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The Ecophysiological Significance of Insectivory As well as Nitrogen and Phosphorus Availability To Sundew Nutrient Cycling, Growth, and Success

by

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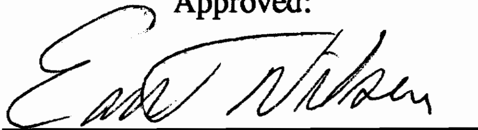

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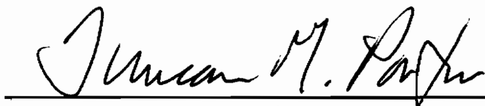

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by

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Abstract

The impact of nutrient addition on growth and nutrient accumulation in insectivorous plants was studied in field populations and greenhouse plantings. Drosera rotundifolia was studied in the field, and D. binata var. multifida and D. capensis were studied in long-established plantings in the greenhouse. In each case experiments were performed by exclosing insects and/or adding phosphorus and/or nitrogen to soil.

None of the species significantly benefitted from insect capture nutritionally or energetically in nutrient-poor or rich soils. Added nutrients to the soil or by foliar insect feeding decreased phosphorus retention in hibernacula by 50% (D. rotundifolia). Nutrient additions reduced D. rotundifolia vegetative growth in both N and P addition treatments. In addition, reproductive output (inflorescences) decreased flowering by 98% when N was added to the soil. Nutrient addition to soil increased nutrient concentration significantly in D. rotundifolia (N and P), and to a greater extent in D. capensis (N and P) and D. binata (P), and increased growth in D. capensis (N and P).

In natural settings insectivory was not found to be a significant source of nutrients for the species of *Drosera* studied. Larger subtropical species such as *D. capensis* and *D. binata* var. *multifida* are found in relatively richer (nutrient) soil than cool temperate species (*D. rotundifolia*) and are better able to utilize available nutrients in substrate by high absorption rates and luxury consumption.

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Table of Contents

Introduction.. 1

Field Experiment: Responses of Drosera rotundifolia to Manipulations of Insect Availability and Soil Nutrient Levels.. 6

Species and Site Description.................................. 6

Materials and Methods.. 11

Results.. 18

Discussion.. 48

Responses of Drosera capensis and D. binata var. multifida to Manipulations of Insect Availability and Soil Nutrient Levels.. 57

Species and Site Description.................................. 57

Materials and Methods.. 60

Results.. 66

Discussion.. 95

Conclusion.. 99

Literature Cited... 102

Vita... 105

List of Figures

1. Interior Bog, Giles County, Virginia, U.S.A.................... 10

2. Soil phosphorus concentration at Interior Bog.................. 21

3. Soil nitrogen (ammonium) concentration at Interior Bog.. 22

4. Soil nitrogen mineralization rates at Interior Bog.............. 23

5. PAR of three microsites at Interior Bog.......................... 26

6. Temperature of three microsites at Interior Bog................ 27

7. Vapor pressure of three microsites at Interior Bog............. 28

8. Mean leaf number of the five largest D. rotundifolia plants per plot at Interior Bog... 31

9. Mean rosette diameter of the five largest D. rotundifolia plants per plot at Interior Bog................................ 32

10. Mean D. rotundifolia density at Interior Bog.................... 33

11. Mean D. rotundifolia flower stalk density at Interior Bog.. 34

12. Mean leaf number per D. rotundifolia at Interior Bog......... 35

13. Mean D. rotundifolia rosette diameter at Interior Bog.. 36

14. Mean D. rotundifolia fresh weight at Interior Bog............ 38

15. Mean D. rotundifolia root to shoot ratio at

Interior Bog.. 39

16. Mean D. rotundifolia hibernaculum fresh weight at

Interior Bog.. 40

17. Phosphorus concentration of D. rotundifolia..................... 43

18. Phosphorus concentration of D. rotundifolia

hibernacula.. 44

19. Nitrogen concentration of D. rotundifolia......................... 45

20. Nitrogen concentration of D. rotundifolia

hibernacula.. 46

21. Soluble Salt concentration: Interior Bog soil..................... 54

22. Phosphorus retention index of D. rotundifolia................... 55

23. Nitrogen retention index of D. rotundifolia....................... 56

24. Soil phosphorus concentration in greenhouse..................... 69

25. Soil nitrogen (nitrate) concentration in greenhouse.............. 70

26. Soil nitrogen (ammonium) concentration in greenhouse.......... 71

27. Soil nitrogen mineralization rates in greenhouse.................. 72

28. PAR of two microsites in greenhouse.............................. 73

29. Temperature of two microsites in greenhouse..................... 74

30. Vapor pressure of two microsites in greenhouse.................. 75

31. Mean leaf number of the five largest D. capensis
plants per plot in greenhouse.................................... 77
32. Mean rosette diameter of five largest D. capensis
plants per plot in greenhouse.................................... 78
33. Mean biomass (dry weight) of D. capensis........................ 80
34. Mean phosphorus concentration of D. capensis.................. 83
35. Mean nitrogen concentration of D. capensis....................... 84
36. Mean total phosphorus of D. capensis............................. 85
37. Mean total nitrogen of D. capensis................................ 86
38. Mean biomass (dry weight) of D. binata var. multifida......... 88
39. Mean phosphorus concentration of D. binata var.
multifida.. 91
40. Mean nitrogen concentration of D. binata var.
multifida.. 92
41. Mean total phosphorus accumulation of D. binata
var. multifida... 93
42. Mean total nitrogen accumulation of D. binata var.
multifida.. 94

List of Tables

1. Drosera rotundifolia plants sampled from Interior Bog.......... 9

2. Soil nutrient levels before treatments; Interior Bog.............. 20

3. Soil nutrient levels after treatment; Interior Bog................. 20

4. Mean dry weight partioning for Drosera rotundifolia plants..... 41

5. Summary of hibernaculum dry weight and nutrient content for C and F treatments (D. rotundifolia)............ 47

6. Summary of flower dry weight and nutrient content for C and F treatments (D. rotundifolia).................... 47

7. Soil nutrient levels before treatments; greenhouse............... 68

8. Soil nutrient levels after treatments; greenhouse................. 68

9. Soil nutrient levels of sundew-supporting Australian bog soils.. 98

10. Soil nutrient levels of sundew-supporting North American bog soil.. 98

Introduction

Insectivorous plants have held the imaginations of researchers beginning at least three centuries before Charles Darwin (Juniper, et al. 1989). Fascinated with the oddity of plant movements, Darwin and other workers began investigating many aspects of physiological phenomena in insectivorous plants. His work with the sundew, Drosera rotundifolia, removed all doubts about the insectivorous properties of this, and other putative insectivorous species (Darwin 1875).

As a matter of definition, insectivorous plants must have these two characteristics, as proposed by Givnish, et al. (1984; p. 480): "1. It must be able to absorb nutrients from dead animals juxtaposed to its surfaces, and thereby gain some increment of fitness in terms of increased growth, chance of survival, pollen production, or seed set; and 2. The plant must have some unequivocal adaptation or resource allocation whose primary result is the active attraction, capture, and/or digestion of prey."

The morphological adaptations to attract and digest insects are thought to be a mechanism to mitigate the poor nutrient availability characteristics of bog soil. Two nutrients thought to be limiting are nitrogen (Chandler and Anderson 1976) and phosphorus (Weiss 1980). Although there have been at least a dozen studies of insectivorous plant nutrition (C. Darwin 1875; F. Darwin 1878; Roberts and Oosting 1958; Plummer 1963; Dore Swamy and Mohan Ram 1969, 1971; Chandler and Anderson 1976; Christenson 1976; Dixon, et al. 1980; Weiss, 1980; Watson, et al. 1982; Aldenius, et al. 1983; Wilson 1985), only one has examined the significance of insectivory in the field (Weiss 1980). Therefore, although it is well documented that several insectivorous

plant species benefit from the application of insects to foliar capture zones or suffer when insects are denied (Juniper, et al. 1989), these results have mainly been derived from laboratory or greenhouse experiments and not from field experiments. Insectivorous plants are often vulnerable to handling and changes in growing conditions, as well as natural stochastic or unknown random variabilities which can effect plant growth. For these reasons it seems that the most realistic and reliable approach to gain knowledge about insectivorous plant nutrition is to perform field experiments.

Nevertheless, much useful information has been accumulated from the myriad of studies that have been performed in the greenhouse or laboratory. The following discussion of insectivorous plant nutrition utilizes studies that represent those in which insectivory has been found to significantly contribute to growth. All of the following except one (Weiss 1980) were performed in the laboratory or greenhouse exclusively.

The first insectivorous plant nutrition study was done by Francis Darwin (1878). He found that Drosera rotundifolia plants which had been "starved" had fewer healthy leaves, flowers, and seeds than "fed" plants. Also, the former had a lower average plant biomass and lower mean seed weight as well when compared to the latter.

Chandler and Anderson (1976) demonstrated that Drosera whittakeri and D. binata, when grown on sand cultures with specific nutrient additions, grew optimally in the absence of inorganic salts, in the absence or in low concentrations of inorganic nitrogen, and in the absence of inorganic sulphate. They also found that the application of Drosophila melanogaster to leaf surfaces enhanced the growth of those plants in media

lacking inorganic nitrogen.

Using the pitcher plant Sarracenia flava in a field study, T.E. Weiss (1980) showed that phosphorus was the primary limiting nutrient supplied by insect capture, and not nitrogen as was previously believed.

These studies, as well as others, have led many to believe that insectivory is an important source of macronutrients for some species. It has also been proposed that insectivory can give an edge against other species in competition for space (Wilson, 1985).

Wilson (1985), in a pseudo-field study (plants were taken from their native site with soil and transplanted in beakers to a more convenient, but environmentally similar site) of Drosera intermedia, observed that plants grown with interspecific competitors present and denied insects accumulated less biomass than did those with no competitors with or without insects available, and also less than plants grown with competitors and insects available. This experiment was done in relatively nutrient-rich sites. Based on these studies, and for other reasons, Givnish, et al. (1984) have developed a cost/benefit model which generally relegates insectivorous plants to sunny, moist, nutrient-poor sites. These conditions are, in almost all cases, where insectivorous plants grow in nature. They point out three possible benefits of the insectivorous habit: 1) increased photosynthetic rate, 2) greater seed production rate or increased seed nutrients, and 3) heterotrophy as opposed to autotrophy. The last one has unequivocally been shown not to occur.

Other researchers have found insectivory to be a less important source of mineral

nutrition to the plant than was previously thought. Dore Swamy and Mohan Ram (1969, 1971) found that Utricularia plants grown from seed in axenic cultures could grow, flower, and successfully propagate in the absence of captured prey. They successfully demonstrated that these plants were not obligate insectivores. Nutrition from insectivory is required for completing the life cycle of an insectivorous plant.

Christensen (1976) found that accumulation of nitrogen and phosphorus in tissues of Sarracenia flava, when grown on complete nutrient media, was not significantly different regardless of insect availability. Insectivory was seemingly not important to plants when ample nutrients were available in the substrate.

For Drosera whittakeri, the same results as above were arrived at by Dixon, et al. (1980). The presence or absence of insects did not make any difference in biomass gain when plants were grown in complete salt solution.

In a similar study by Aldenius, et al. (1983) using Pinguicula vulgaris, insectivory was shown to be important to the plants, but not as important as nutrient concentrations in the substrate. Contrasting with Chandler and Anderson's study, optimal growth occurred in treatments in which insects were available, and a complete nutrient medium was present. These studies dismiss the myth that, because many insectivorous plants have a very limited root system, they cannot absorb the necessary nutrients via the roots.

In general, the importance of insectivory to plant nutrition and growth is not quite as clear cut as Darwin and others once believed. Perhaps to compete for space in their native habitats, insectivory provides an important nutrient source. Or, perhaps insectivory

is not an important source of nutrients for insectivorous plants at all. They may not be metabolically dependent upon large amounts of nutrients. Or, insectivory may be a mechanism to avoid herbivory and nutrient acquisition is secondary.

The main questions of this study are:

1. Does exposure to insects increase nutrient content and/or growth in Drosera species?
2. Will increased soil nutrient levels increase nutrient accumulation, growth, and reproduction in Drosera?
3. Is there any interaction between soil nutrient availability and insect availability on Drosera growth, nutrient accumulation, and reproduction?

My approach was to perform two experiments. One experiment was done in a bog containing a relatively homogeneous stand of Drosera rotundifolia, and the other in a greenhouse using established common plantings of Drosera capensis and D. binata var. multifida. In both experiments (1) insect exclosures were utilized to determine the effect of insect availability to plant growth and nutrition, and (2) soil augmentations were used to determine the effect of soil nutrient availability on plant growth and nutrition.

Field Experiment: Responses of Drosera rotundifolia To Manipulations of Insect Availability and Soil Nutrient Levels

Species and Site Description

Morphology and Phenology Drosera rotundifolia is a small herbaceous plant with a slender stem surrounded by a rosette of leaves (table 1). Flowering scapes arising out of leaf axils bear several perfect flowers. Flowers bloom in mid summer, open one per day, and are either insect pollinated or are selfed as they close in the evening. The root system is generally limited, consisting of a tap root and root hairs (Lloyd 1942).

Leaf blades are orbicular, wider than long, and covered with glandular trichomes which serve to trap and digest insects (Schnell 1976). Trichomes are of two types: stalked and sessile. Stalked glands are capable of movement due to an electrochemical action potential. The tissue of the stalked glands is derived from epidermal and parenchymatous origins and contains tracheids. Both types of glands secrete acidic polysaccharide mucilage which serves to entrap insects. After trapping various enzymatic exudates digest nonchitinous parts of the prey and the absorption of nutrients follows. Sessile glands are physiologically and morphologically similar to stalked glands, except that they are incapable of movements and are of epidermal origin only (Juniper, et al. 1989).

New leaves are produced in mid spring when the plant breaks dormancy. A flush of leaf growth occurs and leaf turnover rate is gradual and slow until autumn. At the onset of autumn, leaves and sometimes roots abscise, and a hibernaculum forms (Swales 1975).

Habitat and Range Drosera rotundifolia is found throughout the northern hemisphere, and in North America it ranges from the southern Appalachians to the Canadian Northwest Provinces and west to California and Alaska (Swales 1975, Schnell 1976). Even though D. rotundifolia has been collected in various habitats such as rotting logs, sand dunes, stream margins, and abandoned pasture land, it is most commonly found in acidic northern peat bogs (Swales 1975). These peatlands are typified by the presence of Sphagnum, or other acidophilic mosses, little or no tree canopy cover, and a large accumulation of organic matter (Mitsch and Gosselink 1986). Sundews often form homogeneous stands on the surface of the Sphagnum, dominating the herbaceous layer of the vascular vegetation.

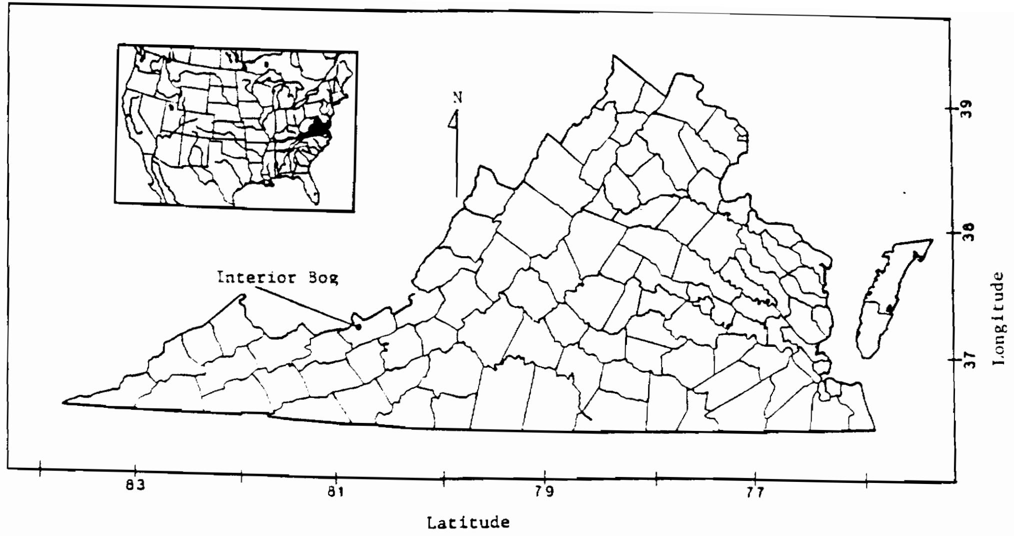
The Study Site

The study site (longitude 80° 36' 00" and latitude 37° 22' 30") was located in northern Giles County, Virginia, U.S.A., in Jefferson National Forest (fig. 1). This particular bog is one of the Interior Bogs, a series of peatlands located at the foot of Big Mountain. The elevation of these bogs is 762 m and the climate of this area can be categorized as cool temperate. The study site bog is roughly elliptical in shape and

occupies an area of about .053 h. The bog is kept in an early secondary successional stage by periodic human removal of Osmunda, Alnus, and other shade producing perennials. As a result, there is a proliferation of Drosera and other heliophytic bog endemics. At this site there is a relatively homogeneous stand of D. rotundifolia. A footpath running through the middle of the bog has compacted the peat and forms a very slow flowing small stream, which empties into a drainage pipe flowing under a road bordering one edge of the study area. The study site was bounded by woodland on three sides and an alder thicket and road on its northern long side.

Table 1. <u>Drosera rotundifolia</u> plants sampled from Interior Bog (Non experimental plants). August 10, 1989.

Leaf number	Rosette Diameter (mm)	Fresh Weight (Dry Weight)(mg)
8	93	414
8	71	202
7	64	251
5	44	74
5	40	83
7	53	163
12	87	319
9	81	641
7	63	125
6	81	189
6	80	313
6	102	593
7	72	364
13	71	693
mean 7.6	71.6	316 (40.3)



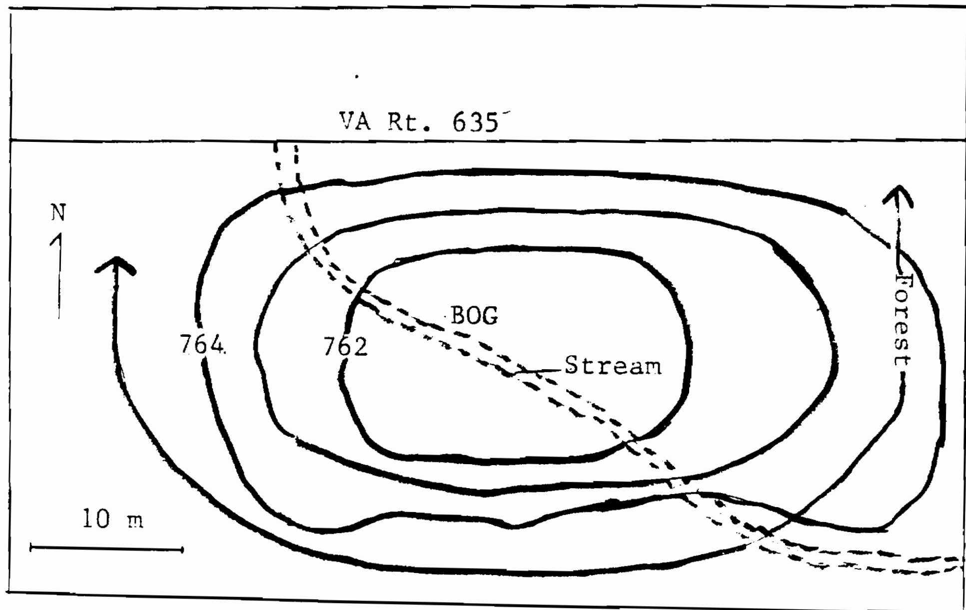


Figure 1: Interior Bog, Giles County, Virginia, U.S.A.

Materials and Methods

Design

The basic design of the experiment is a four-way balanced factorial layout, with the factors being:

1) The presence or absence of complete insect exclosures: Both complete and incomplete insect exclosures (also called partial exclosures or unexclosed plots) had an A-frame made of cpvc pipe and a wooden dowel rod. All materials were light-colored in order to maximize brightness inside the exclosure. Mosquito netting was used as a covering for both designs. Complete exclosure frames were entirely covered with about 10 cm of overhang present at the bottom of the structure. The overhanging fabric was tucked into the substrate to exclude most crawling as well as all flying insects. Incomplete exclosures were made the same way as the others, but fabric terminated approximately 10 cm above the ground surface. Complete exclosures were located along one side of a small stream/footpath and partial exclosures were placed on the other side. This placement was selected to minimize damage to this vulnerable plant community and to represent the variability of bog topography. The structures were placed in rows, spaced as far apart as possible (usually > 2 m), and where sundews were observed to be growing. Each structure occupied 2/3 m^2 of ground area.

2) Blocks: Slight differences in soil and vegetation characteristics were observed the summer before this experiment was set up, and so another replication of the basic experiment was performed in tandem. Five complete exclosures (with nutrient treatments

C, F, P, N, NP) and five incomplete exclosures (with nutrient treatments C, F, P, N, NP) constituted a block. There were two blocks with 10 replications per block.

3) Nutrient treatments: There were five nutrient treatments with four replications per treatment. Five nutrient groups within both complete and partial exclosures were set up randomly within blocks at the beginning of the experiment during the first week of May. They were:

a) Nitrogen addition --(N) 113 g of nitrogen was applied to each N plot in the form of 40-0-0 Osmocote slow release urea fertilizer. It was broadcast evenly over the surface of the soil, being careful to avoid direct application to sundew leaves.

b) Phosphorus addition-- (P) 130 g of phosphorus was applied per P plot in the form of 0-46-0 Super-triple-phosphate. It was applied in a like manner as nitrogen. As this was not a slow release fertilizer, all plots were monitored once a month by soil tests.

c) Nitrogen and phosphorus addition-- (NP) This treatment was a combination of the first two treatments, totalling 243 g of nutrients. The rates for all nutrient additions are similar to those applied by Chandler and Anderson (1976) and Dore Swamy and Mohan Ram (1969).

d) Foliar insect feeding-- (F) Once a month, from June to August, one Drosophila melanagaster was placed on a leaf of each plant in the F treatment.

e) Control--(C) No nutrient manipulations or feedings were done on this group.

4) Time: Four types of phenological measurements of plant growth or success were taken once a month for June, July, and August. Time is not a factor for biomass measurements and plant tissue nutrient analyses, since there was only one destructive harvest in August, and hibernaculum harvest in October.

Abiotic Measurements

Soil Nutrient Concentrations

In March, 1989, random surface layers (10 cm depth) were sampled throughout the bog as an assay of pretreatment conditions. Monthly samples were taken (July through September) from the periphery of each plot, being sure not to disturb any experimental plants. These samples were then air-dried on wax paper, and sent to Virginia Tech's soil testing laboratory where pH, phosphorus, nitrate, and other macronutrient concentrations were obtained, except for ammonium.

After soil was air-dried, ammonium was extracted using 10 ml 2 M KCl. One gram of soil was weighed out from each plot and 10 ml KCl added. The slurry was shaken for one hour and filtered using Whatman #1 filter paper. The filtrate was frozen in a snap-top vial until analysis could take place. Analysis was done using an Orion millivolt meter with a 95-01 ammonia electrode. To each sample 0.1 ml of 10 M NaOH was added to increase the pH of the filtrate and convert ammonium to ammonia so it could be measured by the electrode (Page, et al. 1982). Actual concentration in the soil

is obtained by constructing a standard curve using known ammonium concentrations and back-calculating. The final ammonium concentration refers to air-dried soil.

To obtain a better index of potentially available nitrogen in the various treatments anaerobic incubations were performed. During the incubation ammonifying bacteria convert nitrogen in organic matter to ammonium (Page, et al. 1982; Pearcy, et al. 1989). This procedure, therefore, yields a long-term availability index of soil nitrogen. One gram of air-dried soil from each sample was placed in a small screw-top glass vial. The vial was then filled to the top, leaving no air bubbles in the vial. Incubation at 40° C was done for one week. The soil--water mixture was then quantitatively transferred using 3 M KCl until the soil--water--KCl slurry weighed 11 g. This approximately yields a 10:1 2 M KCl to soil ratio. The extract is shaken and filtered as described previously and frozen until analysis of total ammonium by techniques described previously.

Microclimate

Microclimate of a complete exclosure, an incomplete exclosure, and a plot in which there was no artificial cover, was measured on August 9, 1989. I chose plots that were close to each other and towards the center of the bog to ascertain whether there were microclimatic differences due to the presence of the experimental structures. The following factors were measured: air temperature, soil temperature, leaf temperature, relative humidity, and photosynthetically active radiance (PAR). Measurements were taken every minute and averaged every 15 minutes, beginning at 7:30 A.M. and ending

at 7:00 P.M. using either a Campbell Scientific CR21 or 21X micrologger.

All temperatures were measured using copper/constantan thermocouples. The air thermocouple was shaded and placed at plant level. The soil thermocouple was placed in the root zone (5 cm below the soil surface), and the leaf thermocouple was placed within a randomly selected D. rotundifolia leaf.

Relative humidity was measured in the shade at plant level using either a Campbell XN217, 207, or 201 relative humidity sensor. Relative humidity and air temperature were used to calculate vapor pressure.

PAR was measured using a Li-Cor quantum sensor set at soil level and parallel with the soil surface.

Plant Measurements

Phenology

The flower and density data were analyzed with a 3 way ANOVA since there was only one observation per plot per time period, so the effect of replication was ignored to get a better estimation of the main treatment effects. Leaf numbers and rosette diameters were analyzed using a 4 way ANOVA. All results discussed are the results of multiple comparisons using Fisher's protected LSD at the .05 level (Zar 1974).

The measurements taken were leaf numbers, rosette diameters, flower stalk numbers, and plant density. For each month, the five largest sundews were determined. The number of leaves and the maximum rosette diameter of each plant were measured.

Because of the difficulty of counting each sundew in a 2/3 m^2 area, a subplot under each structure was established to monitor plant density. A circular string enclosing 374 cm^2 of ground area was randomly placed in the plot. The number of flower stalks and the number of plants occurring within the subplot were counted each month.

Biomass

Biomass measurements were analyzed using a two way ANOVA, ignoring the blocking factor in the model to get a better estimate of the main effects. Multiple comparisons were performed using Fisher's protected LSD at $\alpha = .05$ (Zar 1974).

In August clumps of plants within subplots (half of the subplot area) were harvested yielding a minimum of 10 plants per plot. All plants within a particular clump were harvested regardless of size. Individuals were partitioned according to organ type (shoots {stems and leaves}, roots, and flowers {including scapes and seeds}), and fresh weights recorded. Samples were dried at 40° C for two days, and dry weights were taken for bulked samples partitioned by organ and plot. Because of the small mass of individual organs when dried, only bulked weights could be taken. Dried samples were stored in air-tight plastic vials until nutrient analysis could be performed.

Another harvest was done at the onset of die-back in October. At that time, the plants primarily consisted of hibernacula and floral parts. Plants were similarly weighed, but partitioned by vegetative parts and reproductive parts. They were dried and stored the same way as those described above.

Plant Tissue Nutrient Analyses

Nutrient measurements were analyzed using a two way ANOVA, ignoring the blocking factor in the model to get a better estimate of the main effects. Multiple comparisons were performed using Fisher's protected LSD at $\alpha = .05$ (Zar 1974).

Nitrogen concentrations in plant tissues were obtained by using Kjeldahl digestions on a Kjeltec Auto 1030 analyzer according to methods outlined by Chapman (1976).

Phosphorus concentrations were determined colorimetrically using a Gilford spectrophotometer according to the modified Fiske and Subbarrow method (Kabut and Mayer 1948).

Because of the small amount of tissue obtainable from these minuscule plants, samples had to be bulked. However, when this was done, nearly all of the available tissue was used, thus yielding reliable measurements of nutrient concentrations.

Results

Abiotic Conditions

Soil

Soil nutrient levels changed negligibly in plots not receiving nitrogen or phosphorus (tables 2 and 3), so cross-contamination did not occur from nutrient applications. Phosphorus concentration increased as a result of phosphorus applications (treatments P and NP) about ten-fold. Phosphorus levels did not change significantly ($\alpha = .05$) during the course of the growing season for any treatments (fig. 2). Nitrogen applications (treatments N and NP) similarly affected soil nitrogen status. Nearly all of inorganic nitrogen was available as ammonium. Soil nitrogen levels in the foliar feeding treatment did increase slightly, however. There also existed large fluctuations over time in treatments F, N, and NP. This was probably due to undissolved osmocote residue in soil samples, and possibly to some contamination from N and NP treatments into the F treatment (fig. 3). Nitrogen levels did not rise sharply until August. Either fertilizer did not release until then, or a measurement error occurred. Nitrogen mineralization rates were largely unaffected by added nutrients except for the NP treatment (fig 4). It may be that the nitrogen mineralization microorganisms are limited by phosphorus. Therefore, there was a higher nitrogen supply in the NP treatment than in N even though they received the same nitrogen fertilization rates. It is clear from these results that more P and N was available for assimilation in fertilized treatments, while unfertilized plots were not appreciably affected by fertilization. The rates of fertilization of nitrogen and

phosphorus that occurred are comparable to very fertile forest or an agronomic field (Vitousek, et al. 1982; Pearcy, et al. 1989).

Table 2. Soil nutrient levels before treatments; Interior Bog, Va. (March, 1989).

Sample	pH	P (ppm)	K (ppm)	NO_3-N (ppm)	NH_4-N (ppm)
1	5.1	3	26	3	22
2	5.0	2	14	3	22
3	4.9	1	20	3	20
4	4.7	1	31	3	20

Table 3. Soil nutrient levels after treatment; Interior Bog, Va. (July, 1989). U= Unexclosed, E= Exclosed, C= no added nutrients, F= Foliar insect application, P= Phosphorus added, N= Nitrogen added, NP= Nitrogen and Phosphorus added.

Treatment	pH	P (ppm)	K (ppm)	NO_3-N (ppm)	NH_4-N (ppm)
U-C	4.9	5	23	3	17
U-C	4.8	5	15	3	5
E-C	4.5	1	12	3	9
E-C	4.5	1	15	3	5
U-F	5.0	5	34	3	19
U-F	4.8	1	18	5	5
E-F	4.7	1	12	3	6
E-F	4.7	1	8	3	7
U-P	4.9	13	17	3	10
U-P	4.8	60	20	3	3
E-P	4.7	12	14	3	3
E-P	5.2	28	12	3	18
U-N	5.7	2	36	3	280
U-N	5.5	1	17	3	150
E-N	5.5	2	12	3	56
E-N	5.4	7	17	3	38
U-NP	6.4	2	15	3	540
U-NP	5.6	30	14	3	46
E-NP	5.5	17	15	8	120
E-NP	5.0	35	12	3	120

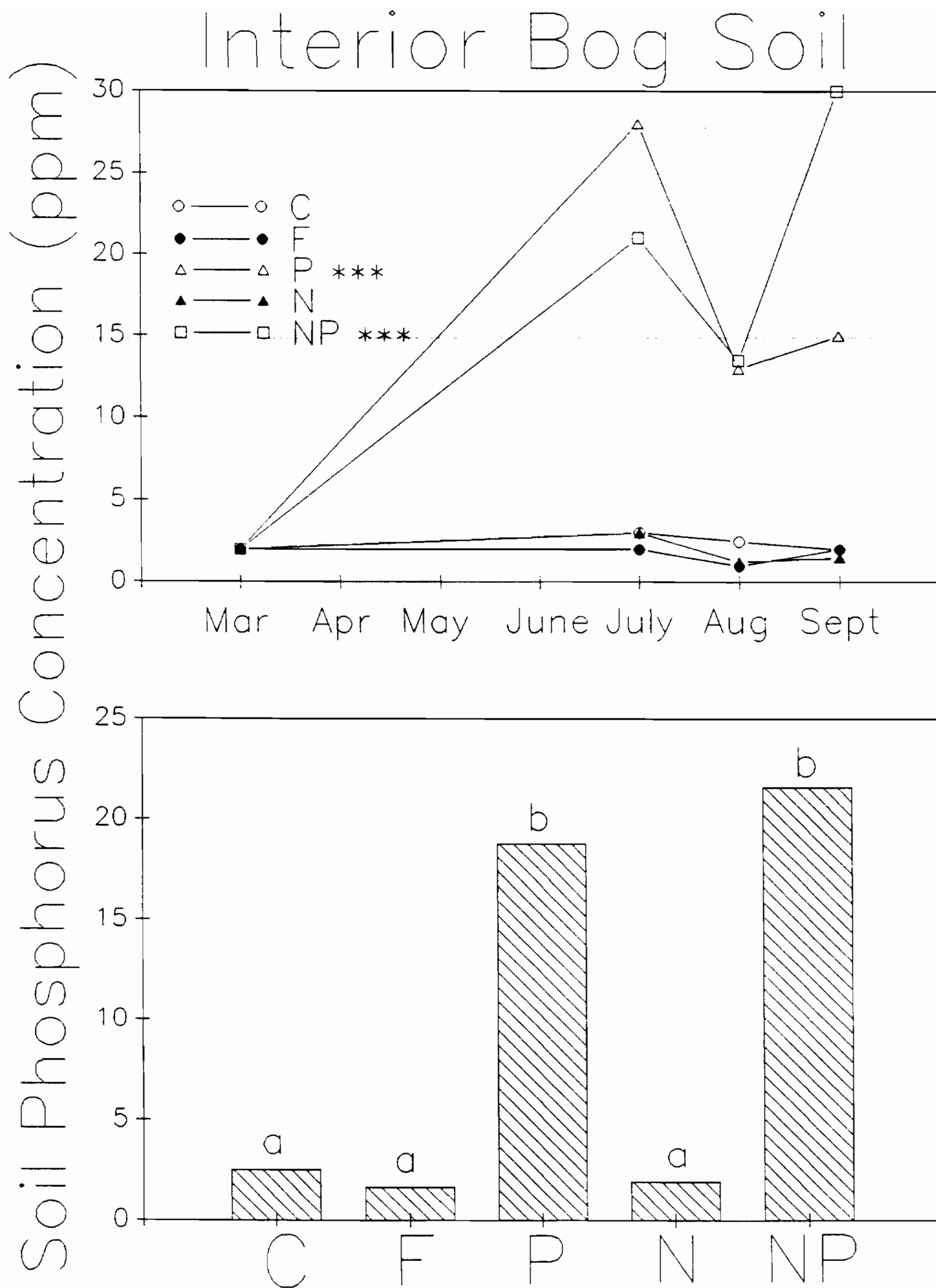


Figure 2: Soil phosphorus concentration at Interior bog. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. (March was before nutrient additions). Comparisons using LSD at .05 level. Same letters are not significantly different. Asterisks denote differences within treatments.

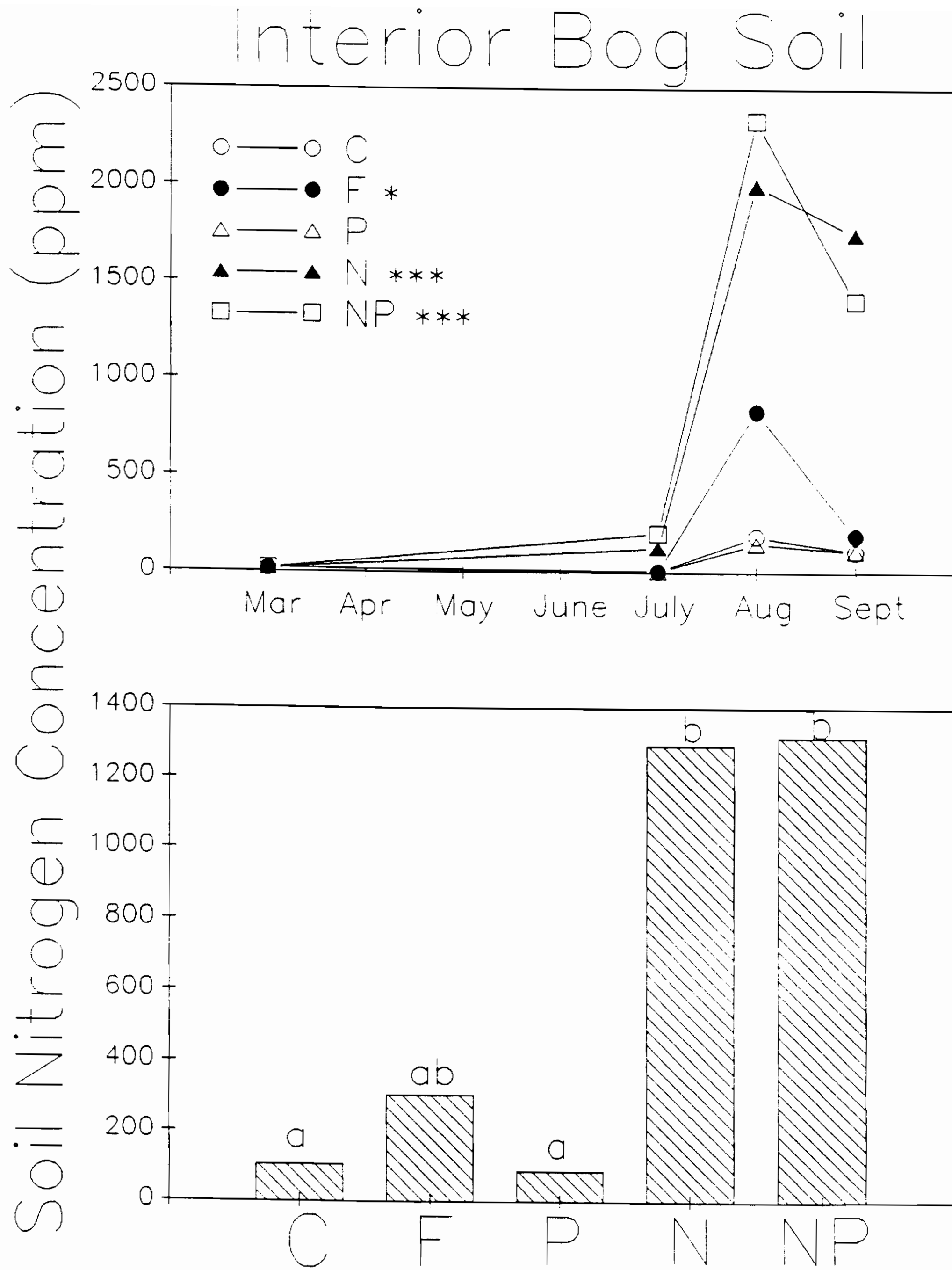


Figure 3: Soil nitrogen (ammonium) concentration at Interior bog. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. (March was before nutrient additions). Comparisons using LSD at .05 level. Same letters are not significantly different. Asterisks denote differences within treatments.

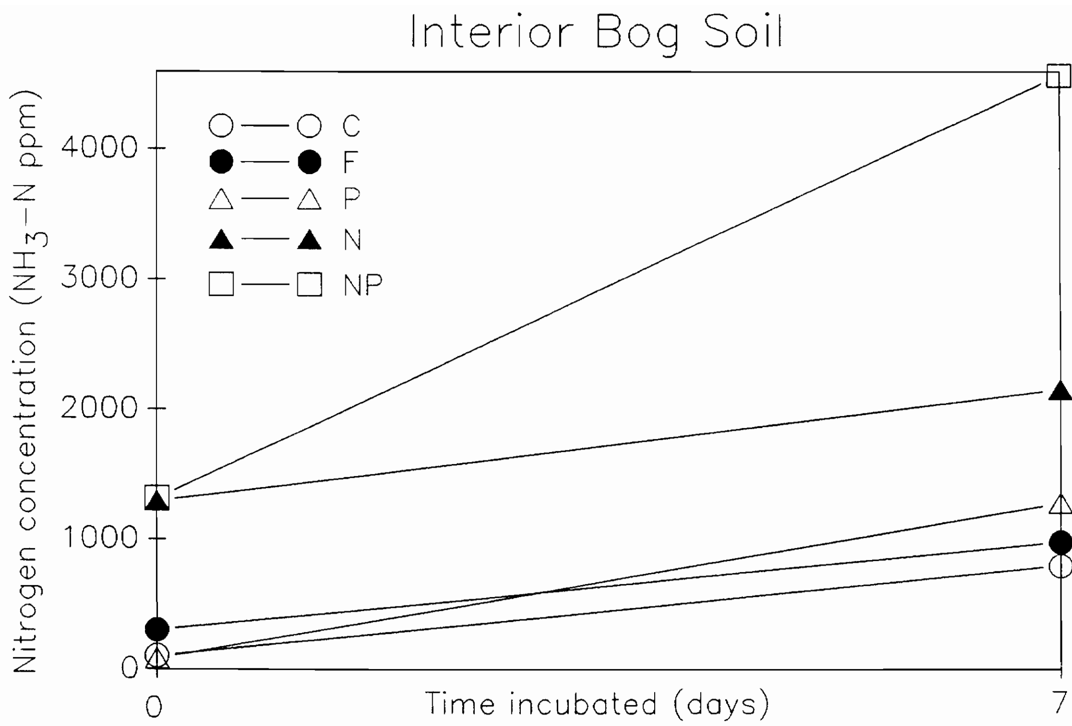


Figure 4 Soil nitrogen mineralization rates at Interior bog. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added.

Microclimate

The daily temperature in the bog did not differ from that of the surrounding area. NOAA's cooperative reporting station closest to the bog (Staffordsville, Va.) reported a high of 21° C and a low of 6° C for August 9 1989. The low temperature recorded in the bog was only 2° C lower than Staffordsville, which is not a large difference for ground level measurements (Biel 1961). Photosynthetically active radiance (PAR, moles of photons between 400--700 nanometers) appeared to be similar for most of the partly sunny day in which microclimate was measured. Figure 5 shows that PAR within a total exclosure more closely followed that of no exclosure during sunflecks. This suggests that the total exclosure sampled was affected by chance sun flecks at times when the partial exclosure was shaded. The reverse is seen (4:00--5:00 p.m.) when PAR within the partial exclosure is highest. However, the low level of PAR on this date reveals that even though this is a canopy-free site, the trees surrounding the site impact light levels in the bog.

Figure 6 shows the relationships among air, soil, and leaf temperatures within and among treatments. Generally regarding temperatures, air > leaf > soil. As with PAR, temperatures within the total exclosure were more similar to temperatures from the plot without an exclosure. Increased PAR levels were probably the reason for this observation.

Relationships among vapor pressure measurements are similar to PAR and temperature with mean vapor pressure in a total exclosure being similar to no exclosure

(fig. 7). Since vapor pressure levels are related to temperature these data are not surprising.

If a greenhouse effect was taking place within exclosures, temperature would be higher with little difference in vapor pressures. This probably did not occur since PAR, temperature, and vapor pressure levels concur. The total exclosure and the plot with no exclosure experienced more similar microclimates than did the partial and total exclosure. Even though chosen sites were relatively close to each other, there seems to be great variability within the bog. Since measurements within the total exclosure were so similar to the no exclosure plot, I conclude that neither the partial nor total exclosures had any substantial effect on microclimate or plant growth.

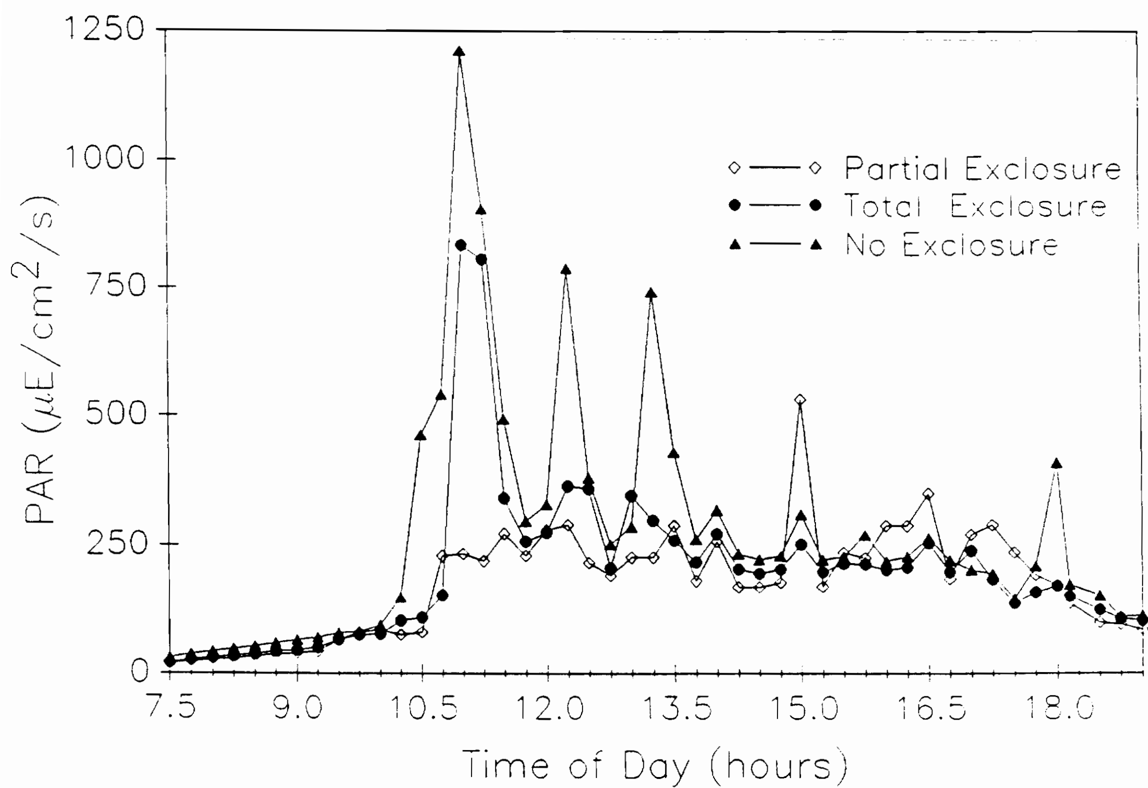
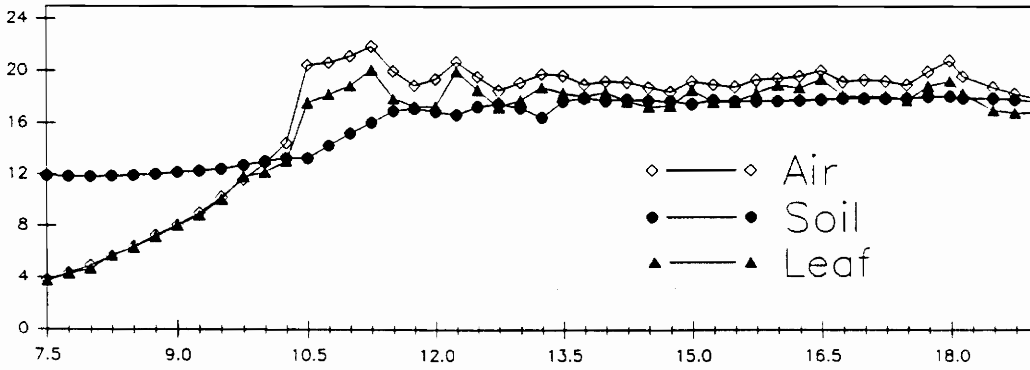
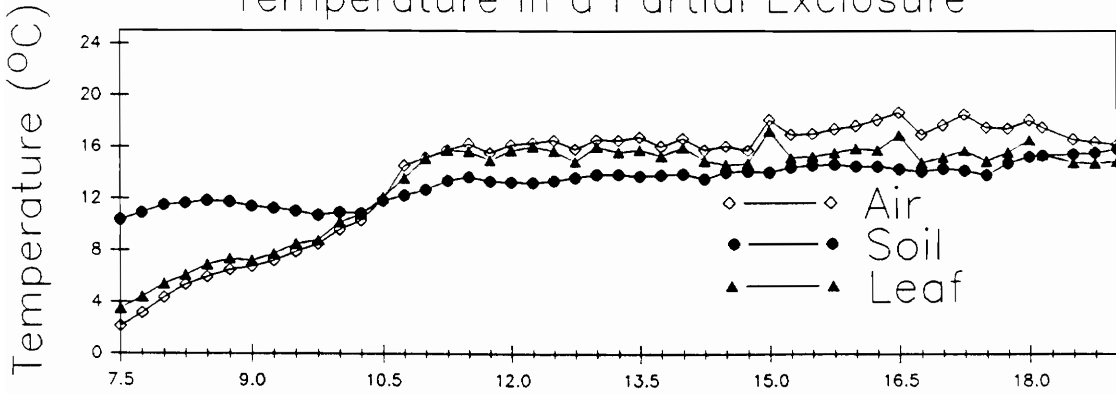


Figure 5: PAR of three microsites at Interior bog. August 9, 1989. (Partly sunny conditions).





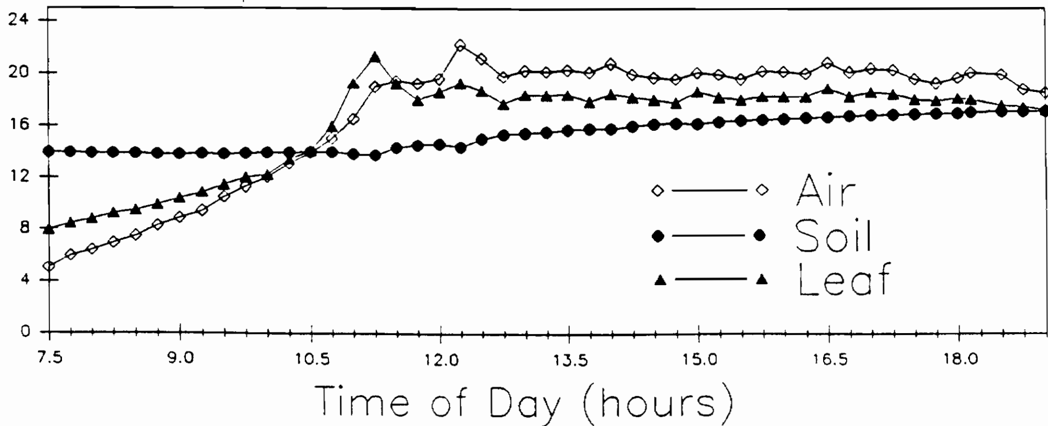


Figure 6: Temperature of three microsites at Interior bog. August 9, 1989.

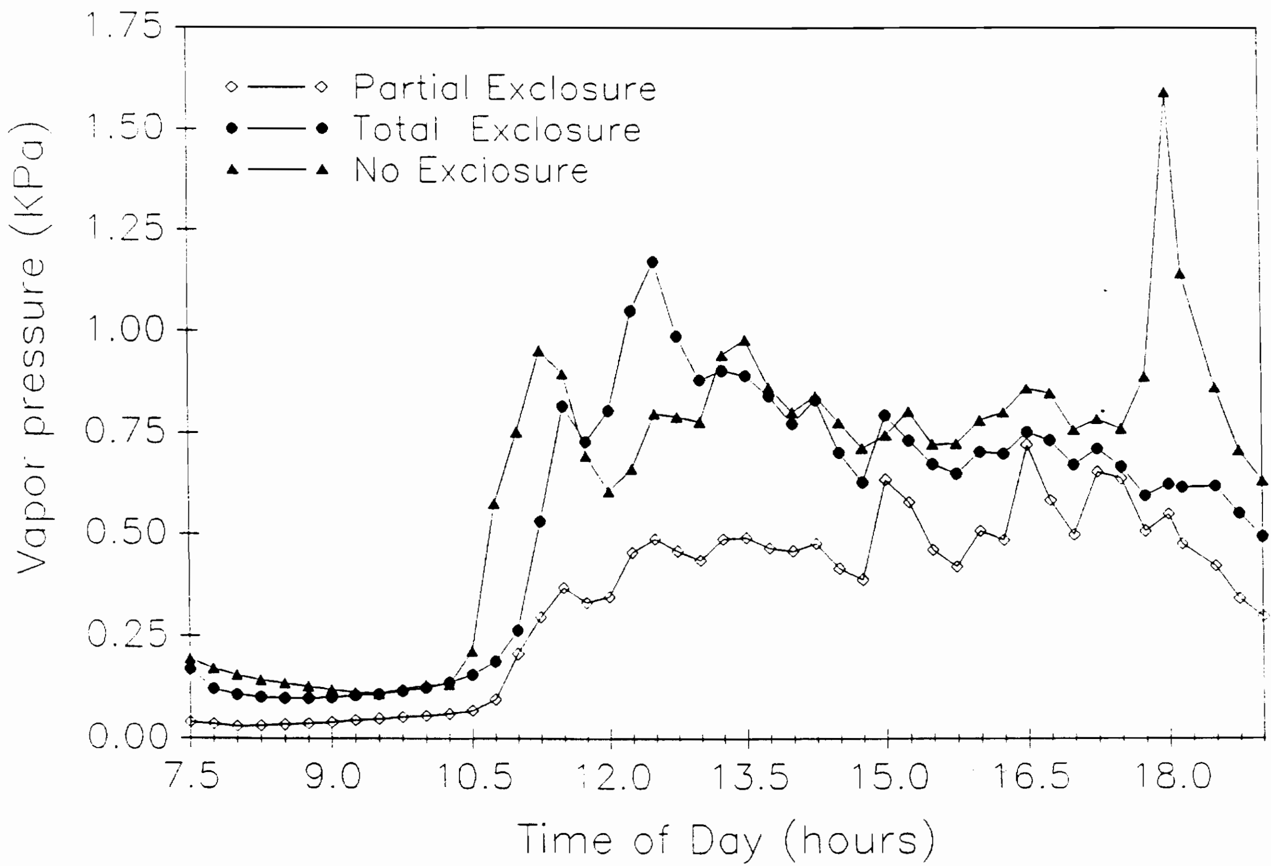


Figure 7: Vapor pressure of three microsites at Interior bog. August 9, 1989.

Plant Measurements

Phenology

The only consistently statistically significant differences were linked to nutrient addition treatments or lack thereof. When nutrients were added sundews usually grew worse, not having as large or as many mature leaves, nor producing as many flowers.

Growth and leaf development seemed to be hampered by the large flux of available nutrients. Figure 8 shows the decrease of leaf numbers in the NP treatment and even greater reductions in the P and especially N treatment. As a result, there were fewer leaves present over time. There was no change due to the presence of complete insect exclosures.

Rosette diameter, which is another indicator of growth (fig. 9), also showed a negative effect of added nutrients. The same trends mentioned above were observed, but F treatment was significantly different from the control. Plant size diminished over time, and plants grown in complete exclosures had a significantly greater mean rosette diameter.

Density of plants (fig. 10) per area is an indicator of survivorship and success. There was an insignificant change during the growing season in density and also no difference due to exclosures. There was not a decline in plant density due to added nutrients, except in the N treatment. In one partially exclosed plot (NP) all plants died two months after nutrient addition.

The number of flower stalks appearing increased significantly with time coincidentally with normal flower initiation (fig. 11). Flowering seemed to be marginally

negatively affected by exclosures ($p = .1023$), but was especially decreased by nutrient additions. This was particularly true in the N treatment, in which flowering was nearly unobserved. Note increase in F treatment.

In addition to these ongoing measurements made on the five largest plants per plot per time, measurements were recorded on all plants sampled at the destructive harvest in August. Trends for leaf number and rosette diameter were similar to above with several exceptions. Figure 12 shows that plants in complete exclosures had significantly more leaves than unexclosed plants. Also, the P treatment had fewer leaves than previously, and the NP treatment did not differ significantly from the F treatment. Rosette diameters were much the same as for the five largest plants, only slightly smaller (fig. 13).

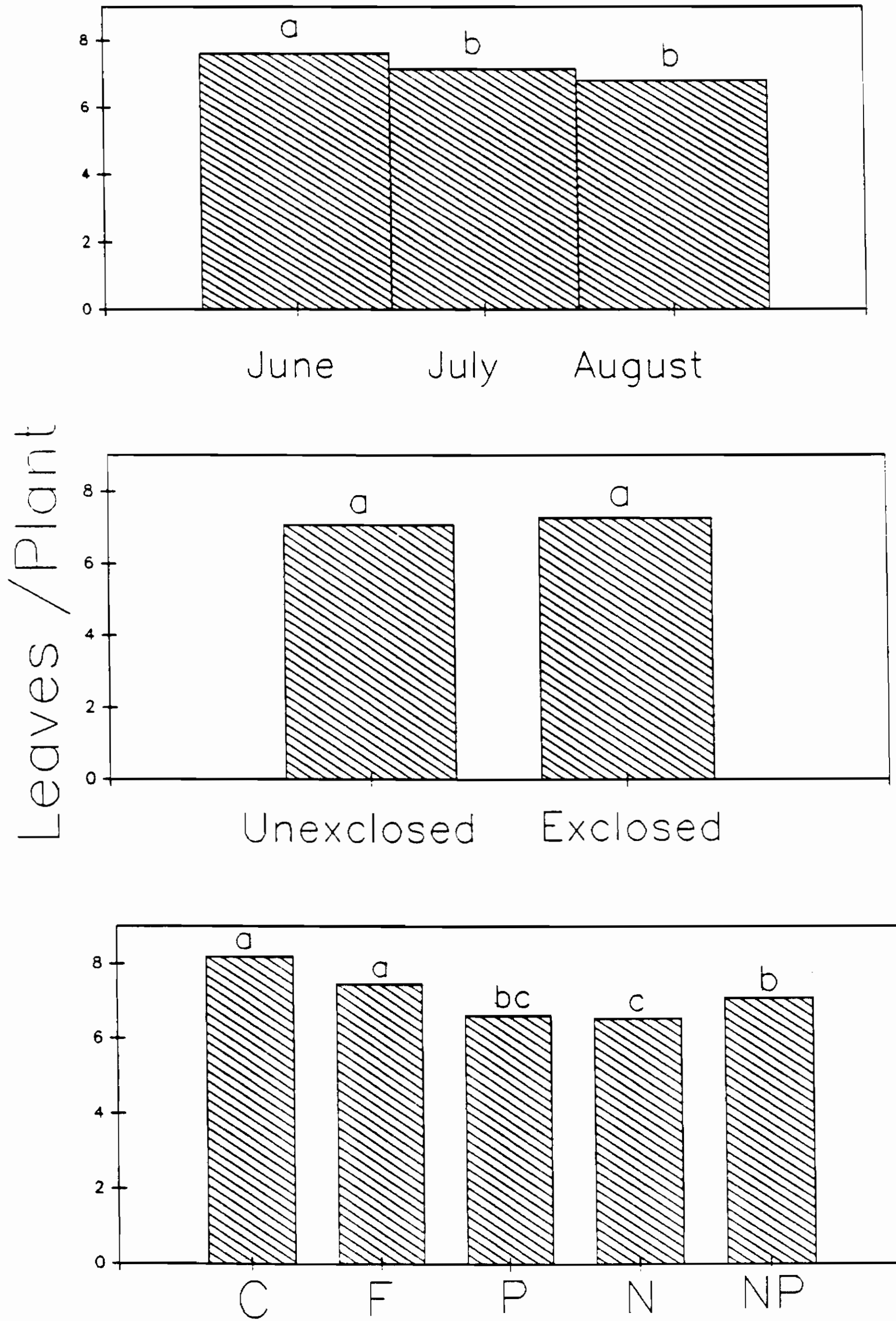


Figure 8: Mean leaf number of the five largest D. rotundifolia plants per plot at Interior bog. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

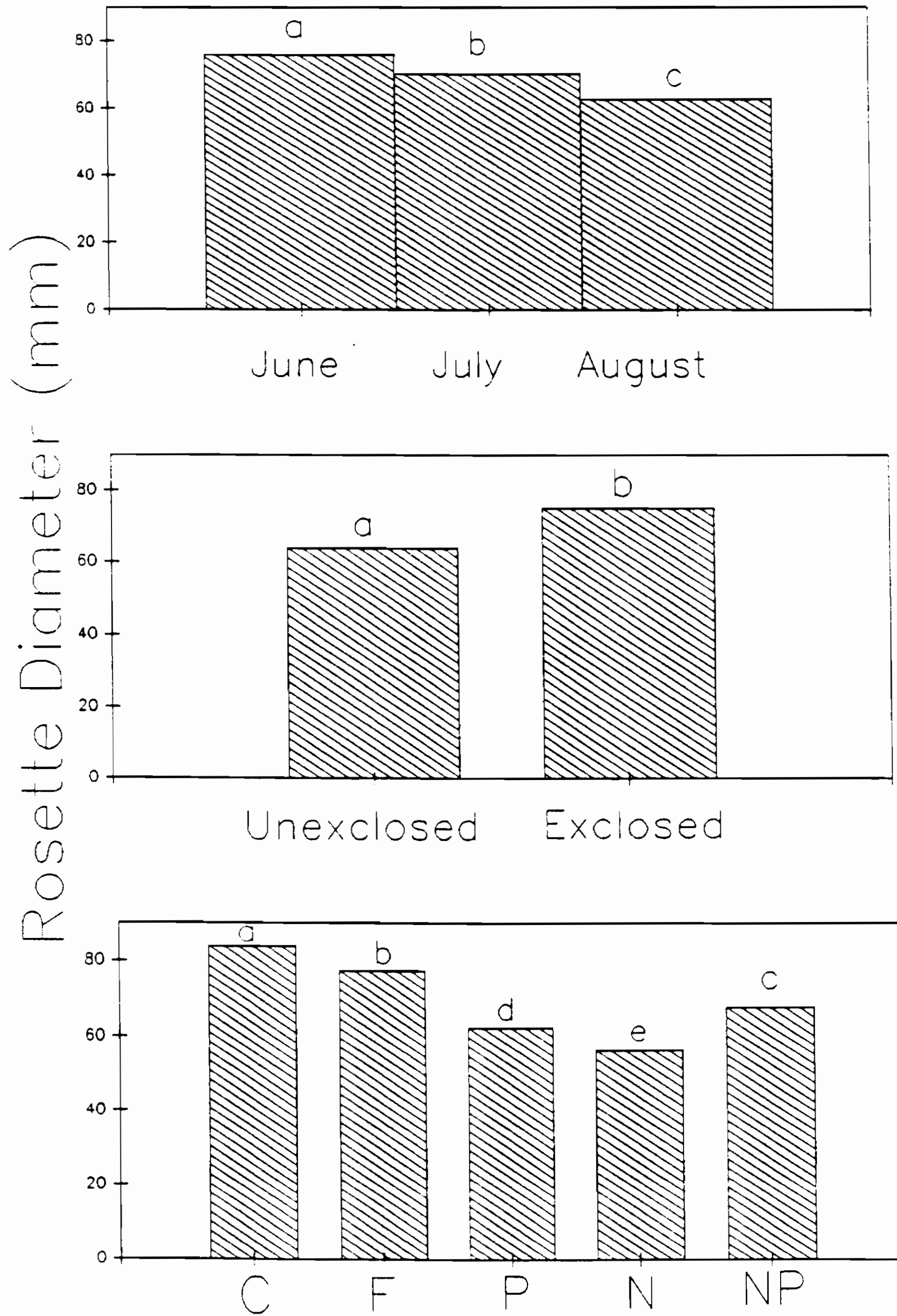
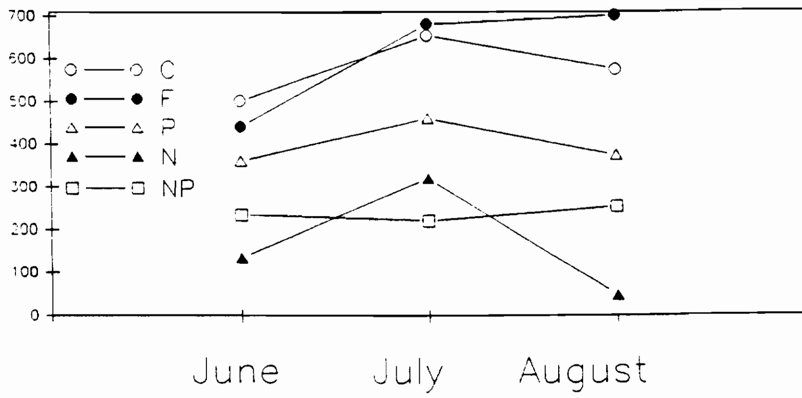
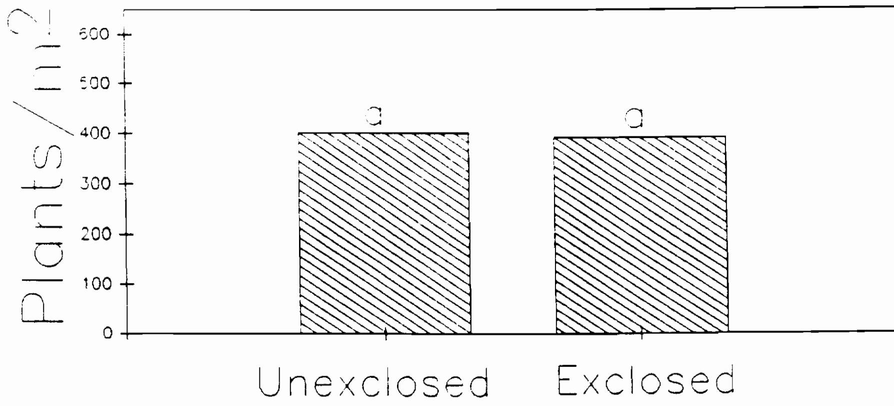


Figure 9: Mean rosette diameter of the five largest D. rotundifolia plants per plot at Interior bog. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.





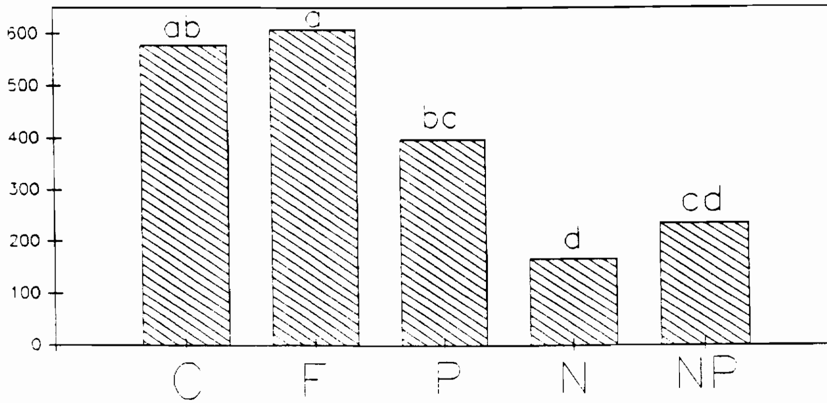


Figure 10: Mean D. rotundifolia density at Interior bog. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

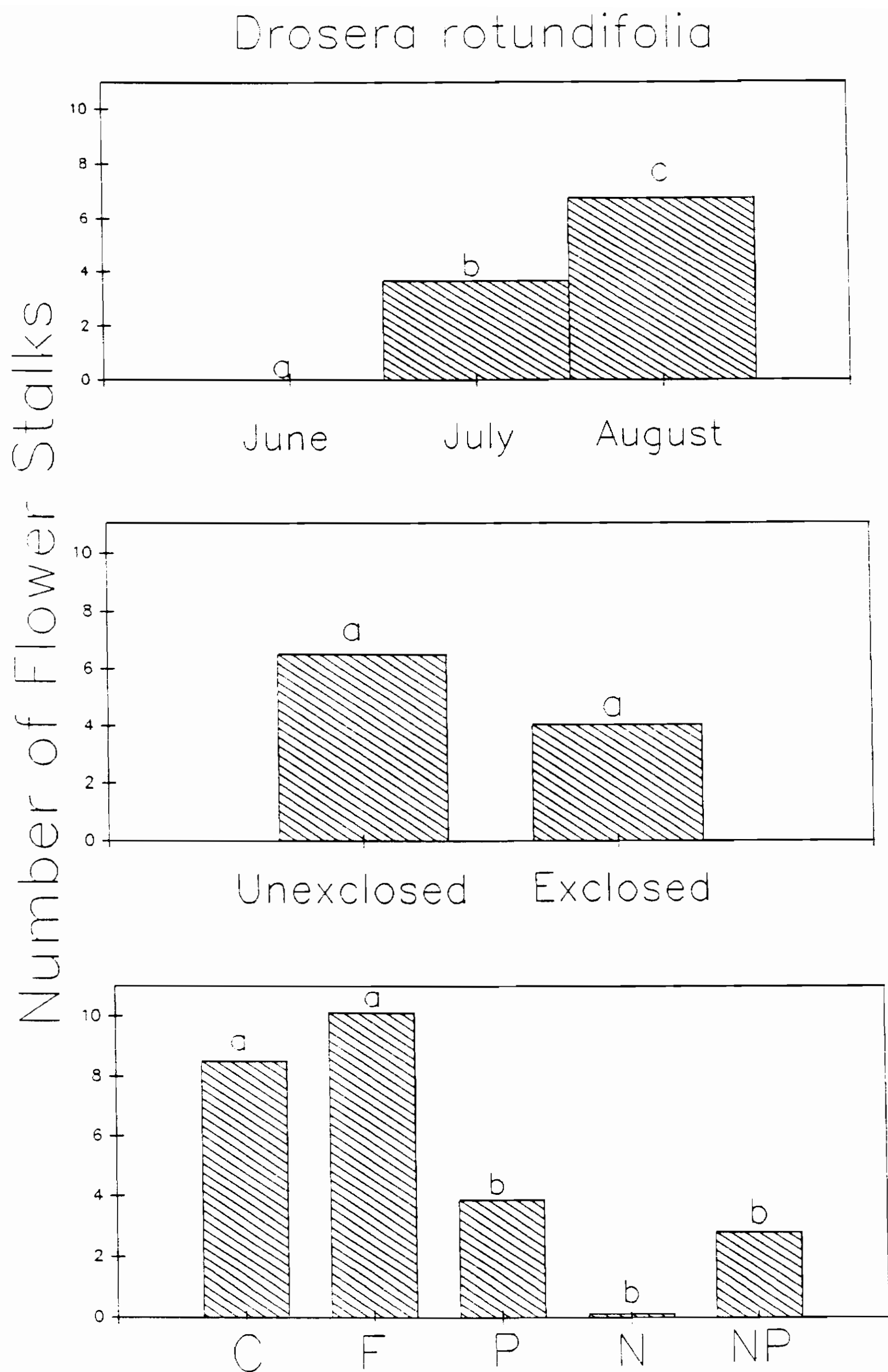


Figure 11: Mean D. rotundifolia flower stalk density at Interior bog. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

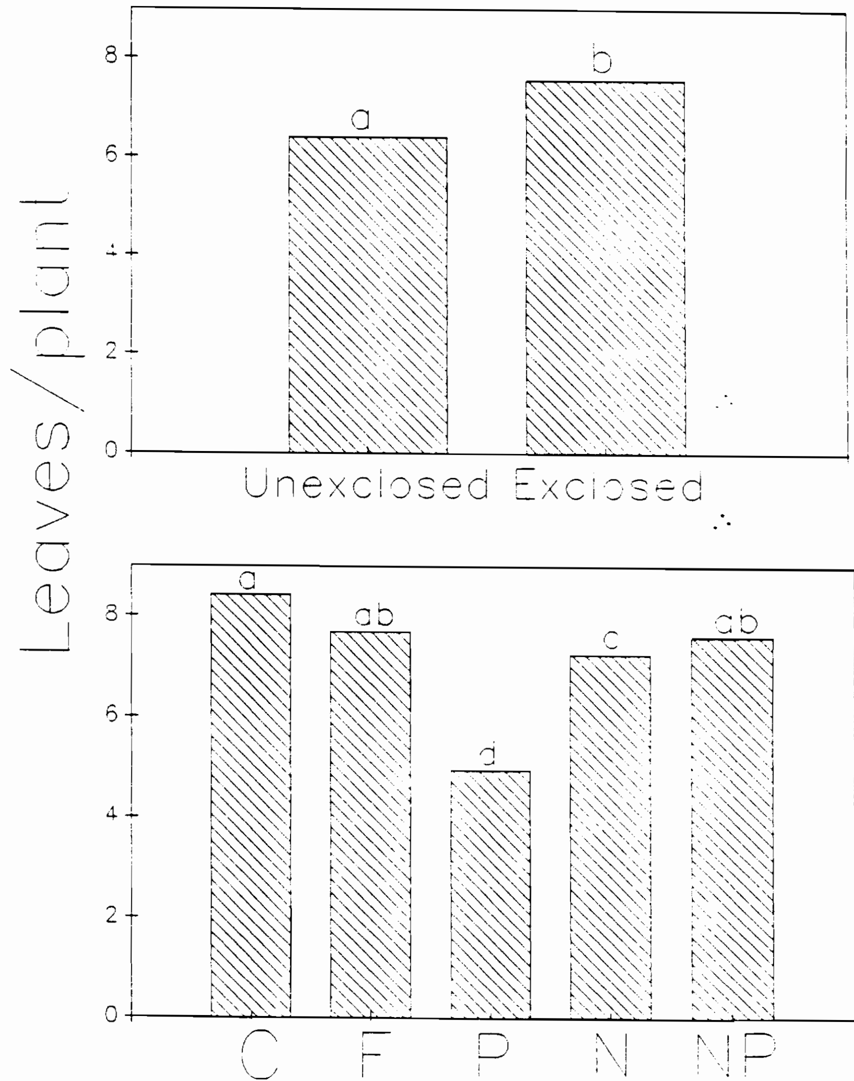


Figure 12: Mean leaf number per D. rotundifolia at Interior bog. August 10,1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

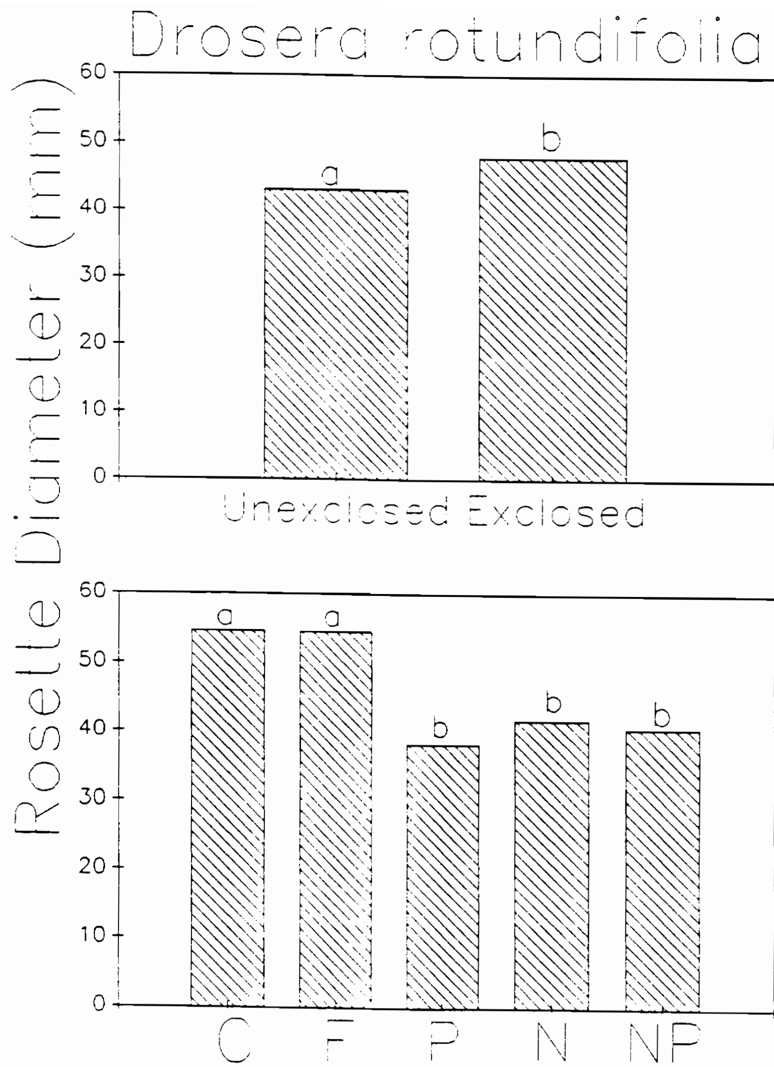


Figure 13: Mean D. rotundifolia rosette diameter at Interior bog. August 10, 1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

Biomass

Mature plants were harvested in August and fresh weights and dry weights were obtained.

Exclosed plants allocated more biomass to their roots, and also had a significantly higher overall weight (fig. 14), but did not have a significantly different root to shoot ratio (fig. 15). As nutrient availability increased, biomass decreased for all organs (fig 14). The largest decrease occurred in the P treatment which had the lowest flower, shoot, and root weight. Dry weight measurements agreed with fresh weights (fig. 14, table 4). Generally, nutrient addition, especially nitrogen, was negatively associated with the root to shoot ratio (fig. 15). Flower to vegetative biomass ratio was tested for significance and none was found at the .05 level.

In addition, a hibernacula destructive harvest was done in October. No effect in biomass was seen due to exclosures (fig. 16), but mixed results resulted from nutrient treatment. C and N treatments had the largest hibernacula weights and P the lowest. C, F, and NP had the highest flower biomass. There was no significant difference observed for the flower to hibernaculum ratio.

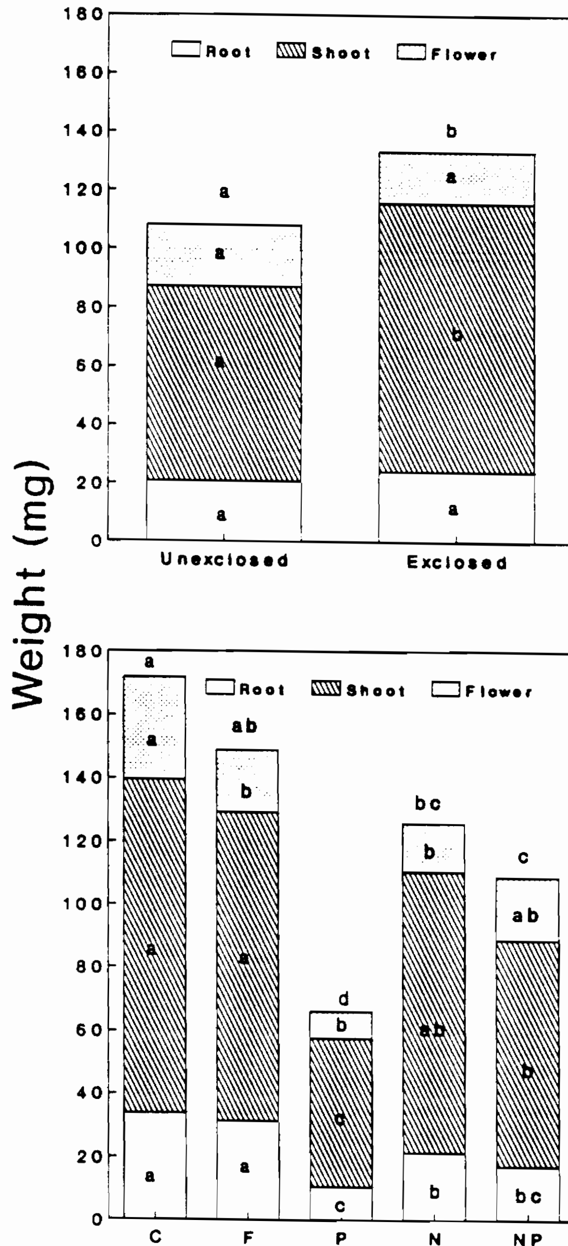


Figure 14: Mean D. rotundifolia fresh weight at Interior bog. August 10,1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

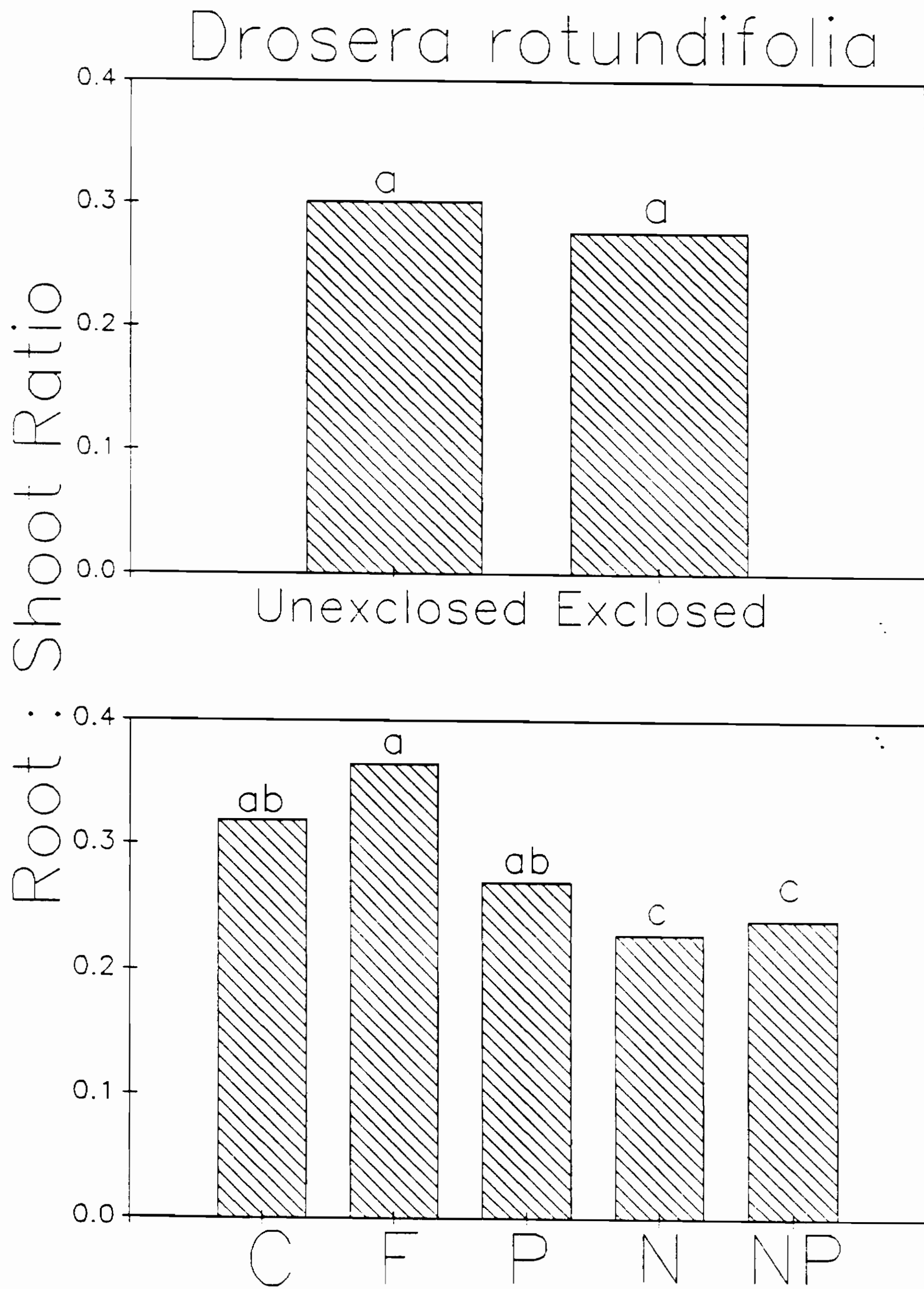


Figure 15: Mean D. rotundifolia root to shoot ratio at Interior bog. August 10, 1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

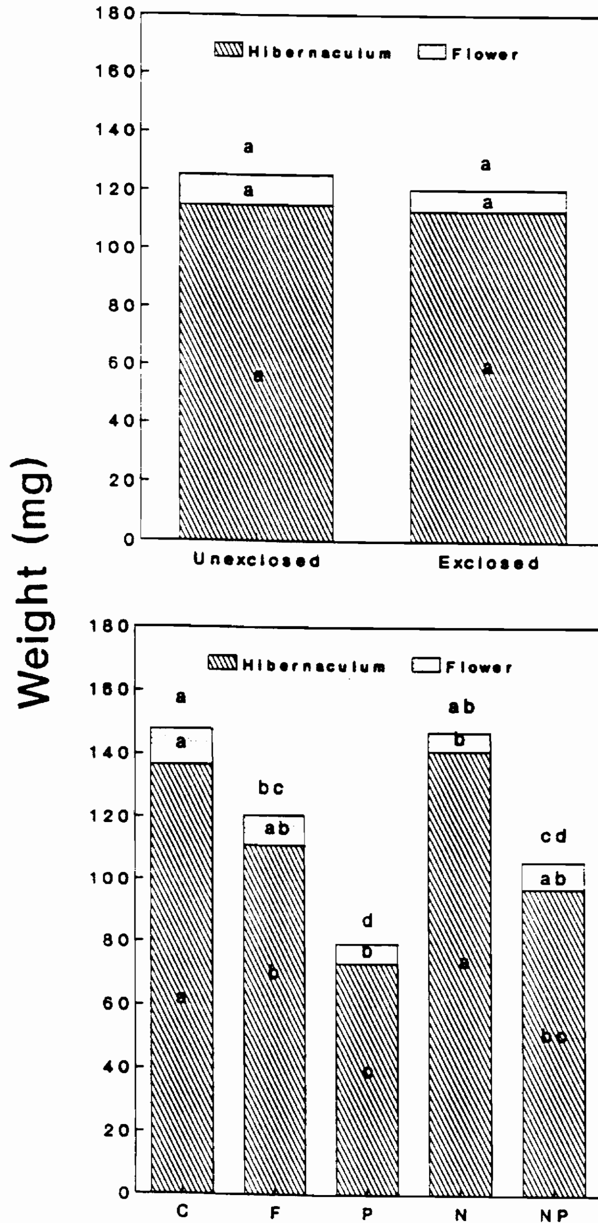


Figure 16: Mean D. rotundifolia hibernaculum fresh weight at Interior bog. October 3,1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

Table 4. Mean dry weight partitioning for *Drosera rotundifolia* plants.

Treatment	Root	Shoot	Flower	Total
	mg			
U-C	5.68	13.10	8.14	26.92
E-C	7.25	21.03	7.22	35.50
U-F	6.08	11.84	7.54	25.46
E-F	6.11	15.09	4.12	25.32
U-P	1.93	5.54	1.52	8.99
E-P	3.13	11.23	1.56	15.92
U-N	4.57	10.96	4.82	20.35
E-N	4.38	17.70	3.49	25.57
U-NP	3.14	10.07	7.81	21.02
E-NP	4.58	10.94	4.96	20.48

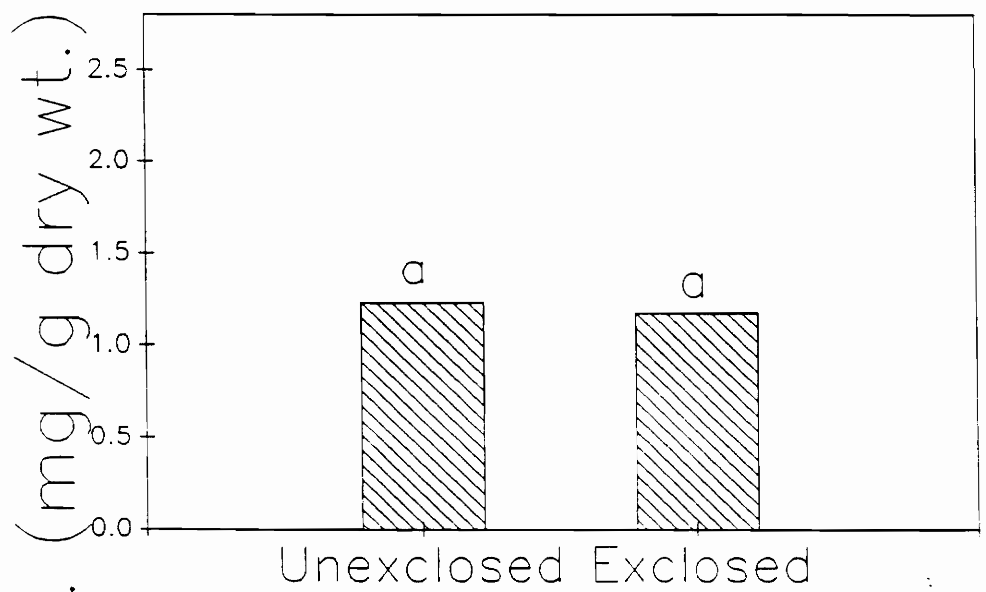
Nutrient Concentration in Tissues

There was not a significant difference in phosphorus concentration due to exclosure effect in either the mature plant harvest or the hibernaculum harvest (figs. 17 and 18).

There were significant differences due to nutrient treatments. In both harvests, P and NP plants (in that order) accumulated the most phosphorus. In the hibernaculum, however, C was not significantly different than P or NP (fig. 18).

Unexclosed plants accumulated more nitrogen in their tissues than exclosed plants in both harvests (figs. 19 and 20). Plants harvested in August showed highest nitrogen accumulation for N and NP treatments (respectively) while hibernacula exhibited highest nitrogen levels in the NP treatment.

When total nutrient accumulation (biomass x nutrient concentration) is examined (tables 5 and 6) for those treatments in which no soil nutrients were added (C and F), hibernacula and flowers contained more nitrogen and phosphorus in the C treatment for exclosed treatments. There were no definite trends in the partially exclosed treatments.



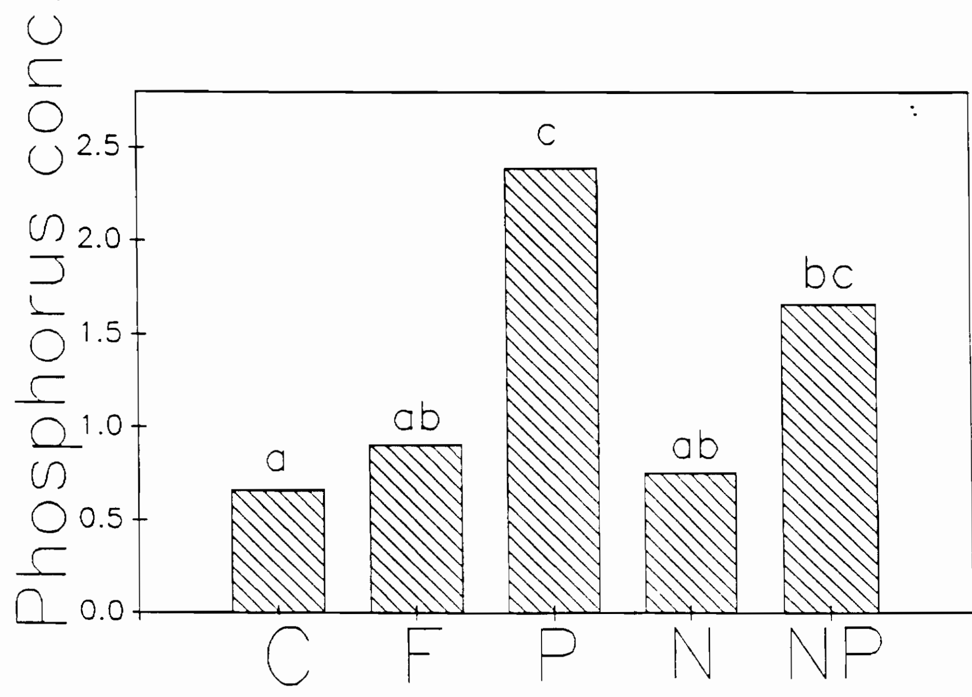


Figure 17: Phosphorus concentration of D. rotundifolia. August 10, 1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

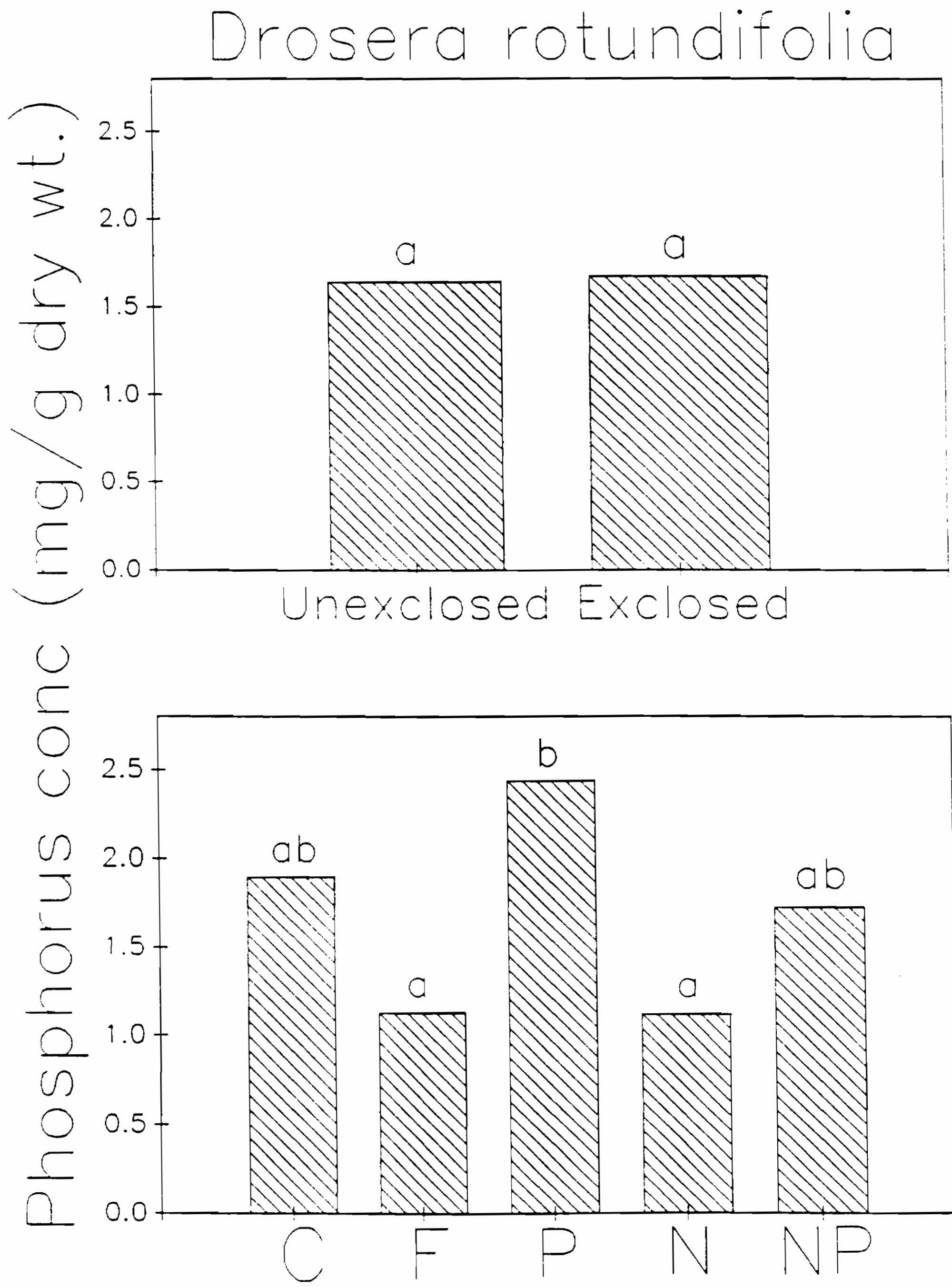
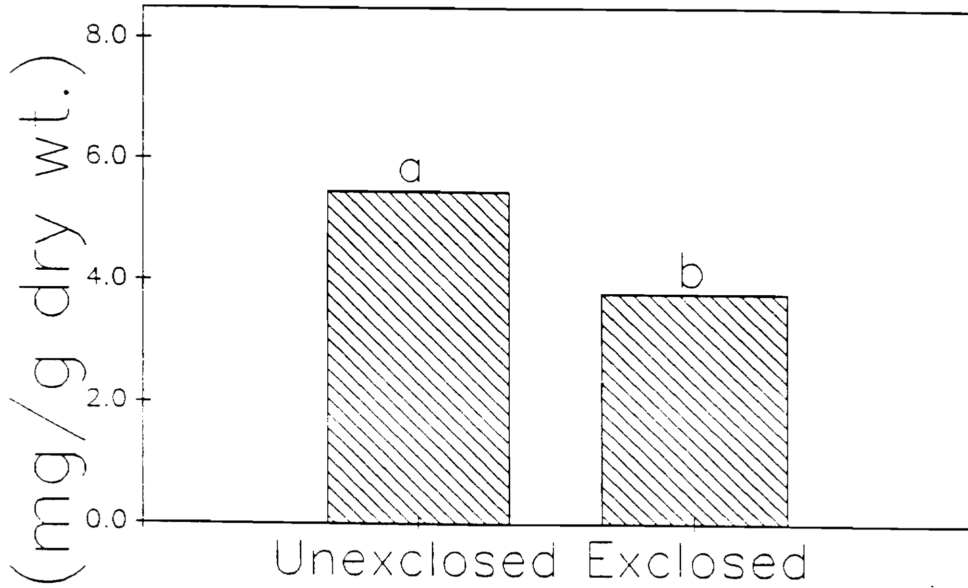


Figure 18: Phosphorus concentration of D. rotundifolia hibernacula. October 3, 1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.



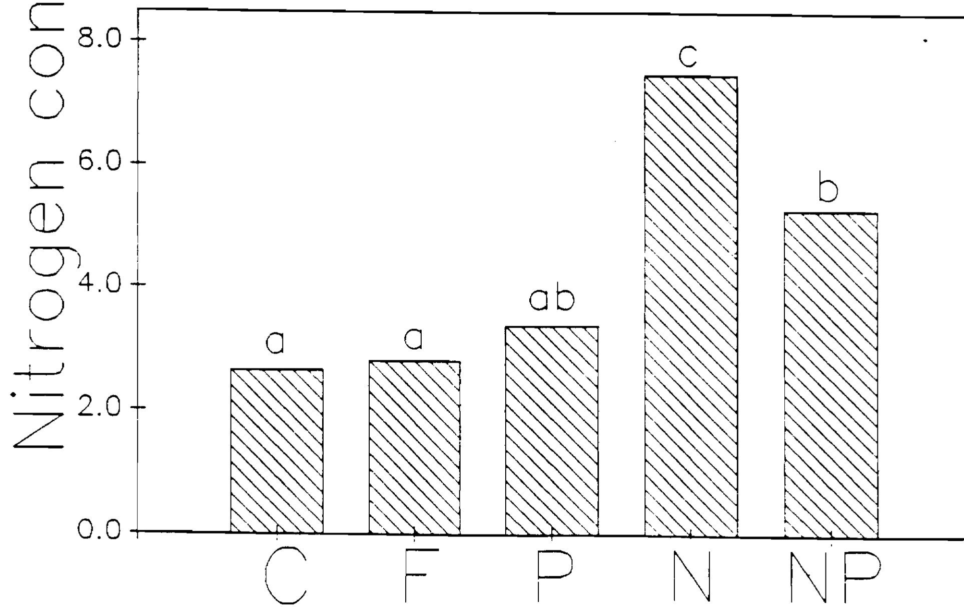


Figure 19: Nitrogen concentration of D. rotundifolia. August 10, 1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

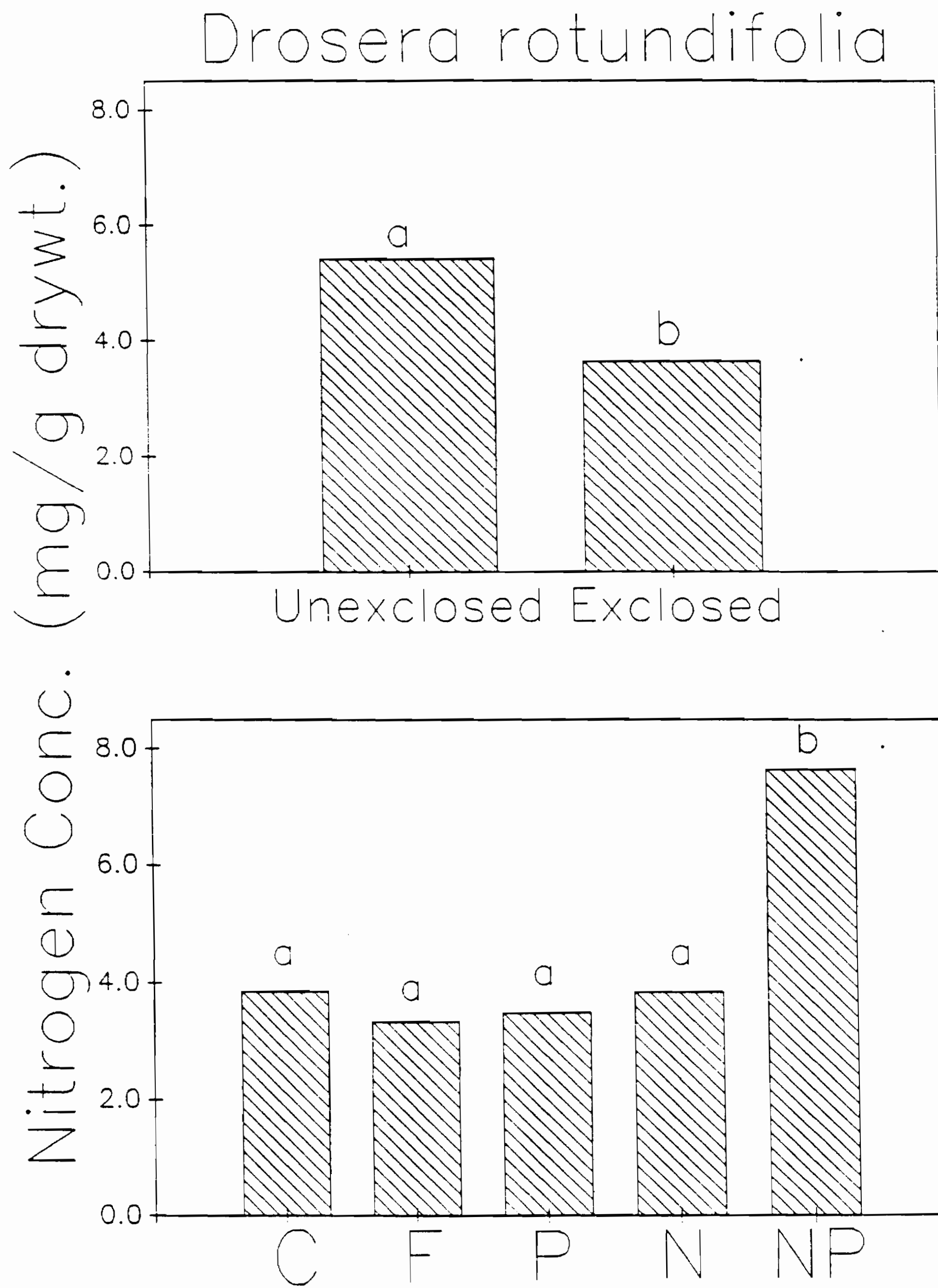


Figure 20: Nitrogen concentration of D. rotundifolia hibernacula. October 3, 1989. C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

Table 5: Summary of hibernaculum dry weight and nutrient content for C and F treatments.

Treatment	Dry wt. (mg)	% N	% P	Total N (mg)	Total P (mg)
UC	22.3	0.543	0.190	12.10	4.237
UF	41.2	0.406	0.128	16.72	5.273
EC	39.4	0.306	0.189	12.05	7.446
EF	22.9	0.340	0.097	7.78	2.221
C	31.0	0.425	0.190	13.18	5.890
F	29.3	0.281	0.113	8.233	3.310

Table 6: Summary of flower dry weight and nutrient content for C and F treatments.

Treatment	Dry wt. (mg)	% N	% P	Total N (mg)	Total P (mg)
UC	7.4	0.363	0.072	2.68	0.532
UF	7.2	0.337	0.092	2.42	0.662
EC	8.1	0.216	0.064	1.74	0.518
EF	4.1	0.253	0.090	1.03	0.369
C	7.8	0.265	0.066	2.06	0.514
F	5.4	0.281	0.091	1.51	0.491

Discussion

Before discussing results of the data, two questions which should be answered are: 1. Were insect exclosures effective in excluding insects from plants? and 2. Was there a specific ion effect as is assumed, or were the nutrient additions toxic primarily because of increased soluble salts?

1. The exclosures, though not perfect at excluding insects, decreased insect populations within plots. While I was at the study site I frequently noticed flying insects in the partial exclosures but not in complete exclosures. When plants were harvested, insects were removed from leaf surfaces. Excluding those plants in which insects were applied to leaf surfaces (F treatment), 10.5% of plants in unexclosed plots had insect residues (8/76) compared with 2.6% (3/114) for exclosed plants.

2. There was not a significant difference in soluble salt levels of soil from any treatments (fig. 21). If soluble salts were the cause for observed growth and flowering differences between treatments, then we would expect to see similar declination in the N and NP treatments (fig. 21). This did not occur, so we can assume that observed differences are due to specific nutrient additions or exclosures.

The first objective of the study was determine whether exposure to insects increases nutrient accumulation or growth in D. rotundifolia. There is no evidence that supports that exposure to insects increases growth. In fact there is evidence to the contrary (see figs. 9, 12, 13, and 14, in which exclosed plants grew better than unexclosed plants). The effect of insect availability did not significantly impact phosphorus concentrations in

tissues, but unexclosed plants had higher amounts of nitrogen in the mature plant and hibernacula (figs. 19 and 20). It appears that insects did contribute to higher nitrogen contents in active tissue and also in overwintering tissue.

The second objective pertains to growth, nutrient accumulation, and reproduction in relation to soil nutrient availability. Added nutrients decreased growth and flowering to some degree, which may be a product of specific ion toxicity (figs 8--16). Phosphorus addition had a more profound effect on growth whereas nitrogen addition greatly affected flowering. This is probably due to a disruption of the carbon to nitrogen ratio in the plant (Krauss and Kraybill 1918; Lyons, et al. 1987). When phosphorus and nitrogen were applied together, there was an ameliorating effect regarding growth and flowering. However, nutrient accumulation in tissues was positively affected by nutrient addition to the substrate (figs. 17--20).

The third objective for this study deals with interactions of nutrient availability via the substrate and insect availability on plant growth, nutrient accumulation, and reproduction. There seems to be little interaction between the two nutrient sources on any of the parameters of interest. The lack of difference in growth between exclosed and unexclosed sites is consistent with other studies in which plants were grown on fertile substrate (Dore Swamy and Mohan Ram, 1969, 1971; Christensen, 1976; Dixon, et al. 1980; Aldenius, et al. 1983; Wilson 1985). This seems to suggest that D. rotundifolia plants are plastic in their nutrient source requirements (substrate versus insectivory).

We observe that Drosera rotundifolia is a small insectivorous plant that needs very

small amounts of nutrients to succeed. The amount of nutrients in mature plants at peak biomass is miniscule (for the UC treatment: phosphorus-- 4.769 mg; nitrogen--14.78 mg) Dixon, et al. (1980) found that Drosera erythrorhiza plants absorbed 76.1% of labelled nitrogen applied to leaves in Drosophila. The nitrogen content of each fly was 26.8 μg. Therefore, the plant would derive 20.39 μg of nitrogen a month from one Drosophila application, or about 0.5% of its requirement. This means in order for its complete nitrogen requirement to be met, it would need to capture at least 200 fruit fly-sized insects per season.

However, it is important that the plant retain and efficiently use the nutrients it obtains for future growth and reproduction. One mechanism for this is the presence of an overwintering vegetative bud, the hibernaculum. Drosera rotundifolia is a shade intolerant early successional species. Successful dispersal of seeds to suitable neighboring sites is important for survival. Since this species is so small, even graminoid species and small shrubs limit light availability. D. rotundifolia would be under a strong competitive disadvantage in nutrient-rich sites, because faster growing species restrict light availability.

There seemed to be a large degree of mortality due to nutrient toxicity, but those plants that survived seemed to acclimate to high nutrient status of the soil. This suggests that roots in this species may have a higher absorption capacity than previously thought. As is consistent with ecological theory (Chapin, 1980, 1987; Tilman, 1982, 1988), a higher root/shoot ratio occurred in plants with low available nutrients (fig. 13). If

insectivory was the most important source of nutrients, then nutrient acquiring tissues (leaves) should predominate under low nutrient conditions, and a lower root/shoot ratio would be observed.

Since sexual reproduction of D. rotundifolia is so crucial, we should examine flower production more closely. Unexclosed plants produced flower stalks and more floral biomass than exclosed plants, although not significantly different at the .05 level (floral numbers $p = .1023$; for floral weight $p = .3917$; and for hibernaculum harvest $p = .0638$. If insectivory is important to this species it may have to do with seed production. However, there is a narrow line between floral initiation (low N), and maximum seed production (higher N). If the plant receives too little nutrition, it does not produce as many flowers and seeds than it would if it receives higher nutrition, but too much nutrient may keep it from initiating flowers. This is seen in tables 5 and 6. If we examine small changes in nutrient availability through insectivory in some of the treatments (UC, UF, EC, EF), control plants contained more total nitrogen and phosphorus in reproductive tissues and hibernacula. This offers no evidence that insectivory is beneficial energetically or nutritionally to D. rotundifolia.

One suggestion is that insectivory may actually be energetically costly to the plant, contrasting to the benefit of nutrient gains. On nutrient rich sites, this benefit would diminish.

Plants growing in nutrient-poor sites are adapted to high nutrient use efficiency (Chapin, 1980, 1987). Nutrient Use Efficiency (NUE) can be described in its simplest

form as the inversion of nutrient concentration in plant tissue. It is advantageous for the plant to have a high NUE during the growing season, and to absorb maximum amounts of nutrients in the hibernaculum to use for next year's growth and especially reproduction. So a small plant like D. rotundifolia can conserve nutrients by an efficient overwintering apparatus. Its NUE (1/nutrient conc [%]) (UC: mature plant phosphorus--1.42, nitrogen--.35) which is higher for phosphorus and lower for nitrogen than that of most crops and wild plants (phosphorus--0.4, nitrogen .58) (Chapin 1987; Pearcy, et al. 1989). It appears that phosphorus efficiency use is potentially critical to species survival.

Figures 22 and 23 show retention indices of phosphorus and nitrogen for plots. Since sample size was small, significance could not be tested, but we can see obvious differences. If plants have a high NUE and also efficiently reabsorb nutrients into their hibernacula, then this NUE accumulation ratio is high, and the plant is more efficient in use and recycling nutrients. For phosphorus (fig. 22), it is evident that UC (unexclosed control) and EC (exclosed control) are much more efficient than any nutrient addition treatment including F (foliar feeding). For nitrogen (fig. 23) the results are not as obvious. This seems to suggest that phosphorus is a more limiting nutrient (if there is one) than nitrogen, because it is more efficiently reabsorbed, since both are mobile in the plant. Except plants in the UNP treatment for nitrogen, plants in the control treatments (exclosed and unexclosed) are most efficient.

Drosera rotundifolia is a small, efficient user of nutrients, and is physiologically adapted, aside from insectivory, to its habitat. It is growing at its genetically realized best

with the environment at its natural state (unexclosed control). Added nutrients negatively affect recruitment and growth, while denying insects only marginally negatively affected flowering. A sudden influx of nutrients (inorganic or insect derived) is apt to upset the nutritional balance both for vegetative growth and flowering. There seems to be a significant amount of morphological plasticity regarding root to shoot ratios, which would imply that if insect populations were low, then absorption of nutrients through roots may increase. Therefore, the importance of insectivory is, at its best, minimal for the survival of D. rotundifolia.

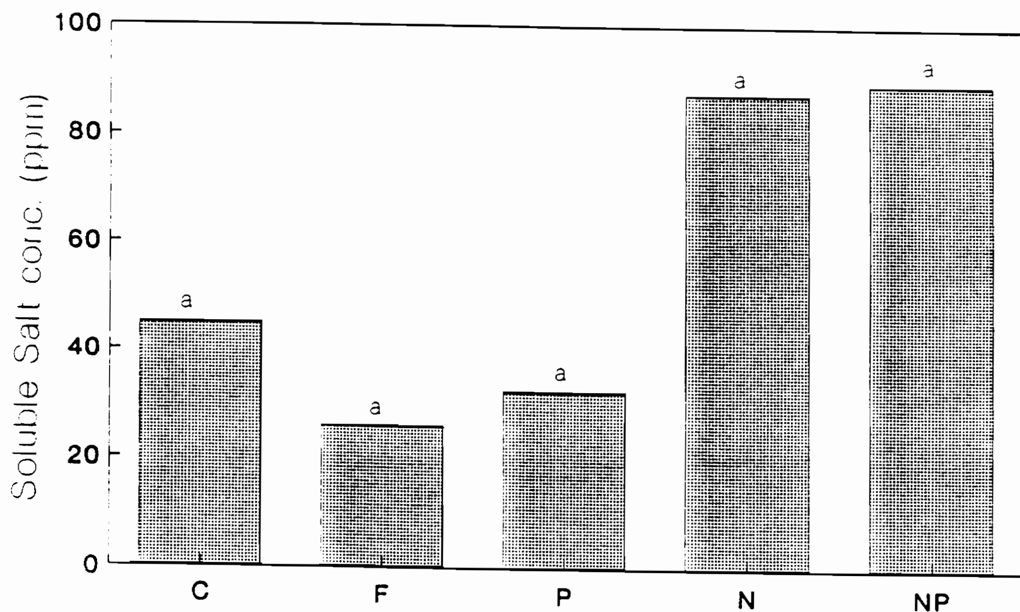


Figure 21: Soluble Salt concentrations: Interior Bog soil. August 10, 1989. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

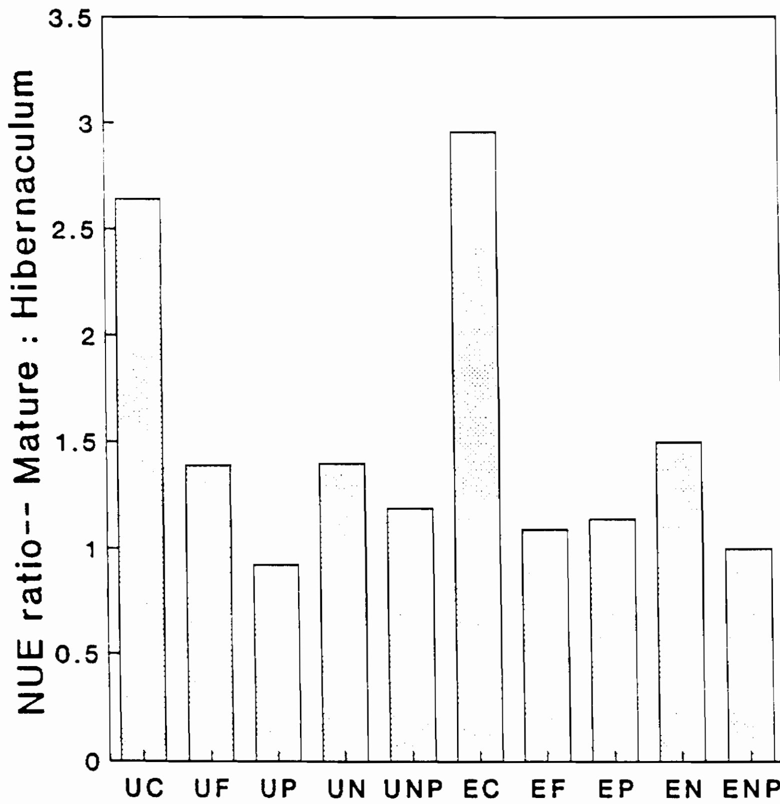


Figure 22: Phosphorus retention index of D. rotundifolia; NUE ratio= (1/P conc mature plant)/(1/p conc hibernaculum). U= Unexclosed; E= Exclosed; C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added.

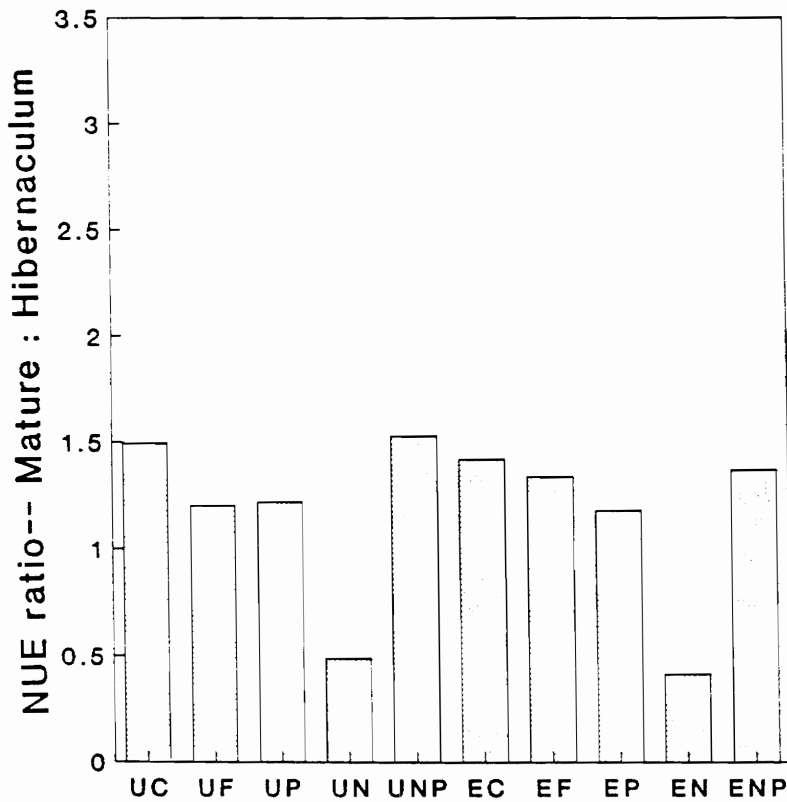


Figure 23: Nitrogen retention index of D. rotundifolia; NUE ratio= (1/N conc mature plant)/(1/N conc hibernaculum). U= Unexclosed; E= Exclosed; C= control, no nutrients added; F= monthly foliar feeding of Drosophila; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added.

Responses of Drosera capensis and D. binata var. multifida to Manipulations of Insect Availability and Soil Nutrient Levels

Rationale

A field study using Drosera rotundifolia was done in which insectivory was not shown to be important regarding growth and nutrition. I wanted to determine whether or not other Drosera species would respond the same way under similar conditions. Therefore I set up a comparable experiment with the two subtropical species, D. capensis and D. binata var. multifida. These species were chosen for two reasons. I had pans with established plantings in a peat substrate available for use. These are evergreen subtropical species that are larger and possibly would have different nutrient requirements. Evergreen plants also lend themselves to fall/winter greenhouse studies. Since I was not able to go to the southern hemisphere to do field studies, I attempted to create the most natural environment as possible under the circumstances.

Species and Site Description

Drosera capensis

Drosera capensis is a stem-forming sub-tropical evergreen sundew endemic to inundated acid peat bogs of South Africa. Leaves turnover at a steady rate with no flush

of growth. Slack (1979) reports rosette diameters of up to 150 mm, but I have observed plants with rosettes well over 220 mm (Stewart, unpublished data). The ribbon-like leaf blades are covered with mucilaginous glandular trichomes which serve to trap and digest insects. Leaf blades of this species are also capable of movements upon insect stimulation, even to the degree of enfolding over its prey (Slack 1979). D. capensis bears one or two flower scapes consisting of up to 20 perfect flowers.

Drosera binata

Drosera binata is a rhizomatous temperate to subtropical Australian sundew. It ranges from 45° to 25° latitude on the eastern shore of the continent. Endemic to inundated peat bogs, this is one of the largest sundews (Charles Darwin (1875) called it "almost gigantic"). Leaves are many-forked and commonly reach 50 cm or more in length (Stewart, unpublished data). White or pink flowers are borne on sometimes bifurcated scapes which have morphology typical of the Droseras. Variety multifida is evergreen and has a steady leaf turnover rate.

Study Site

The site of this study was in the Biology greenhouses on the campus of Virginia Polytechnic Institute and State University. The house was a quonset style, fibreglass-covered structure. Insects were excluded from plants on June 1, 1989, and nutrient treatments begun September 10, 1989. Harvests of all sundews were made on January

21, 1990.

Materials and Methods

Experimental Design

The basic design of the experiment is a three-way balanced factorial layout, with the factors being:

1) The presence or absence of a complete insect exclosure: Both the complete and incomplete insect exclosure were made of cpvc pipe and wood. All materials were light-colored in order to maximize brightness inside of the exclosure. Mosquito netting was used as a covering for both designs. The complete exclosure frame was entirely covered to exclude all insects. The incomplete exclosure was made the same way as the other, but fabric terminated approximately at the top of the structure to only control for shading. The structures surrounded several plastic pans which had an area each of 1600 cm^2. The pans also contained coincidental Dionaea muscipula. The pans had been containers for carnivorous plants for over 10 years and no artificial selection had been performed during that time, except for the periodic removal of non-carnivorous plants. The substrate was Canadian peat with Sphagnum growing on top. Pans containing the species of interest were randomly assigned to the exclosed or unexclosed group.

2) Nutrient treatments: Four nutrient groups were set up randomly within exclosed and partially exclosed pans that contained both D. capensis and D. binata var. multifida at the beginning of the experiment during the first week of September, 1989. They were:

a) Nitrogen addition-- (N) 4 g of nitrogen was applied to each N pan in the form of 40-0-0 Osmocote slow release urea fertilizer. It was broadcast evenly over the

surface of the soil, being careful to avoid direct application to sundew leaves.

b) Phosphorus addition-- (P) 4.6 g of phosphorus was applied per P pan in the form of 0-46-0 Super-triple-phosphate. It was applied in a like manner as N.

c) Nitrogen and phosphorus addition-- (NP) This treatment was a combination of the first two treatments. The total amount of nutrients added were therefore 8.6 g.

d) Control-- (C) No nutrient manipulations were done on this group.

3) Time: Three phenological measurements of plant growth or success were measured approximately every three weeks from October, 1989 through January, 1990. For biomass measures and plant tissue nutrient analyses, time is not a factor, since there was only one harvest in January, 1990.

Abiotic Factors

Soil Nutrient Concentrations

In August, random plots of soil to 10 cm depth were sampled from the pans that were to be used. In October and January samples were taken from the periphery of each pan, being sure not to disturb any experimental plants. These samples were then air-dried on wax paper, and sent to Virginia Tech's soil testing laboratory where pH, phosphorus, nitrate, and other macronutrient concentrations were obtained, except for ammonium.

After soil was air-dried, ammonium was extracted using 10 ml 2 M KCl. One gram of soil was weighed out from each exclosure and 10 ml KCl added. The slurry was shaken for one hour and filtered using Whatman #1. The filtrate was frozen in a snap-top vial until analysis could take place. Analysis was done using an Orion millivolt meter with a 95-01 ammonia electrode. To each sample 0.1 ml of 10 M NaOH was added to raise the pH of the filtrate and convert ammonium to ammonia so it could be measured by the electrode (Page, et al. 1982). Actual concentration in the soil is obtained by constructing a standard curve using known ammonium concentrations and back-calculating. The final ammonium concentration is for oven-dried soil.

To obtain a better index of potentially available nitrogen in the various treatments anaerobic incubations were performed. During the incubation nitrifying bacteria convert nitrogen which is tied up in organic matter to ammonium. This procedure, therefore, yields a more realistic long-term availability index of soil nitrogen (Page, et al. 1982; Pearcy, et al 1989). One gram of air-dried soil from each sample was placed in a small screw-top glass vial. The vial was then filled to the top, leaving no air bubbles in the vial. Incubation at 40° C was done for one week. The soil--water mixture was then quantitatively transferred using 3 M KCl until the soil--water--KCl slurry weighed 11 g. This approximately yields a 10:1 2 M KCl to soil ratio. The extract is shaken and filtered as described previously and frozen until analysis could be performed.

Microclimate

Microclimates of the complete exclosure and the incomplete exclosure were measured on January 10, 1990. This was done to ascertain whether there were microclimatic differences due to the presence of the experimental structures. The following factors were measured: air temperature, soil temperature, leaf temperatures from each of the two species, relative humidity, and photosynthetically active radiation (PAR). Measurements were taken every minute and averaged every 15 minutes. beginning at 7:30 a.m. and ending 7:00 p.m. using a Campbell Scientific 21X micrologger. All temperatures were measured using copper/constantan thermocouples. The air thermocouple was shaded and placed at leaf level. The soil thermocouple was placed at 10 cm below the soil surface, and the leaf thermocouples were placed within a randomly selected leaf of each species.

Relative humidity was measured using a Campbell 207 relative humidity sensor under shade. Relative humidity and air temperature were used to calculate vapor pressure.

PAR was measured using a Li-Cor quantum sensor set at soil level and parallel with the soil surface.

Plant Measurements

Phenology

Phenology data were analyzed using a three way ANOVA. Multiple comparisons

were done using Fisher's protected LSD at $\alpha = .05$ (Zar 1974).

The five largest Drosera capensis plants were chosen and measurements were taken periodically (every three to four weeks). The measurements taken were: mature leaf numbers, plant diameters, and flower stalk numbers. These measurements gave an indication of growth and relative success.

Biomass

Since time was not a factor in biomass measurements (one harvest) statistical analysis was done using a two way ANOVA. Multiple comparisons were done using Fisher's protected LSD at the .05 level (Zar 1974).

In January, 1990 all sundews were harvested (N=152). Plants were dried at 65° for two days and weighed. Weights were recorded by organ biomass partitioning (shoots {stems and leaves}, roots, and flowers {including scapes and seeds}). Dried samples were stored in air-tight plastic vials until nutrient analysis could be performed.

Plant Nutrient Analyses

Since time was not a factor in nutrient measurements (one harvest) statistical analysis was done using a two way ANOVA. Multiple comparisons were done using Fisher's protected LSD at $\alpha = .05$ (Zar 1974).

Tissue nitrogen concentrations were obtained by Kjeldahl digestions and titrations using a Kjeltec Auto 1030 according to methods outlined by Chapman (1976).

Tissue phosphorus concentrations were determined colorimetrically using a Gilford spectrophotometer according to the modified Fiske and Subbarrow method (Kabut and Mayer 1948).

Tissue concentrations were broken down by treatment and organ to determine nutrient partitioning.

Results

Abiotic Measurements

Soil nutrients

Substrate for this experiment was commercial Canadian peat which had been in place for over ten years. Assuming low variability and desiring to conserve soil, only two pans were randomly sampled to estimate before treatment nutrient levels. There seemed to be large variation in potassium (K) and ammonium nitrogen (NH_4-N) (table 7). After treatment levels show only large ammonium variation (table 8).

Phosphorus concentration changed over time for P and NP treatments (fig. 24). Significantly more phosphorus was in soil where added as a nutrient treatment (P and NP).

Nitrate concentration significantly increased over time (fig. 25), and was also greater where nitrogen was added. Ammonium, though at extremely high levels immediately after fertilization, decreased over time (fig. 26). It was also at higher levels where nitrogen was added (though not significant at the .05 level, sample size was small). Nitrogen mineralization rates also changed because of nitrogen addition (fig. 27). N treatment showed an increase in mineralization while NP showed a decreased rate (negative mineralization). This may have slightly affected available nitrogen in the soil between N and NP treatments, but levels were so high this difference was probably negligible.

Microclimate

Photosynthetically active radiance (PAR) was slightly higher in the partial exclosure (fig. 28). Since these readings were taken during winter, PAR was low to begin with. The difference of 10 $\mu E/m^2/s$ was not considered biologically important.

Air temperatures were generally higher in the partial exclosure, and D. binata leaf temperatures higher in the total exclosure (fig. 29). The latter was probably due to the exposure angle.

There were no differences in vapor pressure between the partial and total exclosure (fig. 30).

Microclimate was fairly uniform between exclosure types in the greenhouse. It will be assumed that the presence of exclosures did not affect plant growth significantly, and that the difference in growth was due to nutrient treatments and/or the denial of insects.

Table 7. Soil nutrient levels before treatments; Greenhouse; Virginia Tech. (August 1989).

Sample	pH	P	K	NO_3-N	NH_4-N
		ppm			
1	4.4	5	72	5	115
2	4.2	5	18	5	2240

Table 8. Soil nutrient levels after treatments; Greenhouse, Virginia Tech. October, 1989). U= Unexclosed, E= Exclosed; C= No added nutrients, P= Phosphorus added, N= Nitrogen added, NP= Nitrogen and Phosphorus added.

Treatment	pH	P	K	NO_3-N	NH_4-N
		ppm			
U-NP	4.9	60	26	15	15000
U-C	4.1	4	25	5	270
U-N	4.2	5	18	3	22500
U-P	4.1	60	28	3	1000
E-P	4.5	60	18	5	350
E-N	4.4	4	36	5	650
E-C	4.4	3	22	3	480
E-NP	4.4	60	48	33	6300

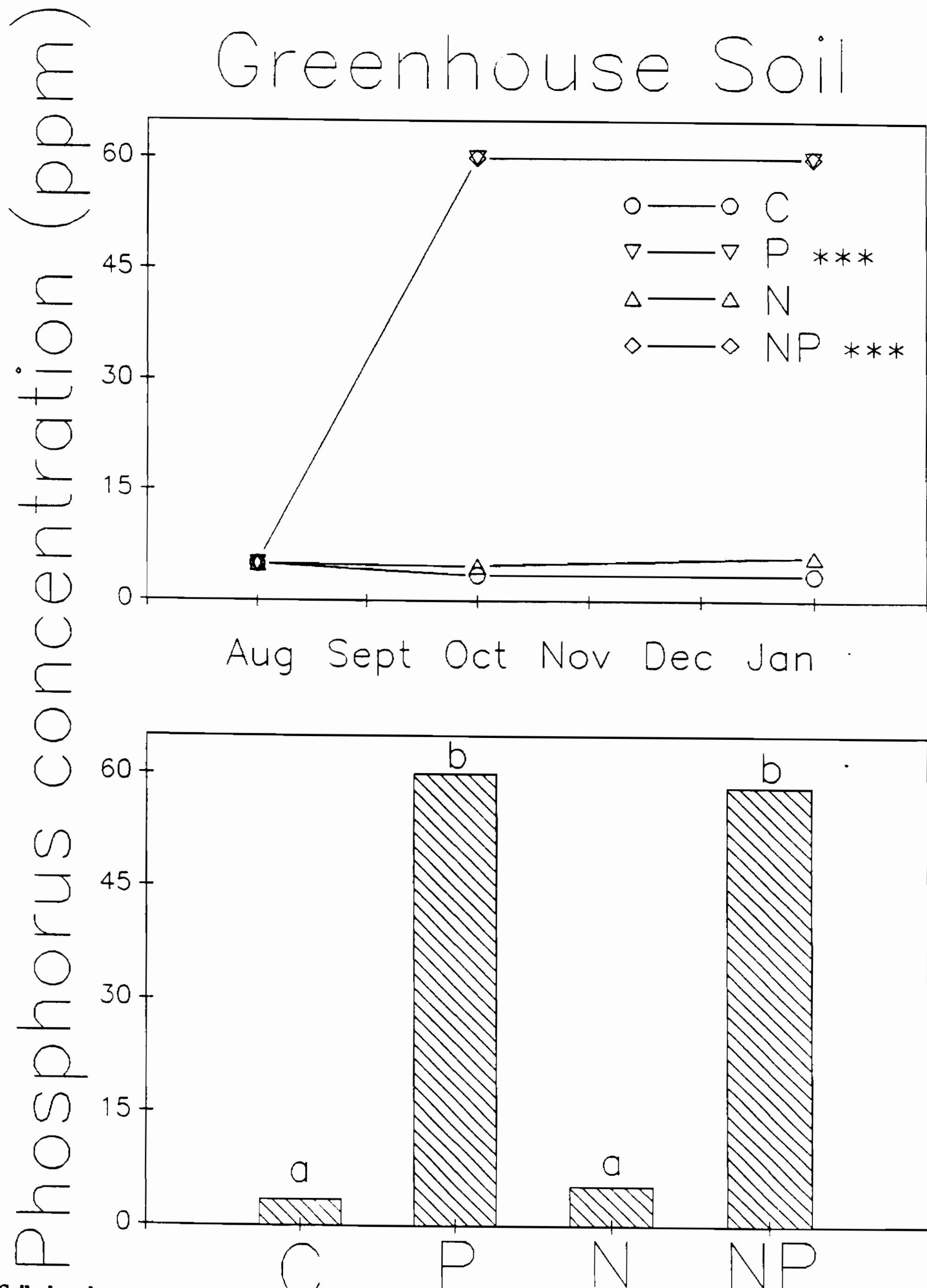
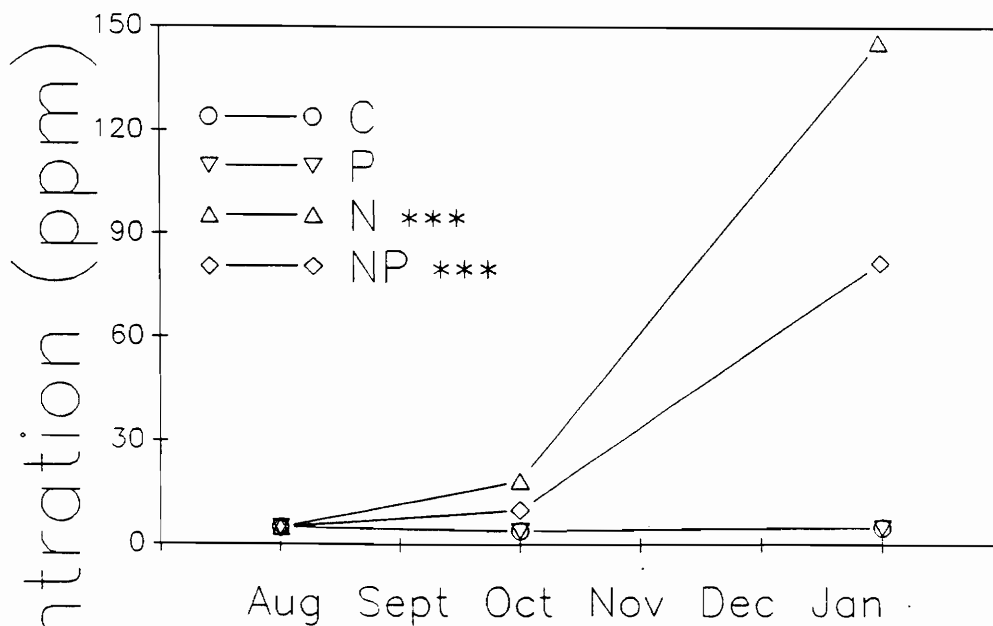


Figure 24: Soil phosphorus concentration in greenhouse. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. August was before nutrients were added. Comparisons using LSD at .05 level. Same letters are not significantly different. Asterisks denote differences within treatments



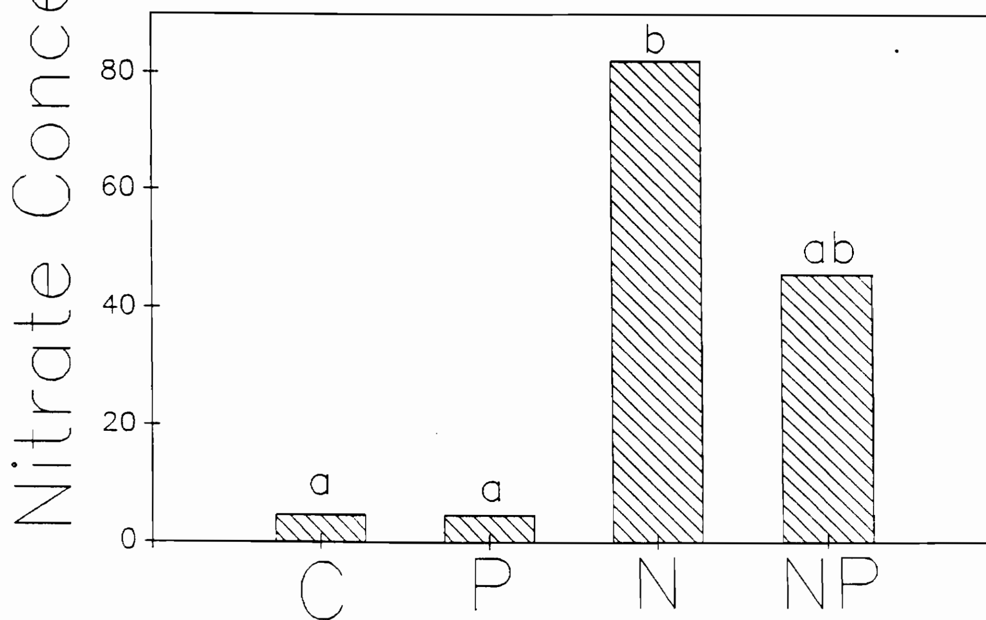


Figure 25: Soil nitrogen (nitrate) concentration in greenhouse. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. August was before nutrients were added. Comparisons using LSD at .05 level. Same letters are not significantly different. Asterisks denote differences within treatments.

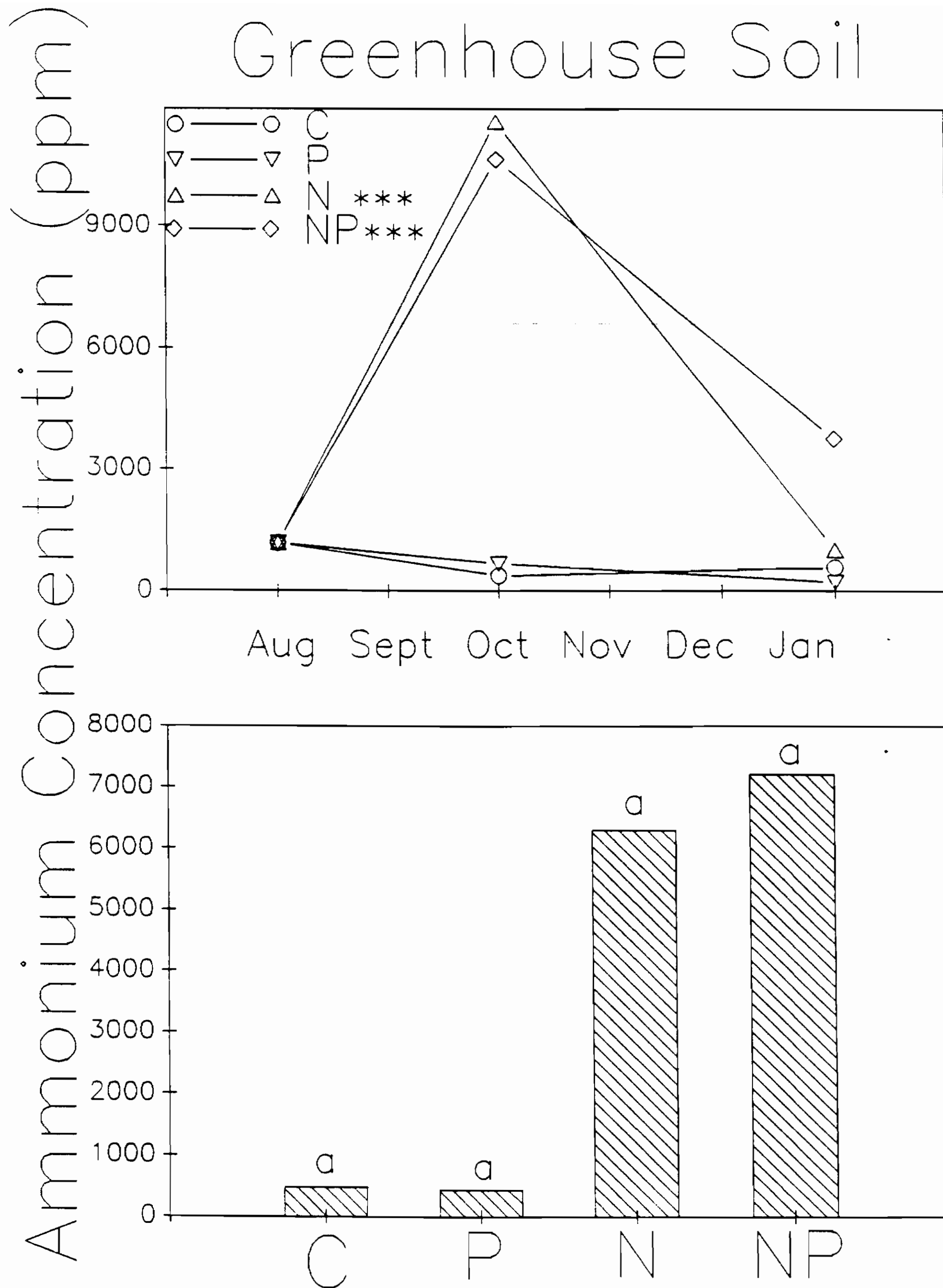


Figure 26: Soil nitrogen (ammonium) concentration in greenhouse. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. August was before nutrients were added. Comparisons using LSD at .05 level. Same letters are not significantly different. Asterisks denote differences within treatments.

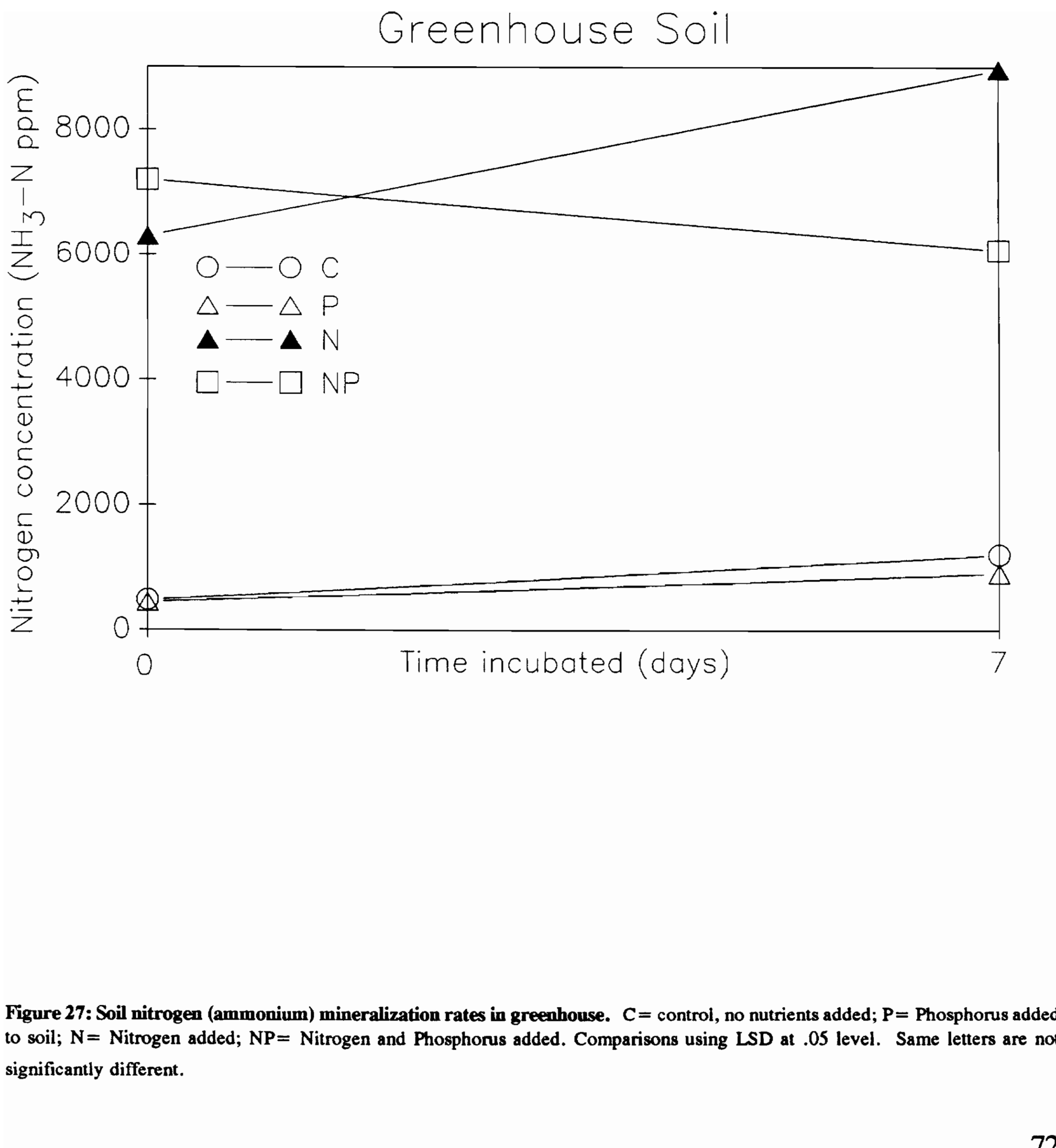


Figure 27: Soil nitrogen (ammonium) mineralization rates in greenhouse. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

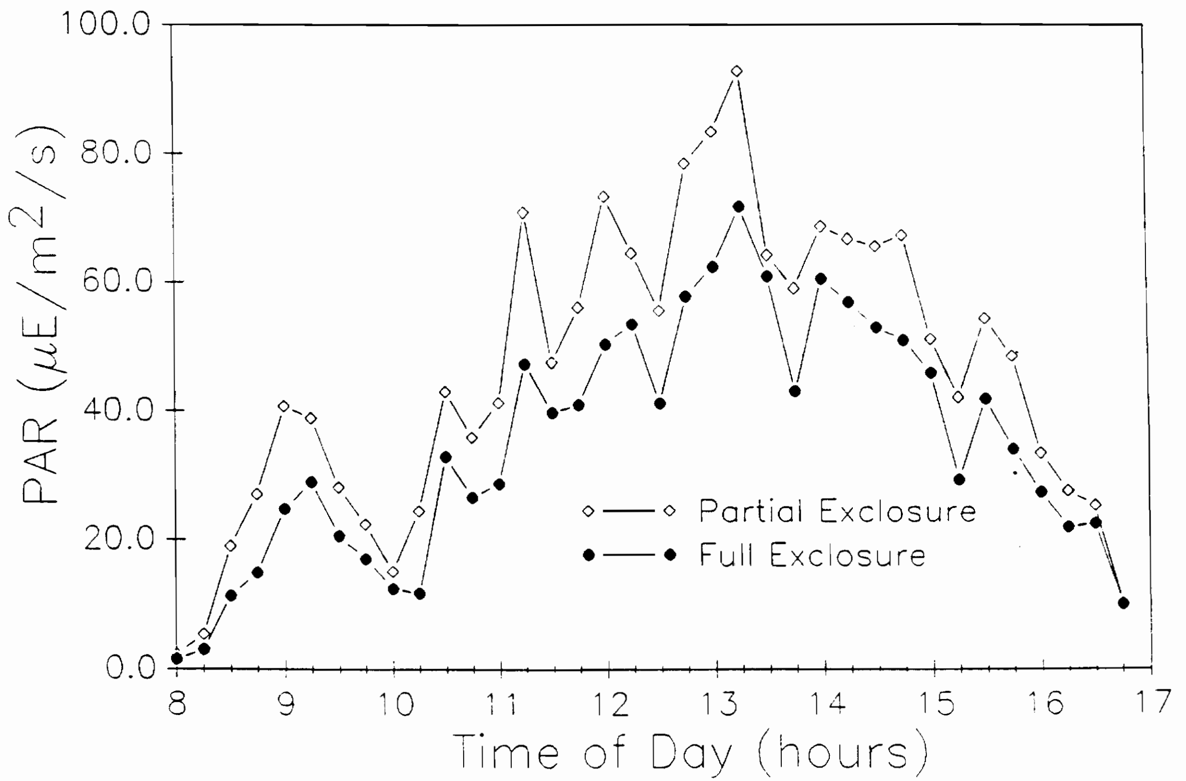


Figure 28: PAR of two microsites in greenhouse. August 9, 1989.

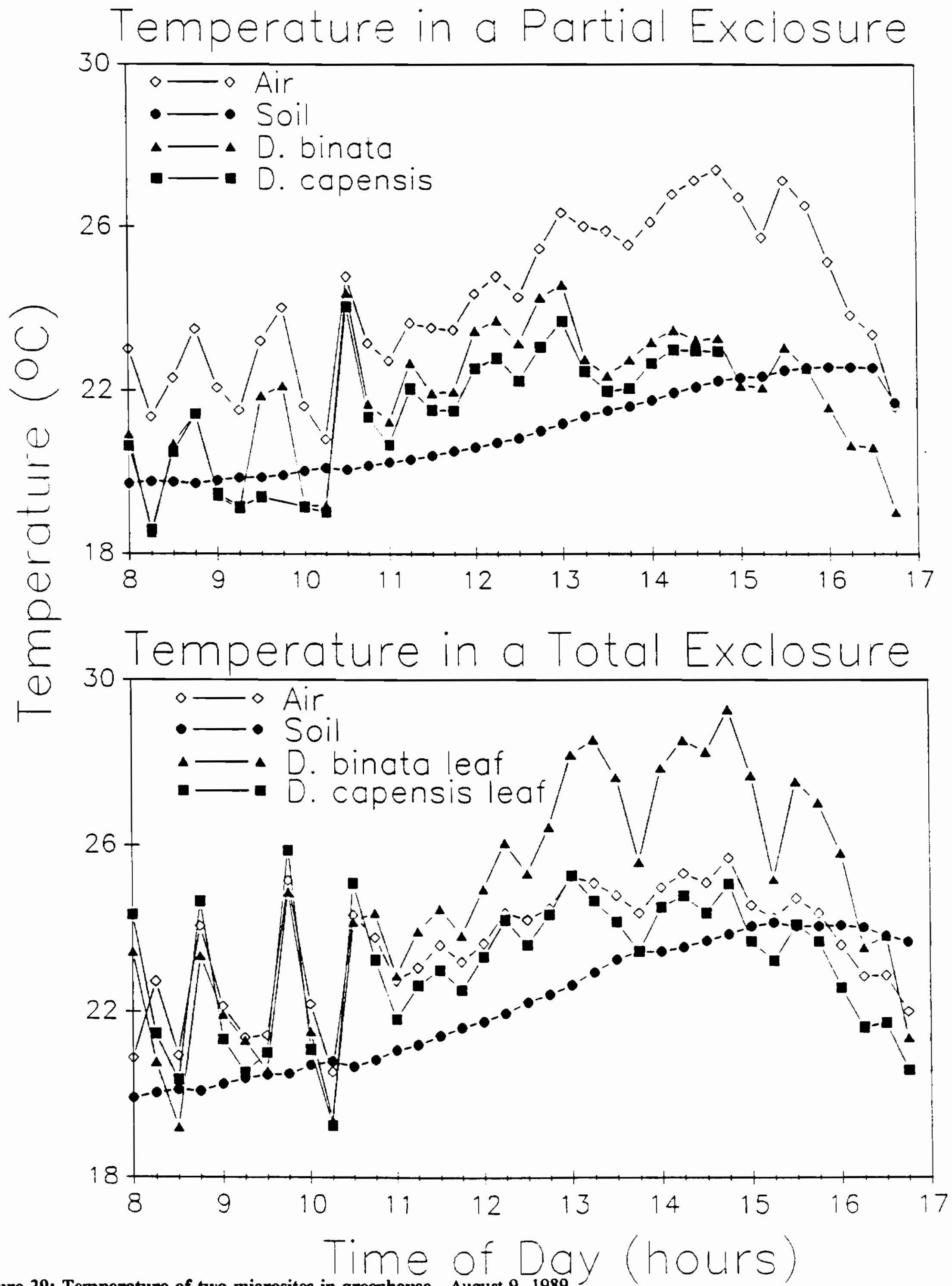


Figure 29: Temperature of two microsites in greenhouse. August 9, 1989.

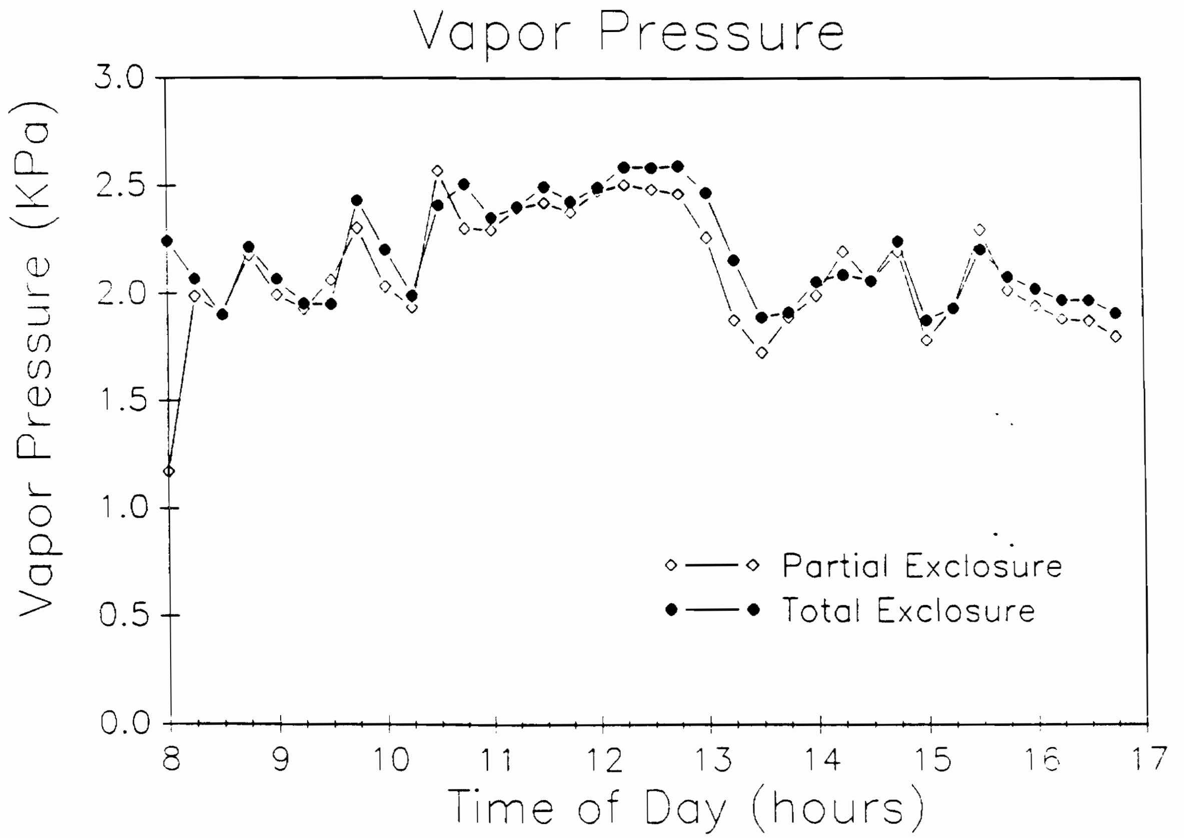


Figure 30: Vapor pressure of two microsites in greenhouse. August 9, 1989.

Plant Measurements: Drosera capensis

Phenology

There were significant differences in leaf numbers as time passed (fig. 31). Plants grew more leaves with time, and also with nutrient treatments, especially NP treatment. There was a marginally significant difference between exclosed and unexclosed plants ($p = .0747$) while exclosed plants had more leaves.

Rosette diameter changed very little over time. There was a marginally significant difference between exclosed and unexclosed plants ($p = .0585$), and exclosed plants had a larger mean diameter (fig. 32). Rosette diameter was larger for plants grown in treatment NP compared to the others.

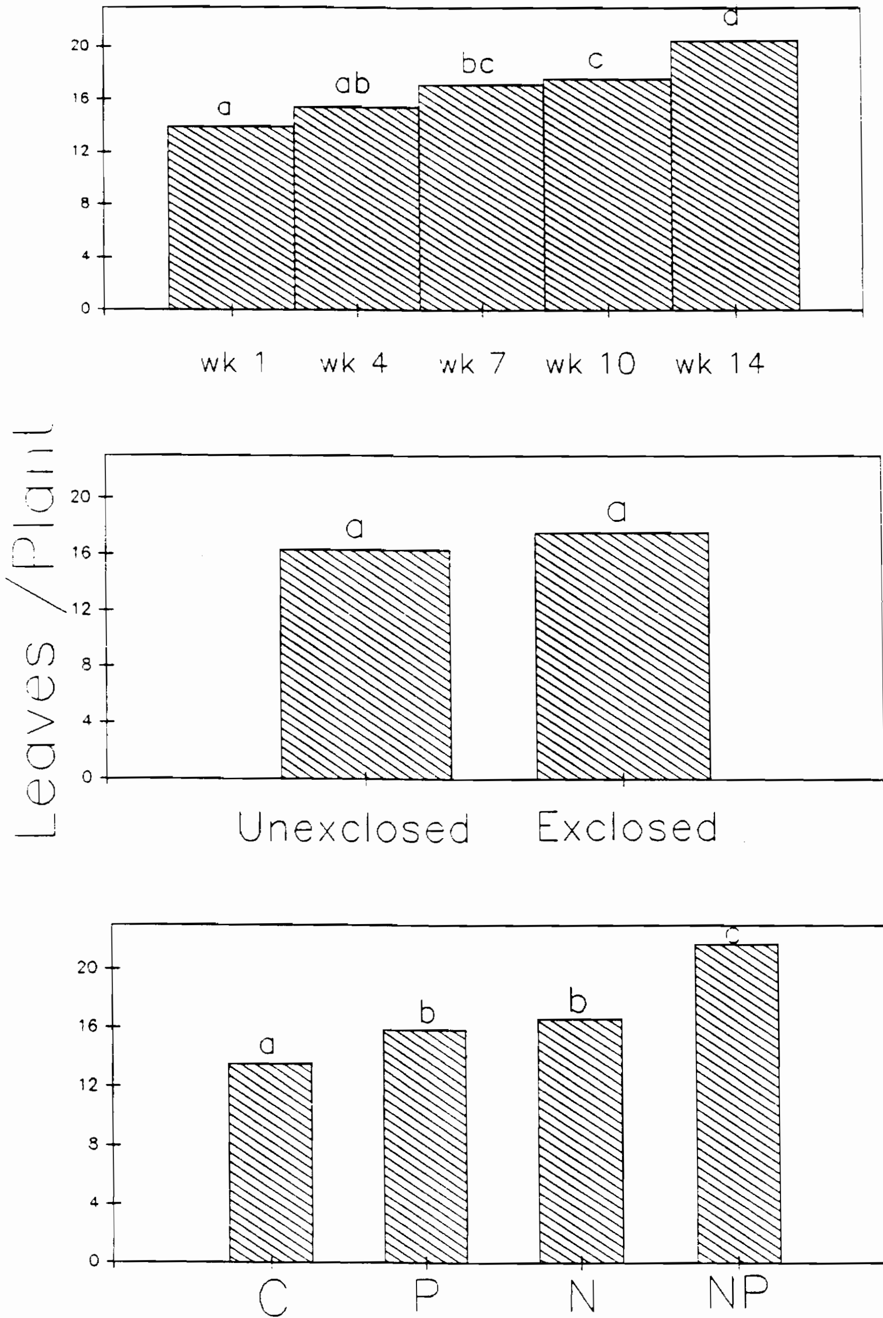


Figure 31: Mean leaf number of the five largest D. capensis plants per plot in greenhouse. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

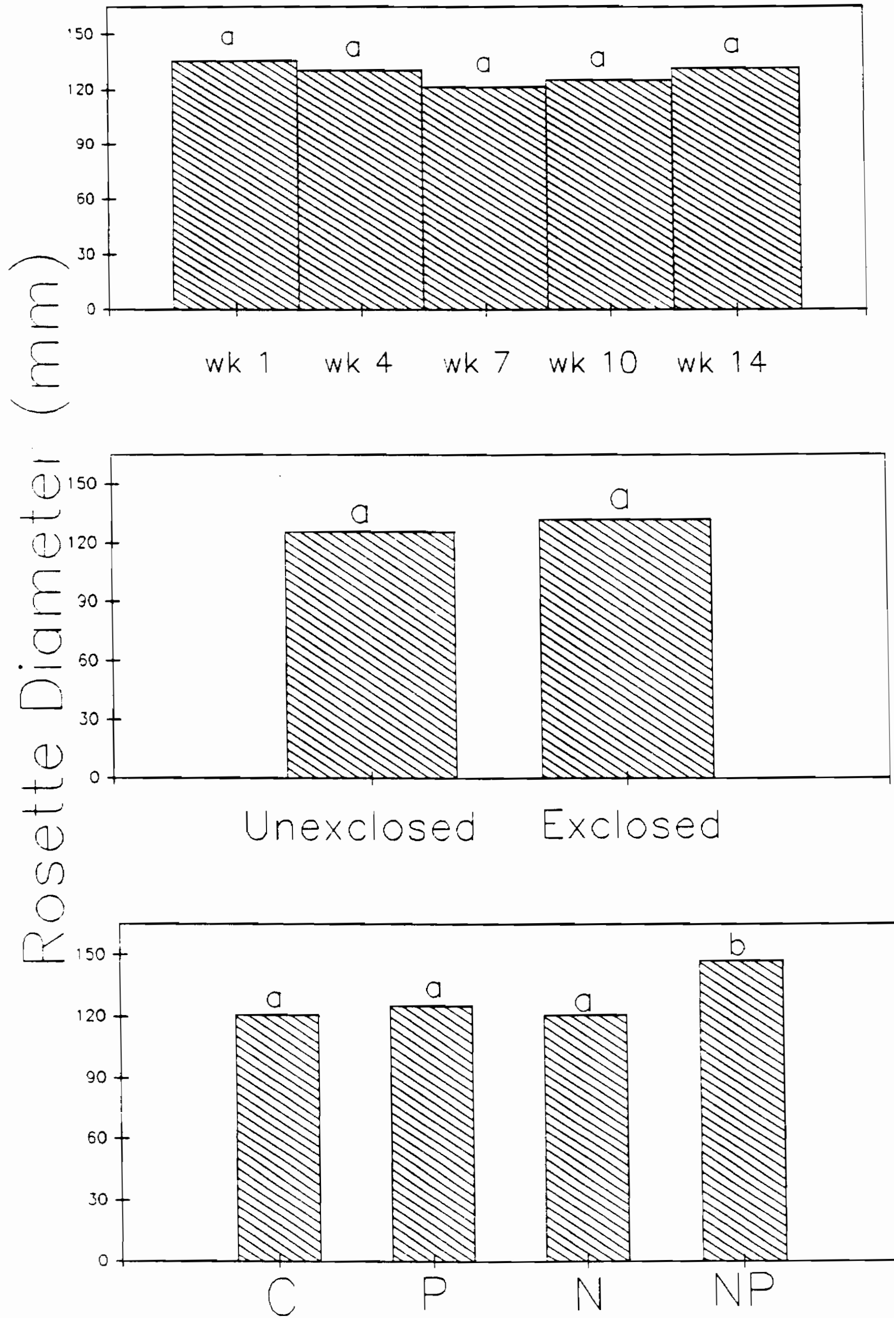


Figure 32: Mean rosette diameter of the five largest D. capensis plants per plot in greenhouse. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

Biomass

Unexclosed and exclosed plants showed no significant difference in biomass (fig. 33). This is true for individual organ biomass partitioning and whole plant biomass. For nutrient addition treatments there were significant differences in root weight. P and N treatments had the largest root biomass followed by NP and C in that order. Most of the biomass for all plants was in stems and leaves. However, the root/shoot ratio was significantly higher for plants in the P treatment (1.2545) compared to the others (NP, .8295; N, .7500; C, .8174). Very little floral production was observed for any groups of D. capensis plants during the experiment.

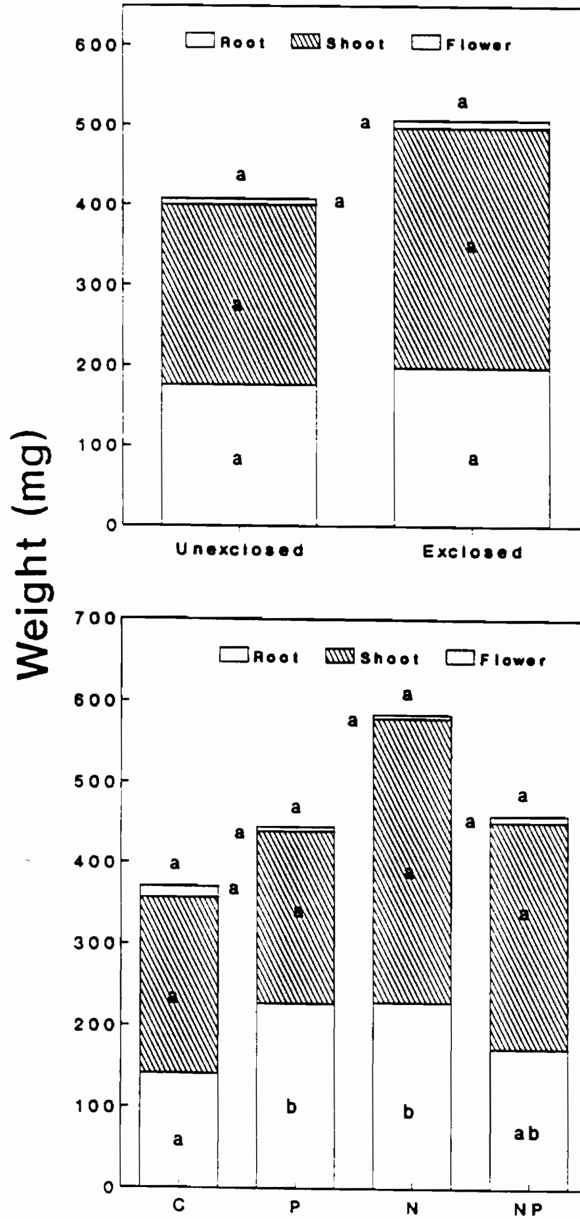


Figure 33: Mean biomass (dry weight) of D. capensis. January 17, 1990. Control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

Nutrient Levels

Figure 34 shows that phosphorus concentration was not significantly different in exclosed and unexclosed plants for any organ or whole plant, but sample size was small (N=8). Roots had a higher phosphorus concentration in unexclosed plants ($p = .1574$). There were significant differences in nutrient treatments. Shoots contained significantly more phosphorus in P and NP treatments. Whole plant phosphorus concentration was greatest in the NP treatment followed by P, N, and C in that order (fig. 36). There were no significant differences in root and flower concentrations. There were no significant differences in nutrient partitioning in spite of greater partitioning to shoots and seemingly higher phosphorus floral partitioning in non-phosphorus addition groups.

Nitrogen concentration (fig. 35) showed moderately significant differences for exclosure type. Nitrogen concentration was higher for roots and shoots in unexclosed plants (roots, $p = .1509$; shoots, $p = .2079$). Nitrogen concentration in flowers was not significantly different. Nutrient treatments containing nitrogen (N and NP) significantly impacted nitrogen concentration in roots, especially treatment NP. Also the whole plant concentration was higher in the NP group (fig. 37). No significant differences were observed for shoots. Not enough floral tissue was available to analyze from treatments N and P. Nutrient partitioning was also not significantly different for exclosure type or nutrient treatments.

Statistical analysis was not possible for total nutrient accumulation in the plant (organs). No phosphorus differences are observed in exclosed versus unexclosed

treatments (fig. 36). Because of large concentrations of phosphorus from P and NP treatments there was seven and eight times respectively more phosphorus in those plants when compared to those in C treatment. Note however that plants from N treatment contained three times

more phosphorus than those in C (most is in roots). Phosphorus found in reproductive structures was minute.

No large differences were observed for total nitrogen between exclosed and unexclosed plants (fig. 37). The patterns of nitrogen accumulation in tissues was similar to phosphorus accumulations. Nitrogen levels per plant (organ) was much higher in plants from N and NP treatments compared to plants from C treatment. To a lesser degree plants from P treatment was also higher. There was little reproductive allocation for nitrogen.

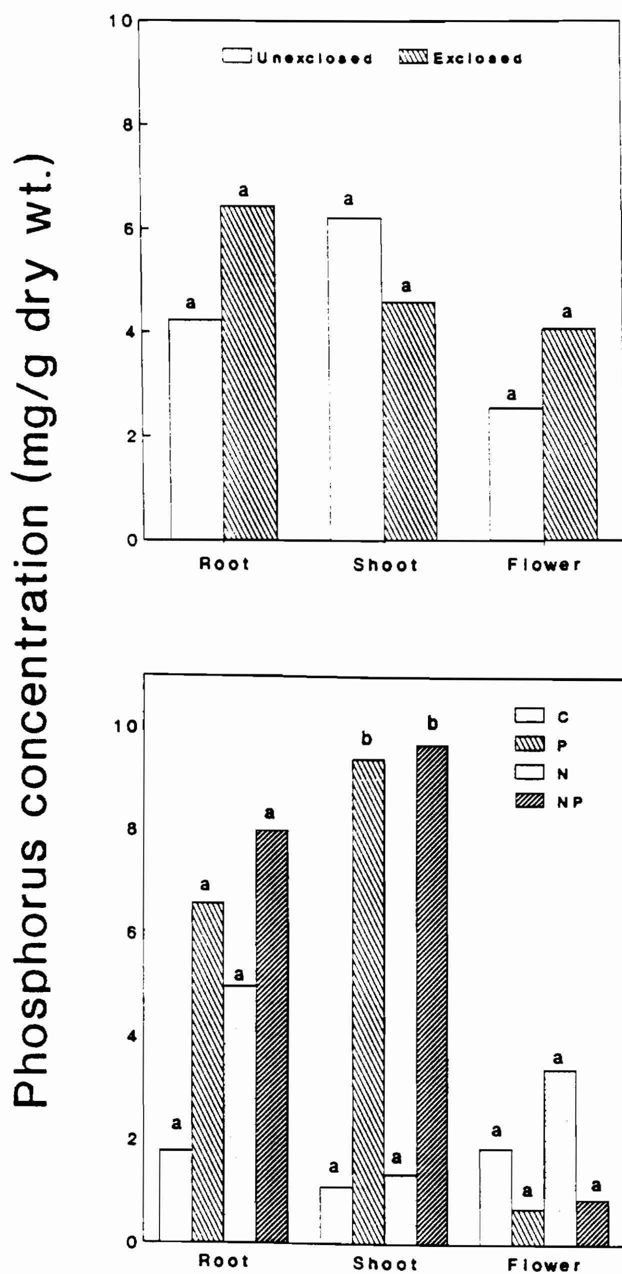


Figure 34: Mean phosphorus concentration of D. capensis. January 17, 1990. Control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

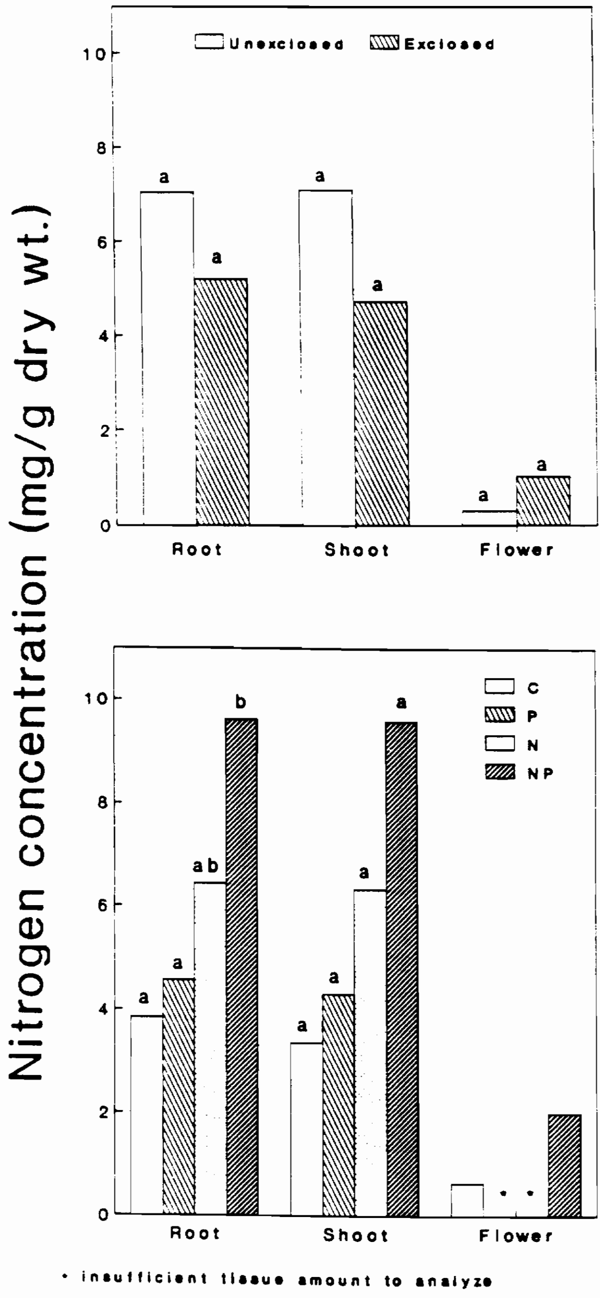


Figure 35: Mean nitrogen concentration of D. capensis. January 17, 1990. Control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

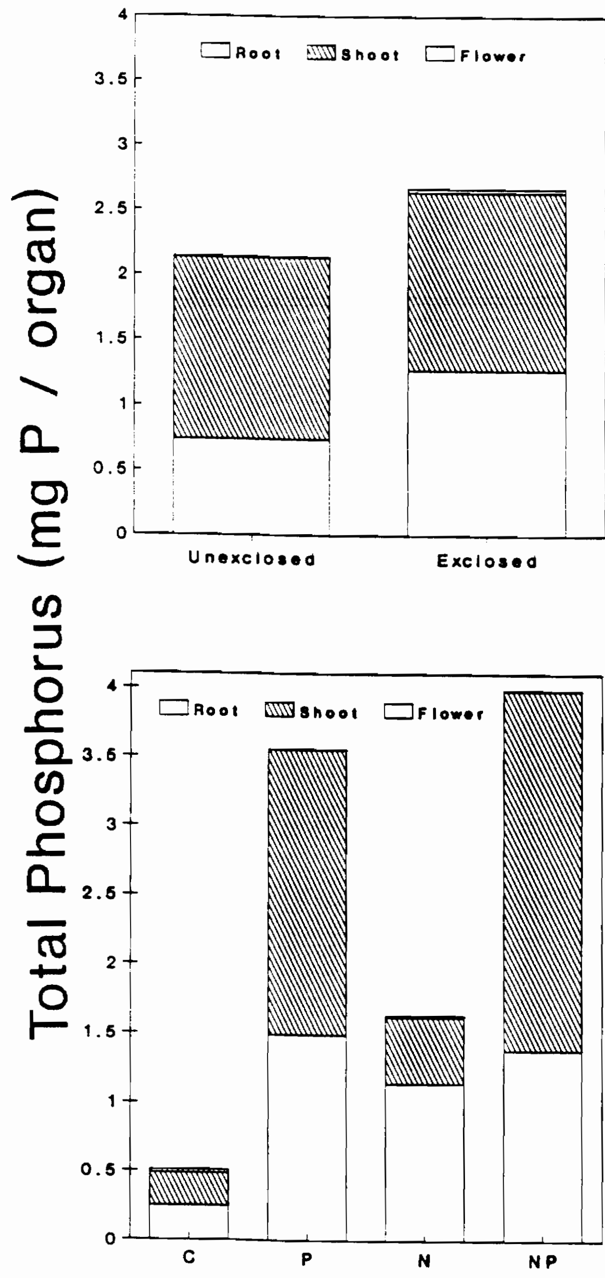


Figure 36: Mean total phosphorus of D. capensis. January 17, 1990. Control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added.

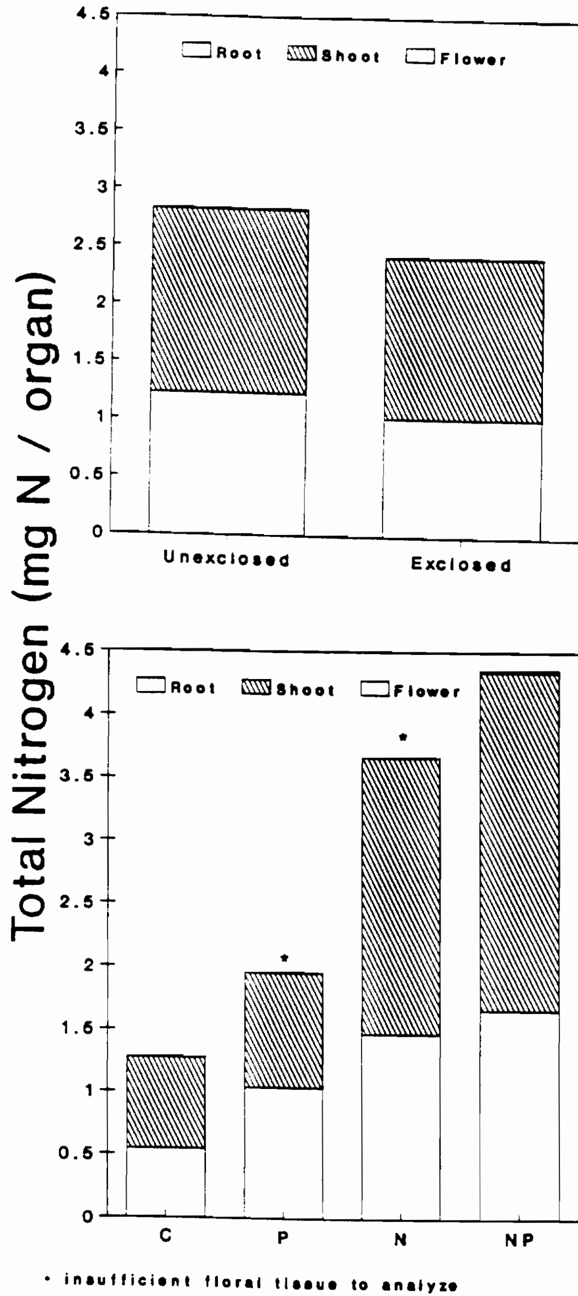


Figure 37: Mean total nitrogen of D. capensis. January 17, 1990. Control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added.

Plant Measurements: Drosera binata var. multifida

Biomass

Significant differences were observed in only one biomass observation (fig. 38). The flower to vegetative ratio was significantly higher in the NP treatment (.2202) than in the others (N, .0342; P, .0066; C, .0150). Nonetheless, some trends can be observed. Exclosed plants had higher biomass, but not significantly ($p = .338$). Only addition of phosphorus increased biomass when compared to C. N and NP treated plants had lower biomass (vegetative).

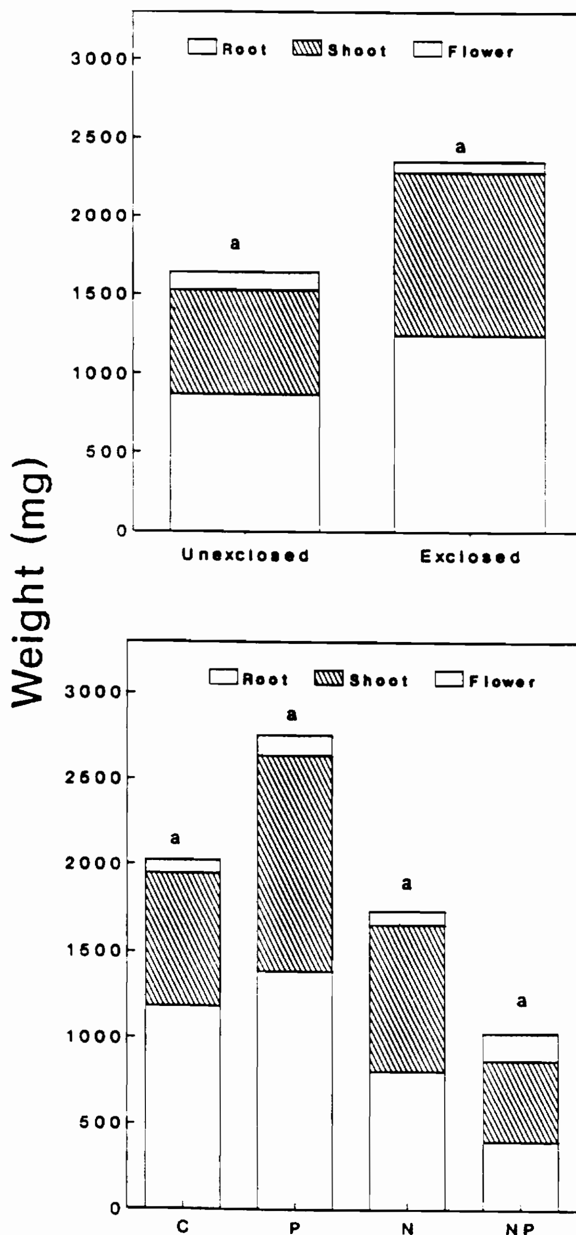


Figure 38: Mean biomass (dry weight) of D. binata var. multifida. January 17, 1990. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different. (Lack of letters signify no significant difference.

Nutrient Concentrations

Phosphorus concentration partitioning showed no significant differences for exclosure type (fig. 39). Flower phosphorus concentrations for exclosed plants were higher with a moderately significant difference (p = .14). In nutrient treatments, however, significant differences were observed. P and NP treatments had higher concentrations of phosphorus in roots and shoots. Moderately significant differences were observed in the flower to vegetative ratio in nutrient treatments (p = .0858), with C (2.5456) being greater than the rest (N, .4692; P, .1835; NP, .3135).

Exclosure types produced no significant differences of nitrogen concentration (fig. 40) with the exception of a moderately significant difference (p = .1171) for flowers. Unexclosed plants had higher nitrogen concentration in flowers. Only shoot nitrogen concentrations were significantly different as a result of nutrient treatments. Shoots in the NP treatment had the highest nitrogen concentration, followed by N, C, and P.

Exclosed plants had slightly higher total phosphorus accumulation than unexclosed due to greater biomass (fig. 41). Nutrient additions show a dramatic difference. P treatment plants exhibited over a 10-fold increase over the control. This was due to higher biomass and higher phosphorus concentration. NP treatment also had higher total phosphorus, but it was due to increased nutrient concentration only (its biomass was only half as much as C). NP treated plants did have higher phosphorus allocation to floral parts.

Figure 42 shows that exclosed plants had slightly more total nitrogen in tissues

than unexclosed because of greater biomass. But, there was more allocation of nitrogen to flowers in unexclosed plants. When compared to phosphorus accumulation, there were not very large differences due to fertilization. N treated plants had somewhat more total nitrogen but NP treated plants had less when compared to control plants. There was higher allocation to reproductive structures in plants in NP treatment.

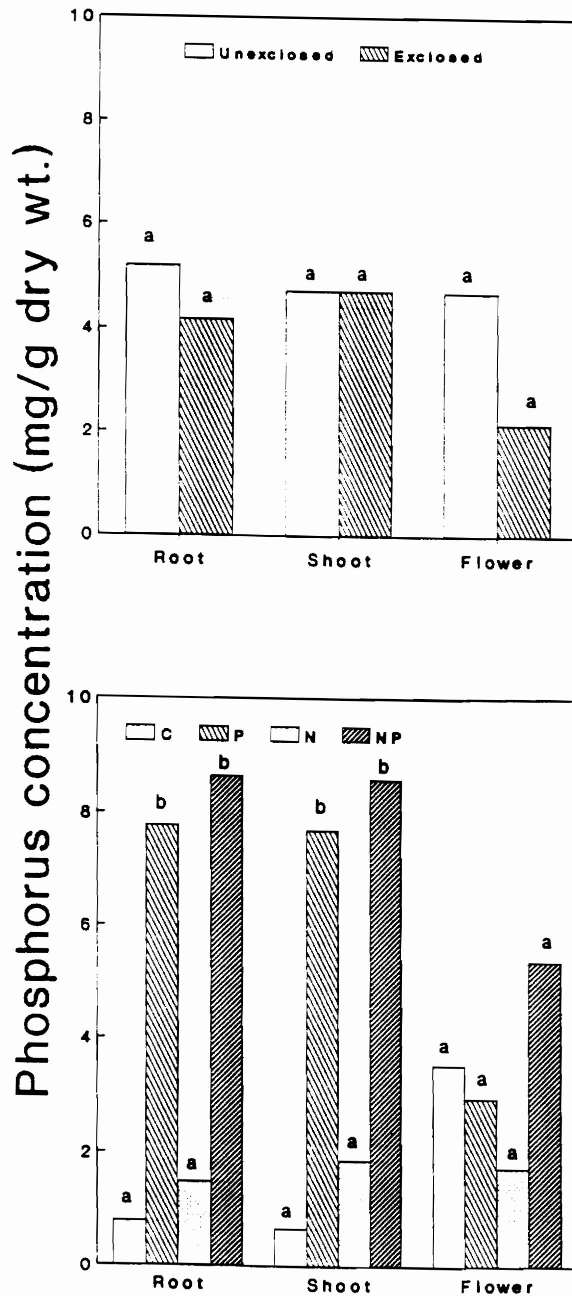


Figure 39: Mean phosphorus concentration of D. binata var. multifida. January 17, 1990. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

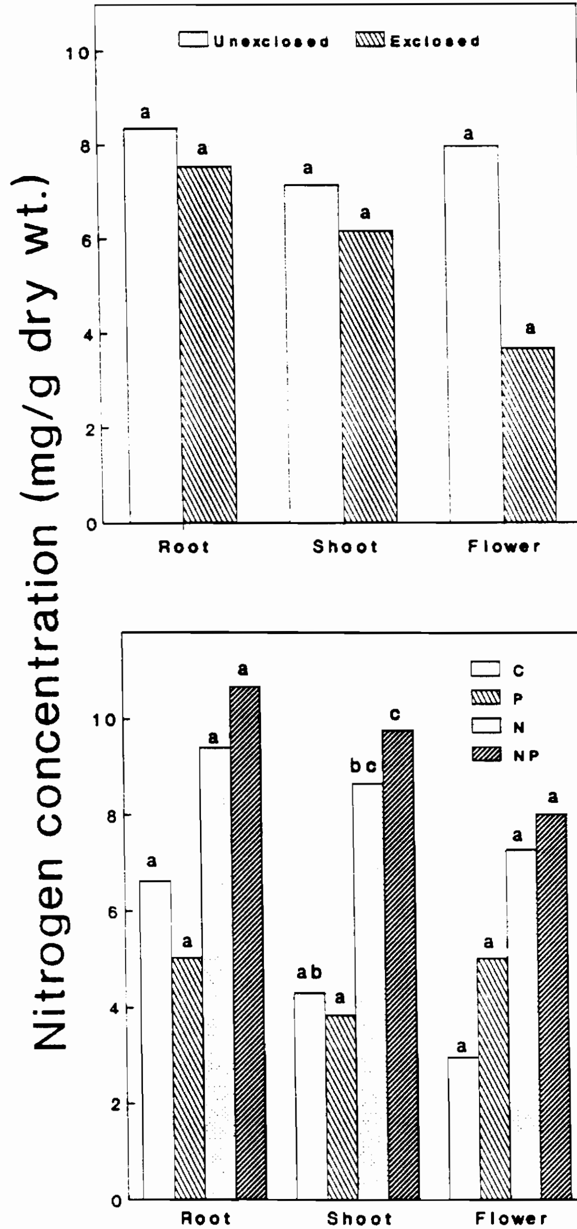
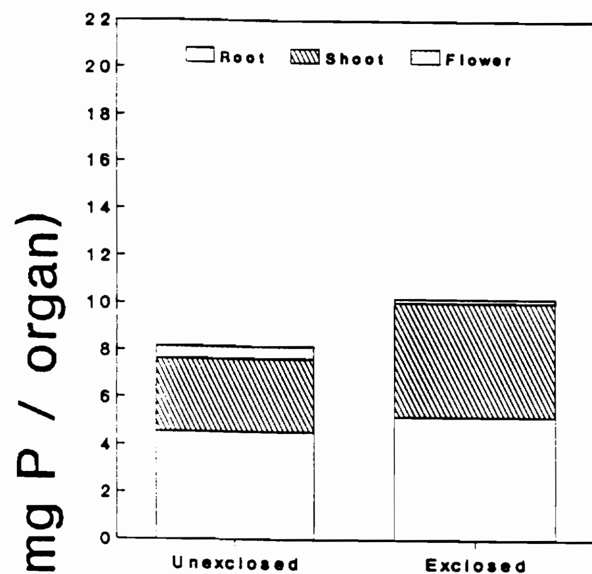


Figure 40: Mean nitrogen concentration of D. binata var. multifida. January 17, 1990. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added. Comparisons using LSD at .05 level. Same letters are not significantly different.

Drosera binata
Total phosphorus



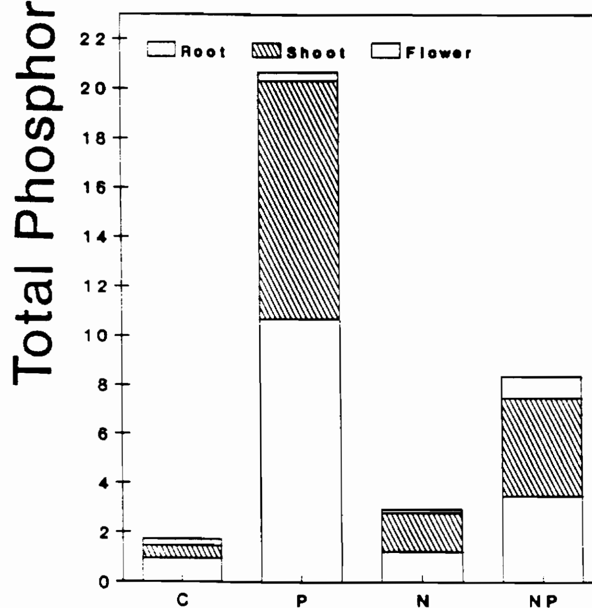


Figure 41: Mean total phosphorus accumulation of D. binata var. multifida. January 17, 1990. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added.

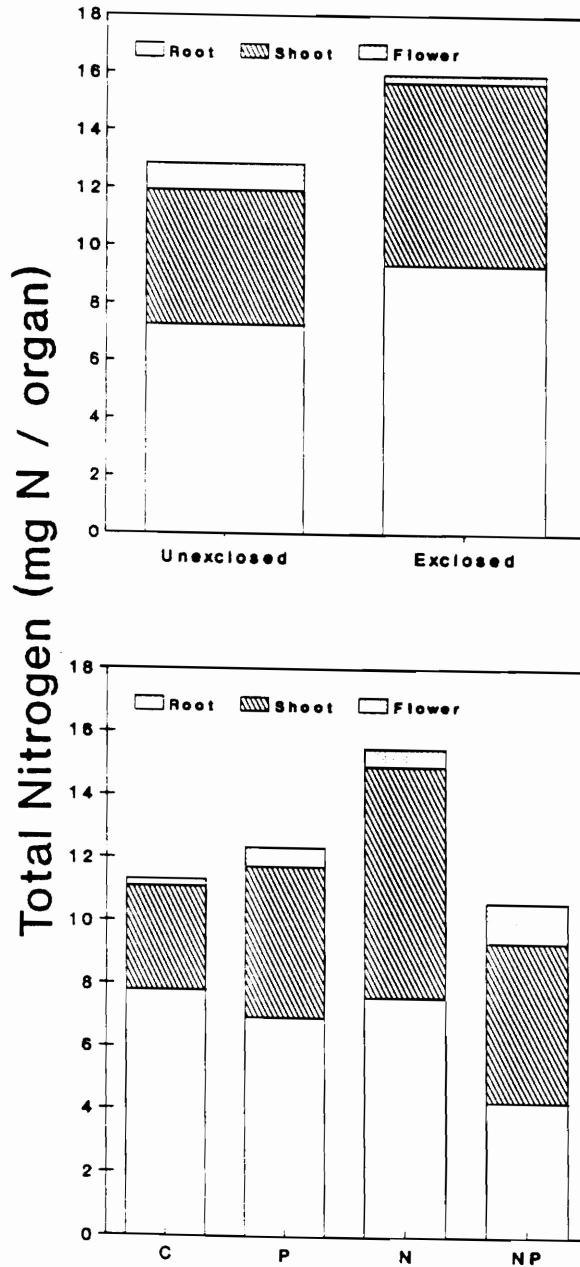


Figure 42: Mean total nitrogen accumulation of D. binata var. multifida. January 17, 1990. C= control, no nutrients added; P= Phosphorus added to soil; N= Nitrogen added; NP= Nitrogen and Phosphorus added.

Discussion

First it must be established that insect exclosures excluded insects from plants. As D. capensis and D binata plants were harvested insect remains were removed and tallied. For D. binata there were an average of 2.34 insects per plant for unexclosed plants and .61 insects per plant for exclosed plants. D. capensis had similar ratios: unexclosed had 2.54 insects per plant, exclosed had .36 insects per plant. Overall, unexclosed plants captured over five times as many insects as exclosed plants. Although the exclosures did not function perfectly, they did an adequate job of excluding most insects.

The first question that I desired to answer pertains to growth, nutrition, and reproduction of Drosera in relation to insect availability. There is no evidence to support the suppopsition that insect availability was positively associated with growth. In fact, exclosed plants actually grew slightly better (figs. 33 and 38). There was also no difference in floral production. There seemed to be no clear patterns regarding nutrient accumulation except that nitrogen levels were higher for all organs in Drosera binata var. multifida, but no significant differences were observed.

The second objective of this study was to determine if nutrient additions to the substrate affected growth, nutrient accumulation, and reproduction in Drosera. Plants grew significantly larger when nutrients were added to the substrate. D. capensis had more mature leaves and larger rosette diameters, especially when nitrogen and phosphorus were added together (figs. 31 and 32). However, the largest biomass occurred in the N

treatment (fig. 33). D binata var. multifida had its largest biomass in the P treatment (fig 38). Both species of Drosera could accumulate nutrients in the tissues. Phosphorus accumulation in tissues was higher where phosphorus was added (P and NP treatments; figs. 34, 36, 39, and 41). Nitrogen was likewise accumulated in tissues (figs. 35, 37, 40, and 42). Reproductive effort seems to be small for both species, but total nitrogen seemed to be slightly higher in NP treated plants (fig. 42).

The third objective refers to interactions between soil-borne nutrients and exposure to insects in growth, nutrient accumulation, and reproduction in Drosera. As with D. rotundifolia, there seems to be little interaction between the two sources of nutrition. Plants responded much stronger to nutrient additions to the substrate, and there seemed to be a lack of nutrient toxicity in these two subtropical species.

D. capensis and D. binata var. multifida are relatively large herbaceous evergreen insectivorous plants. Because of the mild climate of their habitat, a overwintering stage is not necessary. Conversely, their subtropical habitats may be accompanied by more biological pressures, such as competition and predation. Compared to North American species which are highly adapted to nutrient-poor soils, D. binata var. multifida, at least, is found in relatively rich soils (see tables 9 and 10). These sundews also have relatively fast growth rates, growth responses due to pulses of resources, and high nutrient absorption rates through roots. These characteristics approach those found in fast growth species and are not typical of bog plants or insectivorous plants (Chapin, 1980, 1987; Givnish et al., 1984; Coley et al., 1985).

These characteristics suggest that D. binata and D. capensis do not rely heavily upon insectivory for their nutrition, since they are adapted to high nutrient sites. They are also large enough to better compete with fast growing graminoid species for light. In addition, these species are able to accumulate significant amounts of nutrients in shoots and roots through luxury consumption (figs. 35--42). This ability to take advantage of flushes of nutrients or continually high nutrient concentrations in the soil suggest that insectivory may not be necessary for the success of these plants. Because these species form perennial stems for potentially long lives in their habitats, supplementary nutrition through insectivory for seed production may not be as important as some smaller insectivorous plants, although more allocation to reproductive structures was observed in NP treatment for D. binata (fig. 42).

It appears that insectivory could potentially be beneficial to these species, even though exclosed plants grew better than unexclosed plants (figs. 34 and 39). This is because of the slightly positive response of added nitrogen, and to a lesser extent phosphorus, for D. capensis (figs. 36, and 37), and phosphorus for D. binata (figs. 38, 40, and 41), suggesting that these elements were initially limiting. Nutrition through insectivory would only be important on very nutritionally depauperate soils. But, we have seen that these species grow in soils with adequate nutrients. However, there seems to be more than enough absorptive capacity from roots to supply these species with adequate nutrients and to reasonably believe that nutrition through insectivory is insignificant, in natural settings, for D. capensis and D. binata var. multifida.

Table 9. Soil nutrient levels of sundew-supporting Australian bog soils (Chandler and Anderson 1976).

Species	pH	---------ppm--------- Total P	Total N
D. binata	5.0	15	23
D. binata	4.8	22	128
D. binata	4.8	15	146

Table 10. Soil nutrient levels of sundew-supporting North American bog soil (Stewart, unpublished data).

Species	pH	--------ppm---------- Total P	NH_4-N
D. capillaris	4.6	0	13
D. capillaris	4.2	0	10
D. capillaris	4.8	0	10
D. intermedia	5.0	1	9
D. intermedia	4.3	1	15
D. intermedia	4.7	3	8
D. rotundifolia	4.6	0	10

Conclusion

Since the time of Charles Darwin's extensive research on Drosera rotundifolia and subsequent publication of his book Insectivorous Plants (1875), it was assumed by most that insectivory is an important source of nutrition for insectivorous plants in their natural habitat. This conclusion has come about from the rationalization that complex trapping and digestion processes consisting of lures and enzymatic systems which cost energy must have some logical purpose (i.e. nutrition). It has further been suggested that this nutrition source better enables insectivorous plants to compete for resources. This has further been supported by physiological and ecological research primarily in laboratories and greenhouses. Nevertheless, I have attempted to acquire data from experiments performed on plants in their natural environment (D. rotundifolia), or when that has not been practical, in a greenhouse experiment using established populations in common plantings (D. capensis and D. binata).

The data show that insectivory is probably not an important source of nutrients for these three species of sundews for different reasons.

D. rotundifolia seems to be so well adapted to low nutrient habitats through a high nutrient use efficiency and reabsorptive hibernaculum, that additional nutrition negatively affects growth and flowering. D. rotundifolia appears to have such a very specific nutrient regime, that it is detrimental when even slight nutrient excesses are received.

On the other hand, D. capensis and D. binata are more adapted to relatively rich soils and have a high absorptive capacity to exploit high nutrient levels in soils. Because

of highly absorptive roots and the ability for luxury consumption when nutrients are available, there seems to be little need for insectivory for survival. Unlike D. rotundifolia, these two subtropical species may be able to take advantage of insectivory as a significant supplemental source of nutrients without occurring potential detriment. However, the soil status in their natural habitats makes that an unlikely prospect.

Additional study under differing nutrient regimes for various insectivorous plants will perhaps give the answer to the question of significance of insectivory. It appears this answer may be specific for individual species or genera. A more pertinent question is why would a plant expend energy on capturing and digestive devices if resultant insectivory is not significant nutritionally or energetically?

Before these plants were known to be insectivorous it was assumed first by Erasmus Darwin (1791) and then others that the glandular trichomes were an antiherbivory mechanism. Nearly 300 years later Coley, et al. (1985) provided the theoretical framework explaining why this may be the case. They propose that plants with intrinsically slow growth rates and slow leaf turnover rates favor large amounts of antiherbivore defense. No herbivory was noted in any of the sundews used in this research project. Perhaps the glandular trichomes were originally solely an antiherbivore defense mechanism, and the enzymes came later. Perhaps antiherbivory is the primary service trichomes now provide to the plant. It is possible that even though the sundews studied in this project showed little reliance upon insectivory for nutrition, that other insectivorous plants are not so well adapted to their abiotic environments. With additional

research in this field maybe we will be able to theoretize with more confidence about the significance of plant insectivory.

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Vita

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