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The demographic consequences of nitrogen fertilization of a population of sundew, *Drosera rotundifolia*

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SUMMARY

This paper reports the result of a 4-year fertilization experiment using nitrogen, on a level with current deposition, on the demography of a *Drosera rotundifolia* L. population on a raised bog. Five different fertilization treatments were employed: (i) control with no extra nitrogen, (ii) 0·5, (iii) 1·0, (iv) 2·0, and (v) 4·0 g N m^{-2} $year^{-1}$.

Spearman rank correlation test unveiled a significant increase in the daily killing power in relation to the amount of nitrogen fertilization. This was valid for all cohorts studied during the 4 years. The addition of nitrogen fertilizer influenced the reproductive behaviour of the *D. rotundifolia* plants. The proportion of flowering individuals increased in the second year, after which the frequency of flowering gradually decreased compared with the control plots. The number of flowers per individual was not influenced by the nitrogen treatment.

The population size in the control plots remained rather constant over the 4 years. Population size also remained constant when low-concentration fertilizer was added. In these nitrogen-treated plots, however, the three youngest age classes represented more than 55% of the total population compared with less than 40% in the control plots. In the plots treated with 2·0 and 4·0 N m^{-2} $year^{-1}$, the population size decreased dramatically between the first 2 years. From then and up to the end of the study these populations remained at a nearly constant low level.

The nitrogen treatment resulted in a significantly increased density of both *Andromeda polifolia* and *Eriophorum vaginatum*.

Key-words: Drosera rotundifolia, population dynamics, survivorship, reproduction.

INTRODUCTION

During the last 30–40 years, terrestrial ecosystems in Europe have been subjected to an increasing atmospheric deposition of nitrogen compounds (Galloway & Likens 1981; Grennfelt & Hultberg 1986). Besides acting as an acidifying agent, nitrogen is also a major nutrient.

Plant nomenclature follows Krok & Almquist (1984).

This deposition of nitrogen is considered a major threat to the flora of many European countries (Ellenberg 1985). Changes in the floristic composition of vegetation can sometimes be related to nitrogen deposition, but very often the changes are the combined effects of many factors, not only pollutants but also changes in landscape management, and demographical and successional processes. There are several examples indicating that the deposition of nitrogen is causing vegetational change. For example, many coastal heathlands of north-west Europe have changed into grasslands, with subsequent loss of species characteristic of heathlands (Heil & Diemont 1983; Van Dam *et al.* 1986; Van Breemen & Van Dijk 1988).

The concept of 'critical load' has been proposed in an attempt to establish the highest load of an element or nutrient that will not cause long-term effects on ecological systems (Nilsson 1986). However, the use of this concept connecting the biological consequences of an excess load of nitrogen, i.e. changes in individual organisms, in populations and in ecosystems (Nilsson & Grennfelt 1988), is difficult to determine. Nitrogen deposition causes changes in both the abundance of individual species and the structure of communities. The critical load also varies between ecosystems. Therefore, depending on the ecosystem considered, different critical loads may be envisioned for populations or communities. Studies that provide data on the critical load are few, and the levels of nitrogen in most fertilization experiments largely exceed the current rate of deposition of this element.

Plants adapted to nitrogen-poor soils are considered very sensitive to nitrogen deposition (Ellenberg 1985, 1988; Nilsson & Grennfelt 1988). Ombrotrophic bogs receive exogenous nutrients from precipitation and the bog plants are adapted to low levels of nitrogen (Morris 1991). The flora of such bogs is particularly sensitive to atmospheric nitrogen deposition (Nilsson & Grennfelt 1988). Even though increased nitrogen deposition may initially lead to increased primary productivity (Aerts *et al.* 1992), high loads of atmospheric nitrogen are detrimental for *Sphagnum* growth and over a period *Sphagnum* species are likely to disappear from the flora (Ferguson & Lee 1983; Ferguson *et al.* 1984; Woodin *et al.* 1985). Whether the rest of the flora inhabiting raised bogs are equally sensitive to nitrogen deposition is unknown.

The purpose of this study was to examine whether the present deposition of nitrogen might be a threat to species inhabiting raised bogs. The paper reports the result of a 4-year fertilization experiment in which nitrogen has been applied to permanent plots at a rate corresponding to the current deposition rate. The demographic changes of a population of *Drosera rotundifolia* L. have been recorded. In addition, the effects of fertilization on populations of shoots of *Andromeda polifolia* L. and *Eriophorum vaginatum* L. are reported.

MATERIAL AND METHODS

The carnivorous sundew *Drosera rotundifolia* is a small rosette-hemicryptophyte. The root system is generally limited, consisting of a tap root with root hairs (Lloyd 1942). Besides raised bogs, where it mostly grows on the lowest and wettest hummocks of *Sphagnum*, it is also found in blanket bogs, valley mires, and lake mires (Crowder *et al.* 1990). The species is not found on the tops of the driest hummocks or in open water in pools.

An adult *D. rotundifolia* rosette may have 1–7 inflorescences, and generally one-sided racemes (Crowder *et al.* 1990). The seeds are winged and 1·5 mm long and weigh

10–20 μg (Crowder *et al.* 1990; Thum 1988). The plant may spread vegetatively over a few centimetres by the production of axillary buds or by regeneration of parts of moribund plants (Crowder *et al.* 1990).

The study was carried out on a bog named Åtorpsmossen, at Tullgarn 45 km SW of Stockholm in south central Sweden. This raised bog covers 14·5 ha. It has a treeless central part surrounded by a broad marginal pine forest. The ambient nitrogen deposition rate to the area is about 0·6–1·0 g N m^{-2} $year^{-1}$ (Lövblad *et al.* 1992).

The treeless central part of the bog, where the study was carried out, consists mainly of a relatively flat carpet community (*sensu* Sjörs 1948). In the area, *D. rotundifolia* is growing on hummocks of *Sphagnum fuscum* and *S. rubellum* together with *Eriophorum vaginatum, Andromeda polifolia,* and *Vaccinium oxycoccus* L.

In May 1988, twenty 2·5 × 2·0 m plots were marked in the central part of the bog within an area of *c.* 800 m^2. The plots were chosen subjectively to minimize the differences in appearance and vegetation between them. In each plot a 1·0 × 1·0 m frame was laid out. The position of the frame was marked with four 100 × 2 cm plastic tubes securely driven into the peat. The frame was sectioned by strings of fishing-line into a grid consisting of 400 5 × 5 cm squares. Seventy-five of these squares were randomly chosen in each frame and were used throughout the study.

To simulate increased nitrogen deposition, five different fertilization treatments were employed: (i) control with no extra nitrogen, (ii) 0·5, (iii), 1·0, (iv) 2·0, and (v) 4·0 g N m^{-2} $year^{-1}$. Ammonium nitrate was used as nitrogen source. The levels chosen correspond to the range of nitrogen deposition in different parts of Sweden (Lövblad *et al.* 1992).

The five treatments were randomized among the twenty 2·5 × 2·0 m plots, in such a way that each treatment was applied to four of the plots. Application of nitrogen started in May 1988 and continued until September 1991. The total yearly amount of nitrogen was achieved by five applications per year. Due to problems associated with a covering of snow and ice the application of nitrogen was done once a month between May and September.

The nitrogen was added as powder. To minimize the risk of damage to the plant cover when adding nitrogen in the form of powder, each application was done in connection with precipitation. Except for the very dry season in 1990 (during this summer there was evidence of desiccation in *Sphagnum* mosses in all plots), no signs of direct damage to the plant cover were observed.

Starting in September 1988 and twice yearly until 1991, the position of each *D. rotundifolia* plant was mapped by pantograph technique in each of the 75 squares. The measurements were made in late May–early June and at the end of September, so that the fate of individual plants could be traced. The survivorship analysis was based on counts of numbers of seedlings and adults, and no account was taken of the death of seeds before or at germination. The intervals between successive observation dates were unequal in length and therefore the daily killing power (Begon *et al.* 1986) was calculated for comparison of survivorship between years. The survival was studied in the mixed-age 'cohort' of individuals alive at the start of the observations in September 1988 and in the two seedling cohorts originating in 1989 and 1990.

In the middle of the summer (July), the number of flowers was recorded individually for each plant in 10 of the plots (two of each treatment). In 1989 and 1990 the number of leaves, the time of flowering, and the number of dead leaves, were counted. In order to obtain an estimate of the rate at which prey were captured (see Crowder *et al.* 1990),

Table 1. The proportion (%) of *Drosera rotundifolia* individuals overgrown by *Sphagnum* in relation to four levels of nitrogen fertilization (*G*- and *P*-values determined from *G*-test of independence between the control and the various nitrogen treatments, in all cases df=1)

	Year								
N (m^{-2} $year^{-1}$)	1988	*G*	P	1989	*G*	P	1990	*G*	P
0·0	34			16			16		
0·5	27	1·77	NS	21	1·30	NS	34	16·0	<0·001
1·0	37	0·190	NS	26	5·80	0·016	40	27·8	<0·001
2·0	46	2·75	NS	33	8·56	0·003	47	12·9	<0·001
4·0	50	6·07	0·014	52	41·2	<0·001	45	12·2	<0·001

the number of plants with prey on their leaves was counted in July. The number of shoots of *Andromeda polifolia* and leaves of *Eriophorum vaginatum* were also counted in each square.

For the statistical analysis of survivorship, the *G*-test (also known as the likelihood ratio χ^2 test) was used. The *G*-test was also used to test for independence of the nitrogen treatment when the variables were categorical. The presence of any relationship between daily killing power and nitrogen treatment was studied by use of the Spearman rank correlation test. The statistical analyses were performed with the SYSTAT statistical package (Wilkinson 1990).

RESULTS

In the experimental plots the wintering buds of *D. rotundifolia* started growing in the second half of May. The first flowering individuals were seen in late June. The main seedling recruitment occurred at the end of May, but a few seedlings also appeared in September, some of which survived the winter. Due to their low number, however (on average 7% (SD=4) of all recruited seedlings), none of these late-recruited seedlings were included in the analyses of survivorship. Lateral spread by axillary buds was not observed between 1988 and 1991.

The number of leaves produced per individual each year ranged between 1 and 10. The grand mean for the two years 1989 and 1990 was 4·5 leaves per individual, and there were no significant differences between years and treatments. The mean number of dead leaves per individual at the onset of flowering varied between 1·3 and 1·5 in the control plots and in the plots fertilized with 0·5 or 1·0 g N m^{-2} $year^{-1}$. In the plots where the two highest levels of nitrogen were added, the leaf mortality was significantly higher than that in the control plots (Newman-Keuls test, $P<0{\cdot}05$), ranging between 1·9 and 2·5 leaves per individual.

Only a very small number of plants had prey captured on their leaves. In the different plots the percentage of individuals with prey varied between 0 and 5·1%.

During the period from 1988 to 1990 the number of *D. rotundifolia* individuals (seedlings and adult plants) overgrown by *Sphagnum* (spp.) was recorded. There was a clear trend for an increasing proportion of overgrown individuals in fertilized plots in comparison with control plots, and the *G*-test indicated that the proportion of overgrown individuals was dependent on the nitrogen treatment (Table 1).

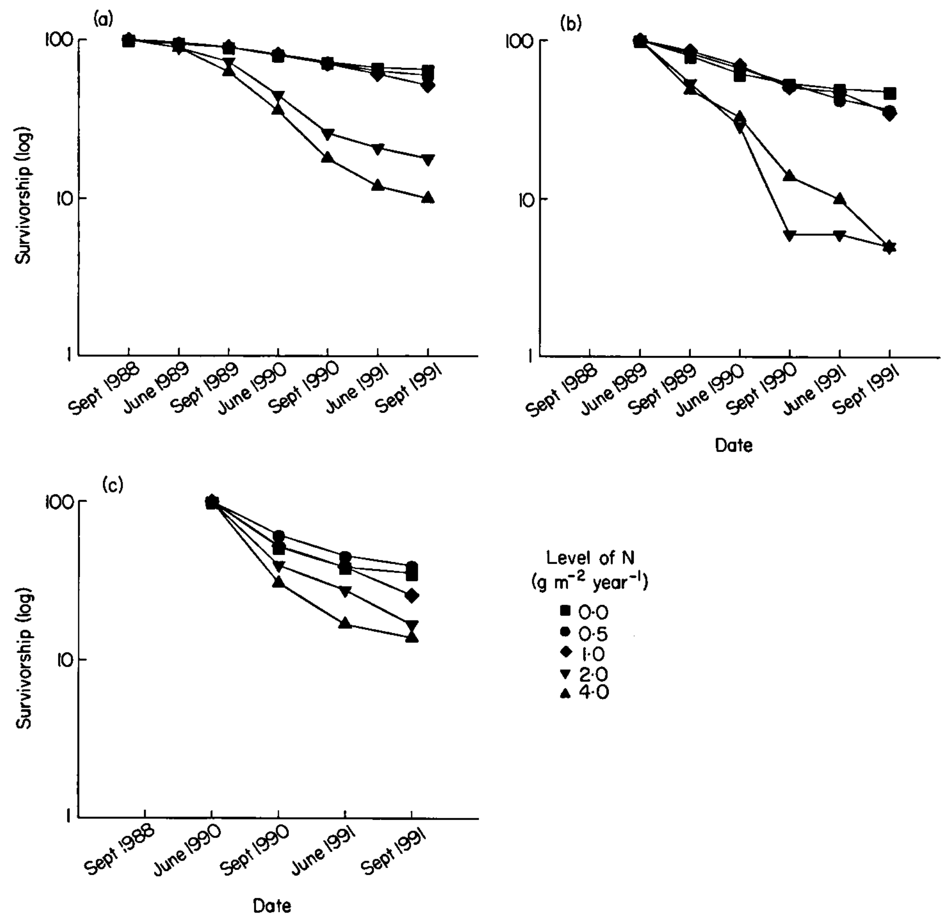

Fig. 1. Survivorship curves for three cohorts of *Drosera rotundifolia* in relation to four levels of nitrogen fertilization. (a) Mixed-age group 1988 (as this cohort is composed of individuals of an uneven age the survivorship curve is referred to as a depletion curve), (b) 1989 cohort, (c) 1990 corhort.

Survivorship

A comparison of survivorship for each cohort between plots within each treatment revealed no significant differences (G-test). Therefore, the data from the four replicates were pooled together when comparing the survival between treatments.

The slope of the depletion curve of the mixed-age population present at the beginning of the study appeared remarkably consistent in the 4 years (Fig. 1a). Around 65% of the individuals observed in 1988 were still alive in October 1991. The daily killing power calculated separately for the winter and for the growing season indicated differences in mortality between years (Table 2). The mortality during the growing season was highest in the driest summer (1990) and lowest in the relatively wet summer of 1991.

Seedlings suffered higher mortality in 1989 and 1990 compared with the adults in the mixed-age cohort for this period (Fig. 1b, c). The mortality of newly established seedlings was comparatively high in the first year for both the cohorts studied (Table 2) and differed significantly from the mixed-age cohort (1989; $G=6{\cdot}61$; df$=1$; $P<0{\cdot}014$,

Table 2. The daily killing power (× 10^{-4}) during winter and during the growing (summer) season in three consecutive years in a population of *Drosera rotundifolia* at four levels of nitrogen fertilization. Mixed-age refers to the population present at the start of the study

	Fertilization (g N m^{-2} $year^{-1}$)														
	0·0			0·5			1·0			2·0			4·0		
	Mixed-age	Cohort 1989	Cohort 1990	Mixed-age	Cohort 1989	Cohort 1990	Mixed-age	Cohort 1989	Cohort 1990	Mixed-age	Cohort 1989	Cohort 1990	Mixed-age	Cohort 1989	Cohort 1990
Winter 1988–89	0·7			0·7			1·1			2·2			2·0		
Summer 1989	2·4	8·2		2·6	6·8		1·8	5·3		6·8	22·7		12·6	25·6	
Winter 1989–90	1·9	4·5		2·0	3·8		1·8	3·7		8·7	11·6		10·2	7·2	
Summer 1990	4·7	5·0	26·5	4·1	8·2	18·1	5·1	12·1	24·0	21·0	56·8	34·6	26·6	32·4	42·7
Winter 1990–91	1·5	1·3	4·1	2·0	3·7	5·2	2·6	1·2	5·1	3·8	0·0	5·7	7·3	5·7	10·0
Summer 1991	1·0	2·8	3·5	2·8	7·6	6·3	7·8	14·2	18·9	12·0	13·4	23·8	12·0	32·4	10·4
Whole observation period	1·8	3·9	9·6	2·1	5·3	8·6	2·7	5·5	12·6	7·5	16·2	15·9	9·5	16·8	18·3

Table 3. The percentage of reproducing individuals in a population of *Drosera rotundifolia* at different levels of nitrogen fertilization. *G*- and *P*-values determined from *G*-test of independence between the control and the various nitrogen treatments, in all cases df=1. No tests were performed on the two highest nitrogen treatments in 1990 and 1991 due to small sample size

N (g m^{-2} $year^{-1}$)	1988	*G*	P	1989	*G*	P	1990	*G*	P	1991	*G*	P
0·0	7			8			6			22		
0·5	17	7·03	0·008	20	10·0	0·002	12	5·12	0·024	21	0·015	NS
1·0	12	2·22	NS	16	5·78	0·016	6	0·02	NS	13	5·00	0·025
2·0	8	0·051	NS	40	31·9	<0·001	0	—		13	—	
4·0	10	0·762	NS	21	9·57	0·002	7	—		0	—	

1990; $G=96{\cdot}7$; df=1; $P<0{\cdot}001$). The 1990 cohort also suffered much higher seedling mortality than the 1989 cohort ($G=11{\cdot}2$; df=1; $P<0{\cdot}001$). After the second growing season, the mortality for the 1989 cohort was already reduced to the level of the mixed-age group.

Treatment effect. The effect of fertilization treatment on survivorship of *D. rotundifolia* differed considerably depending on the amount of nitrogen used (Fig. 1a–c). Only a few significant differences in survivorship were observed between the control plots and the plots treated with low levels of fertilizer, especially in the mixed-age cohorts. Yet, the data in Table 2 show a trend of increased mortality with increased nitrogen fertilization. Spearman rank correlation also indicates a significant increase in the daily killing power in relation to the amount of nitrogen fertilization. This was valid for all seasons starting from the summer of 1990 (summer 1990, Spearman $\rho=0{\cdot}900$; $n=5$; $P<0{\cdot}05$; winter 1990–91, Spearman $\rho=1{\cdot}00$; $n=5$; $P<0{\cdot}05$; summer 1991, Spearman $\rho=0{\cdot}975$; $n=5$; $P<0{\cdot}05$). For all cohorts, the daily killing power during 1988–91 showed a significantly positive correlation to fertilization level (mixed-age group 1988, Spearman $\rho=1{\cdot}00$; $n=5$; $P<0{\cdot}05$; 1989 cohort, Spearman $\rho=1{\cdot}00$; $n=5$; $P<0{\cdot}05$; 1990 cohort, Spearman $\rho=0{\cdot}90$; $n=5$; $P<0{\cdot}05$).

The deposition of 0·5 or 1·0 g N m^{-2} $year^{-1}$ caused only minor and mostly insignificant effects on survivorship. In the growing season of 1991, mortality increased in the plots fertilized with 1·0 g N m^{-2} $year^{-1}$ and was significantly higher than that in control plots ($G=8{\cdot}31$; df=1; $P=0{\cdot}004$). The daily killing power was more than 10 times higher during this period (Table 2).

From the second growing season in 1990, the survivorship of the 1989 cohort was significantly lower than that in the control plots ($G=10{\cdot}8$; df=2; $P=0{\cdot}004$). A significantly increased mortality was also observed in the second growing season of the 1990 cohort in the plots treated with 1·0 g N m^{-2} $year^{-1}$ ($G=10{\cdot}9$; df=1; $P=0{\cdot}001$).

In contrast, 2·0 or 4·0 g N m^{-2} $year^{-1}$ influenced mortality early in the first year of the study, with decreased survival compared with the other treatments. Only 18% and 10% of the original mixed-age cohort survived beyond the end of the study in the plots fertilized with 2·0 or 4·0 g N m^{-2} $year^{-1}$ respectively, compared with 65% for the untreated plots ($G=217$; df=2; $P<0{\cdot}001$).

The influence of high levels of nitrogen was also observed at an early stage in the seedling cohorts. Already in their first growing season the mortality of both seedling cohorts growing in high levels of nitrogen was higher than that of the control seedling population (Fig. 1b and c, Table 2). Of all individuals in the cohort of 1989, only 4% were alive at the end of the study compared with 48% in the unfertilized plots.

Reproduction

In each of the first 3 years (1988–90) the fraction of the population that flowered in the control plots was very small, varying between 6 and 8% (Table 3). In 1991 the proportion increased compared with the previous years and nearly 22% of all the individuals produced flowers. The fraction of reproducing individuals each year in the control plots was correlated to the total precipitation in the spring (Spearman $\rho=0{\cdot}736$; $n=8$; $P<0{\cdot}05$).

Of the individuals in the mixed-age group from 1988 that survived to the end of the study, 43% never produced a flower. None of the individuals produced flowers in all

Table 4. The number of capsules produced m^{-2} in a population of *Drosera rotundifolia* at different levels of nitrogen fertilization

N ($g\,m^{-2}\,year^{-1}$)	1988	1989	1990	1991
0·0	75	100	50	250
0·5	100	150	123	229
1·0	79	146	60	121
2·0	60	140	0	19
4·0	71	127	8	0

4 years. Most of the reproducing individuals only flowered once (41% of the mixed-age group), 13% flowered twice, while only 3% produced flowers in 3 of the 4 years.

None of the individuals in the cohort of 1989 reproduced during their first two growing seasons, but 25% of the remaining individuals produced flowers in 1991. No flowers were produced by the seedling cohort of 1990 during the study.

No individual plant produced more than one flowering stalk, and the number of flowers produced was very small. Most of the individuals produced only one or two flowers but in a few individuals up to six flowers were produced. The mean number of flowers per reproducing individual was 2·2 (SD=1·1). The number of flowers produced by each individual varied between the years ($F_{3,201}$)=3·63; P=0·019). In 1990, for instance, each reproducing individual produced only 1·5 flowers compared with 2·4 in 1991.

The yearly yield of capsules in the control plots varied strongly between years. It was lowest in 1990 and five times higher in 1991 (Table 4).

Treatment effect. Addition of nitrogen fertilizer influenced the reproductive behaviour of plants. The percentage of flowering individuals increased in 1989, after which the frequency of flowering gradually decreased compared with that in control plots.

Apart from the plots given the lowest amount of nitrogen, the flowering frequencies in the first year (1988) were similar in all the plots (Table 3). In plots treated with 0·5 g N m^{-2} $year^{-1}$ the percentage of flowering individuals was significantly higher than in the control plots during 1988–90 (*G*-test, see Table 3).

Flowering increased sharply in all the treated plots in 1989 (Table 3). The percentage of individuals flowering was two to five times higher in the fertilized plots than in the control plots. In contrast to the control plots, flowering decreased in all treated plots in 1990. No reproducing individual was observed in 1990 in plots that were treated with 2·0 g N m^{-2}.

In the fourth year of nitrogen fertilization, no difference was observed in the percentage of plants flowering in the control plots and plots receiving 0·5 g N m^{-2} $year^{-1}$. In all the other treatments the frequency of reproducing individuals was lower than that in the unfertilized plots.

While the number of flowers per individual was not influenced by nitrogen treatment, the effect on the total number of capsules produced m^{-2} was similar to its effect on the flowering frequencies. Initially, this value increased in all plots treated with nitrogen, followed by a gradual decrease compared with the control (Table 4).

Table 5. The number of seedlings recruited m^{-2} in a population of *Drosera rotundifolia* in relation to four levels of nitrogen fertilization (standard deviation in parentheses)

N (g m^{-2} year^{-1})	1989	1990	1991
0·0	144 (45)	146 (90)	38 (9)
0·5	107 (37)	240 (58)	119 (57)
1·0	122 (28)	233 (68)	130 (32)
2·0	88 (38)	49 (18)	18 (7)
4·0	139 (20)	80 (80)	11 (9)

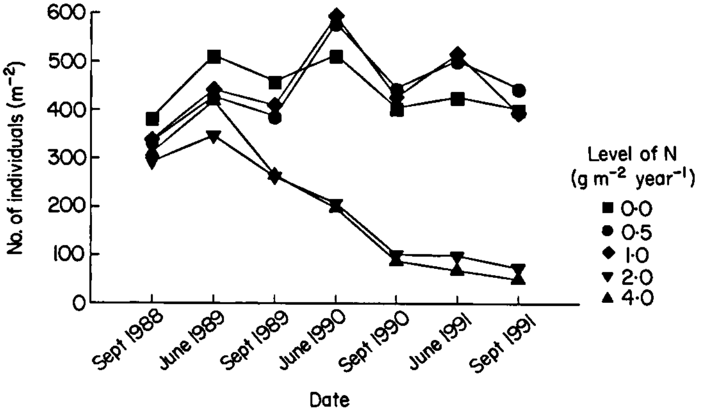

Fig. 2. The density of *Drosera rotundifolia* in four years (1988–91) in relation to four levels of nitrogen fertilization.

Seedling recruitment

The yearly number of seedlings recruited in the control plots varied between 90 and 270 m^{-2}. The mean values for each year are presented in Table 5.

The numbers of seeds per capsule were counted in 25 capsules collected outside the studied plots in 1989. Seed number varied between 37 and 65 per capsule with a mean of 48 seeds per capsule (SD=8). An approximate calculation, using this mean value of number of seeds per capsule and the data on number of capsules per m^2, indicates that the number of seedlings recruited was very low in relation to the seed yield: approximately 0·1%.

Treatment effect. In 1990 the number of recruited seedlings increased more than twice in the two lowest nitrogen treatments. This resulted in a significantly higher representation of seedlings of the total population in 1990 and 1991 in these treatments compared with the control (1990; G=22·7; df=2; P<0·001, 1991; G=49·5; df=2; P<0·001). The density of recruited seedlings decreased considerably when the nitrogen treatment was increased to 2·0 g N m^{-2} year^{-1}.

Population dynamics

At the start of the study, in September 1988, the mean population density of *D. rotundifolia* in all 20 plots was 332 m^{-2} (SD=102). The population size in the control plots remained rather constant during the 4 years (Fig. 2). There were no apparent differences in the development of population size over time between control plots and plots with the lowest levels of nitrogen fertilization added. Yet, a closer look at age structure of the population revealed significant differences. In the nitrogen-treated plots the three youngest age classes represented more than 55% of the total population compared with less than 40% in the control plots. At the end of the study, the three youngest age classes represented 25%, 21% and 9% of the plants present in the plots treated with 0·5 g N m^{-2} $year^{-1}$ and 29%, 15% and 11% of the plants present in the plots treated with 1·0 g N m^{-2} $year^{-1}$. In the control plots, the corresponding figures were 8%, 13% and 17% (G=67·5; df=6; P<0·001).

In the plots treated with 2·0 and 4·0 N m^{-2} $year^{-1}$ the population size decreased dramatically between the autumn of 1989 and the autumn of 1990. From then and up to the end of the study these populations remained at a nearly constant low level.

Fertilization effects on Andromeda polifolia *and* Eriophorum vaginatum

The density of *Andromeda polifolia* shoots increased significantly in all the fertilized plots (Wilcoxon rank test), while the number remained fairly constant in the control plots.

Increased density of *E. vaginatum* was also observed in the fertilized plots, but the increased were only significant for plots treated with 1·0 or more g N m^{-2} $year^{-1}$ (Wilcoxon rank test).

Since *A. polifolia* and *E. vaginatum* shoots were only counted and not individually marked there is no information on whether this increase in the fertilized plots was determined by an increased recruitment or by decreased mortality.

DISCUSSION

Drosera rotundifolia is a short-lived perennial plant. By counting the decayed remains of former rosettes the maximum age of the plants in Britain has been estimated to be 4 years (Crowder *et al.* 1990). However, this study indicates that in other regions the sundew may reach a higher maximum age. Several adult plants that were recorded in the spring of 1988 were still alive in the autumn of 1991, and based upon the linear depletion curve of the mixed-age group the half-life of the population was 4·1 years.

The survival of individuals of *D. rotundifolia* was age-dependent and influenced by season. A smaller percentage of the seedlings and the second-year plants survived compared with older plants. The first-year seedling survival varied between 0·40 and 0·62. The production of the first pair of leaves of a *D. rotundifolia* seedling may be delayed until 2–3 weeks after germination (Crowder *et al.* 1990), and normal rosette leaves are not formed until the plant reaches the moss surface (Backéus 1985). Many seedlings may have died before being recorded or went unnoticed. Consequently, the above figures are likely to underestimate seedling mortality in the population. De Riddler & Dhont (1992) report significantly lower first-year survival (varying between 0·00 and 0·07) in a heathland population of the closely related *Drosera intermedia* growing in a seepage area on and between hummocks of *Sphagnum*.

The fraction of reproducing plants varied with age and years. It was small during the first 3 years and never exceeded 10%, but increased in the last year of the study. The variation between years was to a certain extent determined by the amount of early summer rain. Crowder *et al.* (1990) found considerable variation in the percentage of *Drosera* plants flowering in different bogs in Ireland but the values (ranging between 35 and 73%) were much higher than those observed in this study.

The juvenile phase lasted for at least 2 years, none of the plants reproduced early than in the third growing season. This is in contrast to the study of Crowder *et al.* (1990), according to which *D. rotundifolia* may flower in their first summer and plants can set flower each year thereafter.

In this study, no individual produced more than one flowering stalk, and the average number of flowers per individual never exceeded 2·4. This value is in the lower part of the range of numbers reported in the literature. Typical mean values for number of capsules per plant in Britain lie between five and seven, but data from Ireland and North America show considerable variation between sites and years (Salisbury 1942; Crowder *et al.* 1990).

The demographic data on *D. rotundifolia* from the British Isles indicates a shorter life-span and both earlier and greater reproduction than found in my studies. This dissimilarity in life-history in all probability is a result of differences in climate, which also affect the lengths of the growing season in the two regions. The growing season in the British Isles is about twice as long as in south central Sweden.

As observed in many demographic studies (Silvertown 1987) the largest loss of individuals occurs in the seed state of the life-cycle. The large difference between seed yield and number of recruited seedlings may have at least two causes. First, seeds of *D. rotundifolia* are very light and almost dust-like. Thum (1988) describes the seed shape as an adaptation to wind dispersal. Such seeds are very sensitive even to small wind gusts (Harper 1977) and are easily dispersed over long distances. Secondly, the small seeds may be washed down into the *Sphagnum* layer, which was the case with *Narthecium ossifragum* growing under similar conditions on *Sphagnum* hummocks (Summerfield 1973). Of course, these species may build up a bank of dormant seeds, but Summerfield (1973) observed that a large part of the *N. ossifragum* seeds that moved down into the *Sphagnum* mat lost their viability.

The nitrogen treatment affected both survival and reproduction. For all the cohorts studied mortality increased with nitrogen level. In the plots with the two highest dosages of nitrogen, mortality of plants was rapid. Stewart & Nilsen (1992) also noticed a decline in the density of *D. rotundifolia* after an application of nitrogen.

The cause of the increased mortality is obscure. *D. rotundifolia* has a shallow root system, and drought readily kills the plants (Lloyd 1942; Crowder *et al.* 1990). The summer was very dry both in 1989 and 1990 and there were indications that mortality was related to precipitation during the summer. Seedling mortality in the plots was higher in 1990 than in 1989. Moreover, the effect of fertilization was most pronounced in the driest summer of 1990. In this summer, there was evidence of desiccation even in *Sphagnum* mosses. In the relatively wet summer of 1991, mortality was comparatively low in plots receiving the highest dosage of nitrogen. There are many studies on woody and herbaceous species showing that high levels of nitrogen increase shoot growth relative to root growth (e.g. Hällgren & Näsholm 1988). No increased production of leaves in the fertilized plots occurred, but instead an increase in leaf mortality. Stewart & Nilsen (1992) observed that added nutrients decreased the growth of *D. rotundifolia*, but the levels of nitrogen applied exceeded the levels used in this study.

D. rotundifolia grows on *Sphagnum* hummocks. *Sphagnum* may grow vertically 1–2 cm year^{-1} (H. Rydin, personal communication), and the sundew plants are thus in danger of becoming overgrown (Thum 1988). Fertilization with nitrogen at about the present rate of atmospheric deposition initially leads to increased productivity in ombrotrophic bogs and significantly increases the length growth of *Sphagnum* shoots (Aerts *et al.* 1992). The length increment of *Sphagnum* individuals fertilized with 4·0 g N m^{-2} year^{-1} may be twice that of control plants (Aerts *et al.* 1992). My study indicates that plants of *D. rotundifolia* run a higher risk of being overgrown by *Sphagnum* when nitrogen is applied to plots. Since only survivors were mapped, it is not possible to analyse whether overgrowth by *Sphagnum* confers increased risk of mortality. Yet, the increased seedling mortality in some experimental plots observed in the dry year of 1990 also coincided with an increase in the proportion of individuals that were smothered by the moss.

The most pronounced effect of the addition of nitrogen fertilization on reproduction was the initial increase in the fraction of reproducing individuals, later followed by a gradual decrease compared with the control plot. The number of flowers per individual was influenced to a smaller extent. The reproductive habit in this population of *D. rotundifolia* was very restricted compared with literature data (Crowder *et al.* 1990). Field studies show that the reproductive output of *D. rotundifolia* is highly dependent on the rate of prey capture. Supplementary feeding of insects increases both the fractions of reproducing individuals and the numbers of fruits produced per plant (Thum 1988). The notably low reproduction in the population studied may partly depend on low access to suitable prey and quite consistently the percentage of plants with prey on their leaves was low (never exceeding 5%) compared with the data of Crowder *et al.* (1990) on Irish populations.

Even if nitrogen-containing insect metabolites are more effective in promoting growth than inorganic nitrates (Chandler & Andersson 1976), an increased supply of the latter might possibly have initially enhanced reproduction in the fertilized plots.

With an increased growth of *Sphagnum* in the nitrogen-treated plots, the plants have to allocate more energy to stem growth to avoid overgrowth and consequently fewer resources are left for reproduction. In a study of two *Drosera* species, Chandler & Andersson (1976) observed that addition of inorganic nitrate to individuals supplied with insects inhibited growth. Fertilization with very high levels of nitrogen (about 170 g N m^{-2} year^{-1} mostly in form of ammonium) may cause an immediate reduction in flower production (Stewart & Nilsen 1992).

The age structure and the turnover rate in the plots receiving the lowest amount of nitrogen changed in comparison with the control plot. A higher representation of younger age classes implies that population size was more dependent on yearly reproduction and recruitment of seedlings in these low fertilization treatments. For plants adapted to mires, the water supply may be particularly critical for young seedlings during short periods of drought (Harper 1977). The nitrogen treatment resulted in an increased density of both *A. polifolia* and *E. vaginatum* and an increased competition for light may also imply decreased opportunities for seedling establishment. In addition, this may also influence the survival of adult plants, since *D. rotundifolia* is a physically small and shade-intolerant species (Stewart & Nilsen 1992). Consequently, even if population size remained constant when low amounts of nitrogen were supplied

(0·5 and 1·0 g N m^{-2} $year^{-1}$) it is obvious that the growth of the population became more susceptible to environmental changes.

It is apparent from this study that *D. rotundifolia* inhabiting ombrotrophic bogs is sensitive to atmospheric nitrogen deposition. Changes may be brought about by direct effects and by affecting the interactions between *Drosera* and the *Sphagnum* mosses. There are also reports from Britain and The Netherlands on a decline in *Drosera* species brought about by air pollution (Ashmore *et al.* 1988, p. 118). The critical load for damage of *Sphagnum* communities on raised bogs has been estimated to be 0·5–1 g N m^{-2} $year^{-1}$ (Nilsson & Grennfelt 1988). Morris (1991) suggests that plant species adapted to infertile habitats like ombrotrophic bogs cannot be maintained if nitrogen deposition exceeds 2 g N m^{-2} $year^{-1}$. These figures agree well with the result of this study with regard to *D. rotundifolia*, while other species, such as *A. polyfolia* and *E. vaginatum*, appear to be more tolerant to increased nitrogen deposition.

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REFERENCES

Aerts, R., Wallén, B. & Malmer, N. (1992): Growth-limiting nutrients in *Sphagnum*-dominated bogs subjected to low and high atmospheric nitrogen supply. *J. Ecol.* **80:** 131–140.

Ashmore, M., Bell, N. & Garretty, C. (eds) (1988): *Acid rain and Britain's natural ecosystems.* Contribution to a conference held at Imperial College Centre for Environmental Technology, London, UK.

Backéus, I. (1985): Aboveground production and growth dynamics of vascular bog plants in central Sweden. *Acta Phytogeogr. Suec.* **74.**

Begon, M., Harper, J.L. & Townsend, C.R. (1986): *Ecology. Individuals, Populations and Communities.* Blackwell Scientific Publications, Oxford.

Chandler, G.E. & Anderson, J.W. (1976): Studies on the nutrition and growth of *Drosera* species with the reference to the carnivorous habit. *New Phytol.* **76:** 129–141.

Crowder, A.A., Pearson, M.C. (The Late), Grubb, P.J. & Langlois, P.H. (1990): Biological Flora of the British isles. *Drosera* L. *J. Ecol.* **78:** 233–267.

De Riddler, F. & Dhont, A.A. (1992): The demography of a clonal herbaceous perennial plant, the longleaved sundew *Drosera intermedia*, in different heathland habitats. *Ecography* **15:** 129–143.

Ellenberg, H. (1985): Veränderungen der Flora in Mitteleuropa unter dem Einfluss von Düngung und Immissionen. *Schweiz. Z. Forstwes.* **136:** 19–39.

Ellenberg, H. (1988): Floristic changes due to nitrogen deposition in central Europe. In: Nilsson, J. & Grennfelt, P. (eds): *Critical Loads for Sulphur and Nitrogen.* The Nordic Council of Ministers. Report, 1988:15. Copenhagen, Denmark.

Ferguson, P. & Lee, J.A. (1983): The growth of *Sphagnum* species in the southern Pennines. *J. Bryol.* **12:** 579–586.

Ferguson, P., Robinson, R.N., Press, M.C. & Lee, J.A. (1984): Element concentration in five *Sphagnum* species in relation to atmospheric pollution. *J. Bryol.* **13:** 107–114.

Galloway, J.N. & Likens, G.E. (1981): Acid precipitation; the importance of nitric acid. *Atm. Environm.* **15:** 1081–1085.

Grennfelt, P. & Hultberg, H. (1986): Effects of nitrogen deposition on the acidification of terrestrial and aquatic ecosystems. *Water, Air, Soil Poll.* **31:** 945–964.

Harper, J.L. (1977): *Population Biology of Plants.* Academic Press, London.

Heil, G.W. & Diemont, W.M. (1983): Raised nutrient levels change heathland into grassland. *Vegetatio* **53:** 113–120.

Hällgren, J.-E. & Näsholm, T. (1988): Critical loads for nitrogen; Effects on forest canopies. In: Nillson, J. & Grennfelt, P. (eds): *Critical Loads for Sulphur and Nitrogen.* The Nordic Council of Ministers. Report, 1988:15. Copenhagen, Denmark.

Krok, Th. O.B.N. & Almquist, S. (1984): *Svensk Flora*, 26th edn. Esselte Studium, Uppsala.

Lloyd, F.E. (1942): *Carnivorus plants*. Chronica Botanica Co., Waltham, Mass.

Lövblad, G., Amann, M. Andersen, B., Homand, M., Joffre, S. & Pedersen. U. (1992): Deposition of sulfur and nitrogen in the Nordic countries: present and future. *Ambio* **21:** 339–347.

Morris, J.T. (1991): Effects of nitrogen loading on wetland ecosystems with particular reference to atmospheric deposition. *Ann. Rev. Ecol. Syst.* **22:** 257–279.

Nilsson, J. (ed) (1986): *Critical Loads for Nitrogen and Sulphur*. The Nordic Council of Ministers. Report, 1986:11. Copenhagen, Denmark.

Nilsson, J. & Grennfelt, P. (eds) (1988): *Critical Loads for Sulphur and Nitrogen*. The Nordic Council of Ministers. Report, 1988:15. Copenhagen, Denmark.

Salisbury, E.J. (1942): *The Reproductive Capacity of Plants*. Bell, London.

Silvertown, J. (1987): *Introduction to Plant Population Ecology*, 2nd edn. Longman, Essex.

Sjörs, H. (1948): Myrvegetation i Bergslagen. *Acta Phytogeogr. Suec.* **28.**

Stewart, Jr., C.N. & Nilsen, E.T. (1992): *Drosera rotundifolia* growth and nutrition in a natural population with special reference to the significance of insectivory. *Can. J. bot.* **70:** 1409–1416.

Summerfield, J. (1973): Factors affecting the germination and seedlings establishment of *Narthecium ossifragum* on mire ecosystems. *J. Ecol.* **61:** 387–398.

Thum, M. (1988): The significance of carnivory for the fitness of *Drosera* in its natural habitat. *Oecologia* **75:** 472–480.

Van Breemen, N. & Van Dijk, H.F.G. (1988): Ecosystem effects of atmospheric deposition of nitrogen in The Netherlands. *Environ. Pollut.* **54:** 249–274.

Van Dam, D., Dobben, H.F., Van Ter Braak, C.F.J. & de Wit, T. (1986): Air pollution as a possible cause for the decline of some phanerogamic species in The Netherlands. *Vegetatio* **65:** 47–52.

Wilkinson, L. (1990): SYSTAT: *The system for statistics*. SYSTAT Inc., Evanston, IL, USA.

Wooding, S.J., Press, M.C. & Lee, J.A. (1985): Nitrate reductase activity in *Sphagnum fuscum* in relation to wet deposition of nitrate from atmosphere. *New Phytol.* **99:** 381–388.