

# GROWTH AND REPRODUCTIVE STRATEGIES OF TWO ANNUAL WEEDS AS AFFECTED BY SOIL NITROGEN AND DENSITY LEVELS

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## SUMMARY

The growth and reproductive strategies of two weeds, *Spergula arvensis* L., a weed of croplands, and *Plantago major* L., a weed of wastelands and lawns, were studied in relation to two soil nitrogen and four population density levels. The dry matter yield under the various treatments revealed that *S. arvensis* is less sensitive to density increase than *P. major*. The dry matter allocation pattern with reference to reproductive allocation was, however, not appreciably modified by soil nitrogen or density levels in either of the species, though reproductive allocation was higher in *S. arvensis* than *P. major*. *S. arvensis* produced larger numbers of seeds in nitrogen-rich soil while *P. major* did not. The results indicate that *S. arvensis* is more of an 'r-' strategist and *P. major* is 'K-' selected in the r-K continuum. In the C-S-R strategy model (*sensu* Grime), *P. major* may be assigned a position more towards 'C' and *S. arvensis* more towards 'R'.

## INTRODUCTION

Life history has been envisaged as a point of balance between the conflicting requirements of different activities of an organism such as reproduction, maintenance and growth (Law, 1979). This is basically an elaboration of Fisher's (1958) interpretation of the balance between reproductive and non-reproductive activities, which served as the basis for later studies on 'allocation pattern'. Though biomass allocation pattern has been extensively studied for gaining insight into the reproductive strategies of plants (Harper and Ogden, 1970; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973; Tripathi and Harper, 1973; Werner and Platt, 1976; Hickman, 1977; Abrahamson and Hershey, 1977; Brouillet and Simon, 1979; Weaver and Cavers, 1980), it should not be considered as the sole criterion, as the number and size of propagules are also of considerable significance in reproductive success of a species.

Studies on the pattern of resource allocation in plants, highlighting the reproductive strategies as affected by density and nutrition, are few and far between. Harper and Ogden (1970), Ogden (1974) and Andel and Vera (1977) found for different species that dry matter allocation to the sexual reproductive structures is less variable at different soil fertilizer levels and concluded that reproductive allocation is independent of nutrient level. Density, however, has been reported to influence reproductive effort differently in various species (Abrahamson, 1975; Holler and Abrahamson, 1977; McNamara and Quinn, 1977; Assemat and Oka, 1980; Pitelka, Stanton and Peckham, 1980). Furthermore, the sexual reproductive strategy is also strongly affected by other environmental factors (Whigham, 1974; Hickman, 1975).

We have studied resource allocation pattern with special reference to reproductive strategies for two common weeds, namely *Spergula arvensis* L. and *Plantago major* L., which occur abundantly in the state of Meghalaya (India). *S. arvensis* is a common weed of the high altitude (c. 1500 m) agroecosystems of Meghalaya and is characterized by rapid growth and a short life cycle (up to three life-cycles can be completed in a single year). *P. major* is a perennial, but under extremely cold conditions it may behave as an annual, and Palmblad (1968) considers it as a weedy annual. *S. arvensis* has been reported to prefer light, sandy soils though it may be found growing on soil of all textures (New, 1961), while *P. major* has been reported to occur on a wide range of soil types (Sagar and Harper, 1964) showing no preference. Trivedi and Tripathi (1982) also observed that while in *S. arvensis*, sandy soil supported more vigorous growth than garden soil, in *P. major* the differences in yield due to soil type were not marked. The resource allocation to different plant parts of these two weeds of contrasting habitats has been studied in relation to soil nitrogen and density levels, and the results obtained are discussed in light of the conditions under which these weeds grow in nature.

#### MATERIALS AND METHODS

Seeds of *S. arvensis* and *P. major* were collected from natural populations growing in and around Shillong, Meghalaya (longitude 25.34° N and latitude 91.56° E; altitude 1500 to 1700 m). The seeds of the two species were sown in plastic pots (21 cm diameter and 19 cm depth) with a basal drainage hole. The sowing was done on 26 March 1979 for both the species and the other details regarding the experiment are given in Table 1. *Spergula* was harvested 6, 10 and 20 weeks from

Table 1. *Details of the experiment with regard to sowing, thinning and harvest dates (1979)*

Species	Date of sowing	Date of thinning	Date of Harvest I (H1)	Date of Harvest II (H2)	Date of Harvest III (H3)
<i>Spergula arvensis</i>	26 March	9 April	7 May	4 June	13 August
<i>Plantago major</i>	26 March	16 April	21 May	25 June	27 August

sowing while *Plantago* was harvested 8, 13 and 22 weeks from sowing. During the course of the experiment, from 26 March to 27 August 1979, the temperature in the unheated nethouse where the study was undertaken ranged from 10.4 °C in March to 33 °C in May. Mean monthly minimum and maximum temperature of the nethouse are given in Figure 1. The nethouse was provided with a translucent polythene-sheet roofing while the sides were left uncovered.

Four density levels, 1, 3, 9 and 18 per pot (equivalent to 30, 90, 270 and 540 m<sup>2</sup>), were obtained by sowing 5, 15, 45 and 90 seeds respectively for both species. After germination and establishment, the plants were thinned to the required density levels. The pots were watered on every alternate day with 250 ml water. The amount of water supplied to the plants under different treatments was sufficient to sustain them and except for two occasions on hotter days when plants showed signs of temporary wilting, during most of the experimental period no effect of moisture stress was evident.

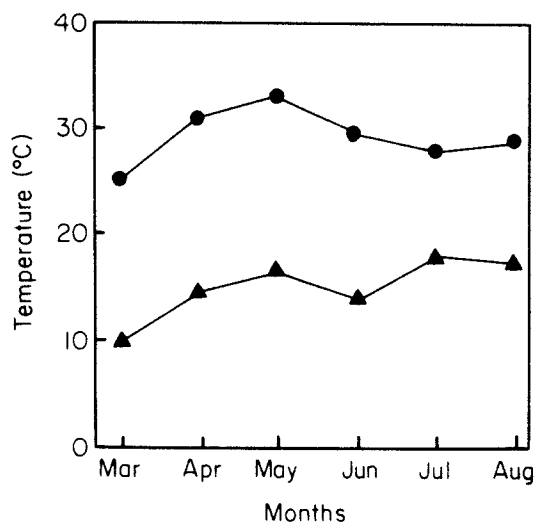


Fig. 1. Mean minimum (▲) and mean maximum (●) temperature of the nethouse during the experimental period.

At the start of the experiment, the nitrogen content of the soil in the pots was analyzed by the Kjeldahl method (Jackson, 1962). The total N content of the untreated soil, which represented the low nitrogen regime, was 0.2%. For the high N regime, 22.85 g of ammonium nitrate per pot was added to the untreated soil to raise the soil nitrogen content to 0.4%. This is henceforth considered as the high nitrogen regime. The populations of the two weeds representing the four density levels as described above were grown in the soils with low and high nitrogen regimes. The experimental plan consisted of two nitrogen regimes  $\times$  four density levels  $\times$  three harvests  $\times$  three replicates, in a factorial manner involving 72 pots for each of the two weeds.

During the time of harvest, plants from the pots representing various treatments were excavated whole and the root system was washed thoroughly with running water. The measurements were based on three and nine plants respectively for D1 and D3 treatments while for higher densities, D9 and D18, four plants from each of the three replicate pots were selected for measurement. The component plant parts were separated, oven-dried at 80 °C to constant weight and weighed. To prevent loss of seeds due to dissemination at the time of the third harvest (H3), the reproductive structures were enclosed in finely perforated polythene bags which served to collect the seeds so as to give an accurate idea of seed weight per plant.

Thompson and Stewart (1981) have highlighted the 'conceptual dichotomy' which differentiates the approach of Harper and Ogden (1970), who measured the proportion of resources devoted to seeds, from that of Gadgil and Solbrig (1972) who have measured allocation to all reproductive structures. In the present investigation, 'reproductive effort' of the two weeds based on both the above concepts has been estimated. In addition, the number of seeds produced per gram of plant weight which is considered as 'reproductive effort' by Bazzaz and Carlson (1979) was also estimated.

The dry matter yield and seed weight per pot, and the ratio between expected and observed yield were calculated after accounting for mortality faced by the weeds in the different treatments. The data obtained were analyzed statistically by means of Student's *t* test and values for the least significant difference (L.S.D.) were calculated.

## RESULTS

*Mortality*

Although both weeds exhibited mortality in dense situations, *P. major* appears to be more sensitive to crowding under both the nitrogen regimes (Table 2).

*Dry matter yield*

Under both the nitrogen regimes, per plant yield decreased with crowding but the magnitude of reduction in yield due to density was much greater in *P. major* suggesting that *S. arvensis* [Fig. 2(a)] is less sensitive to density increase than *P.*

Table 2. *Mortality (%) of Spargula arvensis and Plantago major under two soil nitrogen regimes and four density levels*

Density	<i>Spargula arvensis</i>		<i>Plantago major</i>	
	High N	Low N	High N	Low N
1	0	0	0	0
3	0	0	0	0
9	0	11.1	22.2	22.2
18	16.7	22.2	27.8	38.9

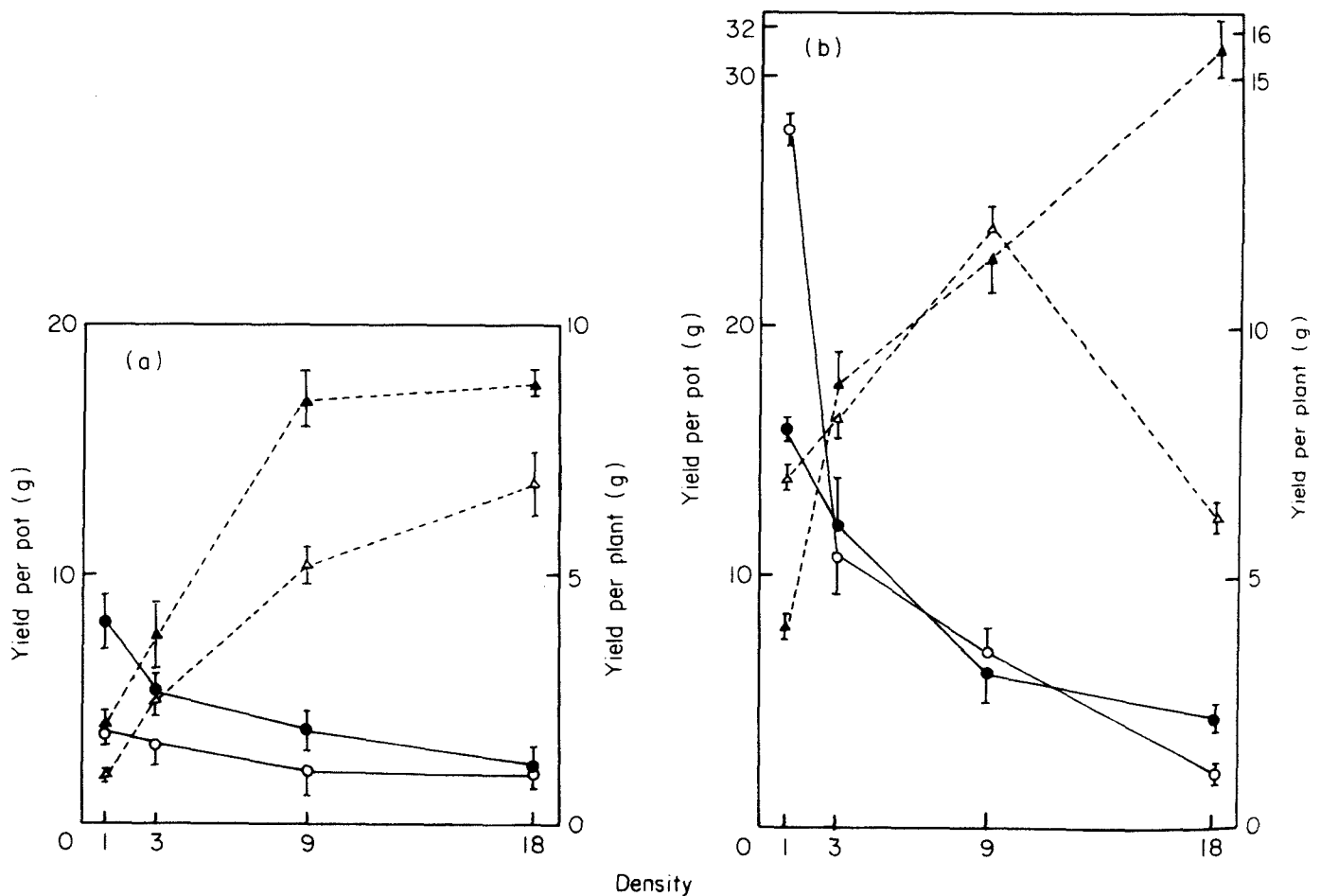


Fig. 2. (a) Per plant and per pot yield (g) of *Spargula arvensis* after 20 weeks growth as related to soil nitrogen and density levels. (Vertical bars denote  $\pm$ s.e. of means). Symbols denote per plant (●) and per pot (▲) yield under the high nitrogen regime. Open circles and open triangles stand for yield at the low nitrogen level. (b) Per plant and per pot yield (g) of *Plantago major* after 22 weeks growth as related to soil nitrogen and density levels. (Vertical bars denote  $\pm$ s.e. of means). Symbols denote per plant (●) and per pot (▲) yield under the high nitrogen regime. Open circles and open triangles stand for yield at the low nitrogen level.

*major* [Fig. 2(b)]. The yield per pot in *S. arvensis* increased with crowding under both the nitrogen regimes while in *P. major*, although under the high nitrogen regime there was a substantial increase in yield per pot from D9 to D18, under the low nitrogen regime a sharp fall was recorded with increase in density beyond D9. In *S. arvensis* the per plant yield differed significantly between high and low N regimes only under D1 ( $t = 3.88$  at 1%), and in *P. major* the yield per plant differed significantly between high and low N regimes under D1 ( $t = 14.02$  at 1%) and D18 ( $t = 3.50$  at 1%). The yield per pot differed significantly due to nitrogen differences under D1 ( $t = 3.88$  at 1%) D9 ( $t = 6.11$  at 1%) and D18 ( $t = 5.63$  at 1%) in *S. arvensis* while in *P. major* the differences due to nitrogen were significant under D1 ( $t = 14.02$  at 1%) and D18 ( $t = 14.52$  at 1%).

### Dry matter allocation

In *S. arvensis* the contribution of root weight towards the total was rather low under all the four densities and both nitrogen regimes (Fig. 3). Maximum

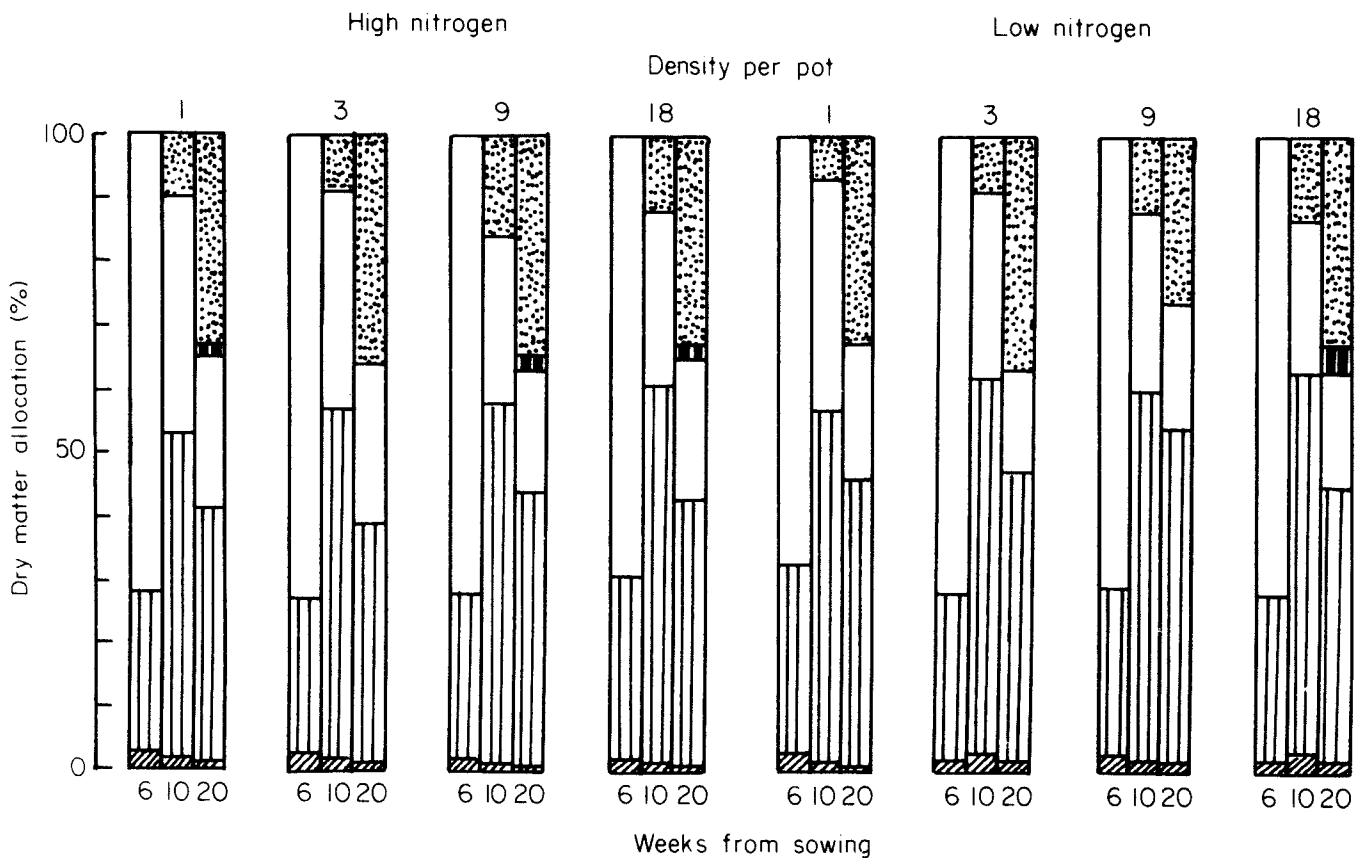


Fig. 3. Dry matter allocation to various plant parts of *Spargula arvensis* after 6, 12 and 20 weeks from sowing as affected by soil nitrogen regime and density. Numbers 1, 3, 9 and 18 denote the density levels under high and low nitrogen regimes respectively. ▨, Root; ▤, stem; □, leaves; ▧, standing dead; ▩, flowers and seeds.

allocation to stem under all treatments was observed during the time of H2, while leaf allocation decreased successively with time under all the treatments. The percentage allocation towards reproductive structures was not much affected by density stress or soil nitrogen level in the case of *S. arvensis*.

In contrast to *S. arvensis*, the allocation of dry matter to the roots was much greater in *P. major*. Under the high nitrogen level, dry matter allocation to the roots increased with increasing density. However, the successive increase in resource allocation to the root with density was not observed in untreated soil although in this case as well the maximum allocation towards root was at the highest density (Fig. 4). Allocation towards photosynthetic structures declined at each successive

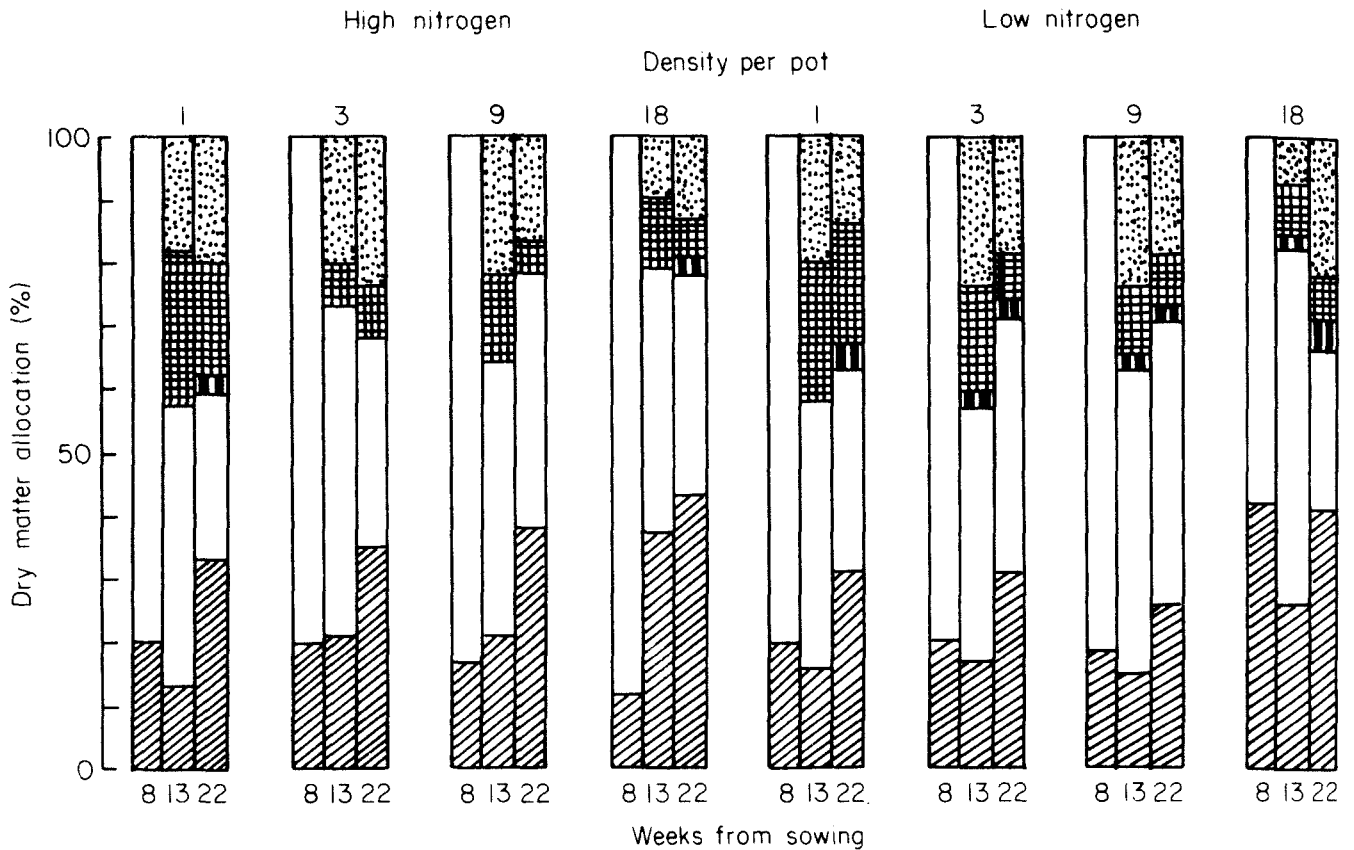


Fig. 4. Dry matter allocation to various plant parts of *Plantago major* after 8, 14 and 22 weeks from sowing as affected by soil nitrogen regime and density. Numbers 1, 3, 9 and 18 denote the density levels under high and low nitrogen regimes respectively. ▨, Root; □, leaf; ▩, rachis; ■, standing dead, ░, flowers and seeds.

harvest under all densities and both nitrogen regimes. The reproductive allocation ranged from about 12% (at D18) to about 26% (at D3) under the high nitrogen regime. At the low nitrogen regime also, the maximum value (24%) was recorded at D3. The minimum allocation (about 13%) was, however, at D1.

#### Seed production.

*S. arvensis* produced greater numbers of capsules per plant under all densities in the high nitrogen regime (Table 3). Increased density resulted in progressively fewer numbers of capsules per plant under both nitrogen regimes. The mean number of seeds per capsule did not vary much with density under the high nitrogen regime (minimum 8.9 and maximum 10.9 seeds per capsule), while the seed production per capsule varied with density from a minimum of 7.3 to a maximum of 12.5 seeds at the low nitrogen regime. Under all the treatments the seed weight (weight per seed = 0.0003 g) remained constant, though seed number per plant showed differences especially under the high nitrogen regime (Table 3). Seed output per plant also decreased with increasing density under both the nitrogen regimes and, correspondingly, the seed weight per plant also showed a similar trend. Increase in soil nitrogen resulted in an increase in seed weight per plant.

In *P. major* too, the number of capsules per plant decreased with increasing density under both the nitrogen regimes (Table 4). The number of seeds per capsule was also negatively correlated with density. Under both the nitrogen regimes, the average seed number per plant exhibited the trend shown by the number of capsules per plant. As the individual seed weight (0.0001 g) remained constant under all the treatments, the average weight of seeds per plant showed differences on account of changes in seed number per plant (Table 4).

Table 3. Number of capsules per plant, seeds per capsule, seeds per plant and seed weight per plant of *Spergula arvensis* under two soil nitrogen regimes and four density levels

Density	No. of capsules per plant ± s.e.	No. of seeds per capsule ± s.e.	No. of seeds per plant ± s.e.	Seed weight per plant ± s.e.
(a) High soil nitrogen				
1	276 ± 47.68	9.6 ± 1.06	2650 ± 458	0.795 ± 0.1373
3	183 ± 52.13	9.6 ± 0.87	1757 ± 500	0.5271 ± 0.1501
9	116 ± 29.80	8.9 ± 0.67	1032 ± 265	0.3096 ± 0.0795
18	83 ± 28.20	10.9 ± 0.96	905 ± 307	0.2715 ± 0.0922
L.S.D.	(34.59)	(4.16)	(341)	(0.1023)
(b) Low soil nitrogen				
1	132 ± 34.63	7.3 ± 9.1	964 ± 275	0.2892 ± 0.0826
3	77 ± 19.44	11.6 ± 1.19	893 ± 313	0.2679 ± 0.0940
9	67 ± 16.48	12.5 ± 1.22	838 ± 94	0.2514 ± 0.0282
18	52 ± 15.73	10.9 ± 0.74	567 ± 237	0.1701 ± 0.0410
L.S.D.	(17.22)	(3.32)	(196)	(0.0589)

The population densities given in tables and figures refer to the numbers of plants per pot at the beginning of the experiment. Figures in brackets at the bottom of the table represent L.S.D. at 5%.

 Table 4. Number of capsules per plant, seeds per capsule, seeds per plant and seed weight per plant of *Plantago major* under two soil nitrogen regimes and four density levels

Density	No. of capsules per plant ± s.e.	No. of seeds per capsule ± s.e.	No. of seeds per plant ± s.e.	Seed weight per plant ± s.e.
(a) High soil nitrogen				
1	705 ± 34.11	14 ± 1.02	9870 ± 478	0.987 ± 0.0478
3	657 ± 25.73	13.3 ± 0.62	8712 ± 341	0.8712 ± 0.0341
9	235 ± 34.59	12.8 ± 0.59	3012 ± 443	0.3012 ± 0.0443
18	177 ± 18.69	10.5 ± 0.46	1867 ± 197	0.1867 ± 0.0197
L.S.D.	(26.90)	(1.81)	(354)	(0.0361)
(b) Low soil nitrogen				
1	879 ± 40.56	12.86 ± 1.85	11304 ± 522	1.1304 ± 0.0522
3	513 ± 52.87	13.40 ± 1.92	6874 ± 708	0.6874 ± 0.0709
9	381 ± 39.47	9.87 ± 3.25	3760 ± 390	0.3760 ± 0.0390
18	158 ± 34.54	9.06 ± 2.15	1431 ± 313	0.1431 ± 0.0313
L.S.D.	(34.52)	(1.97)	(399)	(0.0399)

Figures in brackets at the bottom of the table represent L.S.D. at 5%.

Seed weight per pot in *S. arvensis* increased with crowding and nitrogen regime. Differences in seed weight per pot were significantly higher in the high nitrogen regime under D1 ( $t = 4.41$  at 5%) and under D18 ( $t = 4.67$  at 1%) in *S. arvensis* [Fig. 5(a)], while in *P. major* the differences were not statistically significant. In *P. major*, however, seed weight per pot showed maxima at D3 under the high nitrogen regime and at D9 under the low nitrogen regime [Fig. 5(b)]. The differences in seed weight per pot at the two nitrogen regimes became wider at high density, but were not statistically significant.

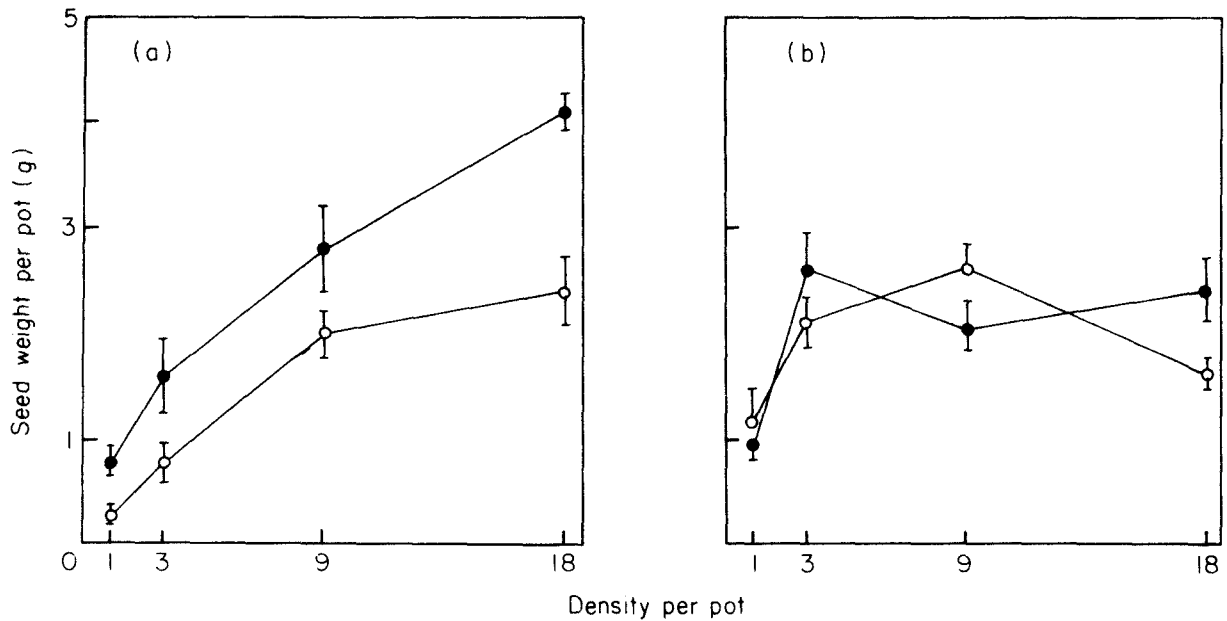


Fig. 5. (a) Seed weight per pot of *Spergula arvensis* at maturity in relation to soil nitrogen and density levels. (Vertical bars denote  $\pm$  s.e. of means). ●, High nitrogen; ○, low nitrogen. (b) Seed weight per pot of *Plantago major* at maturity in relation to soil nitrogen and density levels. (Vertical bars denote  $\pm$  s.e. of means). ●, High nitrogen; ○, low nitrogen.

In *S. arvensis* the crude reproductive effort (CRE) values ranged from 16.2 to 23.3 under the high soil-nitrogen regime and 15.2 to 21.9 under the low soil-nitrogen regime. Differences in CRE were pronounced under the higher levels of crowding, and whereas under the high nitrogen regime the maximum value was obtained at D18, under the low soil-nitrogen regime the maximum was at D9. The number of seeds produced per gram of biomass exhibited the same trend as CRE. In *P. major* under high soil-nitrogen, a minimum 8.1 was observed under D1 and maximum 12.8 under D18. In this species too, the number of seeds produced per gram biomass showed a trend similar to CRE (Table 5).

Table 5. *The crude reproductive effort (%) and number of seeds per gram biomass of Spergula arvensis and Plantago major under two soil nitrogen regimes and four density levels*

Density	<i>Spergula arvensis</i>		<i>Plantago major</i>	
	Crude reproductive effort (%)	No. of seeds per g biomass	Crude reproductive effort (%)	No. of seeds per g biomass
(a) High soil nitrogen				
1	19.3	645	12.4	1237
3	19.4	691	17.7	1473
9	16.2	540	9.2	924
18	23.3	775	7.9	772
(b) Low soil nitrogen				
1	15.2	506	8.1	812
3	16.0	535	12.6	1257
9	21.9	729	10.8	1092
18	17.4	580	12.8	1210

## DISCUSSION

Although *S. arvensis* and *P. major* showed increased mortality at the high densities, increased level of soil nitrogen seems to minimize the density effect in contrast to Sukatschev's observations on *Matricaria inodora*, where he reported greater mortality in fertilized soil (Sukatschev, 1928). The results also differ in this respect from the work of Yoda, Kira and Hozumi, (1963), White and Harper (1970) and Andel and Rozema (1974).

The dry matter yield per plant was progressively reduced with crowding in both *S. arvensis* and *P. major*, as reported in other plant species (Kira, Ogawa and Sakazaki, 1953; Yoda *et al.*, 1963; Bazzaz and Harper, 1976; Tripathi and Gupta, 1980) but the yield per pot showed an increase with increasing density in *S. arvensis* under both the nitrogen regimes. In *P. major*, however, under the low nitrogen regime there was a drastic fall in yield from D9 to D18 although under high soil nitrogen the yield always increased with density. This indicates that the nitrogen requirement of this weed is relatively higher and so in the case of low nitrogen supply, density effects become more pronounced.

Individual plants showed great plastic reduction in growth due to crowding (Fig. 2). It could be assumed that at high population densities, say at D18, if the plants do not suffer from resource competition, the per pot yield ('expected yield') would be 18 times that of D1. But in actual practice this does not happen because of limiting resources and increasing demand by the greater number of individuals at high density, and the 'observed values' are lower. As argued by Tripathi and Gupta (1980), the ratio of expected to observed yield may therefore be used as a measure of competitive stress. *S. arvensis* could be facing more intraspecific competition under the high N regime compared with the low nitrogen regime, as shown by the expected to observed ratio values especially at the highest density (Fig. 6). Conversely, the ratio of expected to observed yield in *P. major* was higher under the low than under the high nitrogen regime, particularly at D18 confirming that reduced soil nitrogen results in an intense competition at high density levels in this weed (Fig. 6).

*P. major* allocated a very high percentage of its resources to the root system and this allocation increased with time suggesting the importance of organs responsible

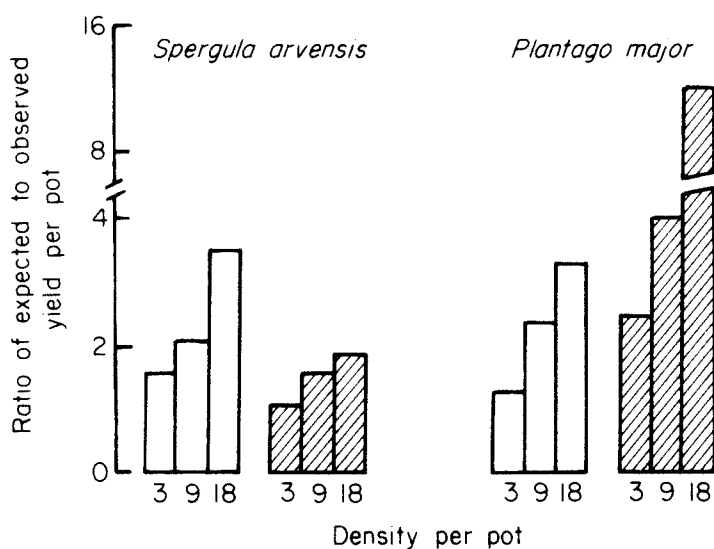


Fig. 6. Ratios of expected to observed values of the total yield per pot of *Spargula arvensis* and *Plantago major* at the time of H3 in relation to soil nitrogen and density levels. Open bars, high nitrogen level; hatched bars low nitrogen level.

for the capture of below ground resources. In *P. major* as in *S. arvensis*, no density-induced variations in biomass allocation towards reproduction could be discerned (Figs 3 and 4). As in an earlier study (Trivedi and Tripathi, 1982), the allocation to reproductive tissues was lower in *P. major* than in *S. arvensis*. In both species the CRE values varied with soil nitrogen and population density although no definite trend was observed (Table 5). The present results are in contrast with the earlier observations of Ogden (1974), Thomas (1974), Abrahamson (1975) and Abrahamson and Hershey (1977), who reported constant seed reproductive effort regardless of density fluctuations. However, some recent reports (McNamara and Quinn, 1977; Zeide, 1978; Assemat and Oka, 1980; Pitelka *et al.*, 1980) showing that sexual reproductive effort varies with density, can be cited in support of our results. Studies on reproductive effort of plants have mostly dealt with perennials and their vegetative–sexual reproductive balance under various imposed levels of crowding and other treatments, and bear limited relevance to the present study.

The present CRE values of *P. major* (Table 5) are below the range 10.6 to 27.7% reported by Kawano (1975). Hawthorn and Cavers (1978) have also determined relatively low values of CRE for *P. major*. Individual seed weight was, however, constant for both the weed species indicating that variation in reproductive effort is evinced by changes in the number of seeds produced. Seed production in *S. arvensis* was greatly reduced by low soil nitrogen while in *P. major* seed output was not so adversely affected. Thus *S. arvensis*, a weed of cropland, appears to have evolved a strategy which ensures greater production of seeds in fertile soil; on the other hand, seed production in *P. major*, which is a ruderal weed, is not much affected by soil nitrogen. This is also confirmed by the data on seed weight per pot in the two nitrogen regimes (Fig. 5).

In the present experiment *P. major* produced much larger numbers of seeds not only in comparison with *S. arvensis* but also compared with its own seed production in an earlier experiment (Trivedi and Tripathi, 1982). Such behaviour is rather intriguing and an explanation possibly lies in differences in environmental conditions prevailing during the experimental period. The present experiment was conducted between 26 March and 27 August 1979, when temperature in the nethouse ranged from a minimum of 10.4 °C in March to a maximum of 33 °C in May (Fig. 1), while the earlier experiment (Trivedi and Tripathi, 1982) was conducted from 10 June to 11 November 1979, during the course of which temperatures in the glasshouse ranged from 10 °C in November to 40 °C in June. Rees and Turquand (1969) have also shown significance of weather in affecting the severity of intraspecific competition in tulip, and Thomas and Dale (1974), on the basis of their studies on *Hieracium floribundum*, have corroborated this view.

However, percentage allocation to reproductive structures in *S. arvensis* continued to be greater than *P. major* indicating that *S. arvensis* tends more towards 'r-strategy' and *P. major* lies closer to 'K-strategy' in the *r*–*K* continuum of MacArthur and Wilson (1967). In our earlier study the allocation to vegetative structures in *P. major* was much greater and emphasis on reproduction was rather low (Trivedi and Tripathi, 1982) while *S. arvensis* allocated a greater proportion of resources to reproduction. The changed allocation pattern of the two weeds due to differences in the time of experiment and the conditions under which the two weeds were allowed to grow, prompt us to believe that the concept of 'r–K strategy' as applied to these weeds earlier (Trivedi and Tripathi, 1982) seems fragile. Barkham (1980) concluded that the strategy or tactics adopted by each species vary from site to site depending on the particular set of environmental

conditions. As opined by Parry (1981), 'reproductive effort' should not be used as an index of ' $r$  and  $K$ ' selection. However, the classification of *S. arvensis* as a  $R$ -selected species and *P. major* as a  $C$ -selected species (Trivedi and Tripathi, 1982) based on the model of Grime (1977) still stands.

## ACKNOWLEDGEMENT

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