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ANALYSIS OF THE DEMOGRAPHY OF RHINANTHUS ANGUSTIFOLIUS POPULATIONS

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SUMMARY

In a secondary succession series in grasslands, which is induced by a drastic change in management regime, the annual hemi-parasite *Rhinanthus angustifolius** appears, builds up a population (phase I) and becomes temporarily abundant (phase II) whereupon the population decreases to a low level (phase III), but with considerable fluctuations. Different vegetational succession stages (corresponding to the three phases of population development) were found in closely adjacent lots which had been managed for different periods of time. In this paper results of four years demographic work on *Rhinanthus angustifolius* in these three succession stages are analysed.

The shown differences in population phases cannot be explained by selection or density dependent behaviour of the plants. The biggest loss factor in the population is in the seed stage in all phases. No clear correlation exists between seed production and number of seedlings the following year. Seedling survival on average is high in phase I but can also be quite high in the other phases. Seed capsule production early in phase I is much higher than in phase II and III, and no difference in seed capsule production occurs between phase II and III. Predation of the seeds in the seed capsules is highest in phase II and can reach 30%. When the seeds are shed seed predation is high just after the shedding, but much seeds disappear in spring when germination begins.

Differences between the phases are clear but the year to year fluctuations are of the same order of magnitude or even greater.

The spatial distribution of a colonizing population of *Rhinanthus angustifolius* was mapped for 4 years, numbers increase continuously despite the yearly fluctuations.

Local environmental conditions are mainly responsible for differences in densities of *Rhinanthus angustifolius* between the succession stages. Fluctuations in numbers are caused by climatological factors and local conditions (e.g. species composition and microclimate).

1. INTRODUCTION

Succession can be studied in terms of changing vegetation types, but succession is the result of processes of appearance and disappearance of species. Populations of each individual species react to changes in the biotic and abiotic environment (DRURY & NISBET 1973; HORN 1976; PICKETT 1976, 1982). How exactly these processes work in a grassland succession series, and how species influence each other in this process has not been the subject of much research (e.g. MUELLER & FOERSTER 1974 and TURKINGTON & HARPER 1979).

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* Nomenclature follows HEUKELS & VAN DER MEIJDEN (VAN DER MEIJDEN et al. 1983).

Population numbers can be influenced by population independent factors such as climate, neighbours (MACK & HARPER 1977), species composition, structure of the vegetation (SCHENKEVELD & VERKAAR 1984), microclimate and predecessors (WERNER 1977), and local abiotic factors (e.g. soil fertility and water regime, GROOTJANS et al. 1985). Factors inherent to the population as density

Table 1. Species composition and cover percentage in a permanent plot recorded in June. In this field management changed from intensive agricultural use, to haymaking without applying fertilizers.

| Year | 1972 | 1973 | 1974 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 |
Number of species	14	15	16	25	23	26	21	24	22	24
Trifolium pratense	4	.	.	.	.	.	.	.	.	.
Alopecurus geniculatus	4	4	4	1	1	1	.	.	.	.
Glyceria fluitans	4	4	4	10	1	1	1	1	.	.
Holcus lanatus	4	10	40	4	30	20	1	2	20	4
Festuca pratensis	10	10	10	4	1	2	8	1	1	2
Poa pratensis	2	2	.	1	.	1	.	.	1	.
Poa trivialis	10	4	.	10	2	1	12	1	1	2
Deschampsia caespitosa	2	2	.	.	.	.	.	.	.	1
Equisetum palustre	2	2	4	1	1	1	1	1	1	2
Cerastium fontanum	1	.	2	1	1	1	.	1	.	1
Cardamine pratensis	2	2	1	1	1	1	2	1	1	1
Rumex acetosa	4	4	4	2	1	1	2	2	1	4
Ranunculus repens	4	10	40	10	30	50	20	4	30	50
Ranunculus acris	2	2	2	1	1	1	2	2	1	4
Festuca rubra	.	2	4	2	1	2	2	1	1	2
Myosotis palustris	.	2	.	1	.	1	1	.	1	1
Stellaria uliginosa	.	1	2	1	.	.	.	1	1	.
Trifolium repens	.	.	10	2	1	1	2	1	1	1
Taraxacum spec.	.	.	2	.	.	1	1	1	1	1
Lolium perenne	.	.	2	.	.	.	.	.	1	.
Eleocharis palustris	.	.	2	.	.	.	.	.	.	.
Anthoxanthum odoratum	.	.	.	2	12	1	12	12	20	12
Galium palustre	.	.	.	2	1	1	1	1	1	1
Ranunculus flammula	.	.	.	2	1	1	1	1	1	1
Cynosurus cristatus	.	.	.	1	1	1	.	.	.	.
Agrostis stolonifera	.	.	.	2	1	1	1	.	.	.
Juncus effusus	.	.	.	1	1	1	1	1	.	1
Juncus articulatus	.	.	.	2	1	1	1	1	1	1
Montia fontana	.	.	.	1	1	.	.	.	.	.
Polygonum hydropiper	.	.	.	1	.	.	1	1	.	1
Rhinanthus angustifolius	.	.	.	.	1	1	12	30	12	20
Sagina procumbens	.	.	.	.	1	.	.	1	.	.
Carex ovalis	.	.	.	.	.	1	.	1	.	.
Bellis perennis	.	.	.	.	.	1	.	.	.	.
Plantago lanceolata	.	.	.	.	.	.	.	1	.	2
Leontodon autumnalis	.	.	.	.	.	.	.	.	1	1
Stellaria graminea	.	.	.	.	.	.	.	.	1	.
Equisetum fluviatile	.	.	.	.	.	.	.	.	.	1

(After BAKKER & DE VRIES 1983)

population   vegetation
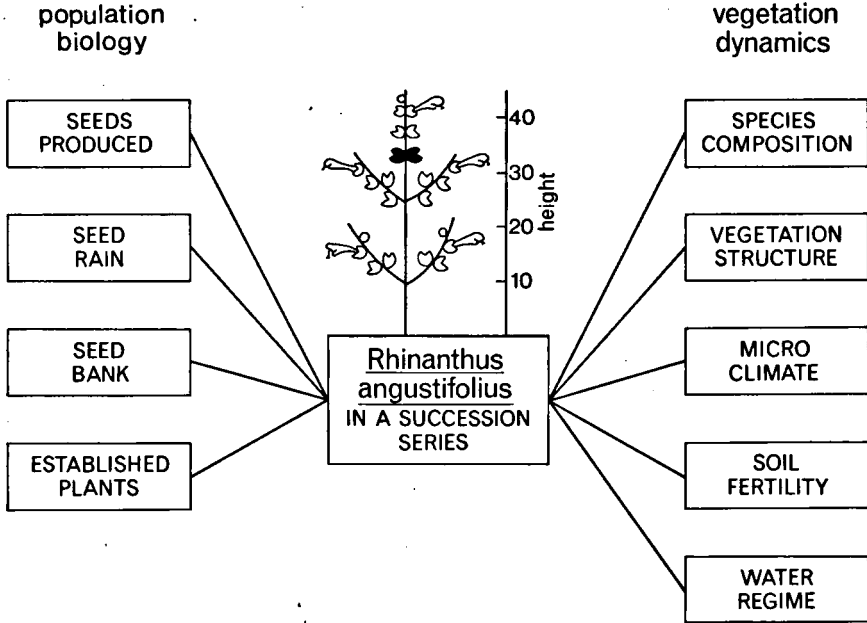biology   dynamics

Fig. 1. Factors which can influence the population density of *Rhinanthus angustifolius* in a succession series.
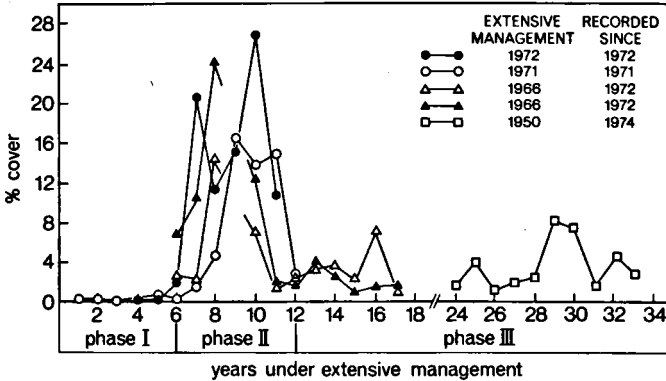

Fig. 2. The cover percentage of *Rhinanthus angustifolius* when colonizing a grassland in a succession series. The data are from permanent plots established in grasslands acquired by the State from 1950 onwards (After TER BORG 1985).

dependent regulation (PUTWAIN et al. 1968; KAYS & HARPER 1974; ANTONOVICS & LEVIN 1980; LAW 1981) or relative growth rate (GRIME 1979) and timing of the germination (VAN BAALEN 1982) can also have bearing on the population composition.

In several grasslands of the Brookvalleys of the Drentsche A a secondary succession occurred following a drastic change in management. The species composition changed from a few fast growing species to a slower growing herb rich vegetation (see Materials and Methods). In general, the annual hemi-parasite *Rhinanthus angustifolius* is one of the invading species in such a succession series. It gradually moves in, and covers up to 30 percent after 6–12 years of changed management whereafter the population decreases again (TER BORG 1985).

The aim of the present study was to analyse the relative importance of the factors which influenced population numbers in the different stages of the succession, in terms of external and internal population regulation (see *fig. 1*).

2. STUDY AREA AND SPECIES

The study area is situated in the Nature Reserve "Brookvalley of the Drentsche A" (ref. 53° NL, 6°40′ EL). Soils are peat with a depth of 1 to 2 metres. Ground water levels are between −20 cm in winter and −100 cm in summer (BAKKER 1976; GROOTJANS 1980). The study area consists of several fields adjacent to each other. They were acquired by the State at different times and the management regime changed correspondingly. The management changed from fertilizing and intensively cropping to mowing once a year (July) without applying fertilizers, and sometimes accompanied by grazing in autumn. After the change in management the total species composition changed noticeably. An example is shown in a permanent plot recording (see *table 1*). The species composition showed considerable fluctuations, but the vegetation development followed a consistent pattern (VAN DUUREN et al. 1981).

The annual hemi-parasite *Rhinanthus angustifolius* is one of the species which reacted to the changed management regime. *Fig. 2* is assembled from data from permanent plot recordings, each permanent plot recorded for about 12 years but started at different times after acquisition.

Three phases in development of a *Rhinanthus angustifolius* population were distinguished (see *fig. 2*): phase I, 2–6 years after a changed management regime, low cover percentage, phase II, 7–11 years after a changed management regime, high cover percentage, phase III, 12 and more years after changed management regime, again with a low cover percentage, but in this phase fluctuations were considerable.

These permanent plot recordings allowed an extrapolation of the spatial variation in the *Rhinanthus angustifolius* populations as they nowadays exist in the brook valleys to a succession series, thus enabling us to make a comparative analysis of the demographic patterns. Vegetational succession stages have been named I, II and III corresponding to the three phases of population development of *Rhinanthus angustifolius*. The vegetation in 1981 in stage I (lots acquired in
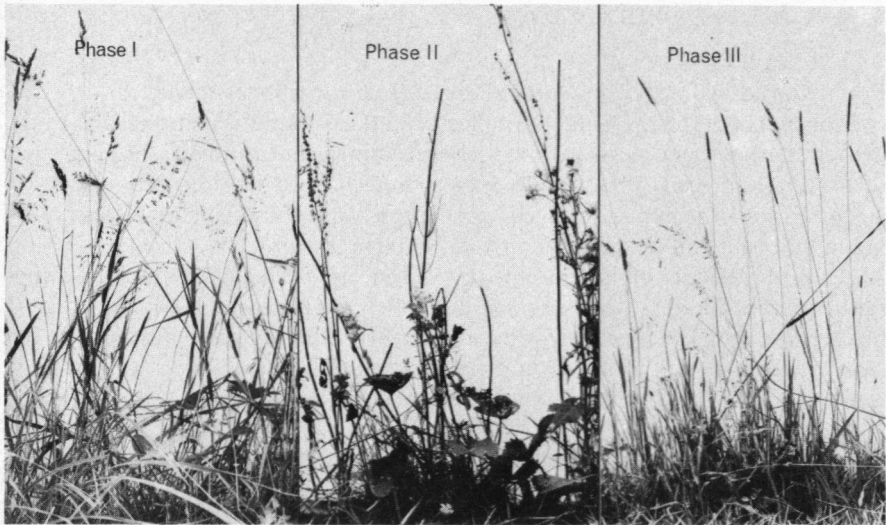
Fig. 3. Photograph of a cross section of a vegetation in July in stage I, stage II, and stage III of the succession.

1974 or 1976) is dominated by *Lolium perenne, Agrostis stolonifera, Poa pratensis* and *Festuca pratensis (Poo-Lolietum)*, stage II (acquired in 1972) is dominated by *Anthoxanthum odoratum, Cynosurus cristatus, Holcus lanatus* and *Festuca rubra (Lolio-Cynosuretum)* and stage III (acquired in 1967) is dominated by *Juncus acutiflorus, Anthoxanthum odoratum, Holcus lanatus* and *Carex nigra (Lolio-Cynosuretum/Juncetum acutiflori)*. Not only the species composition but also the structure of the vegetation differs considerably between the different stages. The difference in structure is already clear in the early spring, the growing season in stage I starts before that in stage II and III, and a difference is maintained throughout the growing season (see *fig. 3*).

Rhinanthus angustifolius germinates in January/February, and emerges in early spring (March/April). The population studied belonged to the aestival ecotype (TER BORG 1972). It is bumblebee pollinated, but self pollination can occur too (KWAK 1980). It is not host specific, most of the hayland species being potential hosts (TER BORG 1972; DE HULLU 1984). The root density in these haylands is extremely high, thus host roots are readily available. As the mowing and haymaking machines are moving freely between the fields seeds are transported from one field to another. The founders of the *Rhinanthus angustifolius* population in the early succession stages will be originating from the later successional stages, but throughout seeds are transported from one field to another.

3. MATERIALS AND METHODS

3.1. Demography
Population dynamics of *Rhinanthus angustifolius* was investigated for a period of four years (1981–1984) and the collected data covered the complete life-cycle, in each stage of the succession. Number of seedlings, mature plants, total number of flowers and seeds per capsule were scored in 6–10 random plots of 30 × 30 cm. In 1981 the number of seeds per capsule was estimated every week, starting in mid May, all seed capsules of the same maturity were collected per plot. The capsule production measurement was done in the same fields as the demography, except phase I (this was done in a field acquired in 1974, also stage I but the *Rhinanthus angustifolius* population was already more developed). To follow the spatial distribution in a field *Rhinanthus angustifolius* was mapped four times in five years in a colonizing population.

3.2. Disappearance of seeds
As disappearance of seeds can be a major loss factor, the number of seeds affected or vanished before and after the seed rain was estimated (1981 and 1982). To calculate the pre-dispersal seed predation the number of healthy seeds and affected seeds – empty, rotten or partly eaten – were counted. The maximum number of seeds produced per capsule is 18. To prevent loss of seeds after drying the capsules were taped.

   To calculate the seed predation after seed shed, seed samples were set out in stage I, II & III in an area of 20 × 20 m² (stage I was the field acquired in 1974 which had a more developed *Rhinanthus angustifolius* population than the 1976 field). Every seed sample contained 50 healthy looking seeds mixed with 50 ml sterilized, sifted soil, which originated from stage II (0–15 cm). To get some information on the rate of predation by different groups of organisms, three treatments were applied (*table 2*). In August when natural seed fall had ended and the haylands were mown, the seed samples were placed on the soil between the vegetation. Monthly 10 samples of each treatment were taken to the laboratory where numbers of seeds were counted and germination rate was determined after stratification (4 °C dark cf. TER BORG 1972).

3.3. Seed bank
To estimate the overall rates of loss from the seed bank and the vertical distribution of the seeds, 15–20 random soil samples from each succession stage (stage

Table 2. Treatment of the seed samples for estimation of the predation of the seeds after the seed rain. TMTD is a fungicide consisting of 50% Thiram.

	TMTD	Aimed organisms
Cheese cloth bags	–	bacteria, fungi
Fine meshed nylon bags (2 mm)	+	soil microfauna
Rings with a bottom of fine meshed nylon	–	all organisms

I acquired in 1974) were taken to the laboratory. After the seeds laying on the soil had been counted, the cores ($\varnothing$ 7.3 cm) were subdivided into two layers: 0–2 cm and 2–5 cm deep. Seeds were washed out of these layers and counted. All seeds were stratified to test viability. (In all cases in which phase I is not specified, it is the field acquired in 1976).

3.4. Density dependence

In order to estimate the importance of density under field conditions, in each phase 7 plots of 40 × 40 cm with different densities of *Rhinanthus angustifolius* were harvested (1983). Regression analysis was performed for seed capsule production on population density.

3.5. Plasticity

Between the phases plant size and capsule production, which are linearly correlated, differed considerably. To get an indication if the origin of this observed difference in size can be plastic, germinated seeds from phase II and III (fields acquired in 1971 and 1950 respectively) were collected in January 1980 from the field and transplanted to the experimental garden (with *Agrostis tenuis* as a host) in a density of 25 per m^2. Seed capsule production and node number were counted. Plants grown in the experimental garden in 1980 (n $\geqslant$ 25) were compared with randomly choosen plants in the field (1980, n $\geqslant$ 40) and with the largest plants in the same fields (1984, n = 15).

One of the parameters which can influence plant size and seed capsule production is the number of nodes. It is the only morphological parameter which to a great extent is genetically determined (TER BORG 1972). Seed capsule production was used as an estimate of seed production, which is the most important parameter for an annual. Statistics used was an analysis of variance.

Table 3. Demographic data of *Rhinanthus angustifolius* collected in four successive years in three stages of the succession (means ± 95% confidence intervals are indicated).

		Seeedlings m^{-2}	Plants m^{-2}	Seed capsules per plant	Seeds per capsule	Seeds m^{-2}	% Seed predation before shed
Phase I	1981	0.0	0.0	0.0	0.0	0.0	–
	1982	1.9 ± 1.4	4.4 ± 3.7	61.4 ± 48.4	9.7 ± 3.2	2,621	19.7
	1983	289 ± 199	109 ± 70	12.9 ± 2.5	10.0	14,061	–
	1984	317 ± 124	166 ± 36	9.5 ± 1.5	–	–	–
Phase II	1981	560 ± 464	219 ± 25	6.1	4.7	6,279	10.6
	1982	489 ± 239	271 ± 93	7.1 ± 3.3	6.1 ± 1.6	11,737	29.5
	1983	598 ± 271	96 ± 45	6.3 ± 1.0	8.5	5,157	–
	1984	60 ± 14	34 ± 13	8.2 ± 1.9	–	–	–
Phase III	1981	90 ± 81	63 ± 17	6.5	5.5	2,252	7.1
	1982	339 ± 161	202 ± 76	10.6 ± 3.1	6.0 ± 1.2	12,847	16.7
	1983	340 ± 214	100 ± 80	5.4 ± 1.1	6.9	3,737	–
	1984	36 ± 9	21 ± 8.5	10.2 ± 1.4	–	–	–

Fig. 4. Spatial distribution of *Rhinanthus angustifolius* when colonizing a grassland from 1979 to 1983. Densities in the patches are at least 100 plants per m².

4. RESULTS

4.1. Demography

The data collected in four successive years show a large variation, but there are some clear tendencies (*table 3*). The number of seedlings tended to be higher in phase II than in the other phases. The number of seedlings in phase I increased every year and in 1984 reached densities comparable with phase II. In phase III the seedling number was lower than in phase II. The differences between the phases hold as well for the mature plants, with the exception of phases II and III for 1983 (these figures do not differ). The survival percentage of the seedlings seemed to depend mainly on weather conditions in that year and to a lesser extent on the succession stage.

In *fig. 4* the spatial distribution of *Rhinanthus* plants is shown. Two years after change of management (phase I), a few plants became established. Every year the average number of plants increased and in 1983 large patches with high densities of *Rhinanthus* occurred.

The number of seed capsules per plant is lower in phases II and III than in
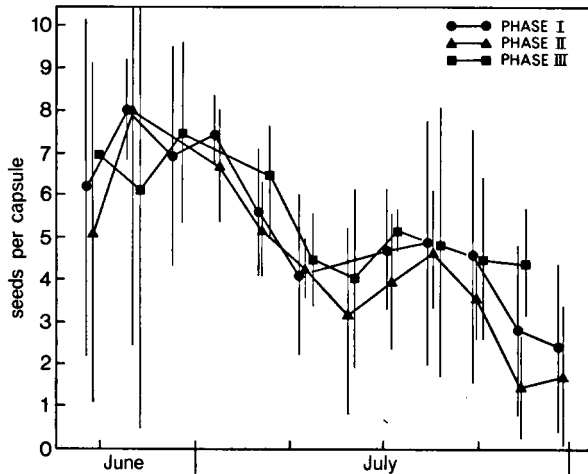
Fig. 5. Number of seeds per capsule produced in the summer of 1982, in three phases of the succession.

phase I. This difference was most extreme in 1982, when seed capsule production was very high (phase I), resulting from large vigorously growing plants. The average number of seeds per capsule was highest in phase I, between phase II and phase III there was no difference. These figures result in a seed production per m² which showed no tendencies dependent on the phase. However, during the season the number of seeds produced per capsule decreased (fig. 5). Predation of the seeds in the capsules depends on the phase, phase II had in both years a higher predation percentage than the other phases. However, in all measured parameters the fluctuations from year to year are extremely high. The differences between years tend to be higher than the differences between phases. For instance a huge number of seeds was produced in 1982 in all phases; this shows as well that no correlation exists between the number of seeds produced and the number of seedlings the following year, with the possible exception during early phase I.

4.2. The fate of the seeds in the soil
Seeds were mainly on the surface of the soil in August (fig. 6), only a few seeds were between 0 and 2 cm depth, and almost none deeper than 2 cm. Two months later the pattern had completely changed. Most seeds were deeper in the soil, mainly between 0 and 2 cm. This remained so until the next seed rain. The germination rate between the three layers differed. Seeds in the upper two layers germinated better than those in the lowest layer (fig. 6). Not only the place of the seeds changed, also the number of seeds in the soil (random soil cores) decreased significantly in late summer and autumn 1981, although this happened very gradually (fig. 7). In this respect there was no difference between the phases. The experiment in which the cause of the disappearance of the seeds was studied
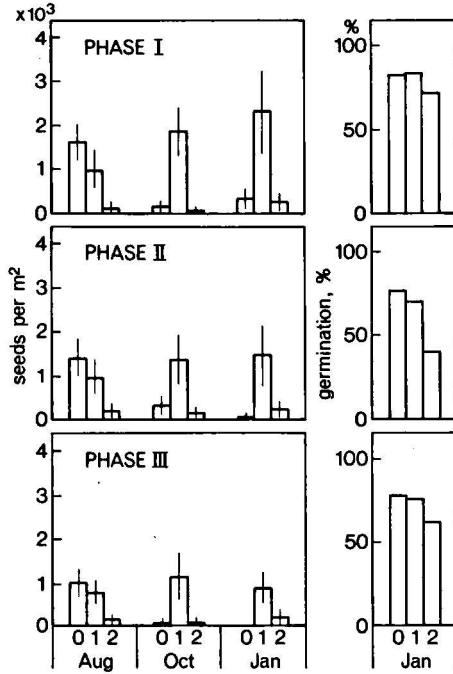
Fig. 6. The distribution of seeds in the soil separated into three layers: 0 on the soil surface, 1 between 0–2 cm, 2 between 3–5 cm, measured in August, September and January in phase I, II and III of the succession (means ± 95% confidence intervals). Also the germination percentage of the seeds in January (under laboratory conditions) in layer 0, 1 and 2 is shown.
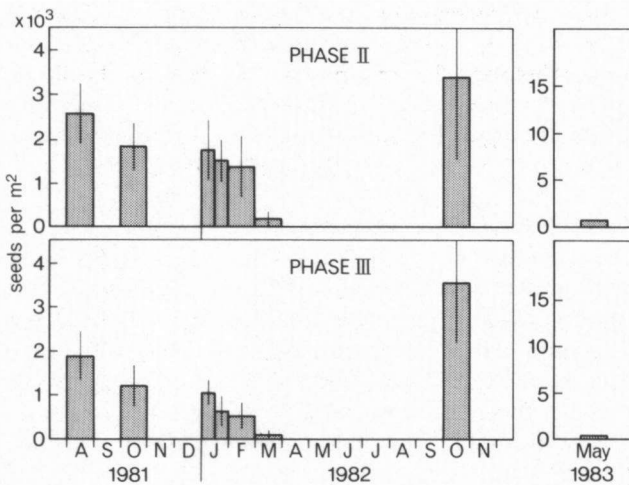

Fig. 7. Number of seeds in the soil (means ± 95% confidence intervals) during winter 1981/1982 and just before seed shedding in 1983 in phase II and III of the succession.
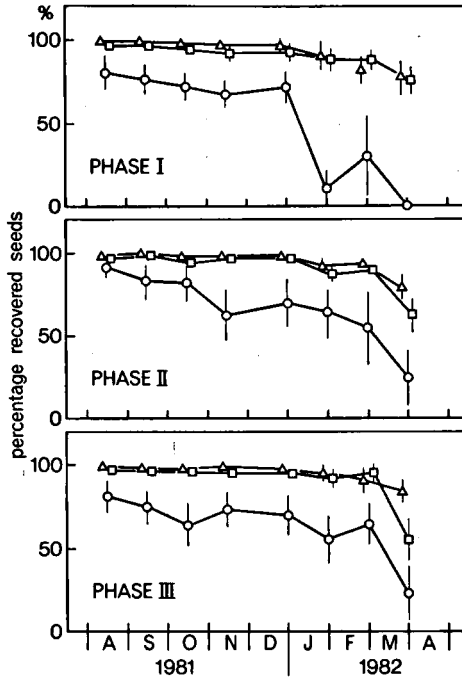
Fig. 8. Percentage recovered seeds in the rings (○), the cheese cloth bags (△) and fine meshed nylon bags (□) (means ± 95% confidence intervals) placed in the field in August 1981 and recovered at monthly intervals throughout the winter.

showed also that seed decreased in all treatments (*fig. 8*). After the first drop in August in the rings, the decline was very gradual in late summer and autumn. Besides differences between the three phases the impact of the different predator groups differed. As expected more seeds disappeared from the rings than from the bags and this divergence increased with time. There were no meaningful dissimilarities between the cheese cloth and fine meshed bags throughout the season.

In February and March the number of seeds in the soil decreased rapidly (*fig. 7*). In this period seed germination starts and losses are severe, probably due to dying in the germination process. The loss of seeds is also seen in the predation experiment, and in this period the different phases started to be distinct as well. In phase I a higher percentage of the seeds disappeared than in the other phases. Just before the seed shedding the seed bank is extremely small (measured in 1983), on average 1–5 seeds per m^2 was found.

4.3. Density
The seed capsule production of plants collected from patches with different densities did not show a significant density dependent behaviour (*fig. 9*) under
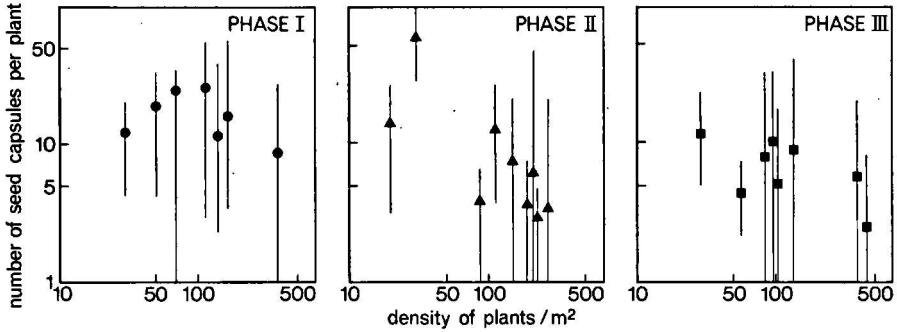
Fig. 9. The average seed capsule production of *Rhinanthus angustifolius* when harvested in different densities in the field. The range (minimum-maximum) is indicated.

field conditions. This is probably due to the high variation in seed capsule production within densities. But in the densities which appear mostly under field conditions (see *table 3* : 100–200 plants/m²) seed capsule production is not likely to be influenced by density of *Rhinanthus angustifolius*. However it is possible that in local spots with densities much higher than 200 plants per m² production may be influenced.

4.4. Plasticity

In the field the average seed capsule production per plant did not differ between stage II and III (*fig. 10*). The seed capsule production between the fields when the germinated seeds had been transplanted to the experimental garden did not differ. The average seed capsule production in the transplanted plants was much bigger than in the random field plants, but did not differ from the largest plants from stage II. The largest plants from stage III were smaller than the plants from stage II. This shows that the potential seed capsule production in all fields of at least some plants is much higher than the actual seed capsule production
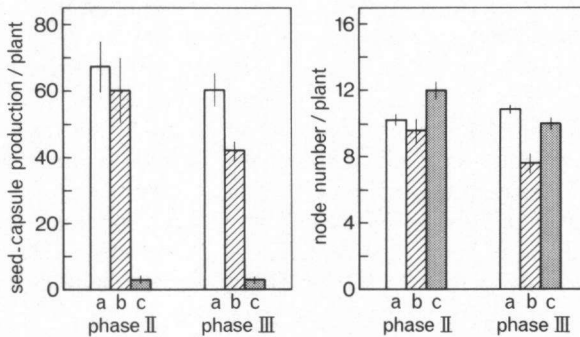

Fig. 10. The seed capsule production and node number of *Rhinanthus angustifolius* when grown in the field and the experimental garden, respectively. The plants from the experimental garden (a)were grown from germinated seeds collected in stage II and III of the succession, and compared with random plants (b) from the stages and with the largest plants (c).

in the field, which makes it very unlikely that reduction in seed capsules is caused by ecotypic differentiation between the different stages (all potentials are still in the plants).

The average node number from the random field plants of stage II and stage III differed, as well as the node number of the largest plants from those two fields. When the plants were grown in the experimental garden the node number from the plants did not differ. The absolute differences between node number are considerably less than those of the seed capsule production. The garden/field (random plants) ratio for node number is for stage II 0.85 and for stage III 1.08. For seed capsule production this ratio is 13.1, 12.1 for stage II and stage III, respectively. Thus although node number is to a high extent under genetic control the plastic effects exceed the genetic differences between the fields.

5. DISCUSSION

In early spring numbers of seedlings in different phases vary remarkably (0–600 m^{-2}). The low densities at the start of phase I are probably due to lack of seeds, but in the other two phases there is no correlation between number of seeds in the soil and the amount of seedlings the following year (*table 3*). This is in contrast with the results from *Rhinanthus minor* in the chalk grasslands in England (GRUBB et al. 1982). The period in which seeds germinate and become established is generally accepted as a very sensitive period (HARPER 1977). Lots of seeds are lost because they are too deeply buried, or because of soil moisture problems and oxygen depletion (SHARITZ & MCCORMICK 1973; HARPER 1977). *Rhinanthus angustifolius* seeds can germinate from a depth of 5 cm (TER BORG 1972) but most seeds are not deeper in the ground than 2 cm (*fig. 6*) which means that few seeds will be lost by burial. The meadows have high water tables, – 20 cm being the lowest in winter, this could possibly result in an extremely high seed mortality (TER BORG 1972). After germination competition for resources starts (HARPER 1977). Losses here are less severe than before seedling establishment (*table 3*). Although the year to year fluctuations in plant survival are very high (*table 3*), this cannot be the explaining factor for the different densities in the different stages of the succession. Factors influencing plant survival within years are related to the succession stages of the meadows. For instance vegetation structure and emergence time can be an important factor (LAW 1981; VAN BAALEN 1982; SCHENKEVELD & VERKAAR 1984), but microclimate and soil fertility are also liable to influence survival.

The habitus of the plants from different sites showed significant differences. Plants from phase I (1982) are much larger and produce more seed capsules per plant than plants from phases II and III (*table 3*) (also seen in other recently colonized fields, TER BORG unpublished). This difference in per plant production could be in principle density dependent. To decide if density dependence is the main regulating factor in a field situation in a mixed stand is very difficult (ANTONOVICS & LEVIN 1980). However, in some natural stands it was shown to exist (PUTWAIN et al. 1968; WATKINSON & HARPER 1978; WATKINSON 1980). As *Rhin-*
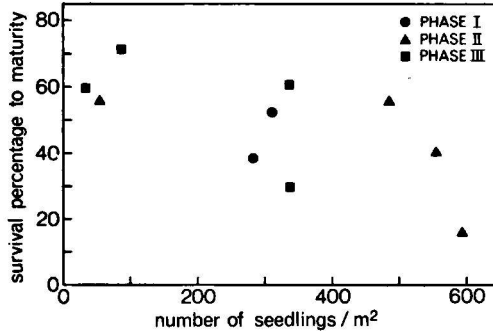
Fig. 11. The survival percentage from the naturally appeared seedlings to mature plants of *Rhinanthus angustifolius* in different succession phases.

anthus angustifolius is a hemi-parasite, analysing density dependence in a field situation becomes even more complex. High density can result in mortality or in a plastic reaction of the plants. *Fig. 9* does not show clear signs of a plastic reaction induced by density. Seed capsule production, between high and low density, does not show a significant relationship. The seed production per plant, however, shows variability independent of the density. Evidence for density dependence is shown by high mortality in the period of most rapid growth. In *Rhinanthus angustifolius* mortality in that period is not density dependent (*fig. 11*), in the densities occurring in the field. Mortality between some years (1982 phase II and III) is the same, independent of the density (*table 3*). When higher densities occur, however, density dependent mortality may occur (TER BORG
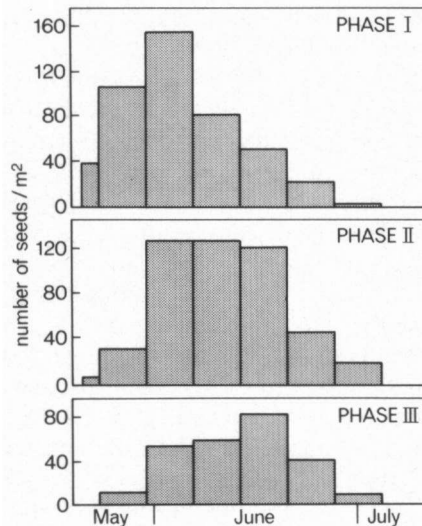

Fig. 12. The total seed production per m² of *Rhinanthus angustifolius* in three succession phases during the summer.

1979). Increasing density usually accelerates the development of an annual and shortens the life cycle (PALMBLAD 1968; SYMONIDES 1978). The different succession stages show a difference in development in the plants. The maximum seed production (in 1981) is in phase I two weeks earlier than in phase III (*fig. 12*). This is not correlated with the density. The huge year to year differences in established plants is another indication that other factors are more important than density dependence. This combination of reasons (each in itself not convincing) makes density dependent regulation as a major regulating factor for population numbers and production very unlikely. The observed habitus differences may have been at least partly caused by the differences in host species (DE HULLU 1984). Host species can have a considerable influence on the production of *Rhinanthus angustifolius* (TER BORG 1972; MIZIANTY 1975; DE HULLU 1984) as also shown in other hemi-parasites e.g. *Odontites* (SNOGERUP 1982) and *Euphrasia* (YEO 1964).

The numbers of seeds per capsule differ as well between the phases and years. The differences in years can be due to the weather conditions during the time of flowering. Since *Rhinanthus angustifolius* is bumblebee pollinated, the number of visits during cold rainy days and warm sunny days can differ considerably (KWAK, pers. comm.). In all phases the earlier formed capsules produce more seeds per capsule than the later formed seed capsules (*fig. 5*), suggesting the influence of the nutritional status of the seed capsule and the decreasing photosynthetic capacity of the leaves (cf. ERNST 1981). If this is the cause of the decreasing seed production it perhaps explains the lower seed production in phases II and III where soil fertility is lower and plants grow less vigorously than in phase I. Another possibility is a different degree of cross-pollination which can influence growth responses (VAN LEEUWEN 1981).

Considerable loss of seeds can occur because of predation from seeds still in the capsule. It is known that *Cidaria albulata* and *Phytomyza rhinanthi* feed on seeds of *Rhinanthus angustifolius* (FÜRST 1931; TER BORG 1972). The intensity of predation varies from year to year. Also in other species this predispersal seed predation is a known phenomenon (ZIMMERMAN 1980; VAN LEEUWEN 1983; LOUDA 1983). In *Rhinanthus angustifolius* predation is not density dependent (*table 3*). After seed shed seeds stay on the soil surface for about a month. During this period the seeds are known to be very vulnerable to predation by large animals such as birds and small mammals (MASSELINK 1980; CRAWLEY 1983). This phenomenon can be traced both in the experiment and in the cores. In October the seeds are more covered and disappearance is slower. HARPER (1977) found also that seeds after burial showed a constant depletion. In autumn eggs of earthworms and worms were found in the samples. During the early stage of the natural germination period seeds are very vulnerable to infection from fungi or bacteria.

These data show in all stages of the life cycle a considerable variation between the phases of population development, the more profound between phase I and II than between phases II and III. But the year to year fluctuation is at least of the same order of magnitude. This large year to year variation is also men-

Table 4. The number of plants on a 30 × 1.5 m transect on a slope in the Scottish Nature Reserve Caih Lochan. Plant height and seed capsule production are given (mean ± 95% confidence intervals). n is the number of plants in the transect.

	Height (cm)	Number of seed capsules	n
1981	14.1 ± 1.5	3.3 ± 0.5	?
1982	12.6 ± 1.0	2.6 ± 0.3	102
1983	11.5 ± 1.2	2.4 ± 0.4	50
1984	11.8 ± 1.2	2.4 ± 0.6	47

tioned by GRUBB et al. (1982) for *Rhinanthus minor* in calcareous grasslands; the density of *Rhinanthus minor* varied from 134–14 plants m^{-2} in a five years period. The year to year fluctuation can in principle be inherent to a population which is part of a succession series. Therefore, population numbers of *Rhinanthus minor* were counted in a stable ecosystem in the Caih Lochan Nature Reserve (Scotland) on a chalk outcrop of the mountains. This area has remained undisturbed for at least 100 years, but probably much longer. In this population the year to year variation is also high (see *table 4*).

Summarizing, a number of demographic parameters differ between the populations of *Rhinanthus angustifolius* corresponding to the stages of the succession. In principle this difference can be caused by the genetic differentiation between the populations in the different succession stages. But as *fig. 5* shows the potential production of seed capsules is much higher than the average production under field conditions and also the largest plants in the field reach a very high seed capsule production. The seed capsule production of the largest plants in the fields was comparable (measured in 1984): for phase I, II and III 53.9 ± 6.5, 59.6 ± 11.2 and 59.4 ± 11.9 (means ± 95% confidence interval) respectively. This indicates a wide range of seed capsule production within one phase. McNEILLY (1981) states that even in an inbreeding species a considerable genetically based variation can exist. *Rhinanthus angustifolius* is not inbreeding, thus it is very likely that genotypes which produce large plants will not be removed in such a short period (3–5 years). This is also expected by the way the fields are managed, seed transport is easily possible between the fields. TER BORG (1985) showed ecotype variation in *Rhinanthus angustifolius*, but could relate this to the different management regimes between the populations. In our study area the management is not different which means that population differentiation as an explanation for the observed differences in *table 3* is very unlikely.

We must conclude that one important regulating factor for the population size will be the weather, or factors induced by climatologic differences. A second important regulating factor will be the environmental conditions in the grasslands which differ depending on the succession stage. The latter influences soil fertility, species composition, vegetation structure and microclimate. The effect of different host species was discussed by DE HULLU (1984) and an indicator of the importance of the vegetation structure is now in print. The influence of

the other environmental factors on population numbers and plant size will be discussed in future papers.

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