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UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

PLANT COMPETITION THEORY: EMPIRICAL TESTS FROM THE TALLGRASS PRAIRIE

A Dissertation
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
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By
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PLANT COMPETITION THEORY: EMPIRICAL TESTS FROM THE TALLGRASS PRAIRIE

A Dissertation APPROVED FOR THE
DEPARTMENT OF BOTANY AND MICROBIOLOGY

BY

Linda L. Wallace

Caryn C. Vaughn

William Ortiz-Leduc

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Preface

This dissertation was written as two chapters. The first chapter was written in the format for submission to the journal *Functional Ecology* authored by myself and L.L. Wallace. The second chapter was written in the format for submission to the journal *Ecology* and is authored by myself, E.M. Steinauer, and L.L. Wallace.

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Abstract

The *resource ratio* and *plant strategies* models of plant competition were empirically tested in a greenhouse (Chapter I) and a field study (Chapter II) conducted in the tallgrass prairie of Oklahoma. The *resource ratio* model predicts that a competitively superior species is one with the ability to acquire limiting vital resources at levels lower than neighboring species. Species with this capability should dominate the community at the expense of competitively inferior species. The *plant strategies* hypothesis, however, asserts that competitively dominant species are those with the capacity to acquire resources in the presence of moderate disturbances (e.g. grazing) and that community structure will reflect a systems disturbance and resource regime.

Chapter I is a greenhouse study designed to address the physiological (gas exchange), morphological (height, tiller and circumference growth rates), and biomass responses of two dominant grasses (*Andropogon gerardii* and *Panicum virgatum*) to nitrogen availability (0.01, 0.1, 1.0 and 10.0 mM nitrate) and disturbance (simulated bison grazing). The experiment was fully crossed. Species responses to these treatments were mixed. Nitrogen availability most strongly affected the above parameters for *P. virgatum*. The responses of *A. gerardii*, however, were regulated by disturbance. These species responses provide support for both competition models and indicate that a single model may not explain interspecific interactions in this system.

Chapter II concerns a field study designed to expand on the findings of the greenhouse study. A fully crossed experiment manipulating light (ambient or 50% shade), nitrogen (bovine urine) and clipping was conducted 30 km south of Norman, Oklahoma. Community structure (species diversity, richness and evenness), plant and soil N, and productivity were measured during 1995 and 1996. Community diversity indices were significantly affected by time (intra- and inter- annually), urine and clipping. Clipping reduced species diversity and evenness. Urine and shade reduced species diversity and richness throughout the duration of the experiment. Detrended correspondence analysis showed clipping to be the strongest influence upon community structure indices; collapsing treatment plots in ordination space. Community structure results support the *resource ratio* model. Nitrogen dynamics and productivity, however, were regulated by clipping. Hence, these parameters support the *plant strategies* model of competition.

Depending upon the parameter and scale of measurement, evidence for each model exists. Further studies of "natural" resource and disturbance regimes (e.g. fire, urine patches, grazing) with greater temporal complexity

are required to determine under what circumstances each model is appropriate in this system.

Chapter I

Implications for Plant Competition Theory: The Effects of Resource Availability and Clipping on the Gas Exchange, Morphology and Biomass of *Andropogon gerardii* and *Panicum virgatum*

Abstract

1. *Andropogon gerardii* (big bluestem) and *Panicum virgatum* (switchgrass) were used to evaluate the appropriateness of the resource ratio and plant strategies models of competition for the tallgrass prairie. The relative importance of resource availability (nitrogen concentration) and disturbance (simulated bison grazing) as regulators of plant characteristics (gas exchange rate, growth, and biomass) indicative of potential competitive success was determined.

2. A fully crossed multifactorial experimental design was employed. Ramets were grown in a range of nitrogen concentrations (0.01, 0.1, 1.0 or 10.0 mM NO_3^-). Plants were clipped to mimic bison grazing (disturbance) in the North American tallgrass prairie. Gas exchange, morphological development and biomass were measured to monitor plant response.

3. Photosynthetic rate was elevated for a short time (ca. 13 days) in *A. gerardii* grown at 0.01 mM NO_3^-. *P virgatum* demonstrated a similar enhancement in response to clipping. Clipping increased *A. gerardii's* height growth rate, though the change in tiller number and circumference were not influenced. *P. virgatum* showed similar responses to nitrogen availability, but was not significantly affected by clipping. While total plant biomass for *A. gerardii* was not affected by clipping, control plants had greater belowground and aboveground biomass. Resource availability did not influence *A. gerardii's* total plant biomass. Clipped ramets of *P. virgatum* had less total biomass than controls. *P. virgatum's* final biomass was also influenced by nitrogen availability.

4. We conclude that grass competition in the tallgrass prairie may not be fully explained by the assumptions of either competition model. The competitive success of *A. gerardii* appears to be more appropriately predicted by the *plant strategies* model while the *resource ratio* hypothesis appears to more fully explain *P. virgatum's* responses.

Keywords: Big bluestem, switchgrass, nitrogen, grazing,

tallgrass prairie, resource ratio, plant strategies.

Introduction

Identifying the mechanisms of competition has long been of interest to ecologists (e.g. Berendse 1985; Berendse & Elberse 1990; Gaudet & Keddy 1995; Grace & Tilman 1990; Grime 1979; Keddy 1989; Tilman 1982, 1988, 1990; Tremmel & Bazzaz 1995; Wallace & Macko 1993). Two plant competition models that have received considerable attention during the past twenty years are the 'resource ratio hypothesis' [R*] (Tilman 1982, 1988, 1990) and the 'plant strategies' or R-C-S Model (Grime 1977, 1979). Because both models have been described in great detail elsewhere (e.g. Grace & Tilman 1990; Grime 1979; Keddy 1989; Tilman 1982, 1988, 1990), we provide only a brief overview.

The resource ratio hypothesis (Tilman 1990) argues that plant competitive success is a function of a plant's ability to acquire and sequester limited resources. The plant strategies model (Grime 1979) asserts that plant competitive success is determined by a species' ability, via life history characteristics, to withstand disturbance.

Empirical support for both constructs exists (e.g. Goldberg 1994; Grace 1995; Grime 1977; Keddy 1991; Tilman 1984; Turkington, Klein & Chanway 1993; Wilson & Keddy 1986; Wilson & Tilman 1991). However, many of these studies have been conducted in the systems in which the models were originally developed or in very similar systems.

Consequently, debate concerning the global applicability of these models has persisted (e.g. Goldberg 1994; Grace 1995; Keddy 1989, 1991). Novel systems must be used to determine the breadth of these competition models (Keddy 1991).

Vegetation in the North American tallgrass prairie is structured both by a suite of disturbances of varying frequency and intensity (e.g. grazing and fire) and by limiting resources such as water and nitrogen (Briggs & Knapp 1995; Collins 1987, 1989, 1990; Knapp & Seastedt 1986; Milchunas, Sala & Lauenroth 1988; Ojima *et al*. 1990; Risser 1990; Seastedt 1985; Steinauer & Collins 1995). Because the dominant grasses in this system persist in large numbers despite disturbance and limited resource availability, these species can be used as indicators of the relative importance of these two factors as regulators of plant competitive success. If the resource ratio hypothesis is correct, one would expect dominant grass species to show less biological or competitive response to changes in disturbance regime, such as grazing. However, if the R-C-S hypothesis is appropriate in this system, then the reverse is true. Alternatively, because both disturbance and limited resources are important agents in tallgrass prairie, it is possible that plant responses may best be predicted by the interaction of resource level and disturbance.

To test these hypotheses, we conducted greenhouse experiments to identify the relative importance of resource availability and disturbance as regulators of plant characteristics (gas exchange, morphology, and biomass) predictive of plant competitive success (Gaudet & Keddy 1988; Hara 1993; Harper 1977; Keddy & Shipley 1989). Two dominant grasses, *Panicum virgatum* and *Andropogon gerardii*, were studied. As dominant species in the tallgrass prairie, these grasses must be able to respond to a wide array of disturbances and fluctuations in resource availability. Thus, these species provide an excellent model for testing these hypotheses.

Materials and Methods

Study Species

Andropogon gerardii [Vitman] (big bluestem) and *Panicum virgatum* [L] (switchgrass) were studied. Both species are perennial, C_4 grasses native to the North American tallgrass prairie (Knapp 1985; Waller & Lewis 1979). These species were selected because of their abundance and importance as forage species for both bison and cattle (Risser *et al.* 1981). *A. gerardii* is found across a wide range of habitats and is obligately mycorrhizal (Hetrick, Kitt & Wilson 1988) while *P. virgatum* is faculatively mycorrhizal (V. Moorthy, pers. comm.) and is more commonly found in moist lowlands of the prairie (Bazzaz & Parrish 1982).

A. gerardii was germinated from seed (Sharp Brothers Seed Co., Salina, KS) in potting soil (50% Oklahoma sandy loam, 50% peat augmented with 14N:14P:14K) in a greenhouse at the University of Oklahoma. Ramets of *P. virgatum* were collected from Great Plains Apiaries Research Area (Washington, McClain County, OK, USA) in spring 1993. Clones were transplanted to 3.6 L pots and maintained in potting soil in the greenhouse. Prior to the experiment all plants were watered daily and fertilized weekly with 14N:14P:14K. A 400 Watt high pressure sodium lamp was used to augment ambient greenhouse light and to maintain a 14 hour light day. Midday PPFD (photosynthetic photon flux density) ranged between 1500 and 1800 μmol/m^2/sec.

Experimental Design

P. virgatum and *A. gerardii* were assessed in individual experiments. Both experiments were fully crossed, with clipping and nitrate availability as treatment effects. Nitrate concentrations for *P. virgatum* were 0.01, 0.1, 1.0 and 10.0 mM nitrate. *A. gerardii* was grown in 0.01, 0.1 or 1.0 mM nitrate. These concentrations range from kinetic saturation, 10.0 mM (Bloom 1988), to observed field values, 0.01 mM (Gropp, pers. obs.).

Experiment One-Panicum virgatum

Hydroponic growth techniques are widely used in the study of nutrient uptake because they provide an easy and inexpensive method for regulating resource availability (e.g. Bloom 1988). However, prior to using this technique, we ensured that *P. virgatum* is not artificially influenced by this growth media. To do so, we conducted an experiment in which gas exchange, morphology and biomass of hydroponically grown ramets were compared to control plants grown in soil. We found no significant differences between plants in the two growth media and thus used hydroponics for this experiment because of the ease of nutrient amendments using this technique (Gropp & Wallace, unpublished data).

Sample size for each clipping*nitrogen concentration cell was n=8, yielding a total N=64. Because of space and equipment limitations, the experiment was divided into two phases. Phase 1 consisted of clipped and unclipped plants grown at either 1.0 or 10.0 mM nitrate. The second phase was identical to Phase 1 with the exception of nitrate concentration (0.1 and 0.01 mM). Ramets of the same approximate height (40 cm) were selected and separated into individual tillers.

Black plastic containers (3.6 L capacity) covered with aluminum foil were used as hydroponic chambers. Each chamber contained 3 L of standard Hoagland's nutrient solution modified to deliver the specified nitrogen concentration. The only source of nitrogen was NO_3^-, as calcium nitrate. Solution pH was maintained at 6.8 with calcium hydroxide and sulfuric acid. Ion selective electrodes (Orion Scientific, Boston, MA) were used to monitor solution nitrate concentration and pH. Chamber solutions were replaced weekly to prevent significant changes in ionic concentration. All chambers received continuous aeration using an air pump and an air line. Because the pump heated the air, a temperature regulated water bath was used to maintain air temperatures at 22°C. Tillers were secured and supported in chambers by wrapping Parafilm wax around the mouth of the hydroponic chamber and the crown of the grass. This allowed the plant to be supported such that roots did not rest on the bottom of the chamber. Though the chambers were not axenic, the wax wrap reduced solution contamination and the opaque covering prevented algal growth. Plants were allowed to acclimate to the hydroponic chambers for 14 days prior to clipping or measurement. To simulate bison grazing, plants were clipped to 10 cm above the crown (Wallace 1990) 19 days after they were placed in the chambers. All material removed was oven-dried, weighed and the weight added to the total final biomass.

Experiment Two-Andropogon gerardii

Since A. *gerardii* is obligately mycorrhizal (Hetrick *et al*. 1988; V. Moorthy, pers. comm.), it did not tolerate hydroponic conditions. After reaching a height of 63 ± 3 cm, tillers were transplanted to 4 L pots containing rinsed calcine clay (pH=6.8). Kjeldahl total nitrogen analysis of the rinsed clay found that [N]<0.001 mM. Three tiller ramets were randomly assigned to each of 48 pots. All pots were watered with 1.75 L of deionized water every three days and with 250 ml of a nitrogen free Hoagland's nutrient solution weekly. All plants were allowed to acclimate for 14 days prior to the start of the experiment.

A fully crossed experimental design was employed, with disturbance (clipped vs. unclipped) and resource availability (nitrogen concentrations of 0.01, 0.1 and 1.0 mM NO_3^-) as treatments, with 8 plants per treatment cell. Plants assigned to the disturbance treatment were clipped to a height of 20 cm aboveground. This height was selected to ensure the presence of leaves for gas exchange measurements. All material removed was oven-dried, weighed and the weight added to the total final biomass.

Measurements

Gas exchange rates per unit leaf area were measured with an LI-6200 (LiCor, Inc., Lincoln, NE) closed gas exchange system, except during Phase 1 of Experiment 1 for *P. virgatum* where an LI-6000 was used. All gas exchange measurements were taken on clear days between 1000 and 1400 hours Central Standard Time. The youngest, fully expanded leaf was sampled. Following gas exchange measurements, leaves were clipped, placed in plastic bags and kept on ice until leaf area measurements were made with an LI-3000 Leaf

Area Meter (Li-Cor, Inc., Lincoln, NE.). Leaf area was measured upon completion of all gas exchange measurements. Tissue removed for gas exchange measurements was dried at 60°C for 48 hours, weighed and added to final aboveground and total plant biomass measurements.

Morphological measurements were plant height, tiller number, circumference, and the change in these parameters per unit time. At the culmination of the experiment, plants were separated into belowground and aboveground components, dried at 60°C for 48 hours prior to weighing.

Biomass data were analyzed with an ANOVA and Duncan's Means Comparison test. Repeated measures ANOVA and Duncan's Means Comparison tests were used for gas exchange and morphological analyses. Arcsine square root transformations were done on all proportional data prior to analysis (Zar 1984).

Results

Gas Exchange

Panicum virgatum

Photosynthetic rate was higher for clipped plants than for controls only on day 7 for Phase 1 plants and on Day 14 for Phase 2 plants (Figure 1a, c). Resource availability did not influence photosynthesis (Figure 1a, c). Stomatal conductance (Figure 1b) increased with clipping during Phase I only (at day 7), but was not affected during Phase 2

(Figure 1d) or by resource availability during either phase (Figure 1b, d). Photosynthesis and stomatal conductance were not affected by the nitrogen*clipping interaction during either phase of the experiment. Water use efficiency (data not shown) was not affected by either main effect or interactions.

This pattern of enhanced photosynthetic response to clipping occurred in each phase of the experiment. Because Phase 1 plants were measured with an LI-6000 IRGA and Phase 2 plants were measured with an LI-6200 IRGA, we are unable to make direct comparisons across the entire N gradient. Within each phase, however, nitrate concentration did not affect photosynthetic rate (Figure 1).

Andropogon gerardii

Clipping decreased water use efficiency (data not shown) only on day 23. The treatments had little affect upon gas exchange rates (Figure 2). The photosynthetic rate was significantly lower in the low N (0.01 mM) treatment only on day 23 (Figure 2a). While photosynthetic rates were greater on day 45 for unclipped plants and those grown at the two higher nitrogen concentrations, the rates were not significantly different. The treatments had no significant effect upon stomatal conductance at any sample date (Figure 2b).

Morphology

Panicum virgatum

The rates of tiller production, change in plant circumference, and height growth rate were all significantly greater for plants grown at low N (0.01 and 0.1 mM) compared to high N (1.0 and 10.0 mM) treatments (Figure 3). Clipping significantly affected only height growth rates (Figure 3b). The clipping*nitrogen interaction did not significantly affect any morphological parameter.

Andropogon gerardii

Nitrogen availability had no affect on any morphological parameter (Figure 4a). Clipping reduced only height growth rate (Figure 4b). In addition to two-way ANOVAs, morphological data were analyzed using repeated measures ANOVA to ensure that sampling time was not solely responsible for observed clipping affects upon plant height growth rate. These analyses also indicate that morphological parameters were influenced by clipping and differences between clipped and unclipped plants increased over time (data not shown). Repeated measures analyses also indicated that neither nitrogen availability nor the interaction of nitrogen and clipping affected morphological parameters.

Biomass

Panicum virgatum

Within each phase of Experiment One, nitrogen availability did not affect final belowground, aboveground or total plant biomass (Figure 5a). However, biomass values for the lower N availabilities (Phase II) were significantly smaller. Clipping significantly reduced final belowground, aboveground and total plant biomass (Figure 5b). The interaction of clipping and nitrate had no affect upon belowground, aboveground or total plant biomass.

Andropogon gerardii

Nitrogen availability and the interaction of nitrogen and clipping had no affect upon belowground, aboveground or total plant biomass (Figure 6a). Clipped plants had more aboveground biomass but less belowground biomass than control plants (Figure 6b). Average total biomass was not significantly affected by clipping (Figure 6b).

Discussion

Gas Exchange

Many studies have shown that grazing increases gas exchange rates in monocots (Detling, Dyer & Winn 1979; Detling & Painter 1983; McNaughton 1983; Painter & Detling 1981; Vickery 1972; Wallace, McNaughton & Coughenour 1985; Wallace 1990). Fire has also been shown to substantially increase photosynthetic rate in grasses such as *A. gerardii* (Knapp 1985). It has been proposed that these grasses may have a competitive advantage over neighboring species that do not demonstrate the same ability to increase photosynthetic rate following disturbance (Wallace & Macko 1993).

In this study, clipping had no effect on photosynthesis in *A. gerardii*. However, *A. gerardii* grown at low NO_3^- availability which mimicked field levels (0.01 mM) showed a short-term increase in photosynthesis (Figure 2). While this response appears counter to that measured by Knapp (1985), it is important to note that fire, unlike grazing, decreases soil N availability (Ojima *et al.* 1990). Thus, *A. gerardii* is likely responding to resource availability in both situations.

Unlike *A. gerardii*, *P. virgatum* showed greater physiological sensitivity to clipping than resource availability. Clipped plants maintained higher rates of photosynthesis and stomatal conductance than control plants for approximately 1.5 weeks (Figure 1). Knapp (1985) found photosynthesis in *P. virgatum* to be less sensitive to fire than resource (water) availability. These findings suggest that the type and timing of disturbance plays an important role in photosynthetic response.

Plant Growth

In the tallgrass prairie, vegetative reproduction is more common and important than sexual reproduction in regulating plant community structure (Collins & Uno 1985; Tonielli, Wallace & Uno, in prep.). For many species long term success in this system is largely dictated by the ability to occupy space which is often governed by vegetative growth and reproduction (Collins & Glenn 1988).

Plant height, circumference, tiller number and the rates of change in these parameters are all indicators of potential competitive success (Gaudet & Keddy 1988). Species that are able to maximize their rates of growth in the presence of disturbance, resource variability or the interaction of these variables should be competitively superior (Connolly & Wayne 1996).

Clipping has been shown to influence morphological performance in North American grasses (Butler & Briske 1988; Olson & Richards 1988). Unlike other studies, we detected no effects of clipping on *A. gerardii* tiller dynamics (Figure 4b). We did, however, find that clipped plants had greater rates of height growth than control plants; at the expense of growth in circumference. Nitrate availability did not influence *A. gerardii's* morphological development (Figure 4a). Clipping had no affect upon *P. virgatum* morphology (Figure 3b). These responses may be the result of long term grazing preferences by native large mammalian herbivores such as bison (Milchunas, Sala & Lauenroth 1988). *A. gerardii* is one of the most preferred forage species in the prairie and thus experiences heavy grazing throughout the growing season. It may have thus developed the capacity to respond quickly to the loss of aboveground tissue to avoid asymmetric competition for light with ungrazed neighbors (Connolly & Wayne 1996). Other species, such as *P. virgatum*, which are not grazed as heavily by bison appear less sensitive to clipping.

Biomass

Resource availability and the interaction of resources and disturbance had no affect upon total *A. gerardii* productivity. The clipping treatment, however, produced plants with reduced belowground and increased aboveground biomass. However, when final biomass was pooled with biomass removed during clipping treatments, total production for *A. gerardii* was similar between clipped and control plants (Figure 6). Thus, this species appeared, on average, to overcompensate for clipping (Brown & Allen 1989).

P. virgatum did not replace biomass lost as a result of clipping and thus did not compensate for grazing (Figure 5). At the end of the growing season, clipped ramets had less biomass than their unclipped counterparts. These responses are also opposite of those measured for *A. gerardii*. As biomass is an indication of the amount of space a species occupies at the end of the growing season and thus its competitive success (Lauenroth, Dodd & Simms 1978), *A. gerardii's* sensitivity to clipping provides support for the plant strategies hypothesis (Grime 1979). Resource availability did not influence *A. gerardii's* productivity, thus the assumption that competition is solely driven by resource levels (Tilman 1990) is not supported.

Conclusions

The responses of *A. gerardii* to clipping and resource availability lend support to the plant strategies hypothesis (Grime 1979). It may be, that as a preferred forage species, *A. gerardii* is continuously exposed to tissue loss and has thus developed the capacity to withstand this form of disturbance (McNaughton 1983). Because one of the best measures of competitive success in the tallgrass prairie is a species' ability to occupy space over time (Collins & Glenn 1988), *A. gerardii's* ability to compensate for tissue lost as a result of grazing may provide this species with a competitive advantage over other grasses (Wallace & Macko 1993). Similarly, *P. virgatum's* inability to replace tissue lost following grazing may put this species at a competitive disadvantage from asymmetric competition when grazed if its neighboring species have the ability to respond to such disturbances. However, it may actually be the competitively superior species when resources such as nitrogen become limited in the absence of a disturbance (i.e. the *resource ratio hypothesis*).

It appears that in a complex system, exposed to a host of disturbances and resource fluctuations, species do not uniformly respond within the assumptions of a single competition model. Species likely show unique strategies for surviving in such a dynamic system. A multiple scale approach is necessary for identifying the mechanisms of competition and the implications of competition for the tallgrass prairie (Lubchenco 1995).

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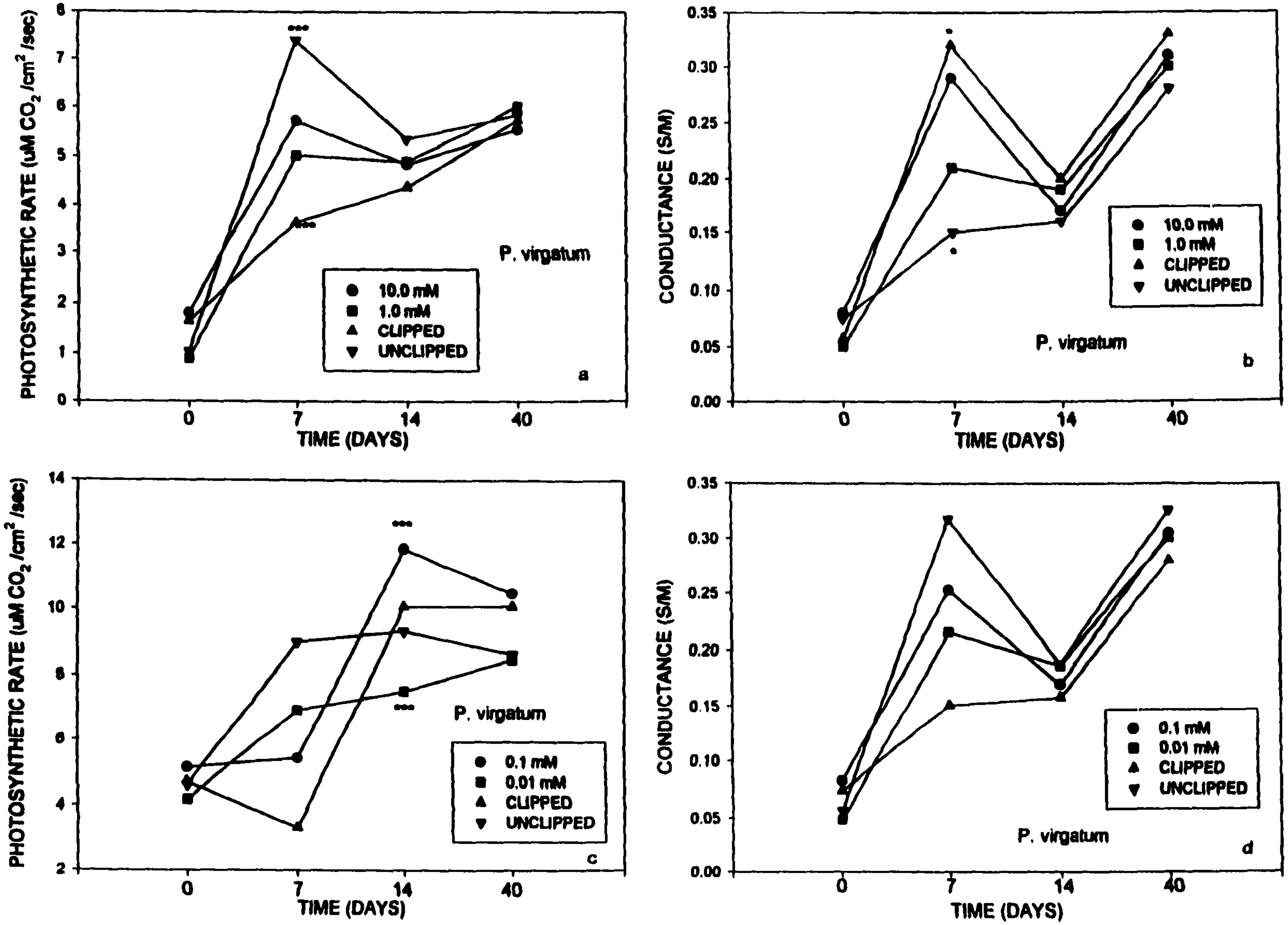
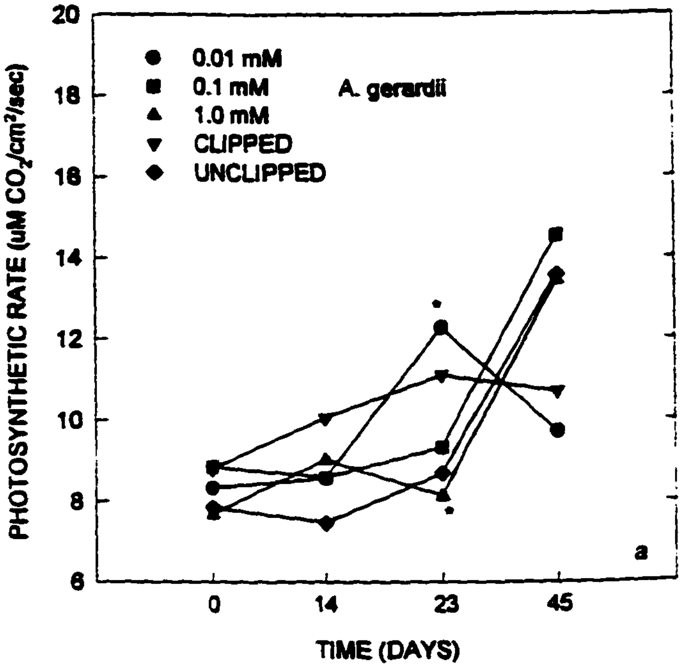
Legend Figure 1

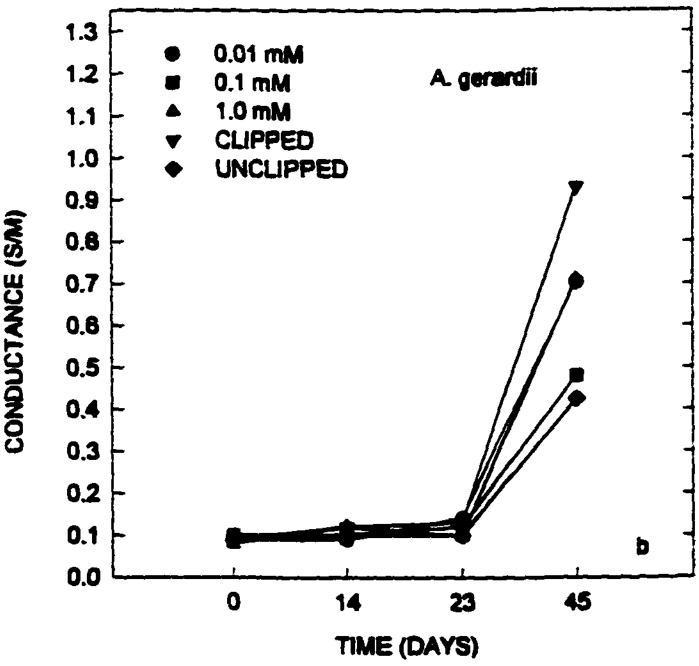
Average rates of photosynthesis and stomatal conductance for *P. virgatum* for Phase 1 (a, b) and Phase 2 (c, d) of Experiment 1. Significantly different treatment effects are indicated with asterisks (*). *=$p \leq 0.05$; **=$p \leq 0.01$; ***=$p \leq 0.001$. Time 0 are preclipping measurements. Days 7, 14, and 40 are days after clipping.


PHOTOSYNTHETIC RATE (uM CO$_2$ /cm^2 /sec)
0
1
2
3
4
5
6
7
8
***
***
P. virgatum
10.0 mM
1.0 mM
CLIPPED
UNCLIPPED
a
0
7
14
40
TIME (DAYS)
CONDUCTANCE (S/M)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
*
*
10.0 mM
1.0 mM
CLIPPED
UNCLIPPED
P. virgatum
b
0
7
14
40
TIME (DAYS)
PHOTOSYNTHETIC RATE (uM CO$_2$ /cm^2 /sec)
2
4
6
8
10
12
14
***
***
P. virgatum
0.1 mM
0.01 mM
CLIPPED
UNCLIPPED
c
0
7
14
40
TIME (DAYS)
CONDUCTANCE (S/M)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.1 mM
0.01 mM
CLIPPED
UNCLIPPED
P. virgatum
d
0
7
14
40
TIME (DAYS)

Legend Figure 2

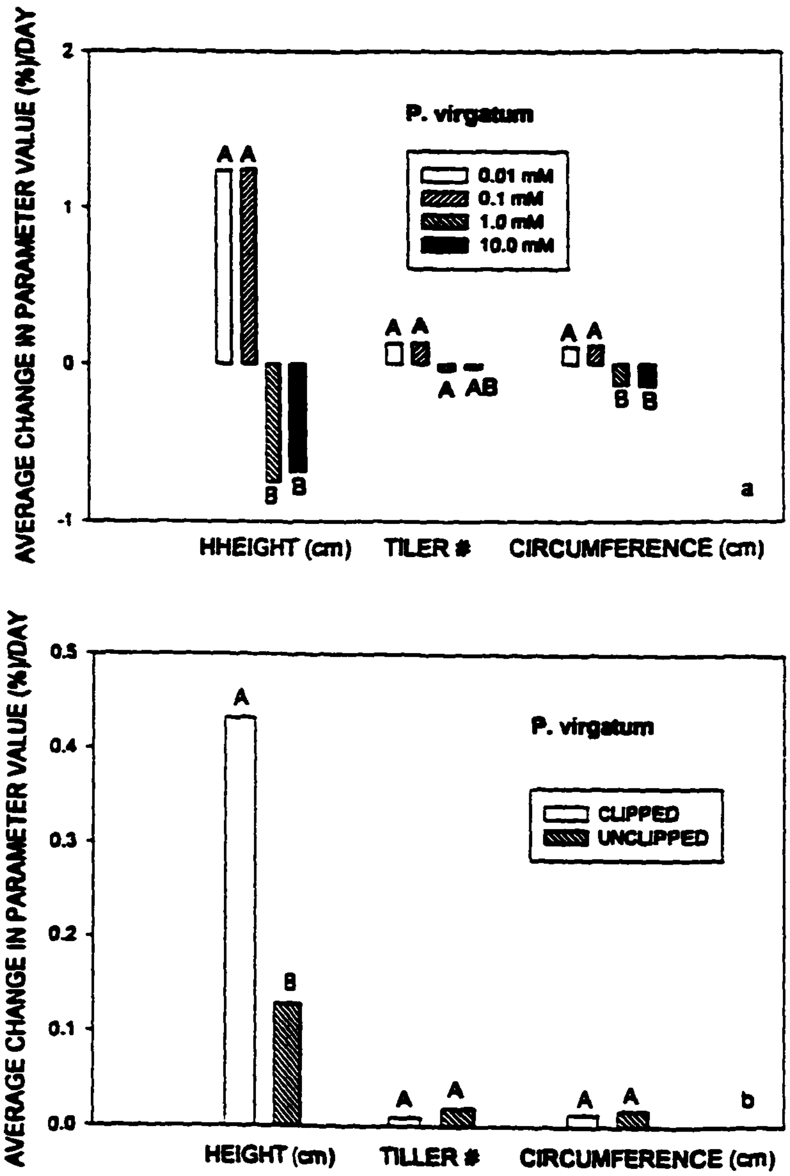
Average rates of photosynthesis (a) and stomatal conductance (b) for *A. gerardii*. Significant treatment effects are indicated with asterisks (*). *=$p \leq 0.05$.


20
18
16
14
12
10
8
6
PHOTOSYNTHETIC RATE (uM CO_2/cm^2/sec)
● 0.01 mM
■ 0.1 mM
▲ 1.0 mM
▼ CLIPPED
◆ UNCLIPPED
A. gerardii
*
*
a
0
14
23
45
TIME (DAYS)


1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
CONDUCTANCE (S/M)
● 0.01 mM
■ 0.1 mM
▲ 1.0 mM
▼ CLIPPED
◆ UNCLIPPED
A. gerardii
b
0
14
23
45
TIME (DAYS)

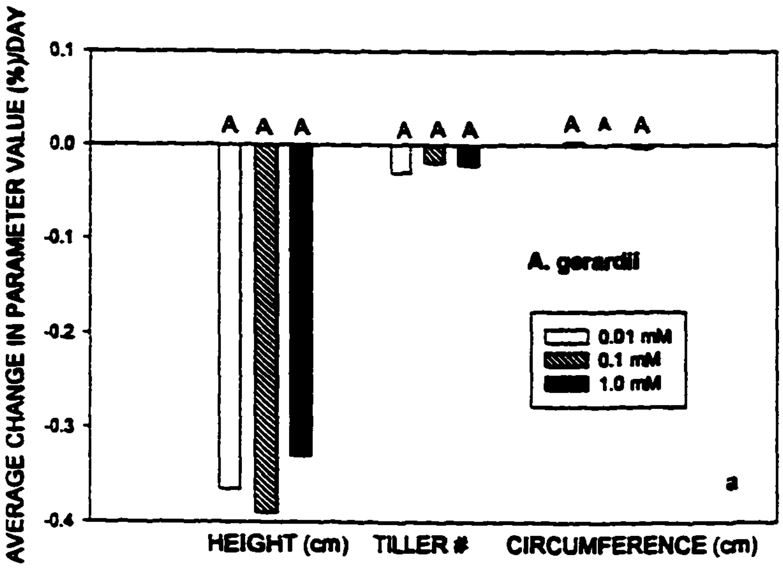
Legend Figure 3

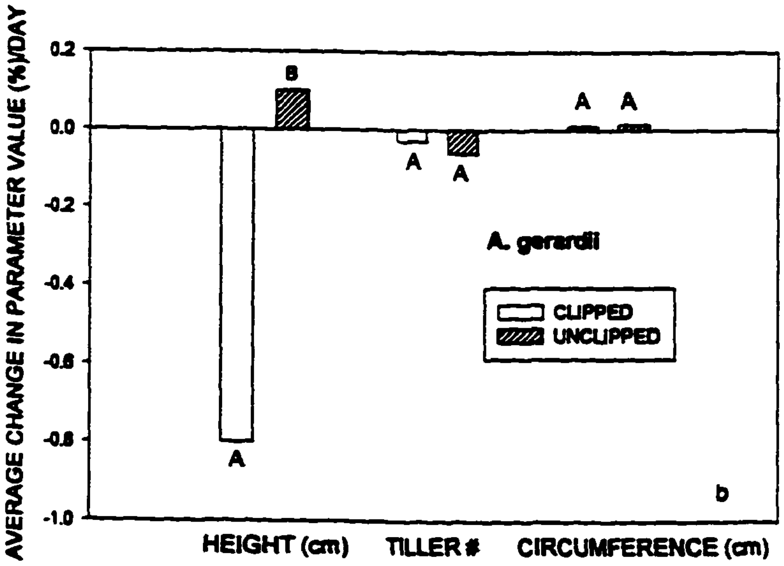
Average rates of growth (% change) per day for *P. virgatum*. Data for the nitrogen and clipping treatments are found in Figure 3a and b, respectively. Significant treatment effects on parameter means are indicated by different letters.


AVERAGE CHANGE IN PARAMETER VALUE (%)/DAY
2
1
0
-1
P. virgatum
0.01 mM
0.1 mM
1.0 mM
10.0 mM
A A
B B
A A
A AB
A A
B B
a
HHEIGHT (cm)
TILLER #
CIRCUMFERENCE (cm)
AVERAGE CHANGE IN PARAMETER VALUE (%)/DAY
0.5
0.4
0.3
0.2
0.1
0.0
P. virgatum
CLIPPED
UNCLIPPED
A
B
A A
A A
b
HEIGHT (cm)
TILLER #
CIRCUMFERENCE (cm)

Legend Figure 4

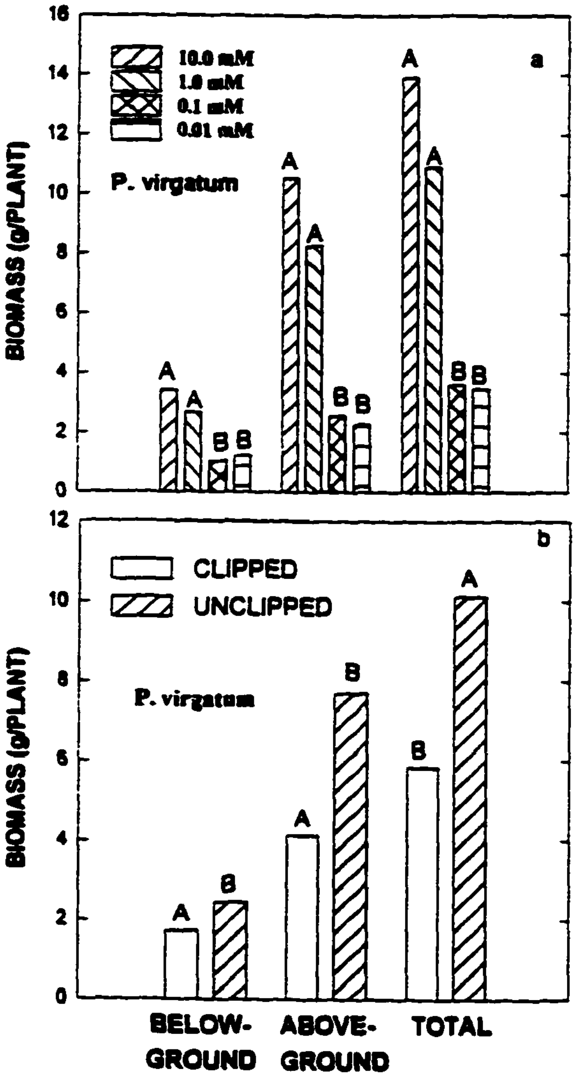
Figure 4. Average rates of growth (% change) per day for *A. gerardii*. Data for the nitrogen and clipping treatments are found in Figure 4a and b, respectively. Significant treatment effects on parameter means are indicated by different letters.


AVERAGE CHANGE IN PARAMETER VALUE (%)/DAY
0.1
0.0
-0.1
-0.2
-0.3
-0.4
A A A
A A A
A A A
A. gerardii
0.01 mM
0.1 mM
1.0 mM
a
HEIGHT (cm)
TILLER #
CIRCUMFERENCE (cm)


AVERAGE CHANGE IN PARAMETER VALUE (%)/DAY
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
B
A
A A
A A
A. gerardii
CLIPPED
UNCLIPPED
b
HEIGHT (cm)
TILLER #
CIRCUMFERENCE (cm)

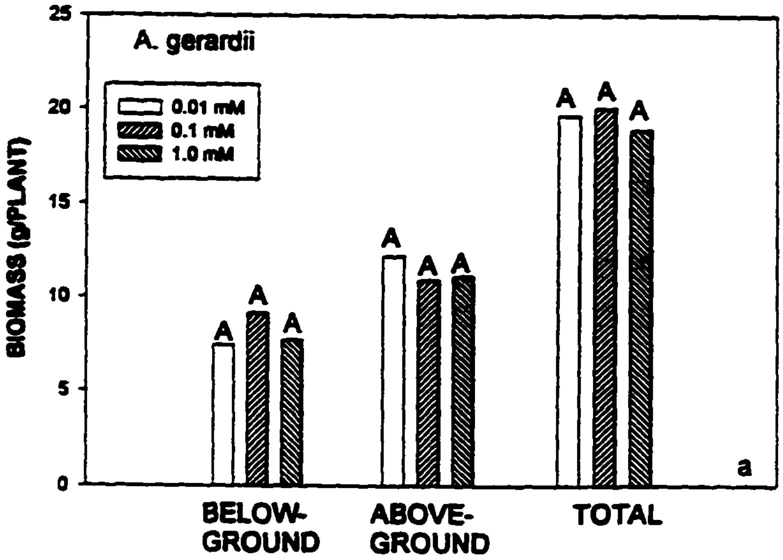
Legend Figure 5

Results of an ANOVA and Duncan's Means Comparison on average final belowground, aboveground, and total plant biomass (g/plant). Different letters represent significantly different means for each biomass component. Data for the nitrogen and clipping treatments are found in Figure 5a and b, respectively.

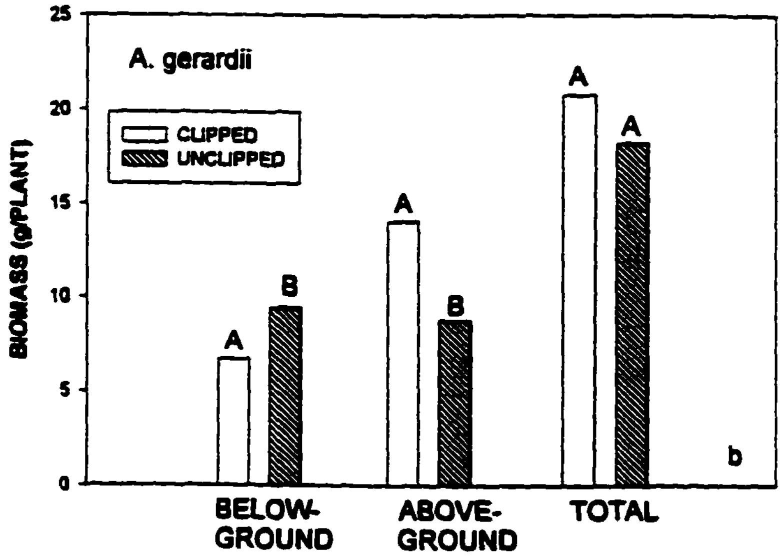

BIOMASS (g/PLANT)
16
14
12
10
8
6
4
2
0
10.0 mM
1.0 mM
0.1 mM
0.01 mM
P. virgatum
a
A
A
B
B
A
A
B
B
A
A
B
B
12
10
8
6
4
2
0
b
CLIPPED
UNCLIPPED
P. virgatum
BIOMASS (g/PLANT)
A
B
A
B
B
A
BELOW-GROUND
ABOVE-GROUND
TOTAL

Legend Figure 6

Figure 6. Results of an ANOVA and Duncan's Means Comparison on average final belowground, aboveground, and total plant biomass (g/plant). Different letters represent significantly different means for each biomass component. Data for the nitrogen and clipping treatments are found in Figure 6a and b, respectively.



A. gerardii
0.01 mM
0.1 mM
1.0 mM
BIOMASS (g/PLANT)
0
5
10
15
20
25
A
A
A
A
A
A
A
A
A
BELOW-GROUND
ABOVE-GROUND
TOTAL
a



A. gerardii
CLIPPED
UNCLIPPED
BIOMASS (g/PLANT)
0
5
10
15
20
25
A
B
A
B
A
A
BELOW-GROUND
ABOVE-GROUND
TOTAL
b

Chapter II

Implications for Plant Competition Theory: The Effects of Light, Nitrogen and Grazing on Tallgrass Prairie Community Structure

Abstract

The resource ratio (R*) and plant strategies or R-C-S models of plant competition were tested in a central Oklahoma grassland. The objectives were to determine the appropriateness of these two models for the tallgrass prairie and to further our understanding of the role of resource availability (light and nitrogen applied as simulated bovine urine) and disturbance (simulated bison grazing) in grassland community structure and function. We employed a fully crossed experimental design with light availability (shade), nitrogen (urine) and clipping as treatments. Community structure (species % cover), light intensity, productivity, and total plant and soil N content were measured.

Species diversity and richness declined with urine and shading. Clipping did not increase plot species diversity or richness. Results of detrended correspondence analysis show that clipping has the most pronounced affect upon community organization, collapsing plots in ordination space. Treatment interactions did not affect community structure. Forb N content was not affected by any treatment. Grasses, however, were strongly affected by clipping and urine application; both increasing grass N content. There is a strong negative correlation between soil N and grass N. Clipping significantly increased grass productivity. Urine and light did not increase plot or functional group biomass. Forb and grass productivity were greater in urine control plots than in urine plots, possibly due to gopher activity (mounding) in urine treated plots. The light*urine*clipping interaction was the only significant interaction (for grass productivity only).

Community structure data indicate that the *plant strategies model* is the most appropriate competition model for this system. Nitrogen dynamics and productivity also provide support for the *plant strategies model* of competition. Further long term studies manipulating resources and realistic disturbances with different temporal relationships are required to elucidate the appropriateness of these models in this system.

Keywords: Resource ratio hypothesis, Plant strategies, R-C-S, grassland, grassland community dynamics, tallgrass prairie productivity, bovine urine, gopher, Oklahoma.

Introduction

Competition has long been argued to be important in predicting plant species richness, distribution and productivity (e.g. Bonser & Reader 1995; Grace & Tilman 1990; Grime 1973, 1977, 1979; Keddy 1989; Tilman 1984, 1985, 1988, 1990; Tilman & Downing 1994; Wilson & Tilman 1991). However, two of the most commonly cited plant competition models, the *resource ratio hypothesis* (Tilman 1988, 1990) and the *plant strategies or R-C-S hypothesis* (Grime 1977, 1979) make several contrasting predictions and have yet to be validated in a system structured by both resource variability and disturbance (Keddy 1991; Gropp 1997; Gropp & Wallace, in prep.). Briefly, the *resource ratio hypothesis* asserts that the competitively superior species in a system will be the species with the lowest requirement for the most limiting vital resource. The *plant strategies hypothesis* predicts that the competitively superior species will have life history characteristics that enable it to acquire resources in the presence of mild to moderate disturbance (e.g. grazing). Not until the mechanisms of competition are understood in an empirical context, will it be possible to build successful predictive models of the dynamics of species richness and distribution in such systems (Bonser & Reader 1995; Keddy 1991).

The North American tallgrass prairie is a spatially and temporally dynamic system dominated by C_4 grasses (Collins

1992). A wide array of mostly C_3 forb species provide this system with its high species diversity (Collins & Glenn 1988; Collins & Wallace 1990; Steinauer & Collins 1995; Turner & Knapp 1996). Tallgrass prairie once occupied wide expanses of land in the eastern great plains, but is now limited to generally small remnants scattered throughout its former range (Axelrod 1985; Risser 1990; Risser *et al.* 1981). For successful management and conservation of these remnants, system dynamics must be understood.

Grassland plant community composition and productivity are regulated by a complex interaction between disturbances (e.g. grazing and fire) and limiting resources (e.g. nitrogen and soil moisture) (Collins & Glenn 1988; Collins & Wallace 1990; Milchunas, Sala & Lauenroth 1988; Steinauer & Collins 1995). Complex canopy and litter dynamics have been found to affect light availability; thereby influencing species interactions and productivity (Connant & Risser 1974; Knapp & Seastedt 1986). Light availability is altered by nitrogen (Wilson & Tilman 1991) and a number of disturbances, including large mammalian grazers such as bison. As grazers remove standing plant tissue, canopy dynamics change and light becomes more available for ungrazed individuals. In the case of bison, which preferentially graze grasses relative to forbs (Krueger 1986; Plumb & Dodd 1993), the quantity of light available for sub-canopy species (e.g. C_3 forbs) increases. Moreover, mega-herbivores influence the resource availability and patchiness of soil resources via urine and fecal deposition (Jaramillo & Detling 1992a; McNaughton 1983a; Stillwell 1983; Stillwell & Woodmansee 1981; Steinauer & Collins 1995). In addition to altering resource levels, grazers serve as a disturbance mechanism (e.g. grazing, wallowing, trampling and soil compaction) in the tallgrass prairie (Collins & Glenn 1988; Collins & Uno 1983; Collins & Wallace 1990; Gessaman & MacMahon 1984; Wallace 1987, 1990). Questions remain, however, as to how the interaction of resource availability and disturbance affect interspecific interactions that may dictate species richness, distribution, and productivity (Turner & Knapp 1996).

We conducted a field experiment in which two resources (light and nitrogen) were varied in the presence/absence of a disturbance (simulated bison grazing) with the following goals: 1) To test the *resource ratio* and *plant strategies* models of competition; 2) To further our understanding of graminoid and forb response to alterations of resource availability and disturbance, thereby increasing our understanding of community and ecosystem dynamics in this highly variable system.

If the *resource ratio hypothesis* (Tilman 1988, 1990) is appropriate for the tallgrass prairie, species diversity, richness and evenness should decline in shaded plots and in plots not augmented with nitrogen. The limited light and nitrogen in these plots should drive competitively inferior species from the plots. The *plant strategies hypothesis* predicts that competition increases with productivity and moderate disturbance (Grime 1977, 1979). Thus, if the *plant strategies hypothesis* is correct, species diversity, richness and evenness will decline in plots with both disturbance (clipping) and greater resource availability (urine addition and/or no shading). Productivity should increase in resource augmented plots. This, coupled with disturbance, should favor *'competitor'* species (e.g. C_4 grasses) at the expense of other species (e.g. C_3 forbs).

Materials and Methods

Study Area

Treatment plots were established in July, 1994 at Great Plains Apiaries Research Area (GPARA). Data were collected in 1995 and 1996. GPARA is a 145 hectare cattle ranch located near Washington, McClain County, Oklahoma (34° 58' N, 97° 31' W) and is managed by the University of Oklahoma for biological and meteorological research. The research area has been a working cattle ranch and farm since it was homesteaded in 1888 (E. Kessler, *personal communication*). The principal vegetation type at GPARA is tallgrass prairie (Risser et *al.* 1981).

The pastures have not been plowed and fire has been suppressed since 1973. Management practices prior to 1973 are not fully documented, however; for the past 23 years, 25 head of cattle (cow/calf) have been stocked at GPARA. The pasture in which this study was conducted has historically been utilized as a winter range for these cattle (E. Kessler, *personal communication*).

A MESONET (OMWD 1996) weather station is located on GPARA, approximately 500 meters from the research plots. MESONET records standard climate data hourly. Average annual precipitation at GPARA is 96.3 cm, with 61.2% of that occurring between April and September (OMWD 1996). Annual precipitation for 1995 was 79.8 cm, with 77.1% occurring during the growing season (OMWD 1996). In 1996, annual precipitation was near the historical average at 95.2 cm, with 83% occurring during the growing season (OMWD 1996). Maximum rainfall occurs in April and May, while July and August are generally dry (ca. 6.8% of annual precipitation, OMWD 1996). Historically, the mean daily growing season temperatures are 23.2°C/17°C (high/low) with maximum high temperatures of 35°C recorded in July and August. In 1995 and 1996 the mean daily growing season temperatures were 28.3°C/16.8°C and 22.4°C/17.6°C, respectively (OMWD 1996).

Experimental Design

A 1.5 m tall cross-bar fence was erected in the pasture to deny cattle access to the study plots. No discernable microclimatic effects of the fence were noted. When plots were established, no small mammal (e.g. gopher) activity was detected. By the second year of the experiment, however, gophers had colonized the surrounding area and gopher mounds were observed in several treatment plots.

Eighty 0.5 m^2 (square) plots were randomly located within the exclosure and marked with survey flags and metal poles. Each plot was randomly assigned to a combination of clipping, shade, and nitrogen treatments in a fully crossed experimental design. Half the plots were shaded using 50% shade cloth fastened 1 m aboveground to rebar poles in each corner of a plot. The other half remained unshaded. To reduce weathering, the cloth was removed from late September through April each year while the dominant C_4 grasses were dormant. To further affect resource availability, we altered soil N availability by applying 2 L of simulated bovine urine (equivalent to 50.9 g N/m^2, Day & Detling 1990a; Steinauer & Collins 1995; Stillwell 1983) to half the plots twice each year; once in late May and again in late July. Control plots received 2 L of deionized water at the time of urine application. Two liters/0.5 m^2 were applied because studies have shown this to be a realistic approximation of bison urine patch size (Day & Detling 1990a; Steinauer & Collins 1995; Stillwell 1983). Urine/water was slowly poured across the plot to prevent runoff and to allow it to soak into the soil. Bison grazing was mimicked by clipping all the vegetation in half the plots to 10 cm aboveground (Wallace 1990) twice each season (immediately prior to urine applications in late May and late July). Half of the plots remained unclipped. All clipped biomass was collected, dried at 60°C for 48 hours, and weighed. These weights were added to total aboveground biomass measures taken at the end of the experiment. Half of the plots remained unclipped.

Percent ground cover of individual grass and forb species was visually estimated in 5% cover classes prior to each clipping and urine application. When less than 5%, cover was estimated in 1% classes. Plants were identified to genera and, when possible, species. At the culmination of the experiment in September, 1996 all plots were clipped at ground level, living biomass was separated into forb and grass, dried at 60°C for 48 hours and weighed. Total plant N was determined for grass and forb samples (for samples with dried biomass greater than 3 g.) collected from each plot at the end of the experiment using the Dumas method (Ward Laboratories, Inc.). Individual species were not isolated for N determination. Thus, the N values reported for the grass and forb components of each plot represent the average N concentrations for these two functional groups on each plot. Soil samples were collected from 10 cm belowground in May 1995 and September 1996, from three randomly selected plots from each treatment. Samples were collected from the same plots at both times. All samples were sifted to remove root fragments, air dried in the laboratory, ground to 5 mm, and analyzed for total N (Ward Laboratories, Inc.).

Photosynthetically active radiation (PAR) was measured in each plot using an LI-189 light meter and wand sensor (Li-Cor, Corp., Lincoln, NE) at solar noon on June 29, 1996 and July 29, 1996. The sensor is one meter long and integrates a light reading over this distance. Because the sensor was longer than the diameter of the plot, half of the sensor was occluded. Thus, we were able to sample radiation intensity across the entire plot. Light measurements were taken at the soil surface (below canopy), and at 1 m aboveground (above canopy). The percent light penetration through the canopy was calculated as (light below canopy/light above canopy)*100. Light penetration measurements allowed us to separate the effects of the shade cloth from the actual amount of light available to plants within the canopy.

Data Analysis

Shannon-Weiner species diversity (H'), species richness (S) and evenness (E) were calculated using canopy cover data that was estimated visually for each plot (McCune & Mefford 1995). The effects of light intensity, urine addition and clipping on the above diversity parameters were analyzed with three-way analysis of variance (ANOVAs) for each sampling period (date). To identify temporal patterns of species and community assemblages, percent cover data for species and plots as they were affected by light, urine, and clipping were analyzed with repeated measures ANOVAs. Detrended correspondence analysis (DCA, McCune & Mefford 1995) was used to examine treatment effects at the level of the entire plant community. The DCA technique was selected because, unlike other ordination methods, it allows for the identification of relatively minor community gradients and does not force species into a fixed gradient and community type (Gauch 1982).

Treatment effects on plant productivity, light, and plant and soil nitrogen data were analyzed with three-way ANOVAs. Percent light penetration data were arcsine-square root transformed prior to statistical analysis (Zar 1984). Pearson's correlation coefficient was used to identify relationships between the nitrogen content of plant functional groups and soil nitrogen. All statistical data were considered significant when $P \leq 0.05$.

Results

Plant and Soil Nitrogen

While forb total % N at the end of the experiment was significantly greater than total % N for grasses, final forb % N content was not affected by light, clipping or urine treatments (Figure 7a). Grass N content at the end of the experiment was significantly increased by urine application and by clipping but was not affected by shade (Figure 7a).

The total N content of soil (parts per million, ppm) was not significantly different between treatments at the beginning of the experiment (May 1995, Figure 7b). At the culmination of the experiment, soil N content (ppm) had increased under ambient light (shade control). However, urine application and clipping decreased soil nitrogen. This pattern is the inverse of grass N levels. There were no significant interactions among treatments for final soil N content. Grass N content was negatively correlated to soil and forb N content (Table 1). Forb N content was not significantly correlated to soil nitrogen.

Productivity

Total plant biomass (forb and grass), including all material removed by clipping over the course of the experiment, was significantly increased by clipping and decreased by urine application (Figure 8a). Light and the interaction of treatments had no affect upon final plot biomass. Overall, the plots had significantly greater grass than forb biomass (ca. 4.5x; $F=180.73$, $p=0.0001$, $df=1$). Forb biomass was significantly less on the urine compared to water plots ($F=6.46$, $p=0.0132$, $df=1$). Though not significant, forb biomass was somewhat greater in full light and clipped plots compared to their respective treatments.

Treatment interactions had no affect upon final forb biomass. There was a significant three-way interaction of light*urine*clipping (df=1, F=4.85, *p*=0.0309) on final grass biomass. The greatest biomass was measured in the ambient light*urine*clipped plots (Figure 9a) while the shade*urine*no clipping plots had the least biomass (Figure 9a). Treatments that included clipping always had significantly greater biomass than their respective unclipped plots. Treatments that included urine applications tended to have less biomass than their respective water controls, with the exception of the shade*urine*clipping plots (Figure 9a).

The % biomass of each three-way treatment was calculated relative to ambient (control) conditions (Figure 9b). Forb biomass was generally decreased by treatments, while grass biomass was lower only in urine*unclipped plots (Figure 9b).

Light Availability

Average ambient light level during the first measurement was greater than during the July measurement. This can be partially attributed to the fact that July 29, 1996 was partially overcast. The clipping*urine interaction had no affect upon % light penetration through the canopy, regardless of sampling date (Table 2). However, the effects of other treatments and interactions changed over time. In

June, shade and water plots had greater % light penetration (69.7 and 73.3, respectively) than ambient light and urine plots (60.6 and 57.1, respectively). The interaction of light*water (74.4%), and shade*water (72.1%) had, on average, 18% more light penetrate the canopy than light*urine (46.8%) and shade*urine (67.3%) plots in June. The three way interaction of light*urine*clipping was significant at both sampling dates (June and July, Table 2), with % penetration decreasing due to the lower light level in July.

Community Structure

Species diversity (H'), richness (S) and evenness (E) were all affected by time (Table 3), demonstrating seasonal and inter-annual changes (Figure 11). While H' was significantly different for all three treatments at the beginning of the study (Figure 11a), only the urine treatment had a significant effect over time (Figure 11b), decreasing H'. Interestingly, clipping reduced plot species diversity and richness. Plot species richness (S) was also significantly different in each treatment in May 1995 (Figure 11c). However, by July 1996, S was no longer affected by clipping (Figure 11d). The light and urine treatments remained significantly different. However, the difference between water and urine plots was greatest, with urine treated plots having the lowest overall species richness. Species evenness (E) did change over time (Table 3), decreasing intra-annually. No significant reduction was measured interannually (data not shown). Other than time, treatments had no affect upon E (Table 3). The interaction of treatments had no affect upon any of these community structure indices (Table 3).

Detrended correspondence analysis (DCA) was employed to determine which treatment most thoroughly explained overall plant community organization. All treatments showed a degree of control over plot variance in May 1995 (Figure 12a-c). However, plots in the clipping treatment were most tightly clustered (Figure 12c) and had the least variability throughout the duration of the study (Table 4). The urine treatment tended to be the second most important regulator of community organization (Table 4). Light played an insignificant role in regulating plant community structure (Table 4).

Discussion

Plant and Soil Nitrogen Content

The results of this study support the general rule that C_3 forbs have a higher N content than C_4 grass species (Larcher 1979; Matson 1980). Though not significant, unclipped forbs receiving water had slightly greater N contents than those not receiving these treatments; the opposite pattern was measured, and was significant, for grasses. While shade did not influence apparent N uptake in grasses, urine and clipping both increased plant N content. This contrasts with Wilsey's (1996) study conducted on *Stipa* from Yellowstone National Park, in which clipping*urine did not increase grass N content. The increase in N content of grasses following urine and clipping treatments in this study may be due to the timing of treatments. In July, forb abundance decreases and community biomass is dominated by warm season grasses. Thus, these grasses have access to N applied early in the growing season, as well as late season (July) applications, with less potential competition from forb species. Additionally, studies have shown that plant acquisition of urine-N can be regulated by precipitation (Vallis & Gardener 1984), the frequency and timing of grazing (Ruess & McNaughton 1984; Sheehy *et al.* 1996), and the availability of other resources, such as CO_2 (Wilsey 1996).

Interestingly, N level in upper soil layers was actually lower on urine treated plots than on water controls. However, N levels were higher in grass tissues on urine treated plots. Steinauer (1995) found that N levels in upper soil layers in tallgrass prairie quickly returned to background levels following urine addition. He attributed this to leaching to deeper in the soil profile, volatization, or absorption by plants. In this study, it appears that grasses strongly absorbed added N while forbs were not able to take advantage of added nitrogen. That grasses were able to quickly absorb added N and reduce soil N levels provides support for Tilman's model. However, the fact that grass N acquisition is greater in the presence of a disturbance, such as clipping (Figure 8, and Ruess & McNaughton 1985), strongly supports the *plant strategies* model of competition (Grime 1977, 1979; Turkington, Klein & Conway 1993).

Productivity

Several of the studies that have investigated the interactive effects of nutrients and disturbance on grassland productivity and community structure have employed severe, "un-natural" disturbances, such as soil tilling (e.g. Wilson & Tilman 1991). It has been found that, in the presence of these extreme and "un-natural" disturbances, productivity does not increase. However, when more "natural" disturbances such as clipping to mimic moderate intensity grazing have been employed, productivity and community structure (Turkington *et al.* 1993) have increased or been altered, respectively. In this study, grasses in clipped plots overcompensated for tissue loss (Brown & Allen 1989; McNaughton 1983b; Ruess & McNaughton 1984; Wallace, McNaughton & Coughenour 1985) while forbs did not. Thus, grazing (clipping) played an important role in governing overall system productivity in this study (e.g. McNaughton

1983b, 1985). It has been proposed that species which overcompensate for herbivory are at a competitive advantage relative to neighboring non-compensating species (Wallace & Macko 1993). Our results support Wallace & Macko's (1993) hypothesis and provide additional support for Grime's (1977, 1979) hypothesis.

Moreover, because the clipping and urine treatment increased grass biomass relative to ambient conditions it might be said that these treatments are serving as system drivers (Lauenroth, Dodd & Simms 1978). Over time, if these treatments were continued, we would expect to see grass biomass continue to increase at the expense of forbs, eventually eliminating forbs from the plots (Lauenroth *et al.* 1978).

Grazing has been shown to significantly alter light limited processes (e.g. productivity) in the tallgrass prairie by reducing canopy complexity and litter accumulation (Knapp & Seastedt 1986). In this study, however, light availability (50% shade) had insignificant effects upon forb, and entire plot productivity. With respect to grass productivity, comparison of shade*clipped*(urine/water) shows that grasses, as a group, are able to acquire sufficient amounts of a limited resource (light) in the presence of a disturbance (clipping); providing further support for the *plant strategies hypothesis* (Grime 1977, 1979).

While several studies have shown that bovine urine and/or, urea, stimulates productivity (Day & Detling 1990a; Jaramillo & Detling 1992a, b; Ruess & McNaughton 1984; Steinauer & Collins 1995), our results, and others (Wilsey 1996), indicate urine is not necessarily stimulatory. In this study, both forbs and grasses had greater biomass in urine control (water) plots than in urine plots. Several hypotheses may explain this counter-intuitive response to N addition. This suppression of productivity was most probably the result of an increased gopher mounding in urine treated plots. Gopher mounds have been shown to greatly reduce plant productivity, with gophers attracted to high nutrient patches (Hobbs, Gulmon, Hobbs & Mooney 1988; Koide, Huenneke & Mooney 1987). Intense gopher mounding was observed on 17 urine treated plots by 1996, compared with only two on control plots. Gopher mounds reduced % plant cover (to < 10% on three plots) and plot productivity. Alternatively, late season (July) urine applications may have induced leaf water stress (Day & Detling 1990b; Wilsey 1996) consequently negatively impacting productivity (Steinauer & Collins 1995). It may be that productivity is more limited by water than N at certain times of the year and the timing of urination in relation to rainfall or soil water potential may be critical with respect to productivity.

Regardless, the fact that light did not increase plot biomass in the absence of a moderate disturbance (simulated bison grazing) suggests that the *plant strategies hypothesis* (Grime 1977, 1979; Turkington et *al.* 1993) may be more appropriate for the tallgrass prairie. However, Knapp & Seastedt (1986) have shown that productivity is light limited in unburned or ungrazed prairie and N is the limiting resource in burned or grazed prairie. Furthermore, the most competitive species tend to shift (i.e. from grasses to forbs) in response to these shifting resource availabilities. Thus, supporting Tilman's model. Although it could be argued that disturbances (e.g. fire and grazing) are responsible for the shift in resources and thus the *plant strategies* model is ultimately what explains plant competition in this system.

Community Structure

With the exception of species evenness, community diversity indices (H' and S) were affected by resource availability and disturbance. Resource treatments (shade and urine) reduced species diversity and richness over time, as forb % cover was reduced; supporting the assertions of the *resource ratio hypothesis* (Tilman 1988, 1990). Clipping late in the growing season (July), after many cool season (C_3) forb species had senesced and plots were dominated by C_4 grasses, did not affect community diversity.

Interestingly, the interaction of resource availability and disturbance, which would support the *plant strategies model*, was not significant. Though in other studies this interaction has affected community structure (Turkington *et al*. 1993).

Results of DCA do not support the above assertions. The clipping treatment had the most profound impact on community structure, significantly reducing plot variability (Table 4). The urine treatment was of secondary importance (Table 4). The shade treatment had insignificant effects on plot organization (Table 4). Thus, these results support Grime's (1977, 1979) *plant strategies model*.

Conclusions

Clipping and urine treatments play an important role in regulating productivity, strongly increasing grass productivity. It appears that, if these treatments were maintained over time, grass biomass would increase at the expense of forbs, eventually leading to the displacement of forbs from the plots (Lauenroth *et al*. 1978).

Aspects of this study support each model of plant competition. Species richness and diversity data provide support for Tilman's (1988, 1990) *resource ratio hypothesis*. Results of detrended correspondence analysis, however, show clipping (disturbance) to be the strongest regulator of plant community organization and thus support the *plant* *strategies model.* Physiological responses (i.e. plant N content and productivity) also support the *plant strategies model* (Grime 1977, 1979).

Additionally, urine patches appeared to profoundly alter the natural disturbance regime. Gophers appear to be attracted to these sites of high N availability, presumably because of the higher plant N content. Thus, urine patches may play a major role in regulating small scale community patch dynamics, resource cycling and productivity (Steinauer and Collins 1995).

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Legend Table 1

Correlation between total plant N (% of sample biomass) for forb and grass functional groups and for total soil N (ppm). Soil 1 samples were collected in May, 1995 and Soil 2 samples were collected in September, 1996. Values in each cell are the Pearson Correlation Coefficient, Prob > |R| under H_o, and Rho=0/number of observations.

	Forb N	Grass N	Soil 1	Soil 2
Forb N n=60		-0.32 0.02 57	0.076 0.75 20	0.14 0.57 20
Grass N n=73			-0.15 0.53 20	-0.65 0.002 20
Soil 1 n=24				0.10 0.63 24
Soil 2 n=24				

Legend Table 2

Results of a three-way ANOVA on % light penetration into the plant canopy (see methods for calculation). Data were arcsine square root transformed prior to analysis. Treatments: Lt=light/shade; U=urine/water; C=clip/unclipped.

Treatment	df	F value	Pr>F
June 29, 1996			
Lt	1	6.00	0.0167
U	1	18.65	0.0001
Lt*U	1	8.35	0.0051
C	1	1.64	0.205
Lt*C	1	0.5	0.4815
U*C	1	0.64	0.4249
Lt*U*C	1	7.19	0.0091
July 29, 1996			
Lt	1	1.24	0.2696
U	1	3.49	0.0656
Lt*U	1	1.17	0.2824
C	1	6.69	0.0117
Lt*C	1	4.5	0.0372
U*C	1	0.46	0.502
Lt*U*C	1	17.68	0.0001

Legend Table 3

Repeated measures analysis of variance for species diversity (H'), richness (S), and evenness (E). Treatments: T=time; L=light; C=clipping; U=urine. Parameters: S=species richness; E=species evenness; H'=Species diversity.

Parameter	Treatment	F	Pr > F
S	T	14.2253	0.0001
	T*L	0.5761	0.5649
	T*C	4.2382	0.0185
	T*U	12.3394	0.0001
	T*L*C	1.0829	0.3445
	T*L*U	0.6578	0.5213
	T*C*U	0.8617	0.4271
	T*L*C*U	0.4293	0.6528
E	T	4.0077	0.0228
	T*L	0.1926	0.8253
	T*C	0.4856	0.6175
	T*U	0.5091	0.6034
	T*L*C	0.0023	0.9977
	T*L*U	0.0001	0.9999
	T*C*U	1.05	0.3557
	T*L*C*U	0.4702	0.6269
H'	T	8.434	0.0001
	T*L	0.9578	0.4186
	T*C	2.6547	0.0566
	T*U	1.9452	0.1319
	T*L*C	0.7332	0.5363
	T*L*U	0.7383	0.5333
	T*C*U	1.1327	0.3431
	T*L*C*U	0.5747	0.6338

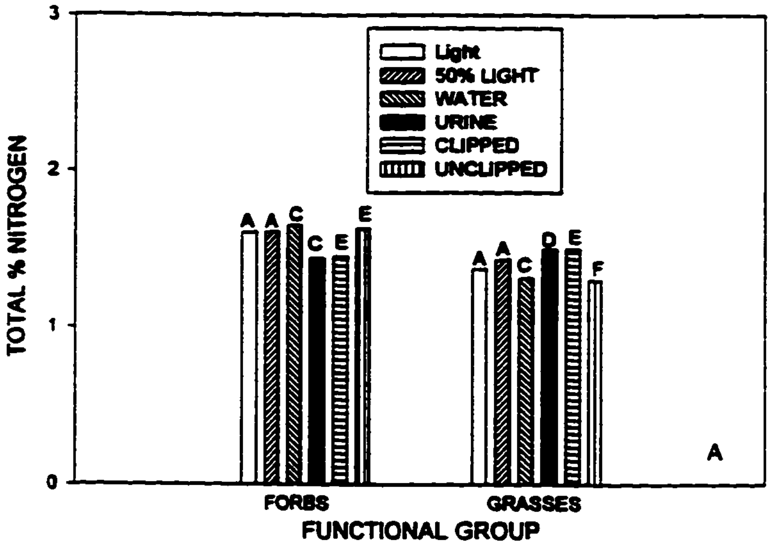
Legend Table 4

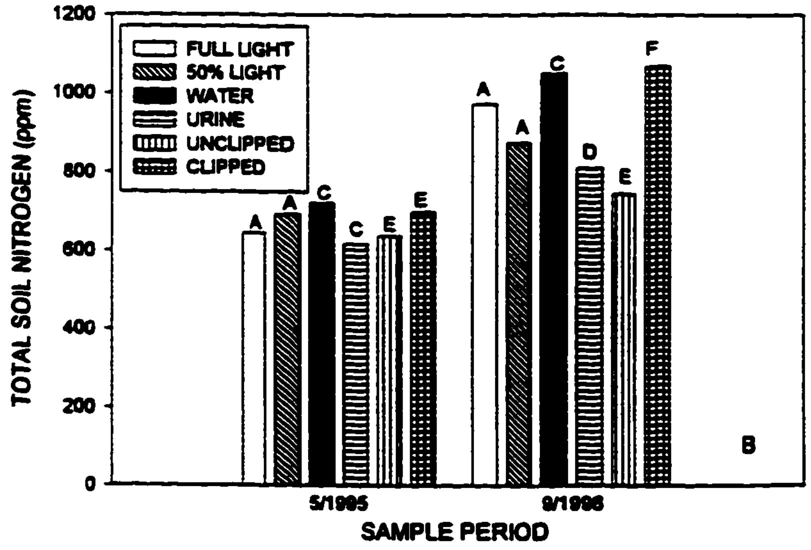
Mean (cv, coefficient of variation) for DCA axis scores for axes 1 and 2 for May 1995 and July 1996. Significant treatment effects upon means are indicated by different letters, as determined by Scheffe's means comparison test.

	Axis Scores			
	May 1995		July 1996	
Treatment	1	2	1	2
Shade	124(72)A	116(42)A	126(72)A	226(32)A
Light	130(81)A	127(45)A	136(83)A	186(130)A
Clipped	98(79)A	147(33)B	101(84)A	257(111)A
Unclipped	156(67)B	96(47)A	162(67)B	155(39)B
Urine	82(99)B	116(35)A	84(98)A	228(127)A
Water	173(52)A	127(50)A	179(54)B	184(39)A

Legend Figure 7

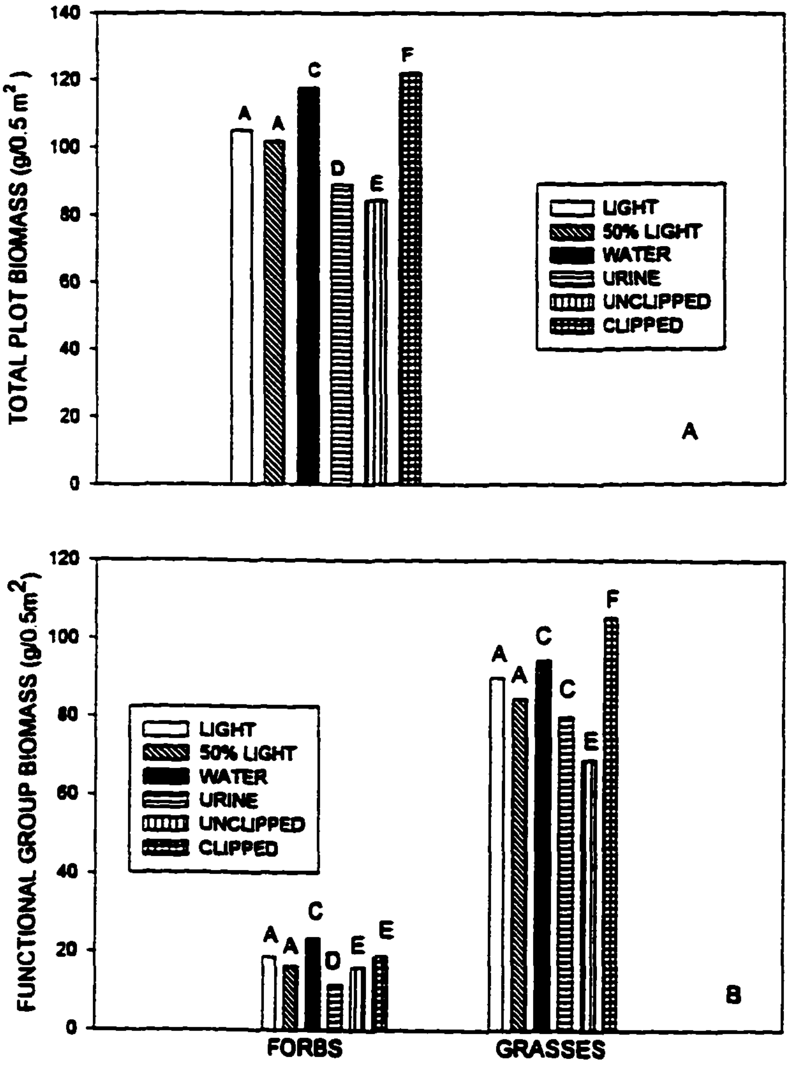
Mean total % plant nitrogen (A) content for functional groups exposed to each treatment as a main effect. No treatment interactions significantly ($p<0.05$) affected plant tissue nitrogen content. B) Mean total soil nitrogen content (ppm) at the beginning and end of the experiment as affected by each treatment as a main effect. Significantly different mean treatment values are indicated by different letters for each main effect, as determined by Duncan's Mean Comparison test.


TOTAL % NITROGEN
0
1
2
3
Light
50% LIGHT
WATER
URINE
CLIPPED
UNCLIPPED
A
A
C
C
E
E
A
A
C
D
E
F
FORBS
GRASSES
FUNCTIONAL GROUP
A


TOTAL SOIL NITROGEN (ppm)
0
200
400
600
800
1000
1200
FULL LIGHT
50% LIGHT
WATER
URINE
UNCLIPPED
CLIPPED
A
A
C
C
E
E
A
A
C
D
E
F
5/1995
9/1996
SAMPLE PERIOD
B

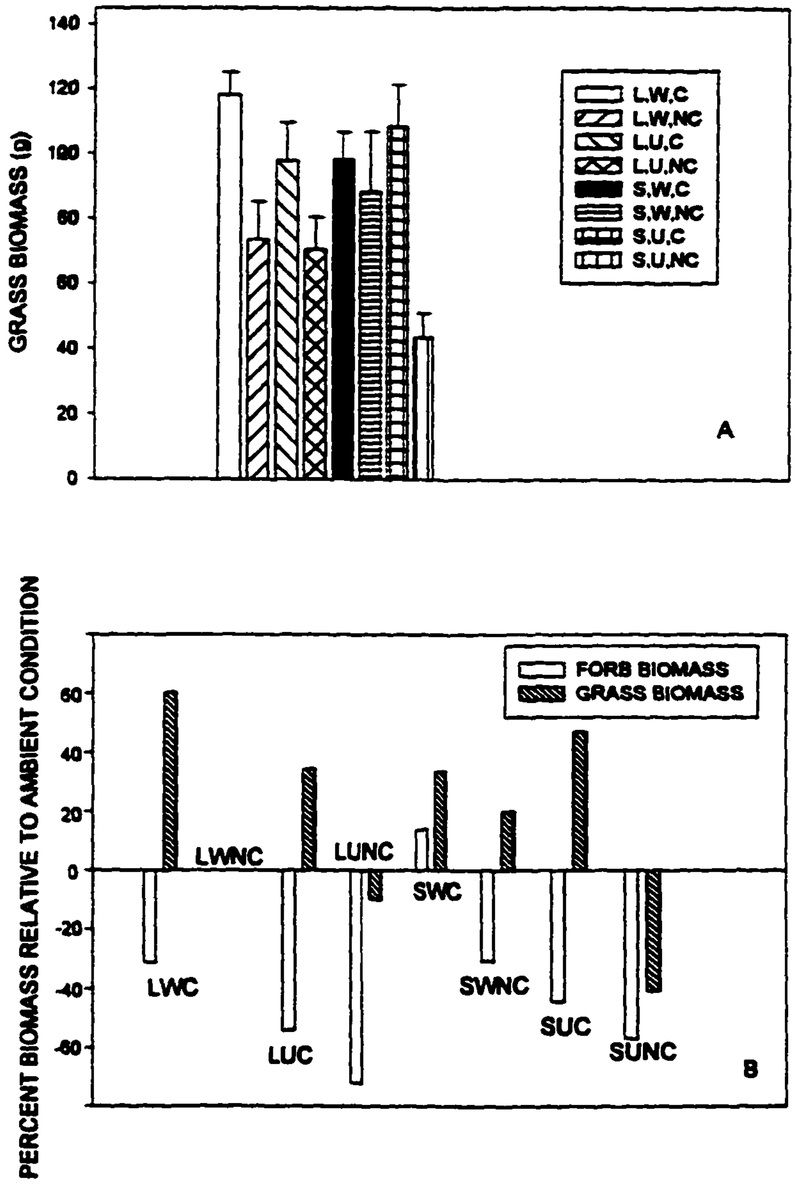
Legend Figure 8

Mean total plot biomass (g/0.5 m^2) (A) for the light, urine and clipping treatments. B) Mean functional group (forb and grass) biomass for the light, urine and clipping treatments. Clipped means include all biomass removed from plots as a result of the clipping treatment. Significantly different treatment effects are indicated by different letters.


TOTAL PLOT BIOMASS (g/0.5 m^2)
0
20
40
60
80
100
120
140
A
A
C
D
E
F
LIGHT
50% LIGHT
WATER
URINE
UNCLIPPED
CLIPPED
A
FUNCTIONAL GROUP BIOMASS (g/0.5m^2)
0
20
40
60
80
100
120
LIGHT
50% LIGHT
WATER
URINE
UNCLIPPED
CLIPPED
A
A
C
D
E
E
A
A
C
C
E
F
B
FORBS
GRASSES

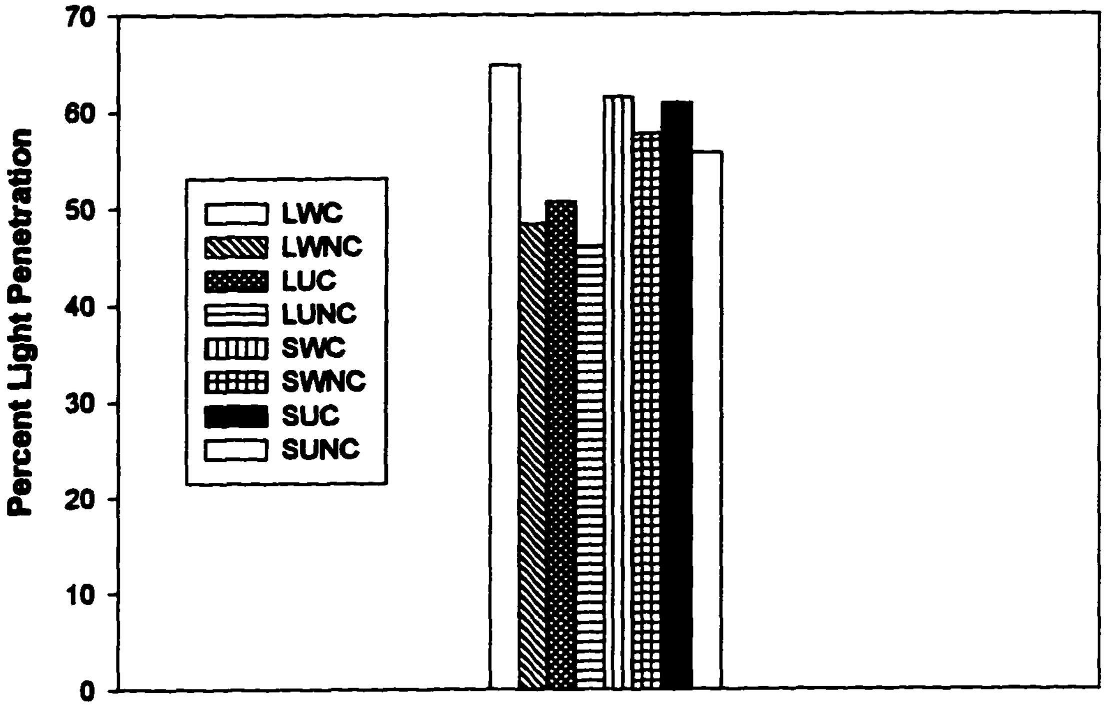
Legend Figure 9

a) Mean grass biomass for the three way treatment interactions. b) Percent grass and forb biomass for each three-way treatment interaction was calculated relative to the experimental control (ambient condition). The formula used was % biomass relative to ambient condition=[(treatment biomass-ambient condition biomass)/ambient condition biomass]*100. L=full light, S=50% light; U=urine, W=water; C=clipped, NC=unclipped. See text for F and *p* values.


GRASS BIOMASS (g)
0
20
40
60
80
100
120
140
L,W,C
L,W,NC
L,U,C
L,U,NC
S,W,C
S,W,NC
S,U,C
S,U,NC
A
PERCENT BIOMASS RELATIVE TO AMBIENT CONDITION
-60
-40
-20
0
20
40
60
FORB BIOMASS
GRASS BIOMASS
LWC
LWNC
LUC
LUNC
SWC
SWNC
SUC
SUNC
B

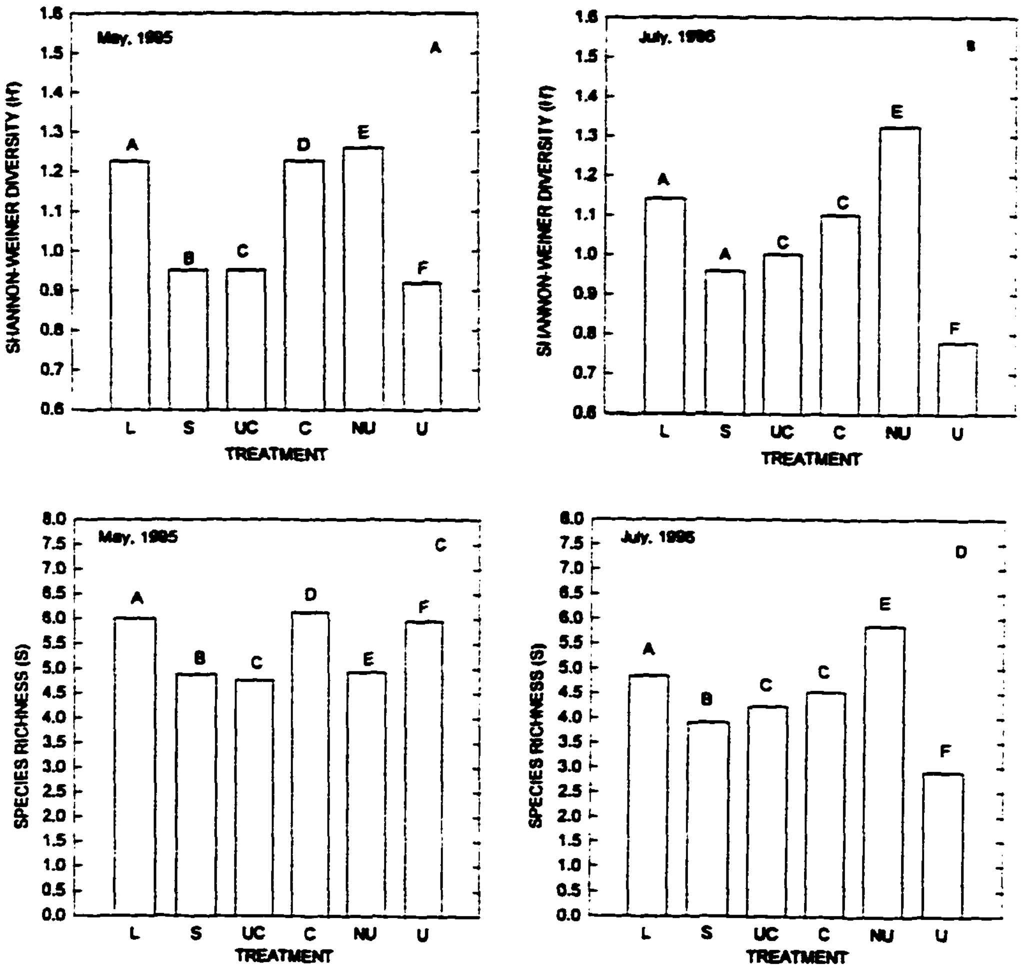
Legend Figure 10

Mean 1996 % light penetration to the base of the plant canopy.


Percent Light Penetration
0
10
20
30
40
50
60
70
LWC
LWNC
LUC
LUNC
SWC
SWNC
SUC
SUNC

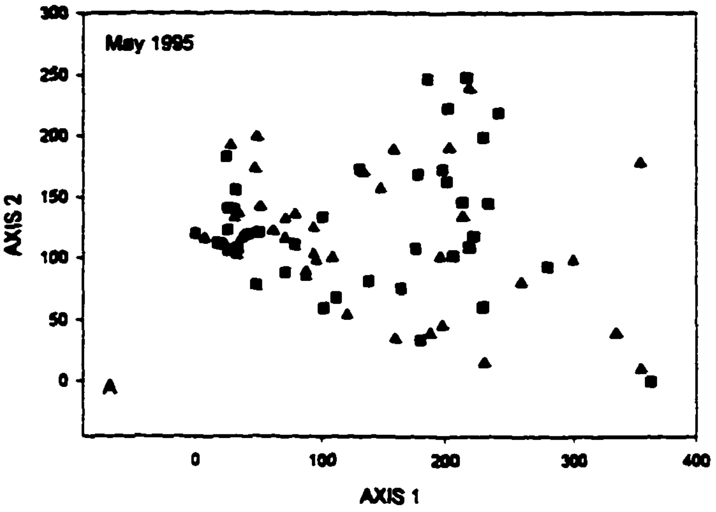
Legend Figure 11

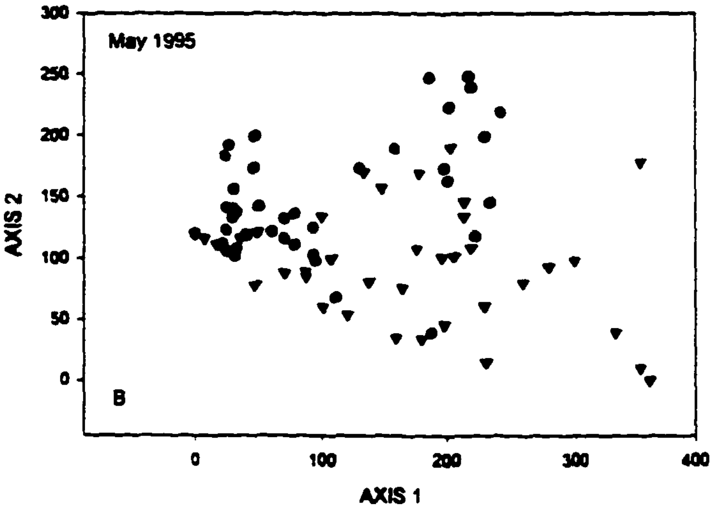
This figure includes Shannon-Weiner species diversity for A) May 1995, B) July 1996, and species richness (S) for C) May 1995, and D) July 1996. Species evenness (E) is not presented because it was not affected by treatments. Treatments: L=full light; S=50% light; UC=unclipped; C=clipped; NU=no urine; U=urine. Significantly different mean values are represented by different letters for the light, clipping and urine treatments as determined by general linear models ANOVAs and Duncan's Mean Comparison tests.


May, 1995
A
SHANNON-WEINER DIVERSITY (H')
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
A
B
C
D
E
F
L
S
UC
C
NU
U
TREATMENT
July, 1995
B
SHANNON-WEINER DIVERSITY (H')
A
A
C
C
E
F
L
S
UC
C
NU
U
TREATMENT
May, 1995
C
SPECIES RICHNESS (S)
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
A
B
C
D
E
F
L
S
UC
C
NU
U
TREATMENT
July, 1995
D
SPECIES RICHNESS (S)
A
B
C
C
E
F
L
S
UC
C
NU
U
TREATMENT

Legend Figure 12

Detrended correspondence analysis (DCA) on plots for May 1995 (A-C) and July 1996 (D-F). Legend: A) and D); inverted triangle=unclipped, circle=clipped; B) and E); triangle=50% light, square=ambient light; C) and F); X=water, O=urine.


May 1995
A
AXIS 2
300
250
200
150
100
50
0
AXIS 1
0
100
200
300
400


May 1995
B
AXIS 2
300
250
200
150
100
50
0
AXIS 1
0
100
200
300
400

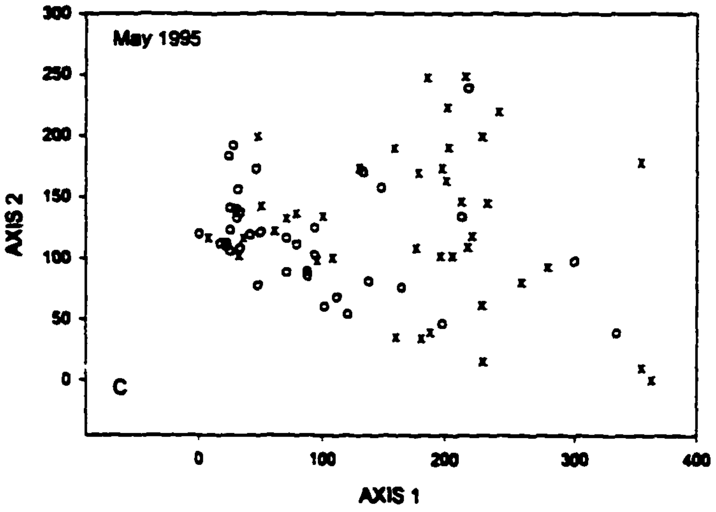
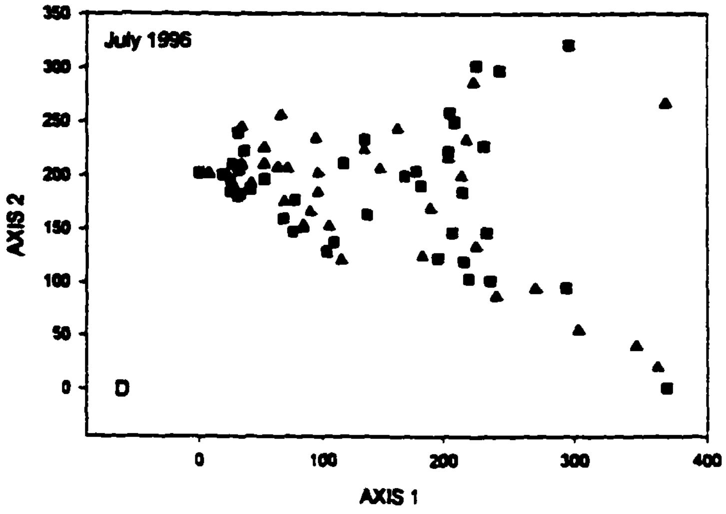
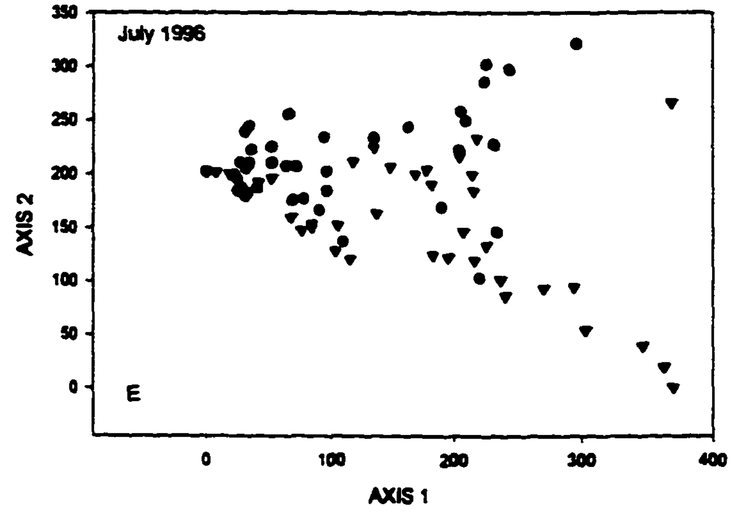
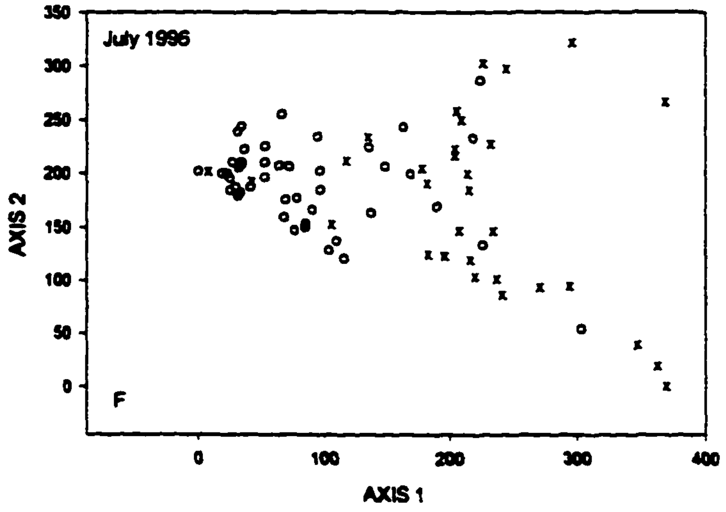

May 1995
C
AXIS 2
300
250
200
150
100
50
0
AXIS 1
0
100
200
300
400

Figure 12 Continued


July 1996
D
AXIS 2
350
300
250
200
150
100
50
0
0
100
200
300
400
AXIS 1


July 1996
E
AXIS 2
350
300
250
200
150
100
50
0
0
100
200
300
400
AXIS 1


July 1996
F
AXIS 2
350
300
250
200
150
100
50
0
0
100
200
300
400
AXIS 1