

# Reproductive allocation in plants of *Scrophularia nodosa* grown at various levels of irradiance and soil fertility

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## SUMMARY

The reproductive allocation of dry matter and mineral nutrients to flowers, capsules and seed was studied in plants of *Scrophularia nodosa* grown in a factorial, three (irradiation) × three (soil fertility), scheme in an experimental garden and in an irradiation gradient (on a natural soil) in a glasshouse. In the irradiation gradient a marked trade-off between sexual reproduction and vegetative propagation was shown: more flowering and seed production at higher irradiation, exclusively rhizome production at the low irradiation. There was no convergence between carbon allocation and nutrient allocation. At decreasing irradiation, biomass production decreased and concentrations of K, N, Na and P increased in all plant parts. In the factorial experiment a reduction of the irradiation from full daylight to 8% of daylight decreased the biomass production and the shoot:root ratio, once more enhanced by decreasing soil fertility, and increased the leaf area ratio. The specific leaf weight was only affected by the irradiation level, except at high soil fertility. The dry weight of the rhizome showed an irradiation and soil fertility interaction.

*Key-words:* *Scrophularia nodosa*, mineral nutrition, irradiation, reproductive allocation, soil fertility.

## INTRODUCTION

*Scrophularia nodosa* is a rhizome geophyte occurring in early as well as later stages of secondary forest succession on alkaline and acid soils (Ernst 1985; Van Anandel & Ernst 1985). Maintenance of established populations of this species during a large part of the successional series is supported by tuberous rhizomes, which show only very restricted vegetative spread (Meusel & Mörchen 1977). For this reason seed formation (after bee and wasp mediated pollination (Antonova 1979)) is particularly important to population expansion. The balance between vegetative propagation and generative reproduction is suggested to be influenced in many plant species by changes in the levels of irradiation, soil moisture and soil fertility (Salisbury 1942; Brix 1967; Anderson & Loucks 1973; Ogden

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1974; Abrahamson 1975; Werner & Platt 1976). The intensity of pollination has also been suggested as a factor determining this balance (Salisbury 1942). In addition, the ratio of fulvic to humic acid, being different for various soil horizons, may also influence the amount of flowers (Ernst *et al.* 1987).

In contrast to studies on annual plant species (e.g. Peace & Grubb 1982), variation in irradiation has been applied experimentally mostly to wild perennial woodland plant species by investigating the biomass allocation in their vegetative phase (Corré 1983a,b; Loach 1970; Lovett Doust 1987; Pons 1977; Slade & Hutchings 1987). Only a few authors (Blackman & Rutter 1947; Björkmann & Holmgren 1963) have considered the effect of irradiation on the mineral nutrition of plants. Generally, reproduction or the reproductive effort has only been measured as the dry matter allocated to the generative organs and the organs of vegetative propagation in individuals, or as the relative abundance of these organs in individual plants or natural populations. With reference to the measurement of the reproductive efforts in plants, Harper (1977) suggested the existence of 'the relevant currency' (differing between species and between habitats) which would be determined by the kind of limiting resource, thus presupposing the existence of only one limiting factor at any one moment (see also Van Andel & Vera 1977; Van Andel & Jager 1981).

The objectives of this study were to examine the effects of shading (i.e. restricting the supply of light) and/or restricting soil resources on the reproductive allocation of dry matter and mineral nutrients in *S. nodosa*. Due to the obligatory entomogamous flowers of *S. nodosa* we will compare the cost of flower and seed production in pollinated and unpollinated plants and the effect of pollination on the balance of carbon and nutrient allocation to generative and vegetative reproduction.

## MATERIALS AND METHODS

### *Experiments*

Seeds of *S. nodosa* L. were collected in a woodland clearing near Orsbach (Aachen, FRG). During the period April–September 1980, seedlings of *S. nodosa* were grown in a factorial design consisting of nine combinations of three irradiation levels and three soil fertility levels outside in an experimental garden. The irradiation levels were (neutrally) adjusted at 8%, 40% and 100% daylight under various numbers of layers of nylon cloth, because *S. nodosa* is not sensitive to changes in red/far-red ratio (Corré 1983a,b). Within each irradiation level three soil fertility levels were adjusted in a garden soil (high level), in dune sand (low level), and in a 50% (v/v) mixture of these two soils (intermediate level). The mineral composition of these soils, as analysed at the start of the experiments, is presented in Table 1. In each of the resulting nine treatments 10 plants were grown individually in pots containing 1 litre of soil. Tap water was added in appropriate amounts, if necessary, every second day depending on the climatic conditions. One- and two-way analyses of variance were used to test the log-transformed dry weight values of plants or plant parts at the end of the experiment.

A second irradiation gradient was set up in a glasshouse (10°C night, 20°C day, 70 ± 5% relative humidity) under several layers of nylon cloth. Three irradiation levels were adjusted by mercury vapour lamps to values of 100–250 W m<sup>-2</sup> (I), 35–45 W m<sup>-2</sup> (II) and 10–15 W m<sup>-2</sup> (III) at a photoperiod of 14 h light/10 h dark. This experiment lasted for 22 weeks. In order to make normal seed development possible all open flowers were artificially pollinated every 2 days with the exception of the plants subjected to an additional non-pollination treatment. In each of the treatments, 10 plants were grown

**Table 1.** Mineral concentrations ( $\mu\text{mol cm}^{-3}$  fresh soil) of the applied soils

Fertility level	N total dry soil	NO <sub>3</sub> -N	PO <sub>4</sub> -P	K	Na	Ca	Mg	Fe	Mn
High	272 (43)	12.74 (1.90)	0.308 (0.008)	6.75 (0.14)	35.5 (3.3)	479 (33)	524 (53)	0.05 (0.01)	0.31 (0.02)
Intermediate	53 (15)	3.25 (0.71)	0.077 (0.031)	1.82 (0.38)	25.4 (5.1)	307 (25)	95 (11)	0.07 (0.01)	0.24 (0.05)
Low	31 (3)	0.13 (0.06)	0.011 (0.001)	0.19 (0.01)	13.7 (6.0)	121 (14)	31 (2)	0.19 (0.05)	0.07 (0.02)
Natural soil	113 (5)	3.30 (0.30)	0.026 (0.003)	0.87 (0.09)	11.8 (5.3)	46 (10)	10 (1)	0.05 (0.02)	0.19 (0.04)

Figures in brackets represent 1 SD ( $n=4$ ).  
For methods of analysis see text.

(immediately after germination on garden soil) on a natural soil obtained from a wood clearing where a population of *S. nodosa* was present. The mineral concentration of this soil is presented in Table 1.

Nectar of protected flowers was collected using calibrated capillaries. Collection was started on the day of the opening of the corolla and finished when the corolla was shed.

Leaf area of the plants grown in the factorial design consisting of soil fertility and irradiation levels were measured immediately after harvesting. Mineral analyses of the soils in both experiments were made in water extracts (1:10, w/w, fresh soil) except for total nitrogen, which was determined after combustion of 100 mg of dry soil in a pure oxygen stream. The plants were separated into different organs, i.e. roots, rhizomes, stem, leaves, flowers, capsules and seeds, after which the organs were dried at 80°C for at least 24 h. All organs were kept separate for each plant. Mineral analyses of plant samples were carried out after homogenization and wet ashing in concentrated HNO<sub>3</sub> and HClO<sub>4</sub>, conforming with the procedures described by Tolsma *et al.* 1987). Nitrate in the soil extracts was measured with a membrane electrode (model ORION).

In a greenhouse, isolated flowering plants of *S. nodosa* were submitted to the following pollination treatments: no active pollination, artificial (brush) self-pollination within individual plants and artificial cross-pollination. Each flower was pollinated once and labelled. Non-pollinated flowers remained in the inflorescence. The degree of fertilization was determined 3 weeks after pollination (20 flowers, four plants per treatment).

### Statistics

One- and two-way analyses of variance were used to test the data from both experiments.

## RESULTS

### Dry matter allocation

The effect of the nine combinations of levels of soil fertility and irradiation on dry matter allocation to rhizomes, to capsules and seeds and on the dry matter production per plant (field experiment) is presented in Fig. 1.

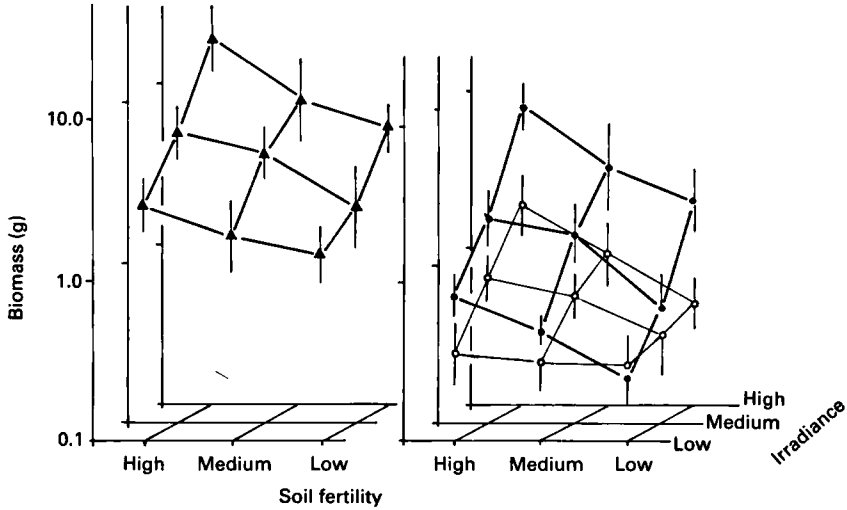


Fig. 1. Dry weight (log scale) of rhizomes (○), capsules and seeds (●) and entire plants (▲) of *Scrophularia nodosa* grown in the nine treatments of a factorial (irradiation × soil fertility) scheme ( $n=10$ ). Vertical lines are  $\pm$  SE.

Table 2. ANOVA tables of the dry weight values in a three (soil fertility) by three (irradiation density) factorial design

Plant part	Source of variation	d.f.	SS	MS	<i>F</i>
Individual plants	Soil fertility	2	28.92	14.46	13.5***
	Irradiation intensity	2	37.76	18.88	17.6***
	Interaction	4	6.48	1.62	1.5 n.s.
	Error	81	86.55	1.068	
Capsules + seeds	Soil fertility	2	31.74	15.87	14.08***
	Irradiation intensity	2	68.77	34.39	30.51***
	Interaction	4	5.19	1.30	1.15 n.s.
	Error	81	91.30	1.127	
Rhizomes	Soil fertility	2	8.53	4.27	8.19***
	Irradiation intensity	2	16.94	8.77	16.81***
	Interaction	4	5.81	1.45	2.78*
	Error	81	42.25	0.52	

\*, \*\* and \*\*\* indicate values significant at  $P < 0.05$ ,  $P < 0.01$  and  $P < 0.001$  respectively.

The response of the rhizome differed from the response of the reproductive structures (capsules, flowers and seeds). A significant ( $P < 0.05$ ) soil fertility and irradiation interaction was present in the rhizome weight only (Table 2). The rhizome weight at the lowest soil fertility level was not significantly ( $P < 0.05$ ) affected by the variation in irradiation and vice versa (Fig. 1b, Table 2). There was no such interaction in the dry weight of the reproductive structures or in the total plant dry weight (Fig. 1, Table 2).

If the allocation of biomass, however, was considered (Table 3), then the allocation pattern to rhizomes was stable at the high irradiation level and independent of the soil

**Table 3.** Generative and vegetative allocation (as percentage of total biomass) of plants of *Scrophularia nodosa* grown at a factorial design consisting of three levels of irradiation (daylight = 100%) and soil fertility

	Soil fertility	Irradiance level		
		100%	40%	8%
Generative allocation (flowers, capsules, seeds)	High	42.1 ± 10.7	28.7 ± 12.3	29.3 ± 10.7
	Medium	37.1 ± 15.6	24.7 ± 17.6	17.3 ± 15.6
	Low	31.5 ± 17.4	10.5 ± 11.6	3.2 ± 6.6
Vegetative allocation (rhizomes)	High	10.6 ± 4.3	11.9 ± 9.2	12.1 ± 4.8
	Medium	14.1 ± 10.5	15.2 ± 7.6	21.1 ± 11.0
	Low	11.6 ± 7.5	22.1 ± 9.3	28.6 ± 7.8

The data are the means, based on 10 plants per treatment.

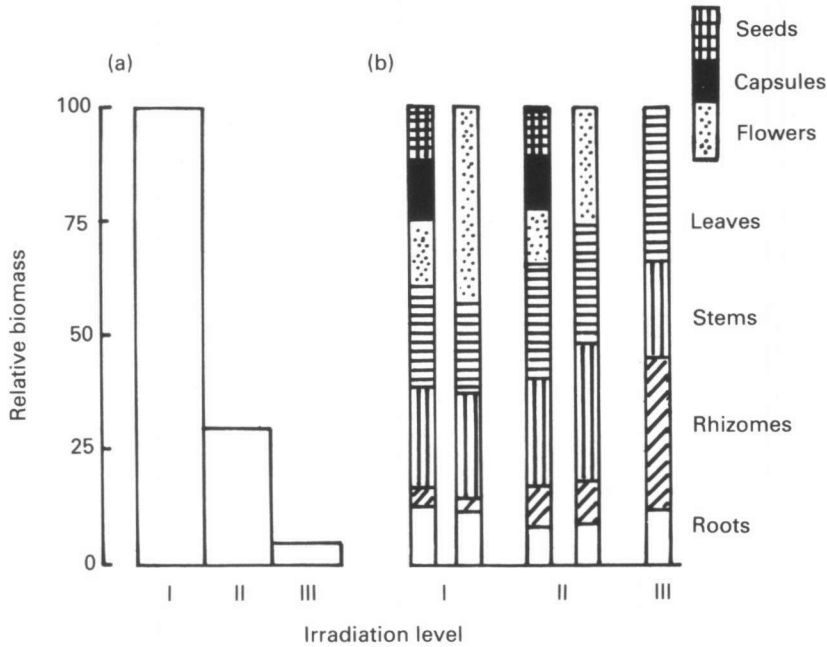
**Table 4.** Leaf area ratio (LAR), specific leaf weight (SLW) and shoot:root ratio (SRR) of plants of *Scrophularia nodosa* grown in a factorial design consisting of three levels of irradiation (daylight = 100%) and soil fertility

Plant parameter	Soil fertility level	Irradiation level		
		100%	40%	8%
LAR (m <sup>2</sup> g <sup>-1</sup> )	High	0.37	0.55	0.68
	Medium	0.39	0.64	1.06
	Low	0.62	0.70	1.37
SLW (mg cm <sup>-2</sup> )	High	5.56	4.32	5.14
	Medium	5.78	4.50	2.56
	Low	4.52	4.51	2.49
SRR	High	4.33	2.16	2.64
	Medium	4.09	2.30	1.65
	Low	3.90	1.70	0.78

The data are the means based on 10 plants per treatment.

fertility, and at high soil fertility independent of the irradiation level. As soon as both environmental factors were decreasing, the allocation of biomass to rhizomes increased to the highest percentage (28.6 ± 7.8%) at the lowest irradiation level, if grown at low soil fertility. Under the same conditions the allocation to the generative plant parts (flowers, capsules and seeds) decreased; it was only 10% of that allocated in plants at high irradiation and high soil fertility.

The combination of irradiation levels and soil fertility had a distinct influence on the leaf area ratio (LAR: leaf area/total plant dry weight) and on the shoot:root ratio (shoot: [roots + rhizomes]). At the same soil fertility level LAR increased by a factor of two (Table 4). At the same irradiation level, however, the increase by a factor of around 1.5 only occurred at low soil fertility. The 'leafiness' of the plants was the same, going from low via



**Fig. 2.** Relative dry weight (a) and dry matter allocation (b) to the various organs of *Scrophularia nodosa* plants grown at three irradiation levels (I = high, II = medium, III = low). The absolute dry weights were 14.1, 4.8 and 0.78 g per plant in the treatments I, II and III, respectively. The right-hand bars at irradiation level I and II represent non-pollinated plants.

medium to high soil fertility, if the irradiation level was decreased from high via medium to low. However, there was an increase by a factor of two if the decrease in the irradiation was accompanied by a decrease in soil fertility (the diagonal from left to right in Table 4). With regard to the shoot:root ratio a high and medium irradiation level had a greater influence than the soil fertility. At low irradiation, however, a decrease of the soil fertility negatively affected the shoot:root ratio.

The effect of the irradiation level and the soil fertility was less clear for the specific leaf weight (SLW: leaf weight/leaf area). Due to the high variability between plants of the same treatment it seemed that at high soil fertility the plants could maintain the leaf quality at decreasing irradiation, whereas at medium soil fertility there was a gradual decrease at decreasing irradiation.

On the natural soil (greenhouse experiment) the irradiation strongly affected the mean plant dry weight (14.1, 4.8 and 0.7 g) as well as the dry matter allocated to the rhizomes and the inflorescence (Fig. 2). With an increase of shading, the portion of dry matter allocated to generative reproduction decreased from 40 to 0% and the proportion of dry matter allocated to the rhizomes increased from 3 to 33% (Fig. 2), thus confirming the results of the field experiment. Absence of pollination hardly affected these proportions at high and medium irradiation. The remaining plant parts were represented by constant (root, stems) or slightly increasing (leaves) dry weight proportions with diminished radiation.

In the absence of a pollinator none of the flowers developed filled capsules (Fig. 2). Artificial cross- or self-pollination nearly always resulted in fertilization and seed

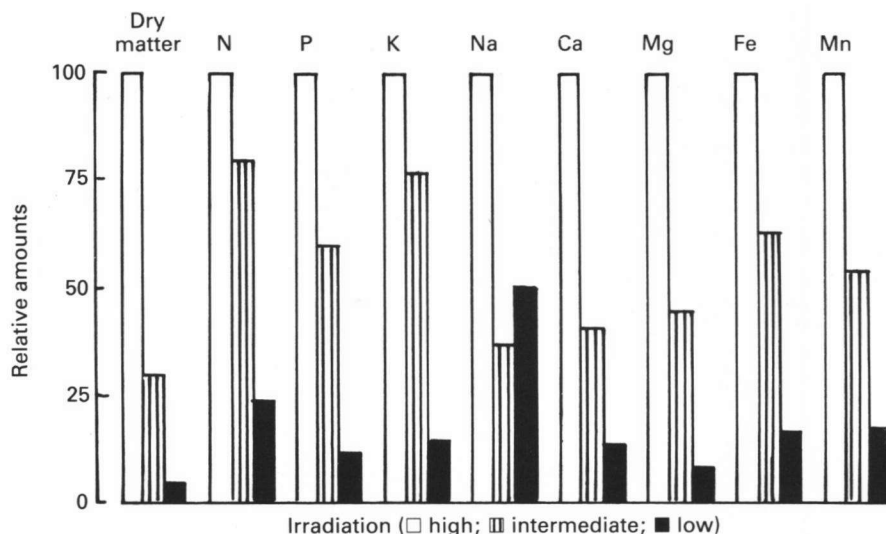


Fig. 3. The relative amounts of dry matter ( $n=8$ ) and mineral nutrients ( $n=4$ ) of *Scrophularia nodosa* plants grown at three irradiation levels. The values at the high irradiation level are adjusted to 100%.

production (self- 95%; cross- 90% of flowers producing filled capsules). In comparison to pollinated plants, unpollinated plants allocated two to three times more biomass to flowers at medium and high irradiation (Fig. 2). Unpollinated plants produced up to five times more nectar than hand-pollinated ones. The absence of seed production of unpollinated plants did not cause another pattern of biomass allocation to the rhizomes.

#### *Mineral amount, mineral concentration*

Compared to the reduction of dry weight in the lower irradiation levels, the absorbed amounts of mineral nutrients were less affected (greenhouse experiment, Fig. 3). Except for calcium, magnesium and sodium, the amount of all mineral elements was far less reduced in the intermediate irradiation (II) than the biomass. At the lowest irradiation (III) Na was the least affected element and Mg the most strongly affected.

These differences in response of dry weight per plant and of absorbed amounts of mineral nutrients per plant caused marked increases in the concentrations of the mineral nutrients in most of the plant parts at the low irradiation (Table 5). Notably, in the rhizomes, stems and leaves the concentrations of some of the elements (N, Na, Fe and Mn) sharply increased. Under high irradiation the highest nitrogen concentration was found in the seeds. At all irradiation levels higher P concentrations occurred in the seeds and the rhizomes, the lowest K concentrations in the seeds, the rhizomes and the flowers. The Na concentrations are low in all parts; relatively high concentrations of Ca, Mg, Fe and Mn occur in the leaves. Comparison of the mineral concentrations in capsules and seeds reveals three distinct patterns: much higher concentrations in the seeds (N, P, Mg and Mn); much higher concentrations in the capsules (K); and about equal concentrations in both organs (Na and Zn) independent of the irradiation.

#### *Mineral allocation*

The result of the differential behaviour of the elements in the various plant parts in the irradiation gradient is a series of markedly differing allocation patterns (Fig. 4). In

Table 5. The concentration ( $\mu\text{mol g}^{-1}$  dry matter) of mineral nutrients in various organs of plants of *Scrophularia nodosa* grown on a natural soil at three levels of irradiation

	N	P	K	Na	Ca	Mg	Fe	Mn	Zn
<b>Roots</b>									
I	586 (145)	14.2 (4.1)	267 (64)	2.94 (0.76)	119 (31)	93.7 (10.4)	15.49 (26.92)	2.52 (1.33)	4.72 (2.57)
II	1168 (263)	26.6 (3.1)	929 (118)	4.35 (0.95)	152 (10)	104.9 (33.3)	7.46 (2.93)	4.28 (0.76)	5.80 (0.92)
III	1907 (409)	41.4 (10.9)	1021 (110)	8.60 (2.34)	104 (24)	59.0 (6.8)	4.40 (1.58)	6.25 (1.43)	—
<b>Rhizomes</b>									
I	428 (156)	17.4 (2.4)	178 (19)	1.91 (0.54)	58 (3)	48.5 (8.4)	0.75 (0.30)	0.63 (0.10)	0.74 (0.13)
II	875 (340)	32.1 (4.7)	294 (76)	3.13 (0.95)	71 (8)	54.4 (7.2)	0.87 (0.82)	0.68 (0.26)	1.65 (0.39)
III	2479 (983)	51.4 (11.5)	458 (68)	9.91 (3.78)	76 (10)	76.0 (10.3)	1.63 (0.84)	2.40 (0.87)	—
<b>Stems</b>									
I	227 (43)	7.0 (1.0)	184 (41)	0.64 (0.21)	118 (30)	42.7 (5.3)	0.09 (0.08)	1.89 (1.06)	0.61 (0.31)
II	764 (214)	14.3 (3.7)	368 (86)	0.41 (0.11)	147 (28)	36.8 (13.7)	0.15 (0.14)	1.94 (0.62)	1.38 (0.40)
III	2016 (561)	32.9 (9.8)	812 (97)	11.53 (4.35)	544 (109)	79.0 (15.6)	1.07 (0.63)	2.43 (0.93)	—
<b>Leaves</b>									
I	628 (61)	14.5 (2.9)	267 (74)	0.38 (0.15)	344 (93)	56.3 (8.7)	0.28 (0.42)	2.52 (0.49)	0.88 (0.36)
II	2417 (376)	35.2 (7.3)	937 (276)	0.45 (0.14)	505 (137)	133.5 (43.4)	1.29 (0.32)	5.81 (1.28)	3.45 (0.98)
III	3821 (507)	44.8 (12.0)	870 (125)	7.50 (2.19)	868 (217)	164.0 (34.9)	3.38 (0.53)	15.19 (3.33)	—
<b>Flowers</b>									
I	471 (27)	10.0 (0.6)	213 (1)	0.27 (0.12)	52 (11)	29.7 (1.8)	0.46 (0.28)	0.51 (0.04)	0.42 (0.00)
II	673 (114)	13.0 (0.07)	352 (11)	0.24 (0.09)	49 (4)	40.4 (0.6)	0.26 (0.01)	0.58 (0.01)	0.79 (0.18)
III	—	—	—	—	—	—	—	—	—
<b>Capsules</b>									
I	370 (80)	13.6 (5.3)	547 (14)	0.95 (0.64)	146 (78)	43.8 (3.7)	0.58 (0.46)	0.53 (0.09)	1.30 (0.95)
II	732 (160)	19.1 (9.8)	1107 (258)	0.78 (0.59)	66 (13)	31.8 (4.9)	0.70 (0.31)	0.50 (0.06)	1.77 (1.29)
III	—	—	—	—	—	—	—	—	—
<b>Seeds</b>									
I	1564 (290)	64.8 (6.7)	145 (12)	0.78 (0.51)	124 (27)	118.4 (23.5)	0.65 (0.08)	1.34 (0.73)	1.10 (0.15)
II	1923 (271)	68.1 (9.8)	261 (96)	0.56 (0.13)	66 (18)	134.2 (27.4)	1.26 (0.71)	1.01 (0.09)	1.58 (0.33)
III	—	—	—	—	—	—	—	—	—

(I = 100–250, II = 35–45, III = 10–15  $\text{W m}^{-2}$ .)  
Figure in brackets represent the SD ( $n=4$ ).



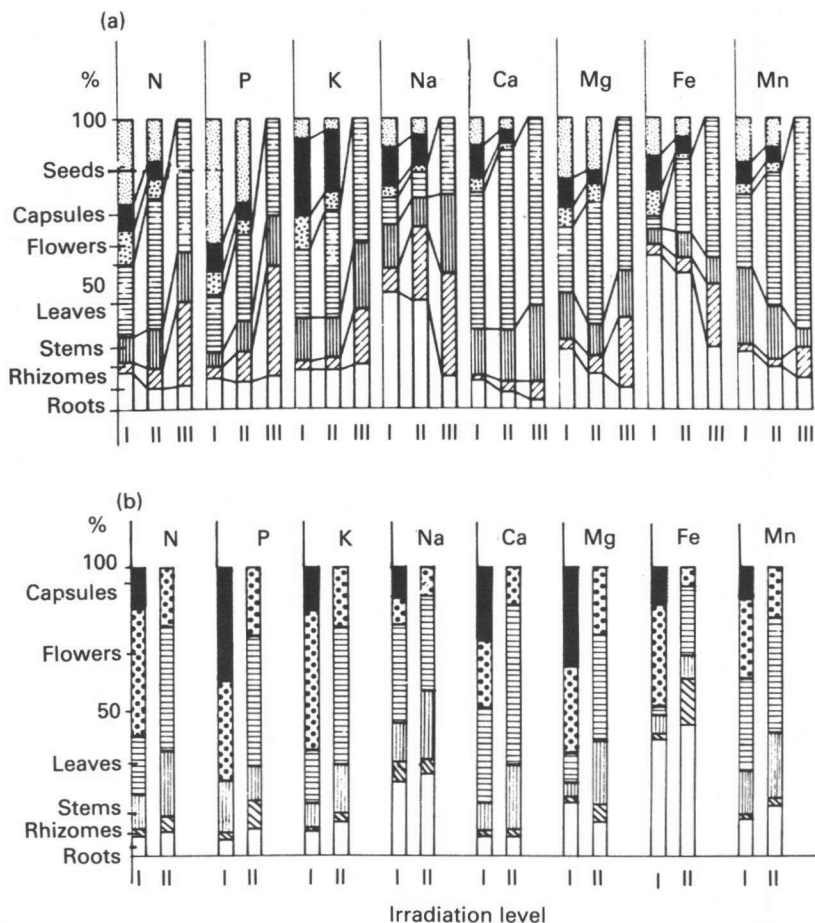


Fig. 4. Patterns of allocation of mineral nutrients to the various organs of *Scrophularia nodosa* plants grown in three levels of irradiation (I=high, II=medium, III=low) ( $n=4$ ) (a) with pollination and (b) without pollination. The total amount per plant is adjusted to 100%.

pollinated plants (Fig. 4a) N, P and K are allocated 48%, 55% and 46% respectively, to the sexual reproductive organs under high irradiation level. Also, a relatively large portion of Mg (19.5 and 23.5%) is allocated to seeds at high and medium irradiation. Large increases of N, P, K and Mg are found in the rhizomes at increasing shade being comparable with the proportional increase of biomass, whereas Ca and Mn did not follow this trend. The root portions of N, P and K are relatively constant over the three radiation levels. Of the Fe present in the above-ground parts at high irradiation, 79% was allocated to the inflorescence. The increase of Fe and Mn in the leaves at increasing shade is very marked, as is the simultaneous decrease of these elements in the roots. The result of the increasing dry matter allocation to the rhizomes and the increasing concentrations of the elements in the rhizomes is presented in Table 6. While the total dry weight per plant at low irradiation is reduced to 5% of the dry weight at the highest level, the rhizome dry weight is only reduced to 42% and the N content of the rhizomes is more than doubled; the contents of P, K and Fe of the rhizomes remain constant.

**Table 6.** The average total amount ( $\mu\text{mol}$ ) of mineral nutrients in the rhizomes of *Scrophularia nodosa* plants grown at different irradiation intensities

Irradiation intensity ( $\text{W m}^{-2}$ )	N	P	K	Ca	Mg	Fe	Mn
100–250	231	22	96	31	25	0.44	0.36
35–45	379	32	115	28	21	0.35	0.27
10–15	575	25	106	18	18	0.38	0.56

Due to the absence of flower production at the low irradiation level, the impact of pollination on the mineral allocation could only be analysed at the high and the medium irradiation level (Fig. 4b). At the high irradiation there was less allocation of nutrients to roots and rhizomes of unpollinated plants, except for Mg. Compared to unpollinated plants, in the rhizomes of pollinated plants the proportion of K increased by a factor of six, that of P by a factor of five, that of Ca, Mn and N by a factor of four, that of Fe and Zn by a factor of two ( $P < 0.05$ ). The proportion of Ca, Mg, K and Zn was significantly ( $P < 0.05$ ) increased in the reproductive organs (flowers, empty capsules) of non-pollinated plants.

At medium irradiation the allocation of nutrients to rhizomes and roots was nearly the same in pollinated and non-pollinated plants. The proportion of nutrients allocated to reproductive organs was nearly twice as high in pollinated plants than in non-pollinated ones.

## DISCUSSION

A variety of parameters have been used to evaluate reproductive effort (Harper 1977; Van Andel & Vera 1977; Thompson & Stewart 1981; Reekie & Bazazz 1987a). We have used the quantity of biomass and nutrients allocated to flowers, capsules and seeds as indicators of sexual reproductive effort, and quantity of biomass and nutrients allocated to rhizomes as indicators of vegetative reproductive effort compared to the total plant biomass and/or nutrient quota. With regard to the most appropriate assessment of reproductive effort, Thompson and Stewart (1981) have suggested mineral resources rather than calorific value, as postulated by Harper and Ogden (1970), whereas Reekie and Bazzaz (1987b,c) assumed that carbon will integrate the allocation pattern of other resources.

First, we will consider the pattern of biomass allocation as the integrator of photosynthesis and mineral supply. In *S. nodosa* the dry matter allocation to the sexual reproduction decreases and that to the rhizomes increases at decreasing levels of soil fertility and irradiation. This shift suggests a competition for resources within individual plants between these two sinks (Harper 1977), although this evidence cannot serve as a direct proof for this hypothesis. High plant density also led to inhibition of flowering in first year seedlings which had all produced rhizomes at the end of the first growth season (Van Baalen 1982).

The sexual reproductive effort in the highest irradiation is 42%. This value is much higher than that found in woodland clearings (20%; Van Baalen 1982) and indicates a lower irradiance exposure during the growing season due to the canopy shadow of the neighbouring woodlands. The sexual reproductive effort of field plants of *S. nodosa* can be compared with a number of perennial herbs, where sexual reproductive effort varied from

5 to 25% (Struik 1965; Williams 1975; van Andel & Vera 1977; Ernst 1983b). Equally high or higher reproductive effort of forest perennials is found in three *Allium* species from deciduous forests in Japan (Kawano & Nagai 1975), in *Allium ursinum* in Europe (Ernst 1979), *Claytonia virginica* (Schemske *et al.* 1978) and *Hieracium venosum* in America (Abrahamson 1979). Other shade-tolerant herbs such as *Anemone nemorosa* (Ernst 1983b) and those reviewed by Bierzychudek (1982) showed a much lower sexual reproductive effort, varying from 5 to 25%.

As in the perennials *Uvularia perfoliata* (Whigham 1974) and *Rubus hispidus* (Abrahamson 1975) the sexual reproductive effort of *S. nodosa* is plastic. Unlike *Chamaenerion angustifolium* (Van Andel & Vera 1977) and *Tussilago farfara* (Ogden 1974), *S. nodosa* shows a strongly variable vegetative reproductive effort. The shift from generative reproduction to vegetative propagation in *S. nodosa* at decreasing soil fertility and decreasing irradiation parallels the decreasing sexual reproductive effort with increasing maturity of secondary succession in species of the genera *Solidago*, *Helianthus* and *Andropogon* (Gaines *et al.* 1974; Roos & Quinn 1977; Newell & Tramer 1978; Abrahamson 1979). The absence of sexual reproductive organs and the presence of rhizomes in *S. nodosa* plants growing at high densities (Van Baalen, 1982) contrast with the enhanced sexual reproduction at higher densities in *Tussilago farfara*, *Rubus hispidus*, *R. trivialis* and *Fragaria virginiana* (Ogden 1974; Abrahamson 1975; Holler & Abrahamson 1977) but is comparable to the density response of *Mimulus primuloides* (Douglas 1977). With respect to some of the species mentioned above the shift towards higher fruit production at higher densities is interpreted as a provision of escape from adverse habitat conditions (Ogden 1974; Abrahamson 1975). This interpretation does not apply to *S. nodosa* because of the restricted spatial and temporal seed dispersal. In *S. nodosa* the opposite response (more seeds at the lower densities and at the higher irradiation and soil fertility levels of early succession) offers prospects of fast population expansion under conditions where the higher growth rates of individual plants (Van Baalen *et al.* 1984), the fast flowering of established plants and the high germination percentage (no innate or induced dormancy in early spring) also contribute to fast population expansion. In later successional stages this ruderal component in the reproductive strategy of *S. nodosa* loses its dominance to a more perennial characteristic: the biomass allocation to the rhizome (and the inhibition of flowering) under shade conditions comparable with biomass allocation of *Ranunculus repens* (Lovett Doust 1987) and *Glechoma hederacea* (Slade & Hutchings 1987) under low light and nutrient conditions. Because the rhizome of *S. nodosa* is not suited to vegetative spread or to the formation of vegetative propagules after fragmentation, non-flowering plants are exclusively focused on maintenance at the growth site. Population maintenance by means of buried seed banks is probably only guaranteed for a few years because of the rapid decay of these seed banks (Van Baalen 1982).

Hampering pollination may be a powerful test on the impact of seed production on the final allocation of biomass and nutrients to vegetative reproduction in self-incompatible plant species. As shown for non-pollinated plants of *S. nodosa*, a lack of pollination evokes an additional production of flowers and nectar, not reported earlier in allocation studies for allogamous plant species. As far as irradiation is sufficient for the initiation of inflorescences, the availability of pollen vectors may affect not only the fertility of a plant, but also its allocation pattern.

Our study has shown that the convergence between carbon allocation and nutrient allocation, as suggested by Reekie and Bazzaz (1987a,b) is not present in *S. nodosa*. A

similar lack of convergence was found for carbon and phosphorus allocation in *Agropyron repens* (Reekie & Bazzaz 1987b). As shown in the greenhouse experiment with plants of *S. nodosa* grown on a natural soil at three levels of irradiation, a decrease of the irradiation diminishes the biomass production, but did not hamper the uptake of N, P, and K so that these nutrients accumulate in all plant parts. Further reasons for this divergence of allocation patterns will be the species-specific chemical composition of fruits, seeds and supporting structures, as shown for some dune annuals (Ernst 1983a), woodland herbs (Van Anandel & Ver 1977; Ernst 1983b) and *Acacia* spp. in an African savanna (Tolsma *et al.* 1987). Plant species with a high ratio of fruit biomass to seed mass will demand more carbon sources and less nutrients than plant species with a low ratio between both reproductive structures. Furthermore, the kind of stored reserve material in seeds (carbohydrate, oil, proteins) will regulate the nutrient and carbon demand.

The species-specific and even genotype-specific demands (Ernst 1987; Reekie & Bazzaz 1987b) will be modified by environmental factors. Variation of the chemical binding of nutrients in the soil solution will affect nutrient uptake and translocation, even with impacts on the reproductive structures, as demonstrated for *S. nodosa* at varying concentrations of humic and fulvic acids (Ernst *et al.* 1987). On the other hand, the high coefficient of variation at each experimental combination indicates that the high genetic variability of *S. nodosa* is not only associated with iron uptake and translocation (Ernst 1985), but will also affect the uptake and translocation of other nutrients, perhaps in relation to the FER genes (Bienfait 1989). Although *S. nodosa* reacts with a rise in LAR at lower irradiation levels as do other typical shade-tolerant species (Blackman & Wilson 1951; Pons 1977), in the present study shading had a striking effect, greatly increasing the concentrations of the recorded elements in most plant parts and there was an enormous proportional increase of nearly all nutrients in the rhizomes. The very high concentration of total N in the leaves at the lower irradiation levels might be in agreement with the high N concentration in the leaves of *Allium ursinum* in beechwoods (Ernst 1979). Ca, K, Mg, N, Na and P also become highly concentrated in the leaves of *S. nodosa* under shade conditions. This phenomenon resembles the P accumulation in the leaves of the slow-growing perennial grasses *Deschampsia flexuosa* (Bannister 1976) and *Agrostis setacea* (Clarkson 1967), although the mechanisms of growth reduction may be different in *D. flexuosa* and *A. setacea*, compared to *S. nodosa*. In the rhizomes and seeds, N and P reach their highest and K reaches its lowest concentration compared to all plant parts at all irradiation levels. Apparently these elements play different roles in the reproduction of *S. nodosa*. Similarly, low K concentrations in seeds or fruits and higher K concentrations in capsules or involucre of *C. angustifolium* and *Senecio sylvaticus* respectively, were found by Van Anandel & Vera (1977). The pool of mineral nutrients accumulated in the rhizome under shade conditions will be drawn on if the growth rate increases at higher irradiation levels. This is of importance when forest plants of *S. nodosa* experience the start of a windfall and the consequent elevation of irradiation intensity. Also in the context of the seasonal irradiation regime in deciduous forests, the mineral nutrient pool in the rhizomes could be of importance because it may sustain fast stem and leaf growth in early spring.

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