

## *Drosera rotundifolia* growth and nutrition in a natural population with special reference to the significance of insectivory

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The impact of nutrient addition on growth and nutrient accumulation in *Drosera rotundifolia* was studied in a field population. Experiments were performed by excluding insects and (or) adding phosphorus and (or) nitrogen to soil. *Drosera rotundifolia* did not significantly benefit from insect capture nutritionally or energetically in native or nutritionally enhanced soils. Added nutrients to the soil or supplemental foliar insect feeding decreased phosphorus retention in hibernacula by 50%. Nutrient additions reduced *D. rotundifolia* vegetative growth in both N and P addition treatments. In addition, allocation to reproduction (inflorescences) decreased by 98% when N was added to the soil. Phosphorus retention in hibernacula was especially high in plots in which no nutrients were added via the soil or by insect applications. Although not statistically significant, flower stalk density and floral biomass were greater where insects were available to plants. The data from this study indicate that insectivory has little impact on growth of field grown *D. rotundifolia*. This species is adapted to low nutrient availability and nutrient enhancement reduces growth. Indices of nutrient retention suggest that phosphorus is conserved more than nitrogen and therefore may be an important limiting nutrient.

*Key words*: insectivory, nitrogen, phosphorus, sundew.

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La force d'impact des nutriments sur la croissance et l'accumulation des nutriments en *Drosera rotundifolia* a été étudiée dans une population naturelle. Les expériences ont été faites par l'exclusion des insectes et (ou) l'addition du phosphore et (ou) de l'azote au sol. *Drosera rotundifolia* n'a pris aucun avantage de la capture des insectes nutritivement ou énergiquement dans des sols naturels ou artificiellement améliorés. L'addition des nutriments à la terre ou l'addition des insectes au feuillage a diminué la conservation du phosphore en l'hibernacle par 50%. L'addition des nutriments a réduit la croissance végétative pour les traitements d'azote et du phosphore. De plus, l'allocation aux inflorescences a diminué par 98% avec l'addition d'azote à la terre. La conservation du phosphore dans les hibernacles était particulièrement élevée dans les lotissements de terre sans nutriments ou insectes. Quoique pas significatif statistiquement, la densité des queues floral et masse floral était accessible aux plantes. La données de cette étude indiquent que manger des insectes ne fait aucun effet sur la croissance des populations natives de *D. rotundifolia*. Cette espèce s'adapte à l'environnement avec peu de nutriments, et l'augmentation des nutriments réduit la croissance. Les indices de la conservation des nutriments suggèrent que le phosphore est conservé plus que l'azote et par conséquent peut être un nutriment limitant important.

*Mots clés* : manger des insectes, azote, phosphore, *Drosera*.

### Introduction

Members of the genus *Drosera* (sundews) possess foliar glandular trichomes that trap insects. The ability to do so makes them insectivorous. As a matter of definition, insectivorous plants must have 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 or prey." This definition assumes a benefit from insectivory and therefore a significant contribution from insectivory to plant nutrition status.

The morphological adaptations to attract and digest insects are thought to be mechanisms that mitigate the low nutrient availability characteristic of bog and acid sandy soils. Two nutrients thought to be limiting are nitrogen (Chandler and Anderson 1976) and phosphorus (Weiss 1980). Although there have been many studies of insectivorous plant nutrition (Darwin 1875, 1878; Roberts and Oosting 1958; Plummer 1963; Dore Swamy and Mohan Ram 1969, 1971; Chandler and Anderson 1976; Christensen 1976; Dixon et al. 1980;

Weiss 1980; Watson et al. 1982; Aldenius et al. 1983; Wilson 1985; Thum 1988; Schulze and Schulze 1990; Krafft and Handel 1991), only a few have examined the significance of insectivory in the field (Weiss 1980; Thum 1988). 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 been derived mainly from laboratory or greenhouse experiments and not from field experiments. Since abiotic and biotic interactions exist in natural plant communities, it is important to perform field experiments.

The objective of this study was to determine if insectivory provides a significant contribution to *Drosera rotundifolia* nutrition. This was determined by examining indices of plant growth, tissue nutrient status, and allocation schedules in a field population in which insect availability to the leaves and N or P availability in the soil are modified.

### Species and site description

*Drosera rotundifolia* is a small herbaceous plant with a slender stem surrounded by a recumbent rosette of leaves. Flowering scapes arising out of leaf axils bear several perfect flowers. Flowers bloom in midsummer, 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

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blades are orbicular, wider than long, and covered with glandular trichomes that serve to trap insects (Schnell 1976). 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 (personal observation). At the onset of autumn, leaves and sometimes roots abscise and a hibernaculum forms (Swales 1975). A hibernaculum is a vegetative overwintering bud.

*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 bog (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 (longitude 80°36'00"E and latitude 37°22'30"N) was located in northern Giles County, Virginia, U.S.A., in Jefferson National Forest. This particular bog is one of the Interior Bogs, a series of small 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 0.053 ha. 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 that empties into a drainage pipe flowing under a road bordering one edge of the study area. The study site was bounded by deciduous forest on three sides and an alder thicket and road on its northern long side.

## Materials and methods

### Design

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

*Presence or absence of complete insect enclosures* — Both complete and incomplete insect enclosures (also called partial enclosures or unenclosed plots) had an A-frame made of cpvc pipe and a wooden dowel rod. All materials were light-colored to maximize brightness inside the enclosure. Mosquito netting was used as a covering for both designs. Complete enclosure 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 enclosures were made the same way as the others, but fabric terminated approximately 10 cm above the ground surface. Complete enclosures were located along one side of a small stream or footpath, and partial enclosures 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 was rectangular (65 cm × 1.05 m) and occupied 2/3 m<sup>2</sup> of ground area.

*Blocks* — Since slight differences in soil and vegetation characteristics were observed the summer before this experiment was set up, another replication of the basic experiment was performed in tandem. Five complete enclosures (with nutrient treatments C, F, P, N, NP) and five incomplete enclosures (with nutrient treatments C, F, P, N, NP) constituted a block. There were two blocks with 10 replications per block.

*Nutrient treatments* — There were five nutrient treatments with four replications per treatment. Five nutrient groups within both com-

plete and partial enclosures were set up randomly within blocks at the beginning of the experiment during the 1st week of May 1989 as follows: (i) Nitrogen addition (N) in which 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. (ii) Phosphorus addition (P) in which 130 g of phosphorus was applied per P plot in the form of 0-46-0 triple superphosphate. It was applied in the same manner as nitrogen. As this was not a slow release fertilizer, all plots were monitored monthly. (iii) Nitrogen and phosphorus addition (NP), which 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). (iv) Supplemental foliar insect feeding (F) in which once a month, from June to August, one *Drosophila melanogaster* was placed on a leaf of each plant in the F treatment. (v) Control (C) in which no nutrient manipulations or feedings were done on this group.

*Time* — Four types of phenological measurements of plant growth or success were taken once a month in June, July, and August 1989. Time was not a factor for biomass measurements and plant tissue nutrient analyses, since there was only one destructive harvest of plants with leaves in August and a hibernaculum harvest in October.

### 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, away from the experimental plants. Soil samples were air dried and ground to pass a 2-mm sieve. Phosphorus, nitrate, and other macronutrient concentrations were obtained using a double acid extract procedure (Page et al. 1982). Soluble salts were determined using a KCl extraction followed by measurements with a conductivity meter. Ammonium pools were analyzed with a 2 M KCl extract procedure (Page et al. 1982) and using a specific ion ammonium electrode system (Orion). We also measured ammonium mineralization rates by using 7-day anaerobic incubations (Page et al. 1982).

### Microclimate

Microclimate of a complete enclosure, an incomplete enclosure, and a plot in which there was no artificial cover was measured on August 9, 1989. This was a partly sunny day. We chose plots that were close to each other and towards the center of the bog to ascertain whether there were microclimatic differences owing 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 min, beginning at 07:30 and ending at 19:00 using a micrologger (Campbell Scientific CR21 or 21X). 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 a relative humidity sensor (Campbell XN217, 207, or 201). Relative humidity and air temperature were used to calculate vapor pressure. PAR was measured using a quantum sensor (Li-cor 190s) set at soil level and parallel with the soil surface.

### Plant measurements

#### Phenology

Measurements taken were leaf numbers, rosette diameters, flower stalk numbers, and plant density. The five largest sundews were measured monthly. 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<sup>2</sup> area, a subplot under each structure was established to monitor plant density. A circular string enclosing 374 cm<sup>2</sup> of ground area was randomly placed in the plot.

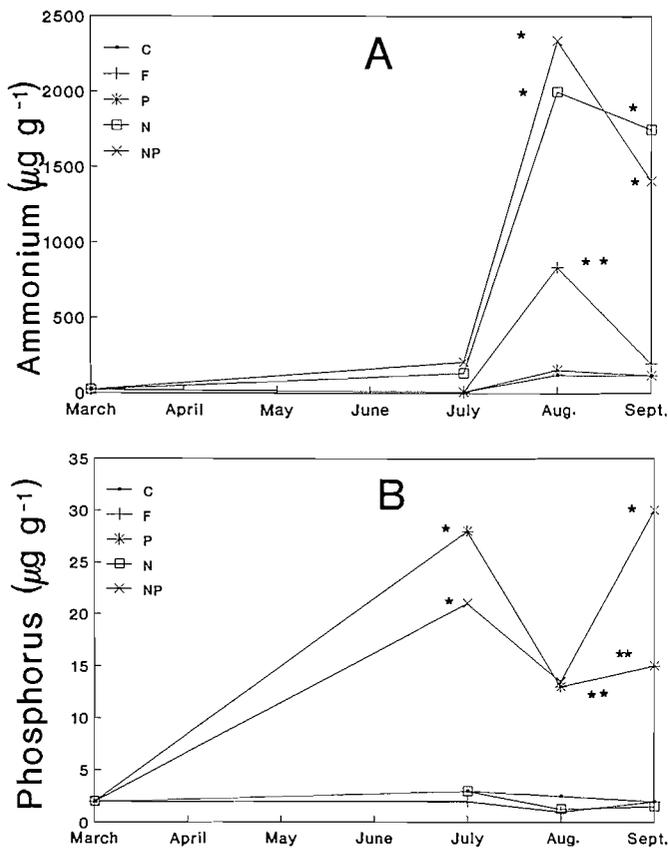


FIG. 1. Interior Bog soil nutrient status during 1989. (A) Ammonium. (B) Phosphorus. Treatments: C, control; F, foliar feeding (one *Drosophila melanogaster* per month during growing season); P, phosphorus addition to soil; N, nitrogen addition to soil; NP, nitrogen and phosphorus additions to soil. Statistical analysis: ANOVA with multiple comparisons using Fisher's LSD. Asterisks denote significant differences at  $\alpha = 0.05$ .

The number of flower stalks and the number of plants occurring within the subplot were counted each month.

Plants were randomly harvested, regardless of size, in October. Rosette diameters, leaf number, and floral output were measured at this time for all harvested plants.

#### Biomass

In August 1989 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. Samples were dried at 40°C for 2 days, and dry weights were taken for bulk samples partitioned by organ and plot. Dried samples were stored in airtight plastic vials until nutrient analysis could be performed. Another harvest was done at the onset of dieback in October. At the 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.

#### Nutrient concentrations

Total nitrogen in plant tissues was obtained by using Kjeldahl digestions (Kjeltec Auto 1030 analyzer) according to methods outlined by Chapman (1976). Total phosphorus was determined colorimetrically (Gilford response) using the modified Fiske and Subbarow method (Kabat and Mayer 1948). Tissue was bulked within treatments and tissue components for nutrient analyses.

All statistical analyses were done using an ANOVA with multiple comparisons using Fisher's LSD at the 0.05 level (Zar 1974).

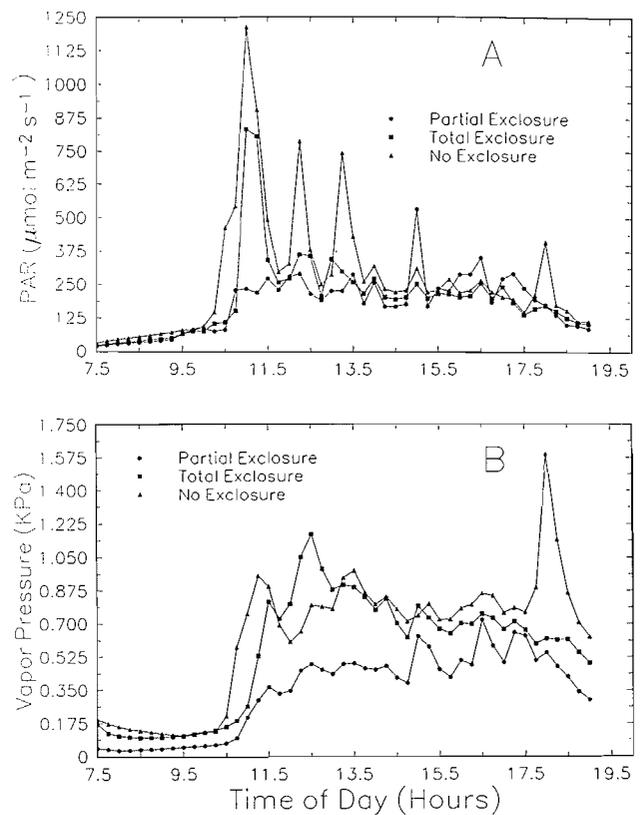


FIG. 2. Climatic conditions at Interior Bog in western Virginia on August 9, 1989. (A) Photosynthetically active radiation (PAR). (B) Air vapor pressure.

## Results

### Soil conditions

Soil nutrient levels changed negligibly in plots not receiving nitrogen or phosphorus, so cross-contamination due to lateral nutrient movement did not occur from nutrient applications, except for a slight rise in the F treatment in August (Fig. 1). Fertilizer treatments did, however, significantly elevate N and P pools in the soil about 10-fold. Nearly all of the inorganic nitrogen was available as ammonium, as the nitrate pool among all treatments was negligible (3–8  $\mu\text{g} \cdot \text{g}^{-1} \text{NO}_3\text{-N}$ ) when compared with ammonium pools. Phosphorus levels in the soil increased by July, but nitrogen levels did not rise sharply until August. Nitrogen mineralization rates were (in  $\mu\text{g}/(\text{g} \cdot \text{d})$ ) as follows: C, 102.9; F, 110.0; P, 168.5; N, 121.4; NP, 471.4. They were largely unaffected by added nutrients except for the NP treatment, which was significantly different at the 0.05 level.

### Microclimate

The daily temperature in the bog did not differ from that of the surrounding area. National Oceanic and Atmospheric Administration's (NOAA) cooperative reporting station closest to the bog (Staffordsville, Va.) reported a daily 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 and 700 nm) appeared to be similar among plots for most of the partly sunny day in which micro-

TABLE 1. *Drosera rotundifolia* phenology at Interior Bog, Giles County Virginia (August 1989)

Treatment	Leaves/plant	Rosette diam. (mm)	Flower scape density (no./m <sup>2</sup> )	Plant density (no./m <sup>2</sup> )
C	8.3a	54a	8.50a	577.1ab
F	7.8b	54a	10.13a	608.3a
P	4.9d	38b	3.88b	398.9bc
N	7.1c	41b	0.13b	167.2d
NP	7.7b	40b	2.83b	236.2cd
Unexclosed	6.3a	43a	6.5a	401.95a
Exclosed	7.7b	48b	4.1a	393.6a

NOTE: Treatments were as follows: C, control; F, foliar feeding (one *Drosophila melanogaster* per month during growing season); P, phosphorus addition to soil; N, nitrogen addition to soil; NP, nitrogen and phosphorus additions to soil. Statistical analysis was ANOVA with multiple comparisons using Fisher's LSD. Different letters in columns indicate significant differences at  $\alpha = 0.05$ ,  $n = 20$  per treatment.

TABLE 2. *Drosera rotundifolia* biomass (mg per organ) for mature plant harvest (August 1989) and hibernacula harvest (October 1989) at Interior Bog, Giles County Virginia

Treatment	Mature plant				Hibernaculum
	Root	Shoot	Flower	Total	
C	6.47a	17.07a	7.68a	31.21a	32.24a
F	6.10a	13.47b	5.83b	25.33ab	24.86b
P	2.77c	8.39c	1.54b	12.46d	19.54c
N	4.48b	14.33b	4.16b	22.96bc	30.92a
NP	3.86bc	10.51c	6.38ab	20.75c	18.69c
Unexclosed	4.28a	10.30a	5.97a	20.55a	25.47a
Exclosed	5.09b	15.20b	4.27a	24.56b	26.17a

NOTE: Root, shoot, and flower biomass partitioning and total indicate mature plant dry weights. Hibernacula are winter bud dry weights. Treatments were as follows: C, control; F, foliar feeding (one *Drosophila melanogaster* per month during growing season); P, phosphorus addition to soil; N, nitrogen addition to soil; NP, nitrogen and phosphorus additions to soil. Statistical analysis was ANOVA with multiple comparisons using Fisher's LSD. Different letters in columns indicate significant differences at  $\alpha = 0.05$ ,  $n = 20$  per treatment.

climate was measured (Fig. 2). PAR within a total enclosure more closely followed that of no enclosure than the partial enclosure during sunflecks. This suggests that the total enclosure sampled was affected by chance sun flecks at times when the partial enclosure was shaded. The reverse is seen (16:00–17:00) when PAR within the partial enclosure is highest. However, the base level of PAR ( $250 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ) on this date reveals that even though this is a canopy-free site, the trees surrounding the site affect light levels in the bog.

Relationships among vapor pressure measurements are similar to PAR with mean vapor pressure in a total enclosure being similar to no enclosure (Fig. 2). Note that the greatest vapor pressure deficit was measured in the no enclosure plot and the partial enclosure has low vapor pressure than the others.

In general the temperatures ranked in the following order: air > leaf > soil (Fig. 3). As with PAR and vapor pressure, temperatures within the total enclosure were more similar to temperatures from the plot without an enclosure than those from a partial enclosure. Leaf temperature is consistently lower than air temperature, and leaf temperature equilibrates with soil temperature by the end of the day. In the morning hours (07:30–10:00) leaf temperature is greater than or equal to air temperature, in contrast with later hours in the day.

### Plant measurements

#### Phenology

The only consistently statistically significant differences in growth among treatments were linked to nutrient addition treatments or lack thereof. When nutrients were added, sun-dews usually grew more poorly, were not as large, and did not have as many mature leaves, or produce as many flowers (Table 1).

Growth and leaf development seemed to be hampered by the large flux of available nutrients. Leaf numbers decreased in the F and NP treatments, with even greater reductions in the P and especially the N treatment. As a result, there were fewer leaves present over time. Exclosed plants had significantly more leaves than unexclosed plants.

Rosette diameter also showed a negative effect of added nutrients. The same trends mentioned above were observed, but the F treatment was not significantly different from the control. Plants grown in complete enclosures had a significantly greater mean rosette diameter. Density of plants per area is an indicator of survivorship and success. There was an insignificant change in density during the growing season and no difference owing to enclosures. There was no decline in plant density because of added nutrients, except in the N treatment.

TABLE 3. *Drosera rotundifolia* plant phosphorus and nitrogen concentrations for mature plant harvest (August 1989) and hibernacula harvest (October 1989) at Interior Bog, Giles County Virginia

Treatment	Mature plant		Hibernacula	
	% P	% N	% P	% N
C	0.667a	2.65a	1.89ab	3.85a
F	0.906ab	2.81a	1.13b	3.34a
P	2.38c	3.38ab	2.44a	3.49a
N	0.752ab	7.48c	1.12b	3.84a
NP	1.66bc	5.26bc	1.72ab	7.64b
Unexclosed	1.23a	5.46a	1.64a	5.40a
Exclosed	1.17a	3.79b	1.67a	3.63b

NOTE: Treatments were as follows: C, control; F, foliar feeding (one *Drosophila melanogaster* per month during growing season); P, phosphorus addition to soil; N, nitrogen addition to soil; NP, nitrogen and phosphorus additions to soil. Statistical analysis was ANOVA with multiple comparisons using Fisher's LSD. Different letters in columns indicate significant differences at  $\alpha = 0.05$ ,  $n = 2$  per treatment.

The number of flower stalks appearing increased significantly with time coincidentally with normal flower initiation (Stewart 1990). Flowering seemed to be marginally negatively affected by exclosures ( $p = 0.1023$ ) but was especially decreased by nutrient additions. This was particularly true in the N treatment, in which flowering was nearly unobserved. Flowering increased in the treatment in which plants were fed with *Drosophila*.

#### Biomass

Mature plants were harvested in August and fresh weights and dry weights were obtained (Table 2).

Exclosed plants allocated more biomass to their roots and shoots and also had a significantly higher overall weight. As soil nutrient availability was increased, biomass decreased for all organs. The largest decrease occurred in the P treatment that had the lowest flower, shoot, and root weight. There did not seem to be any trends with floral biomass, although the control treatment was highest.

In addition, hibernacula were harvested in October after leaf abscission. No effect on biomass was seen because of exclosures. C and N treatments had the largest hibernacula weights and P the lowest.

#### Nutrient concentrations

There was no significant difference in phosphorus concentration because of exclosure effect in either the mature plant harvest or the hibernaculum harvest (Table 3). There were significant differences due to nutrient treatments. In both harvests, P and NP plants (in that order) accumulated more phosphorus than the other treatments. In the hibernaculum, however, C was not significantly different than P or NP.

Unexclosed plants accumulated more nitrogen in their tissues than exclosed plants in both harvests. Plants harvested in August showed highest nitrogen accumulation for N and NP treatments, whereas hibernacula exhibited highest nitrogen levels in the NP treatment.

### Discussion

#### Experimental effect

Before discussing results of the plant measurement data, we need to determine the impact of the experimental manipulations on the plants and the effectiveness of exclosures. Was

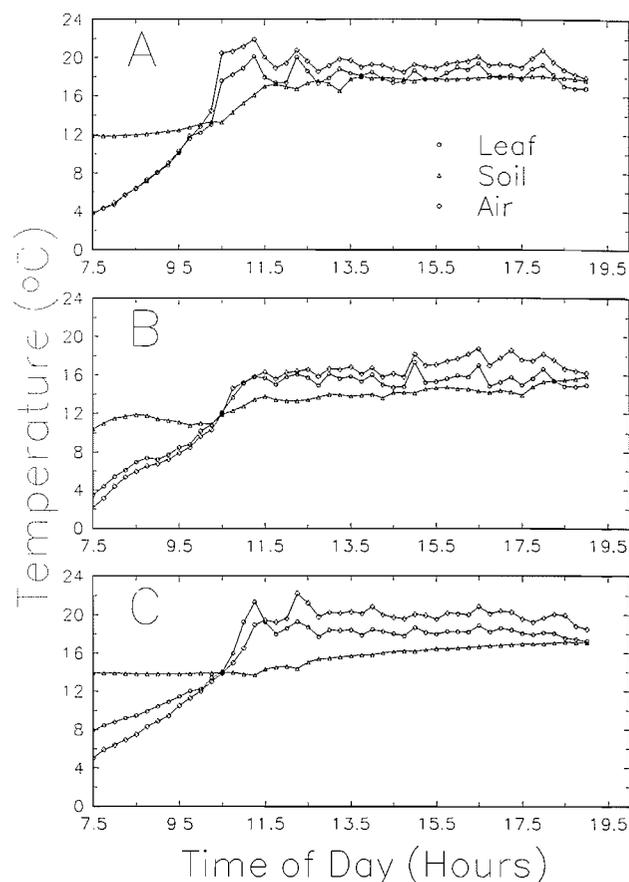


FIG. 3. Temperatures at Interior Bog in western Virginia on August 9, 1989. (A) No exclosure. (B) Partial exclosure. (C) Total exclosure.

there a specific ion effect as is assumed, or were the nutrient additions toxic primarily because of increased soluble salts?

Fertilizer was applied to plots to increase nutrient availability to plant roots. Our nitrogen mineralization data indicate that there was more available nitrogen in the NP treatment when compared with the other treatments. It may be that the nitrogen mineralization microorganisms are limited by phosphorus (Halstead and McKercher 1975). Therefore, there would be a higher nitrogen supply in the NP treatment than in N even though the nitrogen fertilization rates were the same. 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 lateral transfer of fertilizer through the bog. Although the initial soil nutrient status is poor, the rates of fertilization of nitrogen and phosphorus that occurred are comparable with very fertile forest or agronomic field conditions (Vitousek et al. 1982; Chapin and Van Cleve 1989).

Since nutrient treatment effect could conceivably be caused by coincidental conditions such as increased soluble salts in soil and not the specific ions themselves, salt levels were measured in the soil. There was no significant difference in soluble salt levels of soil from any of the treatments (in  $\mu\text{g} \cdot \text{g}^{-1}$ ): C, 43; F, 26; P, 31; N, 82; NP, 83. These levels are within the published range of osmotica for native peatland soil with no external nutrient additions (Succow and Lange 1984). If soluble salts were the cause for observed growth and flowering differences between treatments, then we would expect to see

similar a decrease in the N and NP treatments (those with the highest soluble salt content). This did not occur, so we can assume that observed differences are due to specific nutrient additions or exclusions.

Microclimatic data were taken to determine possible microclimatic changes on the vegetation ground layer due to the presence of the experimental structures. If a greenhouse effect was taking place within exclusions, the temperature would be higher with little difference in vapor pressures. This probably did not occur since PAR, temperature, and vapor pressure levels concur among treatments. The total exclusion and the plot with no exclusion experienced more similar microclimates than did the partial and total exclusion. Even though chosen plots were relatively close to each other, there seems to be great variability within the bog. Since measurements within the total exclusion were so similar to the unexcluded plot, we concluded that neither the partial nor total exclusions had any substantial effect on microclimate.

The exclusions, though not perfect at excluding insects, decreased insect populations within plots. While we were at the study site we frequently noticed flying insects in the partial exclusions but not in complete exclusions. Furthermore, 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 unexcluded plots had insect residues (8 out of 76) compared with 2.6% (3 out of 114) for excluded plants. It was not observed by the researchers but it is possible that ants could have removed the prey from insect surfaces (Thum 1989).

#### Plant measurements

The first objective of the study was to determine whether exposure to insects increases nutrient accumulation or growth in *D. rotundifolia*. Our data indicate that exposure to insects does not increase growth. In fact there is evidence to the contrary (Tables 1 and 2). The effect of insect availability did not significantly impact on phosphorus concentrations in tissues. However, unexcluded plants had higher amounts of nitrogen in the mature plant and hibernacula (Table 3). Conversely, if C and F treatments are compared, there is no difference in phosphorus or nitrogen concentration in mature plants or hibernacula (Table 3). This offers no evidence to support the hypothesis that insectivory is beneficial energetically or nutritionally to *D. rotundifolia*.

*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 was minuscule (for the UC treatment: phosphorus, 4.769 mg/plant; nitrogen, 14.78 mg/plant). Dixon et al. (1980) found that *D. erythrorhiza* plants absorbed 76.1% of labelled nitrogen applied to leaves as *Drosophila*. The nitrogen content of each fly was 26.8  $\mu\text{g}$ . Therefore, the plant would derive 20.39  $\mu\text{g}$  of nitrogen a month from one *Drosophila* application, or about 0.5% of its requirement. For the complete nitrogen requirement of *D. rotundifolia* to be met through insectivory, it would need to capture at least 200 insects the size of a fruit fly per season (Dixon et al. 1980). Furthermore, Thum (1988) found that *D. rotundifolia* captured 0.46 mg/plant of arthropod prey in a small bog in Germany during a growing season. He also reported *Drosophila* mean biomass as 0.179 mg/fly. Therefore, a typical plant would only capture two to three insects the size of a fruit fly per growing season. Most experiments that

emphasize supplementary foliar feedings usually greatly exceed this amount. For example, in other experiments using *D. rotundifolia*, Thum (1988) fed each single plant up to 104 fruit flies during the course of a growing season, and Krafft and Handel (1991) likewise fed each single plant up to 160 *Drosophila* in a single growing season. However, Thum (1989) also found that most of the prey were removed from sundew leaves by ants. Regardless, the experimental design of the present study (three flies per growing season) more closely reflects significant changes in prey capture rates in nature.

The second objective concerned 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 (Tables 1 and 2). There is a large body of data showing that plants adapted to low nutrient status have intrinsically slow growth rates and may not utilize large nutrient fluxes, and in some cases excess macronutrients may affect plant homeostasis (Bradshaw et al. 1964; Coley 1988; Campbell and Grime 1989). 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 (Table 3).

The third objective of this study concerned nutrient availability via the substrate and insect availability on plant growth, nutrient accumulation, and reproduction. There appeared to be little interaction between the two nutrient sources on any of the parameters of interest. The lack of difference in growth between excluded and unexcluded 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).

*Drosera rotundifolia* is a shade-intolerant early successional species. Since this species is physically so small, even graminoid species and small shrubs limit light availability. *Drosera rotundifolia* would be under a strong competitive disadvantage in nutrient-rich sites because faster growing species would restrict light availability. Successful dispersal of seeds to suitable neighboring sites is important for survival. Therefore, allocation to reproductive structures is an important fitness parameter in this species.

Since sexual reproduction of *D. rotundifolia* is so crucial, we should examine flower production more closely. Unexcluded plants produced more flower stalks and more floral biomass than excluded plants, although not significantly different at the 0.05 level (floral numbers,  $p = 0.1023$ ; for floral weight,  $p = 0.3917$ ). If insectivory is important to this species it may have to do with seed production. However, there seems to be a narrow range of nutrient availability required for both floral initiation (low N) and maximum seed production (higher N). If plants receive too little nitrogen, they do not produce as many flowers and seeds compared with higher nitrogen treatment; still higher nitrogen may prevent flower initiation (Tables 1 and 2).

Insectivory may be energetically costly to the plant in contrast with the benefit of nutrient gains (Givnish et al. 1984).

If an insectivorous plant has access to low resources (nutrients), then the energetic or nutrient cost to produce trapping mechanisms, enzymes, etc., may be lower than the energy or nutrient gained by insectivory. On nutrient rich sites, this benefit would diminish and disappear. It may be that this particular site is near or at the cost-benefit junction.

Plants growing in nutrient-poor sites are assumed to be adapted to these nutritionally depauperate conditions (Chapin 1991). It is important that the plants adapted to low nutrient environments retain and efficiently use nutrients for future growth and reproduction (Chapin 1980, 1987). Nutrient use efficiency (NUE) is defined as the amount of nutrient used per carbon gain (Chapin and Van Cleve 1989). One simple index of NUE is the inversion of plant nutrient concentration. It is advantageous for *D. rotundifolia* plants to have a high NUE during the growing season and to absorb high amounts of nutrients into the hibernaculum to use for next year's growth and especially reproduction. A small plant like *D. rotundifolia* can conserve nutrients by an efficient overwintering apparatus such as a hibernaculum. Schulze and Schulze (1990) reported that in *D. rotundifolia* in nature 24–30% of the nitrogen originating from insectivory is overwintered in the hibernaculum. In a pseudo field study they found that insectivory did contribute to slightly higher nitrogen in the hibernaculum. More importantly, however, they found that these small-statured species that have low capture rates relied most heavily on nutrients retained in the hibernaculum from the previous year's growth for current growth (Schulze and Schulze 1990). The NUE (1/nutrient concentration (%)) (unexclosed control treatment, mature plant: phosphorus, 1.42; nitrogen, 0.35) of *D. rotundifolia* is higher for phosphorus and lower for nitrogen than that of most crops and wild plants (phosphorus, 0.4; nitrogen, 0.58) (Chapin 1987; Chapin and Van Cleve 1989). It appears that phosphorus-use efficiency is potentially critical to species survival.

Figure 4 shows nutrient retention indices (NRI = 1/NUE) of phosphorus (PRI) and nitrogen (NiRI) for all treatments. Statistical significance could not be tested, but we can see obvious differences. If plants have a high NRI, they efficiently reabsorb nutrients into their hibernacula, presumably for use in the next growing season. Likewise, if NRI is high, the plant more efficiently uses and recycles nutrients. For phosphorus, it is evident that the unexclosed control (UC) and the exclosed control (EC) are much more efficient than any nutrient addition treatment including F. NiRI contrasts PRI. Unexclosed nitrogen (UN) and exclosed nitrogen (EN) have a lower NiRI when compared with other treatments. This seems to suggest that phosphorus is a more limiting nutrient than nitrogen because it is more efficiently reabsorbed. Plants efficiently reabsorb phosphorus for overwintering when it is in low supply, but reabsorption is hampered by even small phosphorus fluxes (such as in the F treatment). In this way insectivory could be deleterious to phosphorus nutrition. In contrast, NiRI is negatively affected by large fluxes of only nitrogen, and increased phosphorus counteracts the effect of increased nitrogen availability.

### Conclusion

*Drosera rotundifolia* is a small, efficient user of phosphorus and is physiologically adapted to retain phosphorus when in low supply. It is thought that the insectivorous syndrome selectively ameliorates plant nutrient limitations, but this is not

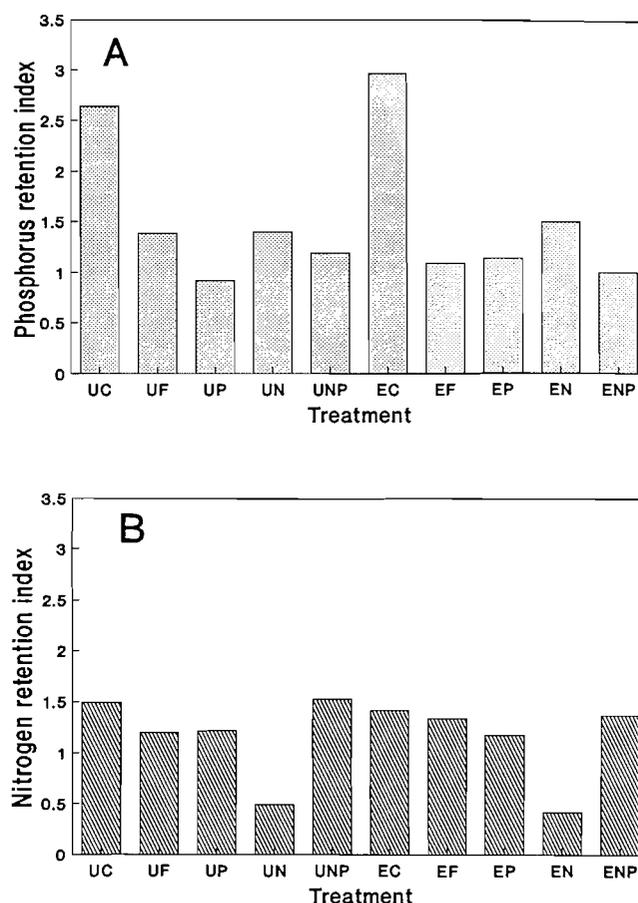


FIG. 4. Nutrient retention indices (NRI) for *Drosera rotundifolia*. (A) Nitrogen. (B) Phosphorus. U, unexclosed; E, exclosed; C, control; F, foliar feeding (one *Drosophila melanogaster* per month during growing season); P, phosphorus addition to soil; N, nitrogen addition to soil; NP, nitrogen and phosphorus additions to soil.

shown to be the case in this field study. *Drosera rotundifolia* is growing at its genetically realized best with the environment at its natural state. Added nutrients negatively affect recruitment and growth, whereas denying insects only marginally and 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. Based on these results the importance of insectivory is, at the feeding level in this study, minimal for the survival of *D. rotundifolia* in natural populations. This conclusion is conditional because this particular site may be nutritionally at or near a cost-benefit junction. In a field study using the approach of foliar insect additions upon *D. rotundifolia*, Thum (1988) showed that similar fitness parameters to those reported here were positively associated with insect additions. The present study using insect exclusions shows the opposite; the absence of prey increased the fitness parameters. The results are not necessarily contradictory, yet they emphasize the need of further research. However, resource environmental manipulations must be based on reasonable levels found in nature. Additional research of this type with *D. rotundifolia* populations at sites with lower soil nutrient status is needed to further resolve the question of the significance of insectivory. Also, other species of insectivorous plants should be studied to

determine the possible effect of other abiotic and biotic interactions with insectivory.

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