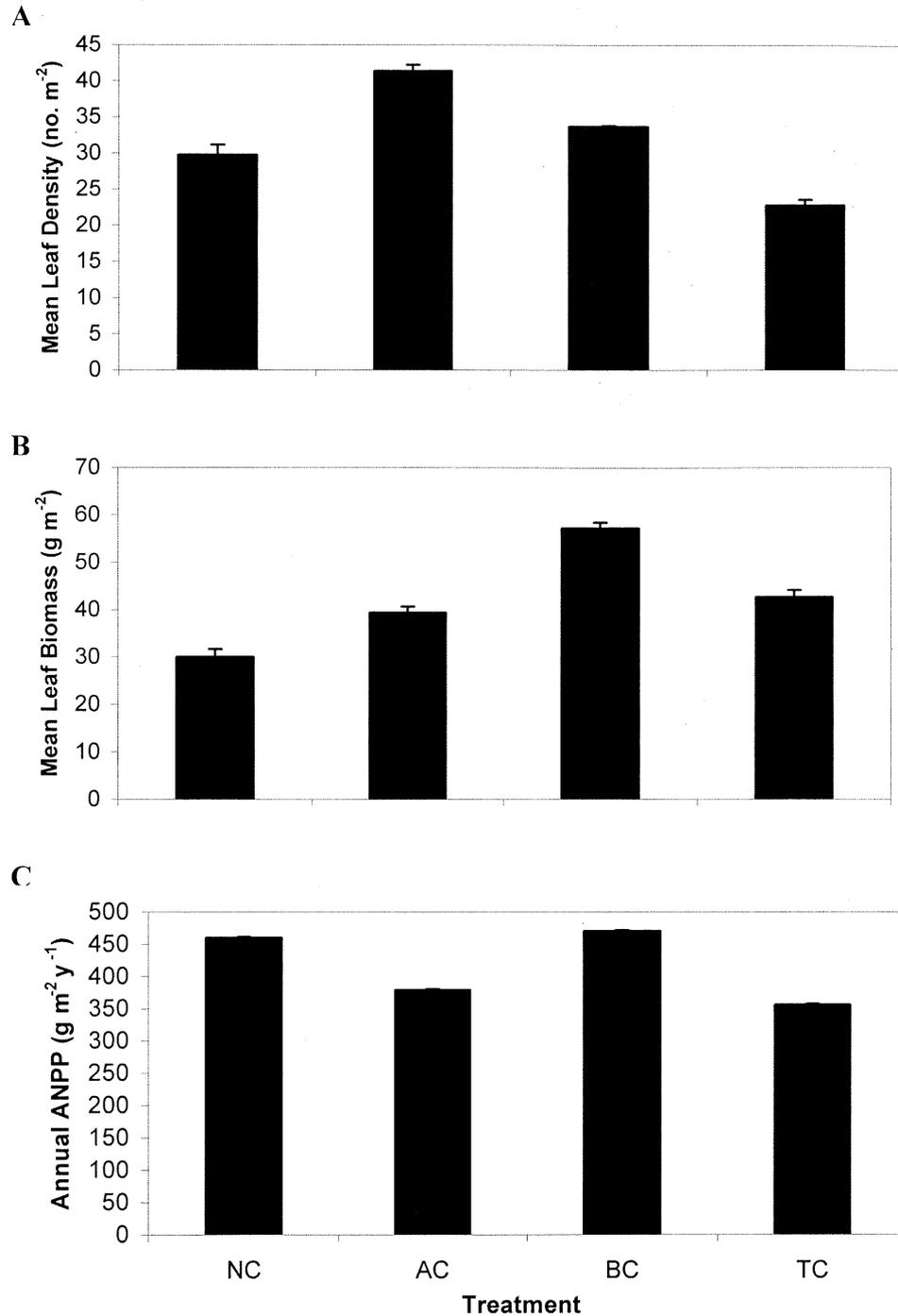


Figure 3-6. Mean leaf A) density (no. m⁻²) ± 1 SE, B) biomass (g m⁻²) ± 1 SE, and C) annual ANPP (g m⁻² y⁻¹) ± 1 SE for *N. odorata* among competition treatments at Lake Ponderosa for 2002. Means and standard errors are reverse square-root transformed values for density and reverse log-transformed values for biomass and ANPP. Treatment abbreviations as in Table 3-1.

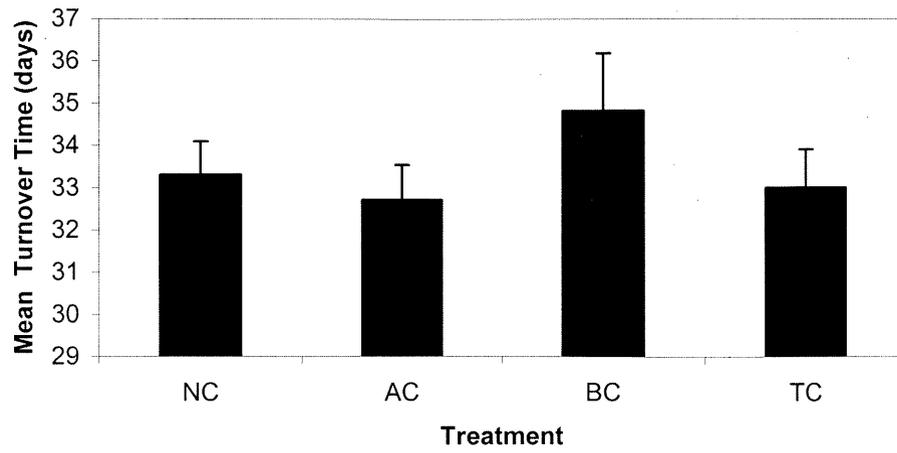


Figure 3-7. Mean leaf turnover time (days) \pm 1 SE for *N. odorata* among competition treatments at Lake Ponderosa for 2002. Treatment abbreviations as in Table 3-1.

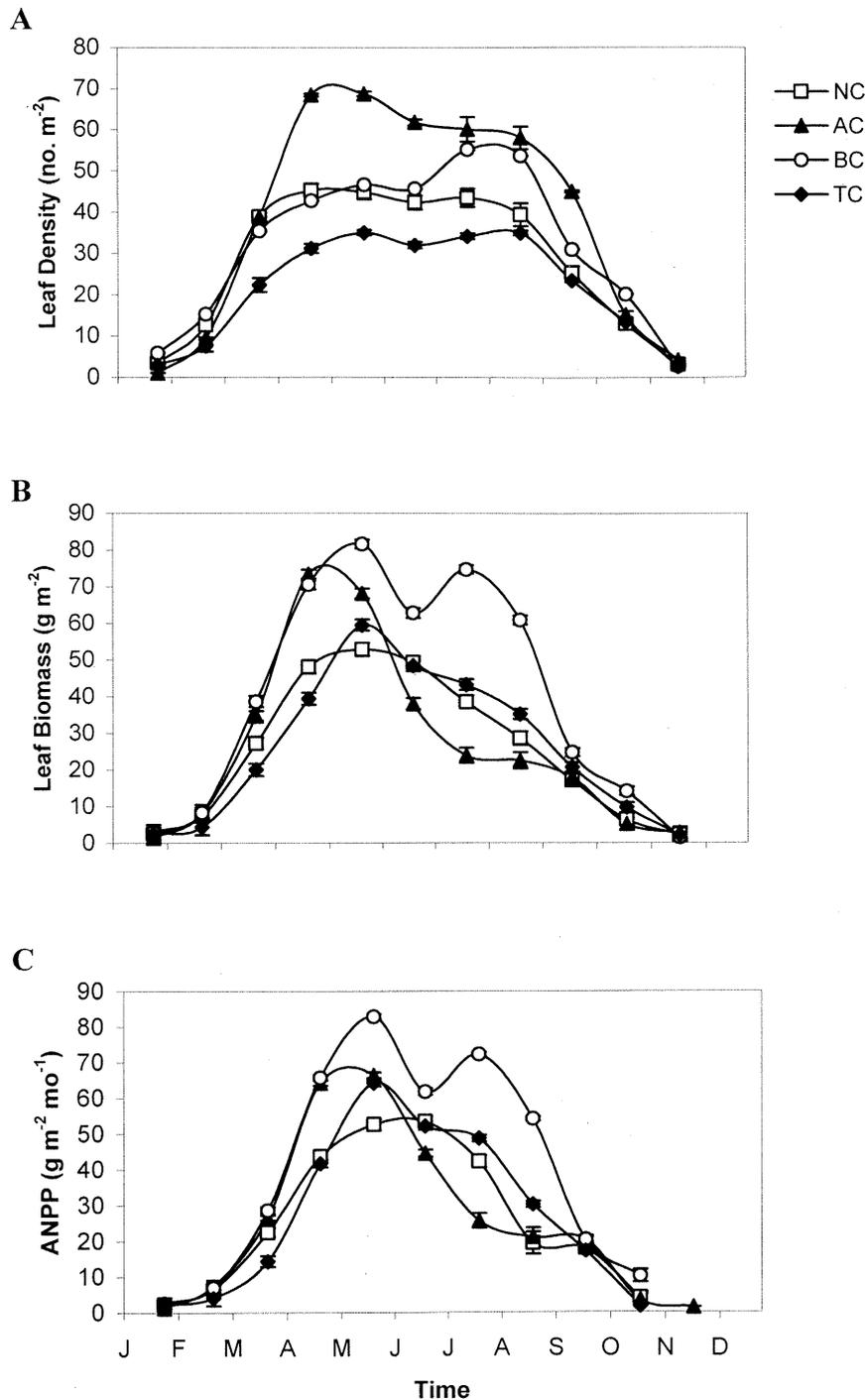


Figure 3-8. Mean monthly leaf A) density (no. m⁻²) \pm 1 SE, B) biomass (g m⁻²) \pm 1 SE, and C) ANPP (g m⁻² mo⁻¹) \pm 1 SE for *N. odorata* among competition treatments at Lake Ponderosa during 2002. Means and standard errors are reverse square-root transformed values for density and reverse log-transformed values for biomass and ANPP. Treatment abbreviations as in Table 3-1.

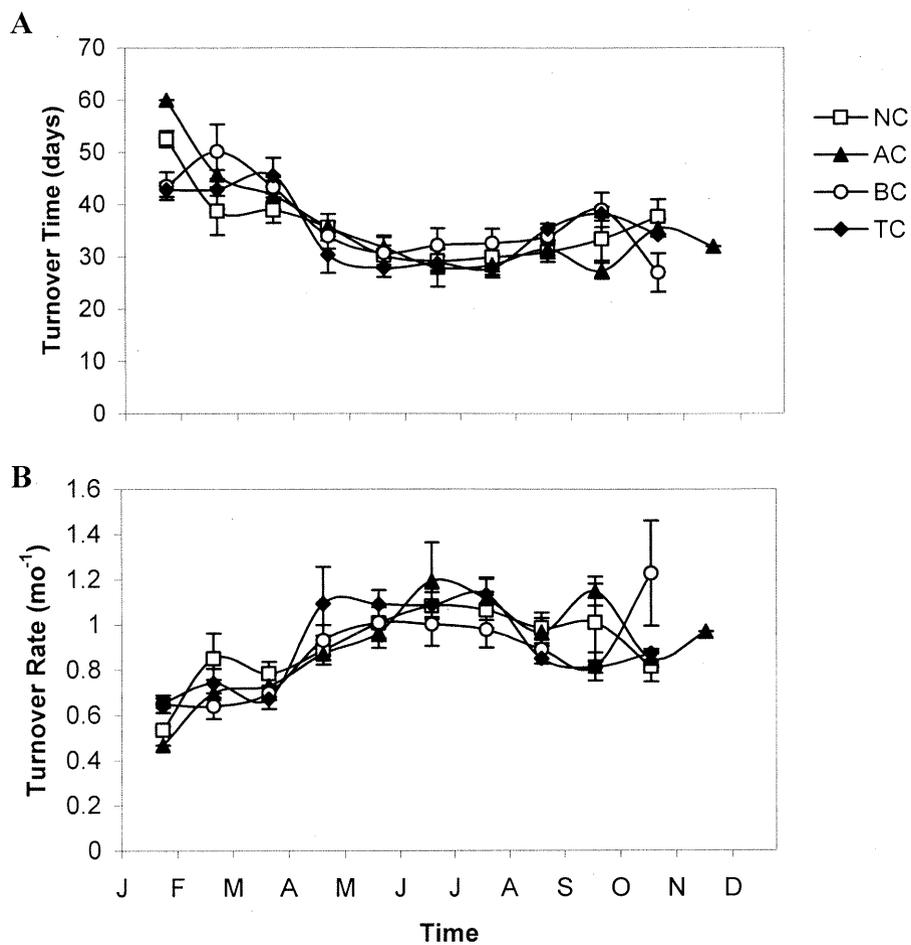


Figure 3-9. Mean monthly A) turnover time (days) \pm 1 SE and B) turnover rate (mo^{-1}) \pm 1 SE for *N. odorata* among competition treatments at Lake Ponderosa during 2002. Treatment abbreviations as in Table 3-1.

interactions, Fig. 3-8). Similarly, competition treatment did not affect monthly turnover times or turnover rates of *N. odorata* at Lake Ponderosa (Fig. 3-9). Turnover times were greatest in early spring months and lowest in late summer months ($F_{7,7} = 5.11$, $P = 0.02$), while the inverse was true for turnover rates ($F_{7,7} = 5.68$, $P = 0.02$). Both turnover time and turnover rates responded similarly over time in all treatments (no AG x BG interactions).

Total competition intensity and its components

Type of competition, when averaged over 2002, did not influence the intensity of competition, regardless of index type or response variable ($P > 0.05$ for all comparisons; data not shown), although when calculated using annual ANPP, CI was greater in the shoreline region than along the littoral-pelagic margin (block effect: $F_{1,12} = 4.83$, $P = 0.04$). When evaluated throughout the year, monthly RCI did not differ with type of competition for any of the response variables (Table 3-2). Moreover, RCI did not change over time for any response variable, and responded similarly over time regardless of competition type (Table 3-2). The same was true when intensity was measured as monthly ACI, except ACI decreased throughout the year when calculated using leaf density and biomass (time effect: $P < 0.04$ for both, Table 3-3).

Competition intensity and productivity

Because CI did not differ among competition types, competition plots were pooled ($n = 15$) to examine how CI changed with plot productivity and if patterns differed between index types. The relationship between plot productivity and CI differed

Table 3-2. Multivariate analysis of two-way split plot repeated measures models for RCI calculated using leaf density, leaf biomass, and ANPP at Lake Ponderosa in 2002. For Wilks' λ tests, error df are shown in parentheses. Between-subject factor abbreviations: AG = aboveground competition, BG = belowground competition.

Response Variable	Source	df	Wilks' λ	MS	F	P value
Leaf Density	AG	1		0.847	0.38	0.55
	BG	1		0.076	0.03	0.86
	AG x BG	1		5.171	2.32	0.15
	Error	16		2.229		
	Month	8	0.394 (9)		1.73	0.21
	Month x AG	8	0.685 (9)		0.52	0.82
	Month x BG	8	0.747 (9)		0.38	0.91
	Month x AG x BG	8	0.711 (9)		0.46	0.86
	Leaf Biomass	AG	1		0.081	0.02
BG		1		0.299	0.08	0.77
AG x BG		1		4.052	1.14	0.30
Error		16		3.550		
Month		8	0.152 (9)		6.26	0.06
Month x AG		8	0.609 (9)		0.72	0.67
Month x BG		8	0.597 (9)		0.76	0.65
Month x AG x BG		8	0.288 (9)		2.79	0.07
ANPP		AG	1		10.735	0.11
	BG	1		2.129	0.02	0.89
	AG x BG	1		164.764	1.67	0.22
	Error	16		98.913		
	Month	8	0.292 (9)		2.73	0.08
	Month x AG	8	0.598 (9)		0.76	0.65
	Month x BG	8	0.776 (9)		0.33	0.94
	Month x AG x BG	8	0.360 (9)		2.00	0.16

Table 3-3. Multivariate analysis of two-way split plot repeated measures models for ACI calculated using leaf density, leaf biomass, and ANPP at Lake Ponderosa in 2002. For Wilks' λ tests, error df are shown in parentheses. Between-subject factor abbreviations as in Table 3-2.

Response Variable	Source	df	Wilks' λ	MS	F	P value
Leaf Density	AG	1		0.273	0.01	0.94
	BG	1		17.533	0.36	0.56
	AGxBG	1		47.005	0.95	0.34
	Error	16		49.272		
	Month	8	0.248 (9)		3.42	0.04
	Month x AG	8	0.674 (9)		0.54	0.80
	Month x BG	8	0.452 (9)		1.37	0.32
	Month x AG x BG	8	0.754 (9)		0.37	0.91
Leaf Biomass	AG	1		0.469	0.25	0.63
	BG	1		0.469	0.25	0.63
	AGxBG	1		0.420	0.25	0.64
	Error	16		1.888		
	Month	8	0.229 (9)		3.80	0.03
	Month x AG	8	0.721 (9)		0.44	0.87
	Month x BG	8	0.691 (9)		0.50	0.83
	Month x AG x BG	8	0.334 (9)		2.24	0.13
ANPP	AG	1		4818.529	0.24	0.63
	BG	1		104.034	<0.01	0.94
	AGxBG	1		175.574	<0.01	0.93
	Error	16		19943.627		
	Month	8	0.276 (9)		2.95	0.06
	Month x AG	8	0.512 (9)		1.07	0.45
	Month x BG	8	0.527 (9)		1.01	0.49
	Month x AG x BG	8	0.622 (9)		0.68	0.70

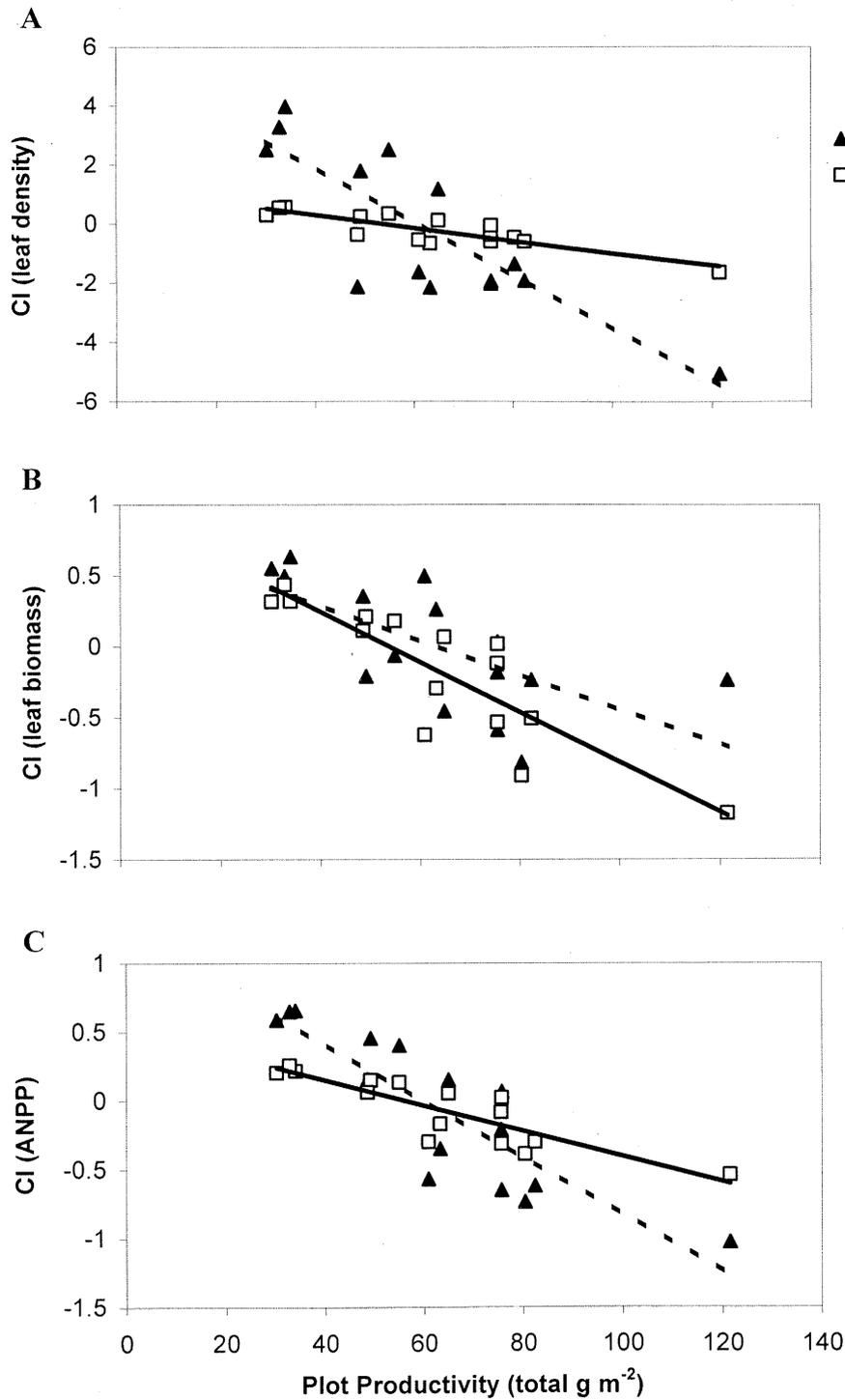


Figure 3-10. Relationship between plot productivity (total g m⁻²) and two competition intensity indices [ACI (---) and RCI (—)] for *N. odorata* leaf A) density, B) biomass, and C) ANPP.

depending on index type and response variable (Fig. 3-10). For leaf density and ANPP, both ACI and RCI declined with increasing plot productivity, although ACI declined more so than RCI (index type x plot productivity interactions: $F_{1,26} = 16.17$, $P = 0.0001$ and $F_{1,26} = 10.39$, $P = 0.0001$, respectively, Fig. 3-10A, C). For aboveground biomass, RCI and ACI responded similarly to changes in plot productivity (no index type x plot productivity interaction) decreasing as plot productivity increased (plot productivity effect: $F_{1,26} = 37.25$, $P = 0.0001$). The relationships between productivity and CI were significant for both index types and all response variables ($P < 0.008$ for all regression lines, Fig. 3-10).

DISCUSSION

Nymphaea odorata and *Nuphar advena* are similar species in that they are both rooted, floating-leaved perennials adapted for life in deep, slow moving water, and can reproduce sexually as well as asexually via horizontal rhizome elongation. Competition between similar species has been shown to be more intense and more symmetrical than competition between dissimilar species (Grace and Wetzel 1981, Pacala and Roughgarden 1985, Keddy 1990, Johansson and Keddy 1991, Keddy et al. 1997, but see Aarssen [1983] and Goldberg [1987]) and, as a result, switches in asymmetric competitive ability between similar species are likely to occur over time (Keddy 1990). However, slight differences in morphology, growth, and phenology may confer an increase in competitive ability to one species, or it may lead to resource partitioning and niche differentiation, lessening the effects of competition and permitting coexistence (Harper 1967, Grace and Wetzel 1981, Engelhardt and Ritchie 2002).

Nymphaea. odorata and *Nuphar advena* did exhibit differences in growth throughout the experiment. In general, *N. advena* emerged later, grew slower, produced fewer leaves, and accumulated less biomass during the year, but had larger, longer-lived leaves than *N. odorata*. *Nuphar advena* was observed encroaching on dense stands of *N. odorata* (J. A. Cherry; personal observation) and may be a successful competitor in the long-term even though it was less dense and less productive than *N. odorata*, and did not

negatively affect *N. odorata* in 2002. Wetland plants can experience trade-offs between energy expended ameliorating environmental conditions caused by inundation (e.g., oxygen depletion, toxic gas accumulation, differences in ion concentrations) and energy devoted to growth. Consequently, some superior competitors may have slower growth rates than their neighbors (Engelhardt and Ritchie 2002). If *N. advena* was in fact a slow-growing, yet superior competitor, then *N. odorata* performance should have suffered from *N. advena*'s presence, which was not the case in this study.

Negligible effects of N. advena presence on N. odorata performance

Examination of unstandardized measures of plant performance in communities of interacting species occurring at natural densities can reflect the actual magnitude of competition in that community (Goldberg et al. 1999). When the performance of *N. odorata* was analyzed without standardizing for plots in which plants grew alone, the magnitude of competitive effects on *N. odorata* leaf density, biomass and ANPP was negligible. *N. odorata* performed similarly when growing alone, and when exposed to aboveground and/or belowground competition, indicating that *N. odorata* was not negatively affected by the presence of *N. advena* and leading to the rejection of hypothesis one.

Moreover, it has often been assumed that the combined effects of aboveground and belowground competition are additive (Wilson and Tilman 1991, 1993, Belcher et al. 1995, Twolan-Strutt and Keddy 1996). This was not the case in this study, where competition from *N. advena* did not affect *N. odorata*, leading to the rejection of the second hypothesis. CI was negligible for all competition treatments, which suggests that

competition from *N. advena* may not be important for *N. odorata* regulation.

Furthermore, assuming *N. odorata* did not negatively affect *N. advena* through asymmetric competition, these results suggest that interactions between rooted, floating-leaved plants may be fundamentally different from interactions documented for other wetland species.

Rejection of the first two hypotheses occurred despite a trend for leaf densities to be highest in AC plots, and aboveground biomass and ANPP to be highest in BC plots. This trend for differences among response variables may have been caused by changes in water depth. For instance, in shallower water, *N. odorata* leaves tended to be smaller than in deeper water (J. Cherry, data not presented), and when subjected to adverse conditions, leaf size can be diminished (Godfrey and Wooten 1981). Formation of floating islands resulted in localized patches of unusually shallow water relative to the surrounding deep-water marsh, which occurred primarily within AC plots. As a result, these plots tended to have more leaves, but the leaves were smaller and contributed less to plot biomass and production. In addition, all plots exhibited a wide range of leaf densities, biomass, and ANPP due to natural variation in water depths among plots.

Possible factors contributing to lack of competition between N. odorata and N. advena

The lack of statistical support of competition could be attributable to environmental or biotic factors that mediated the response of *N. odorata*. For example, when plants are subjected to both competition and herbivory, the effects of competition are often less severe, or reduced by, the presence of herbivores (Bonser and Reader 1995, Van et al. 1998, Gurevitch et al. 2000, van der Wal et al. 2000). Furthermore, herbivory

may influence aboveground plant responses and potentially result in overcompensation (e.g., McNaughton 1983, Louda 1984, Huntly 1991, Hunter 1992, Crawley 1997, Karban and Thaler 1999). Aboveground compensation to herbivory has been demonstrated to increase in plants simultaneously experiencing aboveground competition for light (Rand 2004). The same could be true for *N. odorata* at Lake Ponderosa, which has been shown to compensate for herbivory when approximately three percent of leaf biomass is removed (J. Cherry, see previous chapter). Because plants were not protected from herbivores, they may have compensated for grazing and masked the potential negative effects of competition.

The dominant species in a pairwise interaction is thought to suffer more from intraspecific competition than interspecific competition (Pimentel et al. 1965 as discussed in Harper 1967). Thus, *N. odorata* and *N. advena* could co-occur at Lake Ponderosa if intraspecific competition was a more important factor influencing *N. odorata* performance than interspecific competition (Harper 1967, Goldberg 1987, Keddy and Shipley 1989). Conversely, resource partitioning and niche differentiation between interacting species could minimize negative interactions and permit coexistence. For example, *N. advena* has larger, more stable rhizomes with rootlets that may achieve greater rooting depths than those of *N. odorata*, which would permit resource partitioning belowground. Moreover, *N. advena* leaves typically do not experience shading at Lake Ponderosa, while *N. odorata* leaves can be shaded by *N. advena* (J. A. Cherry, personal observation). Thus, their interaction may not be substantially negative if *N. odorata* has a greater tolerance for shade.

At Lake Ponderosa, the co-occurrence of *N. odorata* and *N. advena* in the absence of competition may be due to the distribution of *N. advena* along the periphery of the *N. odorata*-dominated deep-water marsh. Interactions between species in habitat peripheries are thought to be less intense than those within habitats, which may permit coexistence along habitat margins (Keddy 1990). The short duration of this study is another possible explanation for the lack of competition between *N. odorata* and *N. advena*. For long-lived species such as *N. odorata* and *N. advena*, one year simply may not have been long enough to detect changes in competitive effects for all response variables. If *N. advena* continues to encroach into the *N. odorata* zone, *N. odorata* performance could be negatively affected if competition becomes more intense or more important relative to other factors.

CI - productivity patterns differed with response variable and index type, but not over time

Several scientists have predicted that CI should be greatest when productivity is high (Grime 1979, Huston 1979, Keddy 1990, Campbell and Grime 1992). Therefore, it was expected that competition between *N. odorata* and *N. advena* would be most intense when productivity was high relative to other plots, and during the summer when biomass of both species was greatest. This was not true in this study, leading to the rejection of the third and fourth hypotheses. Instead, neither ACI nor RCI changed significantly over time, nor were there consistent patterns between CI and productivity for the population-level response variables measured.

When using leaf densities to calculate CI, ACI and RCI both decreased as productivity increased, regardless of the response variable used to calculate CI. This

pattern conflicted with other studies that demonstrated an increase in ACI, and no change in RCI, as productivity increases (Wilson and Tilman 1991, 1993, Campbell and Grime 1992, Turkington et al. 1993). Negative correlations between competition and productivity have been demonstrated, and in several cases, CI values were near zero or negative at high productivity levels (Davis et al. 1998, Goldberg et al. 1999), as was the case at Lake Ponderosa. This negative relationship is not well understood, but suggests that positive interactions between plant species may become increasingly important in productive habitats.

Advocates for RCI as an index of intensity have argued that it is more likely than ACI to reflect the true response of target species to competition from neighbors (Wilson and Tilman 1993, Grace 1995). For *N. odorata*, both ACI and RCI demonstrated negative correlations between competition and productivity, which further emphasizes the importance of a previously under-recognized pattern in nature (see Goldberg et al. 1999). This also underscores the importance of using consistent response variables and indices of competition when quantifying competitive interactions so that comparisons among experiments can be made.

Summary

Competition between *N. odorata* and *N. advena* at Lake Ponderosa was negligible, and did not differ between above- and belowground components. This suggests that competition between these species was not important in this study, and that interactions between rooted, floating-leaved plants may be fundamentally different from interactions documented for other wetland species. The lack of competition in this

experiment is explainable if other factors, such as herbivory, mediated the effects of competition, if differences in rooting depth or tolerance to shade existed between interacting species, or if intraspecific competition was a more important structuring force for *N. odorata* than interspecific competition. Additionally, interactions between species occurring along habitat margins may not be intense enough to negatively affect plant performance, or the experiment may have been too short to capture negative effects of competition on a productive, long-lived perennial such as *N. odorata*. Furthermore, ACI and RCI decreased from positive to negative values with increasing productivity, suggesting that positive interactions between species may become increasingly important as productivity increases. In general, interactions between the two rooted, floating-leaved macrophytes in this study were different than those observed for other wetland plants and from those predicted by predominant plant models of competition, providing a unique example of plant interactions previously undocumented for wetland plants.

LITERATURE CITED

- Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: towards a general evolutionary theory of coexistence in systems of competition. *American Naturalist* **122**:707-731.
- Aarssen, L. W., and E. A. Epp. 1990. Neighbor manipulations in natural vegetation: a review. *Journal of Vegetation Science* **1**:13-30.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology: Individuals, Populations and Communities*, 3rd edition. Blackwell Scientific Publications, Oxford.
- Belcher, J. W., P. A. Keddy, and L. Twolan-Strutt. 1995. Root and shoot competition intensity along a soil depth gradient. *Journal of Ecology* **83**:673-682.
- Bonser, S. P., and R. J. Reader. 1995. Plant competition and herbivory in relation to vegetation biomass. *Ecology* **76**:2176-2183.
- Cahill, J. F. 1999. Fertilization effects on interactions between above- and belowground competition in an old field. *Ecology* **80**:466-480.
- Cahill, J. F. 2002. Interactions between root and shoot competition vary among species. *Oikos* **99**:101-112.
- Callaway, R. M., and S. C. Pennings. 2000. Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *American Naturalist* **156**:416-424.
- Campbell, B. D., and J. P. Grime. 1992. An experimental test of plant strategy theory. *Ecology* **73**:15-29.
- Carter, S. 1995. Herbivory by *Donacia rufescens* Lacordaire and *Donacia cincticornis* Newman on the white water-lily, *Nymphaea odorata* Aiton. University of Alabama, Tuscaloosa.
- Catling, P. M., K. W. Spicer, and L. P. Lefkovitch. 1988. Effects of the introduced floating vascular aquatic, *Hydrocharis morsus-ranae* (Hydrocharitaceae), on some North American aquatic macrophytes. *Naturaliste Canadien* **115**:131-137.

- Clark, M. W. 2000. Biophysical characterization of floating wetlands (flotant) and vegetative succession of a warm-temperate aquatic ecosystem. Dissertation. University of Florida, Gainesville.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**:710-723.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35**:131-138.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122**:661-696.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Connolly, J. 1987. On the use of response models in mixture experiments. *Oecologia* **72**:95-103.
- Crawley, M. J. 1997. Plant-herbivore dynamics. Pages 401-474 in M. J. Crawley, editor. *Plant Ecology*. Blackwell Press, Malden, Massachusetts.
- Davis, M. A., K. J. Wrage, and P. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* **86**:652-661.
- Engelhardt, K. A. M., and M. E. Ritchie. 2002. The effect of aquatic plant species richness on wetland ecosystem processes. *Ecology* **83**:2911-2924.
- Gause, G. F. 1934. *The Struggle for Existence*. Williams & Wilkens, Baltimore, Maryland.
- Godfrey, R. K., and J. W. Wooten. 1981. *Aquatic and wetland plants of the southeastern United States: Dicotyledons*. University of Georgia Press, Athens, GA.
- Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. *Ecology* **68**:1211-1223.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* **139**:771-801.
- Goldberg, D. E., T. Rajaniemi, J. Gurevitch, and A. Stewart-Oaten. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* **80**:1118-1131.

- Goldberg, D. E., and S. M. Scheiner. 2001. ANOVA and ANCOVA: Field competition experiments. Pages 77-98 in S. M. Scheiner and J. Gurevitch, editors. *Design and Analysis of Ecological Experiments*. Oxford University Press, New York.
- Gough, L., and J. B. Grace. 1997. The influence of vines on an oligohaline marsh community: results of a removal and fertilization study. *Oecologia* **112**:403-411.
- Grace, J. B. 1990. On the relationship between plant traits and competitive ability. Pages 51-66 in J. B. Grace and D. Tilman, editors. *Perspectives on Plant Competition*. Academic Press, New York.
- Grace, J. B. 1993. The effects of habitat productivity on competition intensity. *Trends in Ecology and Evolution* **8**:229-230.
- Grace, J. B. 1995. On the measurement of plant competition intensity. *Ecology* **76**:305-308.
- Grace, J. B., and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist* **118**:463-474.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester.
- Grime, J. P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*, 2nd edition. John Wiley & Sons, New York.
- Gurevitch, J. 1986. Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology* **67**:46-57.
- Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: a meta-analysis of field experiments. *American Naturalist* **155**:435-453.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* **140**:539-572.
- Hairston, N. G. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* **61**:817-826.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:357-361.
- Harper, J. L. 1967. A Darwinian approach to plant ecology. *Journal of Ecology* **55**:247-270.

- Hogg, E. H., and R. W. Wein. 1988. The contribution of *Typha* components to floating mat buoyancy. *Ecology* **69**:1025-1031.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* **144**:741-771.
- Hunter, M. D. 1992. Interactions within herbivore communities mediated by the host plant: The keystone herbivory concept. Pages 287-325 in M. D. Hunter, T. Ohgushi, and P. W. Price, editors. *Effects of Resource Distribution on Animal-Plant Interactions*. Academic Press, San Diego.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* **22**:477-503.
- Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81-101.
- Johansson, M. E., and P. A. Keddy. 1991. Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. *Oikos* **60**:27-34.
- Karban, R., and J. S. Thaler. 1999. Plant phase change and resistance to herbivory. *Ecology* **80**:510-517.
- Keddy, P. A. 1990. Competitive hierarchies and centrifugal organization in plant communities. Pages 265-290 in *Perspectives on Plant Competition*. Academic Press.
- Keddy, P. A., and B. Shipley. 1989. Competitive hierarchies in herbaceous plant-communities. *Oikos* **54**:234-241.
- Keddy, P. A., L. Twolan-Strutt, and B. Shipley. 1997. Experimental evidence that interspecific competitive asymmetry increases with soil productivity. *Oikos* **80**:253-256.
- Keddy, P. A., C. Gaudet, and L. H. Fraser. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *Journal of Ecology* **88**:413-423.
- King, G. M., T. Berman, and W. J. Wiebe. 1984. Methane formation in the acidic peats of Okefenokee Swamp. *American Midland Naturalist* **105**:386-389.
- Louda, S. M. 1984. Herbivore effect on stature, fruiting, and leaf dynamics of a native crucifer. *Ecology* **65**:1379-1386.

- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- McCreary, N. J. 1991. Competition as a mechanism of submersed macrophyte community structure. *Aquatic Botany* **41**:177-193.
- McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. *Oikos* **40**:329-336.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **110**:351-369.
- Miller, T. E. 1996. On quantifying the intensity of competition across gradients. *Ecology* **77**:978-981.
- Moen, R. A., and Y. Cohen. 1989. Growth and competition between *Potamogeton pectinatus* L. and *Myriophyllum exalbescens* Fern. in experimental ecosystems. *Aquatic Botany* **33**:257-270.
- Morin, P. J. 1999. *Community Ecology*. Blackwell Science, Inc., Malden, Massachusetts.
- Moser, E. B., A. M. Saxton, and S. R. Pezeshki. 1990. Repeated measures analysis of variance: application to tree research. *Canadian Journal of Forest Research* **20**:524-535.
- Munger, J. C., and J. H. Brown. 1981. Competition in desert rodents: an experiment with semipermeable enclosures. *Science* **211**:510-512.
- Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. *Nature* **244**:310.
- Pacala, S. W., and J. Roughgarden. 1985. Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. *Ecology* **66**:129-141.
- Pimentel, D., E. G. Feinberg, P. W. Wood, and J. T. Hayes. 1965. Selection, spatial distribution, and the coexistence of competing fly species. *American Naturalist* **94**:97-109.
- Rand, T. A. 2004. Competition, facilitation, and compensation for insect herbivory in an annual salt marsh forb. *Ecology* **85**:2046-2052.
- Reader, R. J., and B. J. Best. 1989. Variation in competition along an environmental gradient: *Hieracium floribundum* in an abandoned pasture. *Journal of Ecology* **77**:673-684.

- Reader, R. J., S. D. Wilson, J. W. Belcher, I. C. Wisheu, P. A. Keddy, D. Tilman, E. C. Morris, J. B. Grace, J. B. McGraw, H. Olf, R. Turkington, E. Klein, Y. Leung, B. Shipley, R. van Hulst, M. E. Johansson, C. Nilsson, J. Gurevitch, K. Grigulis, and B. E. Beisner. 1994. Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology* **75**:1753-1760.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240-285.
- Setälä, H., and I. Makela. 1991. *Galerucella nymphaeae* (Col., Chrysomelidae) grazing increases *Nuphar* leaf production and affects carbon and nitrogen dynamics in ponds. *Oecologia* **86**:170-176.
- Spence, D. H. N. 1982. The zonation of plants in freshwater lakes. *Advances in Ecological Research* **12**:37-126.
- Taylor, D. R., L. W. Aarssen, and C. Loehle. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat template for plant life history traits. *Oikos* **58**:239-250.
- Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* **58**:338-348.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2-16.
- Tilman, D., M. Mattson, and S. Langer. 1981. Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. *Limnology and Oceanography* **26**:1020-1033.
- Turkington, R., E. Klein, and C. P. Chanway. 1993. Interactive effects of nutrients and disturbance: an experimental test of plant strategy theory. *Ecology* **74**:863-878.
- Twolan-Strutt, L., and P. A. Keddy. 1996. Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology* **77**:259-270.
- Van, T. K., G. S. Wheeler, and T. D. Center. 1998. Competitive interactions between *Hydrilla* (*Hydrilla verticillata*) and *Vallisneria* (*Vallisneria americana*) as influenced by insect herbivory. *Biological Control* **11**:185-192.

- Van, T. K., G. S. Wheeler, and T. D. Center. 1999. Competition between *Hydrilla verticillata* and *Vallisneria americana* as influenced by soil fertility. *Aquatic Botany* **62**:225-233.
- van der Wal, R., M. Egas, A. van der Veen, and J. Bakker. 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* **88**:317-330.
- von Ende, C. N. 2001. Repeated Measures Analysis: Growth and Other Time-Dependent Measures. Pages 134-157 in S. M. Scheiner and J. Gurevitch, editors. *Design and Analysis of Ecological Experiments*. Oxford University Press, Inc., New York.
- Weigelt, A., and P. Jolliffe. 2003. Indices of plant competition. *Journal of Ecology* **91**:707-720.
- Welden, C. W., and W. L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. *The Quarterly Review of Biology* **61**:23-44.
- Wiersema, J. H. 1997. Nymphaeaceae Salisbury - Water-lily Family. Pages 66-77 in *Flora of North America. Magnoliophyta: Magnoliidae and Hamamelidae*. Oxford University Press, Inc., Oxford.
- Wilson, J. B. 1988. Shoot competition and root competition. *Journal of Applied Ecology* **25**:279-296.
- Wilson, S. D., and P. A. Keddy. 1986. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *American Naturalist* **127**:862-869.
- Wilson, S. D., and D. Tilman. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia* **88**:61-71.
- Wilson, S. D., and D. Tilman. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* **74**:599-611.
- Wilson, S. D., and D. Tilman. 1995. Competitive responses of 8 old-field plant species in 4 environments. *Ecology* **76**:1169-1180.

CHAPTER FOUR: CONTRIBUTION OF SEED BANK TO VASCULAR PLANT RICHNESS ON TEMPORARY FLOATING ISLANDS

ABSTRACT

In wetlands, disturbances resulting in fluctuating water levels create opportunities for recruitment of new individuals from seed banks. Drawdown periods favor the establishment of species adapted for life in shallower water. In this study, floating island formation functioned similarly to drawdowns in water level by creating patches of sediment that were less inundated relative to the surrounding deep-water marsh. To examine if and how seed banks contributed to temporary formation of distinct plant assemblages on these islands, field surveys of plant percent cover on and off of islands were conducted over two years, along with a controlled greenhouse experiment in which levels of inundation were manipulated to mimic conditions of differing water levels.

Plant assemblages differed significantly on and off of floating islands. Floating-leaved perennials dominated the undisturbed deep-water marsh, while emergent species dominated floating islands. Moreover, species richness was greater on islands than in the undisturbed deep-water marsh. Plant assemblages in the greenhouse seed bank experiment also differed among water level treatments in a manner consistent with differences observed in field surveys. These results demonstrate that floating island

formation temporarily altered levels of inundation favoring the germination of a more species-rich, emergent wetland plant assemblage. Because these islands persisted long enough for several species to set seed, their formation may be one mechanism contributing to the maintenance of the seed bank within the deep-water marsh, and may help maintain populations of otherwise rare species in the area.

INTRODUCTION

Regeneration from seed banks in wetlands often results from fluctuating water levels and is largely dependent on the frequency and duration of flooding and drying (van der Valk and Davis 1978, Keddy and Reznicek 1982, Gerritsen and Greening 1989, Brock and Rogers 1998). Without fluctuating hydrological conditions or other disturbances, the same suite of species is expected to dominate a community over time (Leck and Simpson 1995). Disturbances resulting in a decline in water level create opportunities for the establishment of species adapted to life in shallower water (van der Valk and Davis 1978, Wisheu and Keddy 1991, Baldwin and Mendelsohn 1998, Nicol et al. 2003), and the presence of sizeable seed banks in many wetlands promotes rapid plant responses after drawdown events (van der Valk and Davis 1979, Leck and Graveline 1979, Kirkman and Sharitz 1994).

Floating island formation within deep-water marshes is a disturbance that functions similarly to drawdowns in water level by changing hydrological conditions so that new germination niches are created. Unlike periods of drawdown, however, floating islands are less inundated relative to the surrounding deep-water marsh because islands float high in the water column, not because overall marsh water levels decline. More specifically, floating islands form when live vegetation, associated organic matter, and sediments separate from the underlying substrate or continuously float over it due to the

accumulation of gases in the sediment and aerenchyma tissue of existing vegetation (King et al. 1984, Hogg and Wein 1988, Clark 2000). Documented cases of floating islands, often referred to as flotant, suggest that development occurs when underlying sediment subsides or during periods of high water levels (Swarzenski et al. 1991).

Contrary to this paradigm of formation, temporary floating islands in this study were not associated with subsidence or changes in overall water level. Rather, they likely formed as increasing temperatures during summer months accelerated decomposition rates and gas accumulation creating small patches of sediment that detached from the underlying substrate and floated up in the water column.

Differences in adult vegetation between areas with and without floating islands have been documented in other wetlands (e.g., Swarzenski et al. 1991, Clark 2000), as well as successional changes in vegetation following formation of long-term floating islands (Clark 2000). Because wetlands are dominated by clonally reproducing vascular plants (Barrett et al. 1993, Grace 1993) many of which are also capable of reproducing sexually (Barrett et al. 1993; Vasseur et al. 1993; Eckert et al. 1999), recruitment of plants on floating islands likely results from a combination of regrowth from vegetative fragments and germination from the seed bank. However, studies of adult vegetation alone provide little information on the specific contribution and potential importance of seed banks to plant assemblages following disturbance.

To examine if and how seed banks influence the temporary formation of distinct plant assemblages on floating islands, field surveys of vegetation on and off of islands were completed. In addition, a controlled greenhouse seed bank experiment was conducted in which levels of inundation were manipulated to mimic conditions on and

off floating islands. The field surveys and greenhouse experiment were designed to test three main hypotheses. First, assemblages on floating islands would differ from and be more species-rich than assemblages in the surrounding deep-water marsh. Second, assemblages germinating from the seed bank would differ with inundation level, and those experiencing minimal inundation would be more species-rich than those experiencing higher levels of inundation. Third, seed bank assemblages experiencing high levels of inundation would most closely resemble assemblages observed in the undisturbed, deep-water marsh, while those experiencing lower levels of inundation would most closely resemble assemblages observed on floating islands. Because many wetland plants primarily reproduce clonally (Barrett et al. 1993, Grace 1993), seed production and recruitment may be vital to maintaining plant diversity, and temporary floating islands may provide essential opportunities for rare species in this marsh ecosystem to replenish their seed bank.

METHODS

Study site and floating island formation

Lake Ponderosa is a small (12 ha), privately owned freshwater reservoir located within the Oakmulgee District of the Talladega National Forest, Bibb County, Alabama (N 32° 55', W 87° 19'). Lake Ponderosa drains two unnamed intermittent first-order streams, one of which flows through an extensive emergent marsh at the north end of the lake dominated by *Alder serrulata* and *Myrica cerifera* at higher elevations, and tall graminoid and rush species at lower elevations. Adjacent to the emergent marsh, there is a deep-water marsh dominated by the rooted floating-leaved perennial, *Nymphaea odorata* Aiton. Continual inputs from the two streams and the presence of a dam prevent all but minor fluctuations in overall lake water level (J. A. Cherry, unpublished data), and therefore, the deep-water marsh rarely experiences periods of drawdown.

The study was conducted in a small portion (500 m²) of the deep-water marsh, in which floating islands formed during 2001. This area was relatively shallow and homogeneous, in close proximity to the emergent wetland, and dominated by mature *N. odorata*. Water depths in undisturbed sites of the study area ranged from 20 cm to 48 cm. However, water depth was less than 15 cm above floating islands. Within the study area, water pH (Orion Model 250A; Orion Research Group, Inc., Beverly, MA) was 5.48 ± 0.03 (± 1 SE) and 5.25 ± 0.01 during 2001 and 2002, respectively.

Floating islands at Lake Ponderosa formed in late May of 2001 and early June of 2002, and persisted until early October of both years, at which time the islands subsided and were completely inundated throughout winter and spring. When sediment rose to the surface during island formation, the rooted, floating-leaved plants growing within the deep-water marsh also floated to the surface. The leaves of these plants either died or hung off the islands into the surrounding water. As a result, shading from floating leaves and light attenuation through the water column were diminished on floating islands as compared to the surrounding, undisturbed marsh.

According to the owners of the lake, floating islands do not form every year at Lake Ponderosa, and were not present during the summer of 2000. Moreover, there can be as many as five consecutive years without floating islands at Lake Ponderosa before experiencing one to three consecutive years of floating island formation. When islands form in consecutive years, they do not necessarily reform in the same places from year to year, nor is all of the deep-water marsh affected (J. A. Cherry, personal observation). In 2001 and 2002, floating islands ranged in size from approximately 1 m² to 6 m², with most smaller than 3 m². Moreover, islands were more common in 2002 and occurred throughout a greater percentage (approximately 60%) of the deep-water marsh area than in 2001, when islands were limited to a smaller area (approximately 25%) of marsh (J. A. Cherry, personal observation).

Field measurements

In early August, two months after floating island formation was first documented in 2001, 15 permanent 1 m x 1 m plots were established systematically along three

transects spaced 20 m apart (5 plots per transect) within the area of floating island formation. The first transect was located a random distance (approximately 35 m) from, and ran parallel to, the closest shoreline. Percent cover of adult vegetation, water depth, and presence or absence of floating islands were documented at all fifteen sites twice while floating islands persisted in 2001 (August and September), twice after floating islands subsided (November 2001 and March 2002), and twice after floating islands reappeared in 2002 (August and September).

Aerial percent cover of adult vascular vegetation, as well as open water and exposed sediment, were estimated visually using a 1 m² quadrat divided into 0.1 m x 0.1 m sections. Smaller plants occurring once within a plot were documented as covering 1% of the quadrat area. To provide a measure of inundation, an average plot water depth was calculated from two readings taken with a meter stick. In plots lacking floating islands, water depth was measured from the surface of the water to the bottom of the lake, and in plots with floating islands, depth was measured from the water's surface to the top of the floating island. Floating island presence was confirmed if there was positive buoyancy of sediment when physically pushed down into the water column, mean water depth was less than 15 cm, and/or there was a lack of connectivity between the organic and mineral layers determined by physically reaching under the floating substrate.

Greenhouse experimental design

On March 6, 2002, five sediment cores (5 cm diameter, approximately 10 – 15 cm deep) from each of the 15 plots were collected for seed germination studies using an Ogeechee River corer (Wildlife Supply Company, Saginaw, MI). Samples were limited

to the upper 15 cm of the organic layer because species richness, and perhaps seed viability, decline with depth (Leck and Graveline 1979). Moreover, the top 15 cm would be more likely to germinate after floating island formation because this constituted the top layer of islands.

Sediment samples from within each of the fifteen 1 m² plots were homogenized in the field. Upon return to the laboratory, all detritus, roots and rhizomes were removed in order to isolate the contribution from the seed bank. Samples were stored in 15 separate five gallon buckets over night so that sediments could settle out from the lake water. The sediment remained inundated during this period. The following day, a 1 cm layer of sediment was distributed over 3 cm of sand in clear plastic containers (4 cm deep, 11.2 cm diameter), in which holes had been drilled 2 cm up on the sides and in the bottoms to permit water exchange. Upon settling, each container had at least a 0.5 cm layer of sediment, which was not disturbed again during the experiment. There were three containers (i.e., subsamples) per treatment-plot combination for a total of 180 containers. These containers were evenly distributed among tubs (55.5 cm x 39.5 cm x 14 cm), which were placed on tables in the greenhouse of the Experimental Mesocosm Facility at the University of Alabama and subjected to ambient light levels. The sixteen tubs (4 tubs per treatment) had been randomly designated for one of four treatments, which were designed as small-scale representations of inundation patterns observed at Lake Ponderosa. The tubs were randomly rotated weekly to control for variations in light and temperature in the greenhouse.

The four water level treatments were as follows:

1) drawdown (DD), in which the water level remained below the holes in the sides of the dishes so that water entered only through holes in the bottom to simulate islands floating above the water's surface,

2) saturated (SA), in which the water level was maintained above the holes in the sides of the dishes but not over the surface to simulate islands that float just below or at the water's surface,

3) flooded (FL), in which the water level was maintained 5 cm above the sediment surface to mimic total inundation, and

4) switched (SW), in which the sediment was flooded for the first 84 days and saturated for the last 40 days to mimic the change in inundation caused when floating islands first form.

For this experiment, there were 15 field plots, four water level treatments, 16 tubs, and three containers per treatment-plot combination for a total of 180 containers. The average of the three containers per treatment-plot combination was used in analyses to ensure a more accurate estimate of seed bank response. For statistical analyses, there were 15 replicates in each of the four treatments for a total of 60 samples. Data were also analyzed prior to obtaining averages to test for tub effects, which revealed that tubs did not affect seedling number or species richness in this experiment.

All treatments were maintained for 124 days beginning on March 7, 2002. Seedling emergence was monitored on nine dates over the 124 days, five dates before switching the water level treatment (days 8, 15, 55, 74 and 84) and four dates after

switching (days 96, 105, 113, and 124). During the course of the experiment, crowding of seedlings within containers did not occur. Within the flooded and switched treatments, there was some algal cover, but it developed after seedling establishment and did not affect seedling numbers. Many of the more common seedlings were easily identifiable, but there were several that did not flower after 124 days. After completing the experiment, the sediment was allowed to dry to induce flowering; those that did not flower were identified to the lowest taxonomic level possible. All seedlings were identified according to Godfrey and Wooten (1981*a, b*).

Statistical analyses

Multi-dimensional scaling (MDS) was used to compare similarities of adult plant assemblages on and off floating islands at Lake Ponderosa. MDS graphically represents, in two dimensions, relationships between plots in multidimensional space based on similarity matrices calculated using the Bray-Curtis Similarity Index (Bray and Curtis 1957). The relative spacing of points in an ordination plot is indicative of similarity in the samples analyzed. The data used were percent cover estimates collected at the end of the floating island season in September, and therefore represented a product of vegetation response and survival of changes in inundation caused by floating island formation. A two-way Analysis of Similarities (ANOSIM), a non-parametric analog of MANOVA, with floating island (presence and absence) and year (2001 and 2002) as main effects was performed to test for assemblage differences. When ANOSIM revealed significant differences, similarity percentage analysis (SIMPER) was also conducted to identify species responsible for observed differences in assemblages. Additionally, simple linear

regression was used to analyze the relationship between water depth and species richness of adult vegetation at Lake Ponderosa in 2001 and 2002.

For the greenhouse seed bank experiment, MDS was used to compare assemblages among water level treatments (DD, SA, SW, and FL) using the final number of individuals for each species present from each of the 15 sampling sites. Use of the final number of individuals represented a product of seed bank response and survival of individuals in different water level treatments. A one-way ANOSIM with water level treatment as the main effect was performed to test for assemblage differences, which was followed by SIMPER analysis to identify species responsible for differences among treatments. To examine changes over the duration of the experiment, a Repeated Measures ANOVA was performed to test the main effects of water level treatment and time (day 8, 15, 55, 74 and 84) on species richness. When the assumption of sphericity could not be met (Mauchly's criterion for orthogonal components > 0.05), multivariate tests of hypotheses for within-subject effects were used instead of using univariate tests (Moser et al. 1990, von Ende 2001). For Repeated Measures analysis, pairwise comparisons were made using Tukey's HSD. A MANOVA with water level treatment as the fixed factor was performed to analyze differences in the final number of seedlings among four plant habits (emergent, rooted floating-leaved, free-floating, and submerged). Multiple comparisons within groups were made with a Bonferroni correction. Data were log-transformed to meet distributional and variance assumptions.

To compare assemblages from the greenhouse seed bank experiment to those obtained during field surveys, MDS was used to compare assemblages based on presence/absence of species among water level treatments. A one-way ANOSIM with

field habitat or water level treatment as the main effect was performed to test for assemblage differences. ANOSIM was followed by SIMPER analysis to identify species responsible for differences among groups.

When data were transformed, reverse transformed means and standard errors are presented as indicated in figure legends. For all statistical analyses, hypotheses were tested at the $\alpha = 0.05$ level. MDS, ANOSIM, and SIMPER analyses were performed in Primer 5 (version 5.2.9, PRIMER-E Ltd., Plymouth, U.K.). All other analyses were performed in SAS (version 8.1e, SAS Institute, Cary, NC).

RESULTS

Plant assemblages at Lake Ponderosa

A total of 22 plant taxa from 13 families were identified in the field plots, 17 of which were unique to floating islands and one of which was unique to the deep-water marsh (Table 4-1). In the absence of floating island formation, no more than four species were observed in a plot, all of which were rooted floating-leaved or free-floating aquatic plants with the exception of the rarely present sedge, *Eleocharis baldwinii*. No fewer than three, and as many as 16 species were found in 1 m² plots on floating islands. Vegetation surveys throughout the entire deep-water marsh revealed no additional species other than those identified from the sampling sites. However, there were species present along the lakeshore and in the emergent marsh that were not present in the deep-water marsh (J. A. Cherry, unpublished data). Moreover, many of the small, emergent species present on floating islands rarely occurred along the lakeshore or within the emergent marsh, most likely due to the presence of dense stands of large graminoid and rush species. This group of otherwise rare species common on floating islands included *Cyperus albomarginatus*, *C. erythrorhizos*, *Eleocharis baldwinii*, *E. obtusa*, *E. olivacea*, *Eupatorium* sp., *Fimbristylis autumnalis*, *Fuirena pumila*, *Ludwigia decurrens*, and *Sagittaria latifolia*.

Table 4-1. Species list and corresponding plant habit for plants identified in field surveys and in the greenhouse seed bank experiment. Mean aerial percent cover of adults in the field and the mean percentage of total individuals in each water level treatment are presented for every species.

Family	Species	Habit	Seedlings in the Greenhouse					Adults in the Field	
			Drawdown	Saturated	Switched	Flooded	Island	No Island	
Alismataceae	<i>Sagittaria latifolia</i> Willd.	emergent	0	0	0	0	1	0	
Asteraceae	<i>Eupatorium</i> sp. 1	emergent	<1	0	0	0	<1	0	
	<i>Eupatorium</i> sp. 2	emergent	<1	<1	0	0	0	0	
Cabombaceae	<i>Brasenia schreberi</i> J. F. Gmel.	rooted, floating- leaved	0	0	<1	0	<1	<1	
Clusiaceae	<i>Hypericum walterii</i> (Gmel.) Gl.	emergent	0	0	0	0	<1	0	
Cyperaceae	<i>Cyperus albomarginatus</i> Mart. & Schrad.	emergent	<1	0	0	0	0	0	
	<i>Cyperus erythrorhizos</i> Muhl.	emergent	3	3	0	0	0	0	
	<i>Cyperus</i> sp.	emergent	9	17	5	1	<1	0	
	<i>Dulichium arundinaceum</i> (L.) Britt.	emergent	<1	0	0	<1	1	0	
	<i>Eleocharis baldwinii</i> (Torr.) Chapm.	emergent	53	36	22	1	11	3	
	<i>Eleocharis obtusa</i> (Willd.) Schult.	emergent	6	4	0	<1	0	0	
Juncaceae	<i>Eleocharis olivacea</i> Torr.	emergent	1	1	<1	0	16	0	
	<i>Eleocharis</i> sp.	emergent	7	13	47	67	0	0	
	<i>Fimbristylis autumnalis</i> (L.) Roem. & Schult.	emergent	<1	0	0	0	<1	0	
	<i>Fuirena pumila</i> (Torr.) Spreng.	emergent	0	0	0	0	<1	0	
	<i>Juncus nodatus</i> Coville	emergent	8	11	3	0	<1	0	
	<i>Juncus repens</i> Michx.	submerged	<1	<1	<1	0	0	0	
	<i>Juncus</i> sp.	emergent	<1	<1	0	0	0	0	
	<i>Utricularia gibba</i> var. <i>biflora</i> Lam.	free- floating	<1	3	4	8	6	<1	
	Mayaceae	<i>Mayaca fluviatilis</i> Aubl.	submerged	0	<1	0	0	2	0
	Nymphaeaceae	<i>Nymphaea odorata</i> Ait.	rooted, floating- leaved	1	5	15	19	27	56

Table 4-1, continued.

Family	Species	Habit	Seedlings in the Greenhouse				Adults in the Field	
			Drawdown	Saturated	Switched	Flooded	Island	No Island
Nymphaeaceae, cont.	<i>Nuphar advena</i> (Ait.) W. T. Ait.	rooted, floating- leaved	0	0	0	0	0	2
Onagraceae	<i>Ludwigia decurrens</i> Walter	emergent	5	4	2	2	<1	0
	<i>Ludwigia</i> sp.	emergent	0	0	0	0	<1	0
Poaceae	<i>Leersia oryzoides</i> (L.) Swartz.	emergent	0	0	<1	0	<1	0
	<i>Panicum</i> sp.	emergent	<1	0	0	<1	<1	0
	Unidentified	emergent	0	<1	0	<1	<1	0
Potamogetonaceae	<i>Potamogeton diversifolius</i> Raf.	submerged	4	0	<1	<1	0	0
Xyridaceae	<i>Xyris</i> sp.	emergent	0	0	0	0	4	0
Unidentified dicot		emergent	0	0	0	0	<1	0
TOTAL NUMBER OF SPECIES:			19	17	12	11	21	5

Of the fifteen plots studied in 2001, eight were floating at or near the surface with at least three species present as adults, and in 2002, ten were floating with at least four species in each. Plant assemblages differed on and off of floating islands according to MDS ordination. Moreover, there was a greater degree of dissimilarity among assemblages on floating islands than undisturbed plots (Fig. 4-1). ANOSIM confirmed that assemblages on floating islands were significantly different from those in the undisturbed deep-water marsh (Global $R = 0.42$, $P = 0.001$), and that assemblages differed between years (Global $R = 0.35$, $P = 0.001$). *N. odorata* dominated the deep-water marsh in both years and was twice as abundant than when found on floating islands, while a combination of *Eleocharis baldwinii*, *E. olivacea*, and stranded individuals of *U. gibba* var. *biflora* dominated floating islands in both years.

Floating island formation was associated with water depths under 15 cm in the field whereas undisturbed sites maintained depths greater than 20 cm throughout the year. Species richness in September declined significantly with increasing water depth in 2001 and 2002 (Fig. 4-2), reflecting that richness was greater on floating islands than undisturbed sites. At the deepest site within the sampling area, more species were present than predicted by the regression line. However, three of the four species were aquatic (*N. odorata*, *Brasenia schreberi*, and *Utricularia biflora*), and the fourth, *Eleocharis baldwinii*, is capable of germinating in flooded conditions when space is not limited.

Assemblages of the seed bank experiment

In the greenhouse, a total of 23 taxa were identified from 10 plant families, eight of which were unique to the seed bank experiment (Table 4-1). MDS analysis indicated

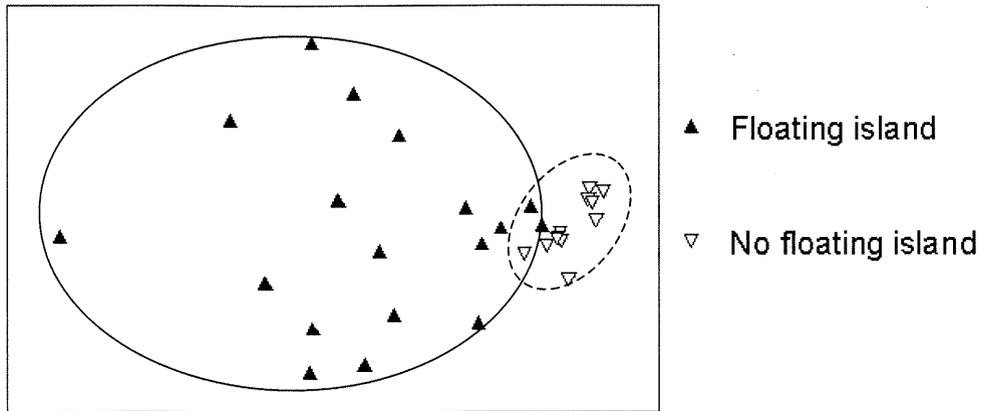


Figure 4-1. MDS ordination of plant assemblages on and off of floating islands in the field for both years. Ordination is based on percent cover of plants in each plot. Circles distinguish assemblage types [floating islands (---) and no floating islands (—)].

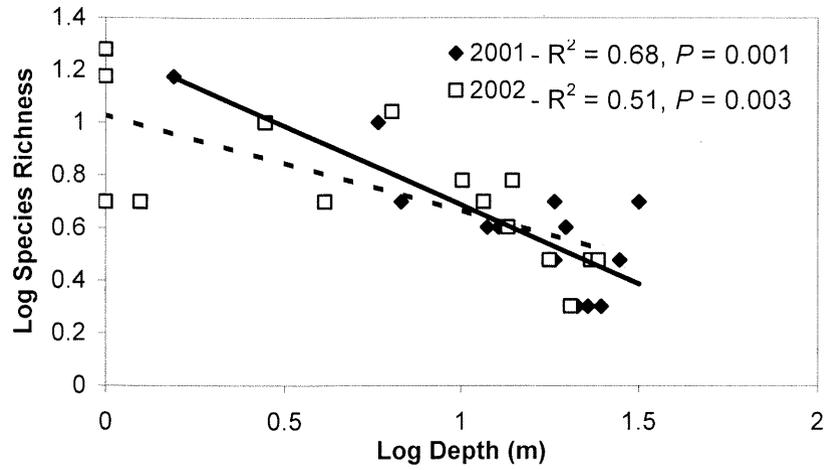


Figure 4-2. The relationship between water depth and the number of species in each field plot in 2001 (—) and 2002 (---).

overlap in plant assemblages germinating in the four water level treatments (Fig. 4-3). Despite this overlap, assemblages differed significantly among water level treatments (Global $R = 0.32$, $P = 0.001$). Moreover, assemblages differed significantly between all treatment pairs ($P < 0.04$), except drawdown and saturated treatments ($R = 0.07$, $P = 0.09$). Drawdown and saturated assemblages were dominated by *Eleocharis* spp., *Cyperus* spp., and *Juncus nodatus*, switched assemblages were dominated by *Eleocharis* spp. and *N. odorata*, and flooded assemblages were dominated by *N. odorata*.

Water level treatment significantly affected the number of species germinating from the seed bank during the course of the experiment (treatment: $F_{3,56} = 4.34$, $P = 0.008$), and the number of species increased significantly over time for all treatments (time: $F_{7,50} = 20.15$, $P < 0.0001$, Fig. 4-4). There was no significant treatment x time interaction. The drawdown treatment had the greatest number of species on all but one sampling date, although these differences were only significant between drawdown and flooded treatments. The number of species germinating from the seed bank increased significantly in the first 84 days of the experiment before stabilizing. Water level affected the number of seedlings germinating in the different plant habit groups, but this effect was only significant for rooted, floating-leaved plants ($F_{3,56} = 13.998$, $P = 0.001$, Fig. 4-5). Rooted, floating-leaved perennials were more abundant in the flooded and switched treatments than in the saturated and drawdown treatments. Emergent plants were common in all treatments, whereas free-floating and submerged plants were rare in all treatments.

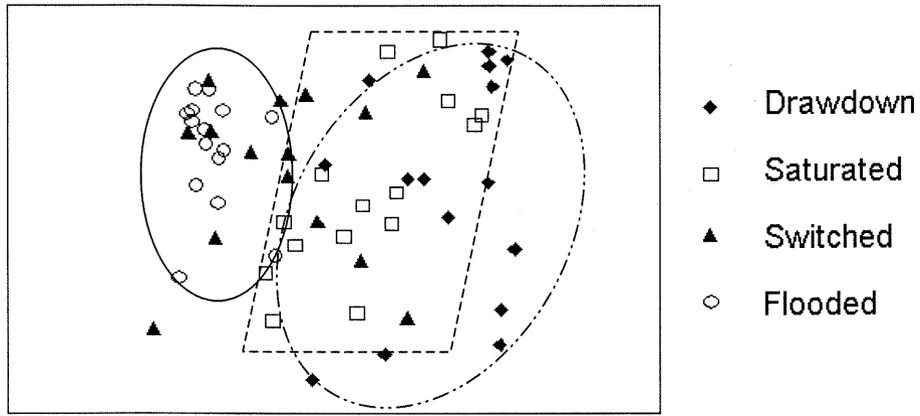


Figure 4-3. MDS ordination of plant assemblages in each of the four seed bank water level treatments. Ordination is based on species' abundances in seed bank samples for each treatment. Shapes distinguish assemblage types [flooded (—), saturated (---), and drawdown (-·-·)]. Switched assemblages are not delineated.

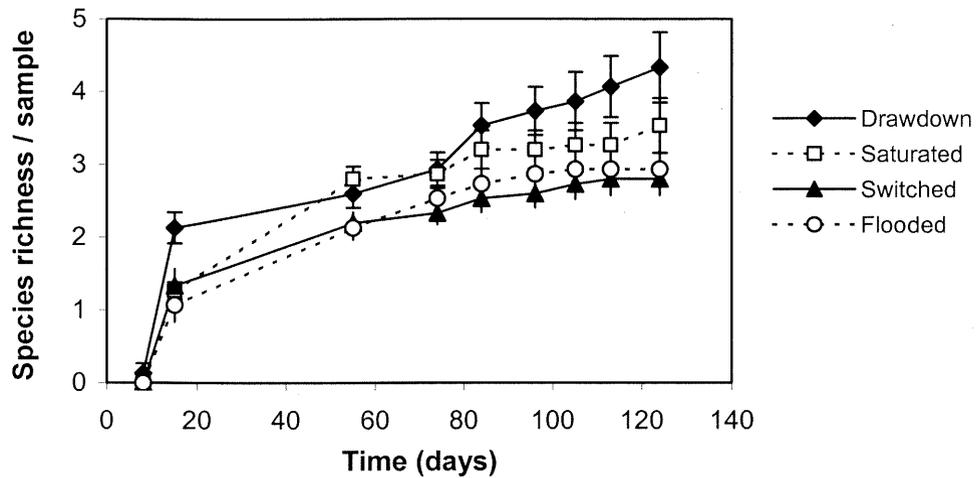


Figure 4-4. Change in total number of species per sample (98.53 cm^2 per container) present as seedlings in each of the four seed bank water level treatments ($n = 15$ samples per point; error bars are ± 1 SE). Means and standard errors are reverse log-transformed values.

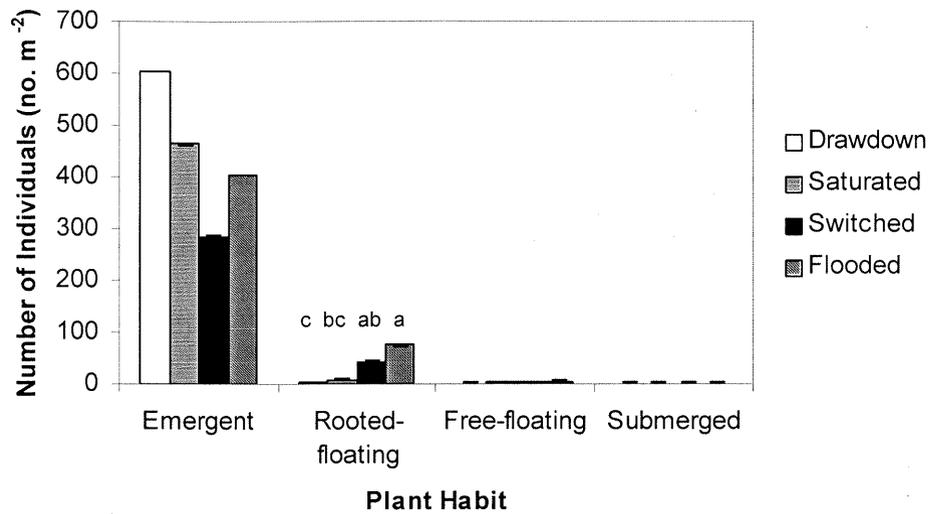


Figure 4-5. Mean number of seedlings per m^2 in different seed bank water level treatments for each plant habit group (error bars are ± 1 SE). Letters denote significant differences within groups at the $\alpha = 0.05$ level. Means and standard errors are reverse log-transformed values.

Comparison of field and greenhouse assemblages

MDS analysis of presence/absence data for species on and off of floating islands in the field and in each of the water level treatments indicated overlap among all plant assemblages (Fig. 4-6). Despite this overlap, assemblages differed significantly (Global $R = 0.53$, $P = 0.001$). Moreover, assemblages differed significantly between all pairwise comparisons ($P < 0.007$) except saturated and switched treatments in the greenhouse ($R = 0.07$, $P = 0.09$). SIMPER analysis revealed that assemblages typical of saturated and switched treatments were more similar to those of floating islands than either drawdown or flooded. Furthermore, assemblages typical of the flooded treatment were most similar to undisturbed, deep-water marsh assemblages, while those in the drawdown treatment were most unlike the undisturbed, deep-water marsh assemblages.

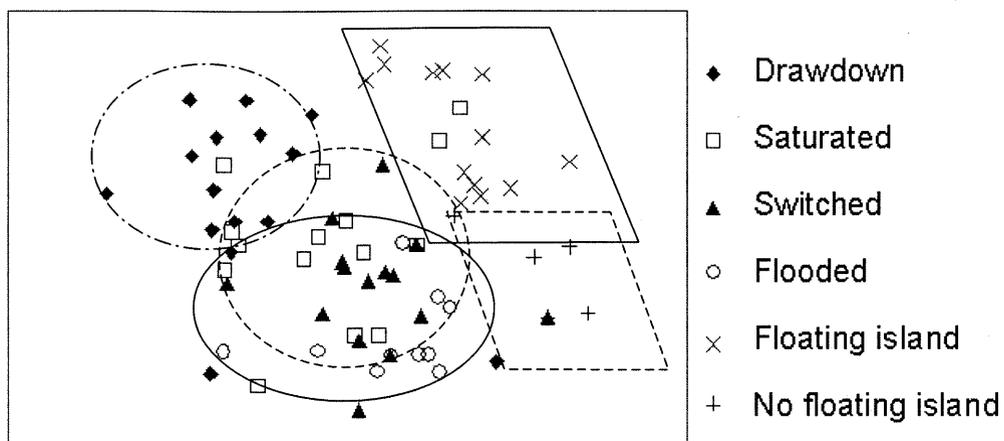


Figure 4-6. MDS ordination of plant assemblages on and off of floating islands in the field and in each of the four seed bank water level treatments. Ordination is based on presence/absence of species. Shapes distinguish assemblage types [flooded (—, ○), switched (---, ○), drawdown (---, ○), floating island (—, □), and no floating island (---, □)]. Saturated assemblages are not delineated.

DISCUSSION

Floating island assemblages more species-rich than in undisturbed marsh

Plant assemblages on floating islands differed significantly from and were more species-rich than those in undisturbed deep-water marsh, supporting the first hypothesis. In many freshwater wetlands, seed banks vary among vegetative zones, such as emergent and deep-water zones, while within a zone they are less variable (e.g. van der Valk and Davis 1978, Leck and Graveline 1979, Keddy and Reznicek 1982). Therefore, assuming seeds were evenly dispersed by water currents throughout the study site, differences observed on and off of floating islands likely resulted from localized changes in water level due to island formation, not initial differences in seed bank composition (Kirkman and Sharitz 1994, Collins and Wein 1995, Nicol et al. 2003). In this study, undisturbed deep-water marsh sites were dominated almost exclusively by the rooted-floating leaved perennial, *N. odorata*, while assemblages on floating islands were much more variable. A number of emergent species absent in undisturbed sites, as well as free-floating and submerged species that became stranded after island formation, were present on floating islands.

Floating island formation resulted in lower levels of inundation relative to the surrounding marsh, and as a result, created habitat no longer suitable for *N. odorata*. The floating leaves of adult *N. odorata* either dried up or hung off the sides of islands,

creating new germination sites for emergent plants. As a result, species richness on islands was greater than that of undisturbed sites, largely because of the presence of a variety of emergent species. The change in inundation above islands explained between 51% and 68% of the variation in species richness within the deep-water marsh. Other factors potentially controlling richness in the field included island size, time of island formation, presence of clonal fragments in the sediment, distance of islands from other seed sources, and the density and composition of adult plants at sites of island formation.

The pattern of increasing species richness with decreasing inundation has been observed in other wetlands (e.g. Wilson et al. 1993) and, for many wetland species, can be attributed to inhibition of germination in flooded conditions and the requirement of drawdown for successful recruitment (van der Valk and Davis 1976, 1978, Smith and Kadlec 1983, Leck and Simpson 1995). Even species that can survive in deeper water often only set seeds when stranded or in shallow water (Keddy and Reznicek 1982), as was observed for *U. gibba* var. *biflora* in this study. This difference suggests that without the changes of inundation caused by floating island formation, the community at Lake Ponderosa would continue to be dominated by the same suite of species throughout the year (Leck and Simpson 1995). The formation of floating islands at Lake Ponderosa likely releases some seeds from flooding inhibition so that a greater number of species is available to colonize islands. Furthermore, declines in inundation associated with island formation resulted in a shift from assemblages dominated by *N. odorata* to ones characterized by emergent plants. Sudden declines in water levels in other wetlands have resulted in similar changes in composition as plants colonizing newly-exposed habitat replace the dominant species (van der Valk and Davis 1976, 1978, 1979, Leck and

Graveline 1979, Wisheu and Keddy 1991, Kirkman and Sharitz 1994, Baldwin and Mendelssohn 1998, Le Page and Keddy 1998, Arrington et al. 1999).

Seed bank assemblages differed among water level treatments

Seed bank assemblages differed with inundation level, and assemblages experiencing minimal inundation (i.e., drawdown) were more species-rich than those experiencing higher levels of inundation in the greenhouse experiment, supporting the second hypothesis. Additionally, as predicted by the third hypothesis, seed bank assemblages exposed to high levels of inundation were dominated by *N. odorata* as were assemblages observed in the undisturbed, deep-water marsh. Seed bank assemblages in treatments designed to mimic floating island formation or islands floating at the surface (i.e., switched and saturated) were dominated by a mix of emergent and rooted, floating-leaved species, as were assemblages on floating islands. These results suggested that low inundation levels are necessary for the recruitment of many species present in the seed bank (van der Valk and Davis 1978, Smith and Kadlec 1983, Gerritsen and Greening 1989, Wilson et al. 1993, Leck and Simpson 1995), and that assemblage differences are influenced by species' abilities to tolerate and respond to changes in inundation (Cassanova and Brock 2000).

For instance, emergent species, especially in the Cyperaceae family, were common throughout the seed bank experiment, and tended to increase in abundance with decreasing inundation. The dominance of small sedges in all treatments may be indicative not only of their persistence in the seed bank, but also their role as early-successional species capable of taking advantage of newly available habitat (Harper 1977). Free-

floating and submerged species were rare in all treatments, which could be due to their infrequency in the seed bank, short seed longevity and viability, or the lack of favorable germination conditions in the greenhouse. Rooted, floating-leaved plants were also present in low abundances for all treatments. This was not surprising given that most aquatic perennials persist vegetatively without reliance on seed production (Kirkman and Sharitz 1994) and often lack seed banks (Leck and Simpson 1987, Collins and Wein 1995). However, they did significantly increase in abundance as inundation increased, suggesting that flooded conditions enhanced their germination, as has been documented for seed banks of the Okefenokee Swamp (Gerritsen and Greening 1989). These results demonstrate that recruitment from seed is important for the species observed in the seed bank experiment, even though most are also capable of reproducing clonally. Therefore, floating island formation may be an important mechanism for maintaining genetic diversity within the ecosystem because it creates additional habitat favoring the germination of otherwise rare emergent species.

Other studies of wetland seed banks have suggested that deep-water marshes dominated by floating perennials often have shallow, species-poor seed banks that are unable to persist due to constant inundation (Leck and Simpson 1987, Collins and Wein 1995). The number of species observed as adults and germinating from the seed bank at Lake Ponderosa was lower than in some studies of wetlands (e.g. Leck and Graveline 1979, Leck and Simpson 1987). However, because many of the plants observed on floating islands survived long enough to flower and set seed, floating island formation, along with seed inputs from the adjacent wetland likely helped maintain the seed bank within the deep-water marsh.

Implications of floating island formation

Formation of floating islands resulted in localized changes in hydrological conditions that reduced the cover of *N. odorata*, and created new, temporary germination niches for other species. It has been demonstrated that disturbances that reduce the cover of dominant perennials, as floating island formation did for *N. odorata*, must be lethal for seedling recruitment to result in changes in community composition (Baldwin and Mendelssohn 1998). Because floating islands were not permanent and *N. odorata* was capable of regrowing from rhizomes once islands subsided, differences in plant assemblages at Lake Ponderosa were not indicative of long-term shifts in assemblage composition. For observed changes in assemblages at Lake Ponderosa to be permanent, floating islands would have to persist from year to year, a condition that would drastically reduce or eliminate *N. odorata* in the long-term. However, islands did persist long enough for several species to set seed, and their formation may be one mechanism contributing to the maintenance of genetic diversity at this site, especially given that many of the small, emergent species found on islands were rare along the lakeshore and within the emergent marsh (J. A. Cherry, personal observation).

Summary

An increase in species richness with a decrease in water depth as observed in this study has been documented in other freshwater marsh systems as well (Keddy and Reznicek 1982, Wilson et al. 1993). Within the deep-water marsh of Lake Ponderosa, the presence of emergent species was limited to floating islands where inundation was lower

than in the surrounding undisturbed marsh. The disturbance of floating island formation created a temporary habitat in which a greater number of species could germinate and eventually set seed. Functionally, the formation of temporary floating islands was similar to water level fluctuations in other systems where species richness increased during natural or human-induced low-water phases or drawdown (Keddy and Reznicek 1982, Smith and Kadlec 1983, Collins and Wein 1995). This depth-species relationship, which existed in the field over the two years of this study and in the water level treatments in the greenhouse, suggests that temporary island formation contributes to the maintenance of the seed bank within the deep-water marsh and may help maintain locally rare populations.

LITERATURE CITED

- Arrington, D. A., L. A. Toth, and J. W. Koebel, Jr. 1999. Effects of rooting by feral hogs *Sus scrofa* L. on the structure of a floodplain vegetation assemblage. *Wetlands* **19**:535-544.
- Barrett, S. C. H., C. G. Eckert, and B. C. Husband. 1993. Evolutionary processes in aquatic plant populations. *Aquatic Botany* **44**:105-145.
- Baldwin, A. H., and I. A. Mendelssohn. 1998. Response of two oligohaline marsh communities to lethal and nonlethal disturbance. *Oecologia* **116**:543-555.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **27**:325-349.
- Brock, M. A., and K. H. Rogers. 1998. The regeneration potential of the seed bank of an ephemeral floodplain in South Africa. *Aquatic Botany* **61**:123-135.
- Cassanova, M. T., and M. T. Brock. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities. *Plant Ecology* **147**: 237-250.
- Clark, M. W. 2000. Biophysical characterization of floating wetlands (flotant) and vegetative succession of a warm-temperate aquatic ecosystem. Ph. D. Dissertation. University of Florida, Gainesville, FL, USA.
- Collins, B., and G. Wein. 1995. Seed bank and vegetation of a constructed reservoir. *Wetlands* **15**:374-385.
- Eckert, C. G., M. E. Dorken, and S. A. Mitchell. 1999. Loss of sex in clonal populations of a flowering plant, *Decodon verticillatus* (Lythraceae). *Evolution* **53**:1079-1092.
- Gerritsen, J., and H. S. Greening. 1989. Marsh seed banks of the Okefenokee Swamp: effects of hydrologic regime and nutrients. *Ecology* **70**:750-763.
- Godfrey, R. K., and J. W. Wooten. 1981a. Aquatic and wetland plants of the southeastern United States: Dicotyledons. University of Georgia Press, Athens, GA, USA.

- Godfrey, R. K., and J. W. Wooten. 1981b. Aquatic and wetland plants of the southeastern United States: Monocotyledons. University of Georgia Press, Athens, GA, USA.
- Grace, J. B. 1993. The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. *Aquatic Botany* **44**:159-180.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, England, UK.
- Hogg, E. H., and R. W. Wein. 1988. The contribution of *Typha* components to floating mat buoyancy. *Ecology* **69**:1025-1031.
- Keddy, P. A., and A. A. Reznicek. 1982. The role of seed banks in the persistence of Ontario's coastal plain flora. *American Journal of Botany* **69**:13-22.
- King, G. M., T. Berman, and W. J. Wiebe. 1984. Methane formation in the acidic peats of Okefenokee Swamp. *American Midland Naturalist* **105**:386-389.
- Kirkman, L. K., and R. R. Sharitz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. *Ecological Applications* **41**:177-188.
- Le Page, C., and P. A. Keddy. 1998. Reserves of buried seeds in beaver ponds. *Wetlands* **18**:242-248.
- Leck, M. A., and K. J. Graveline. 1979. The seed bank of a freshwater tidal marsh. *American Journal of Botany* **66**:1006-1015.
- Leck, M. A., and R. D. Simpson. 1987. Seed bank of a freshwater tidal wetland: turnover and relationship to vegetation change. *American Journal of Botany* **74**:360-370.
- Leck, M. A., and R. D. Simpson. 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. *American Journal of Botany* **82**:1547-1557.
- Moser, E. B., A. M. Saxton, and S. R. Pezeshki. 1990. Repeated measures analysis of variance: application to tree research. *Canadian Journal of Forest Research*. **20**:524-535.
- Nicol, J. M., G. G. Ganf, and G. A. Pelton. 2003. Seed banks of a southern Australian wetland: the influence of water regime on the final floristic composition. *Plant Ecology* **168**: 191-205.
- Smith, L. M., and J. A. Kadlec. 1983. Seed banks and their role during drawdown of a North American marsh. *Journal of Applied Ecology* **20**:673-684.

- Swarzenski, C. M., E. M. Swenson, C. E. Sasser, and J. G. Gosselink. 1991. Marsh mat flotation in the Louisiana Delta Plain. *Journal of Ecology* **79**:999-1011.
- van der Valk, A. G., and C. B. Davis. 1976. The seed banks of prairie glacial marshes. *Canadian Journal of Botany* **54**:1832-1838.
- van der Valk, A. G., and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**:322-335.
- van der Valk, A. G., and C. B. Davis. 1979. A reconstruction of the recent vegetational history of a prairie marsh, Eagle Lake, Iowa, for its seed bank. *Aquatic Botany* **6**:29-51.
- Vasseur, L., L. W. Aarssen, and T. Bennett. 1993. Allozymic variation in local apomictic populations of *Lemna minor* (Lemnaceae). *American Journal of Botany* **80**:974-979.
- von Ende, C. N. 2001. Repeated Measures Analysis: Growth and Other Time-Dependent Measures. Pages 134-157 in S. M. Scheiner and J. Gurevitch, editors. *Design and Analysis of Ecological Experiments*. Oxford University Press, Inc., New York.
- Wilson, S. D., D. R. J. Moore, and P. A. Keddy. 1993. Relationship of marsh seed banks to vegetation patterns along environmental gradients. *Freshwater Biology* **29**:361-370.
- Wisheu, I. C., and P. A. Keddy. 1991. Seed banks of a rare wetland plant community: distribution patterns and effects of human-induced disturbance. *Journal of Vegetation Science* **2**:181-188.