Acta Bot. Neerl. 34(1), February 1985, p. 23–32.

THE INFLUENCE OF SWARD DENSITY ON THE POPULATION DYNAMICS OF RHINANTHUS ANGUSTIFOLIUS IN A GRASSLAND SUCCESSION

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SUMMARY

Five till ten years after once intensively used grasslands are taken out of agricultural use, the hemi-parasite *Rhinanthus angustifolius* may locally build up a population (phase I) and becomes temporarily dominant (phase II). *Rhinanthus angustifolius* remains dominant for some time, whereupon the population decreases to a low level (phase III). Some aspects of population behaviour are studied experimentally in the field.

In early successional stages, more seedlings established themselves where the vegetation had been cut short. During late succession fewer seedlings were found among the cut vegetation. The creation of 36 cm^2 gaps reduce capsule production per plant when compared with 7 cm^2 gaps, during early succession. In late succession stages no difference had been found between no gaps, 7 cm^2 gaps, and 36 cm^2 gaps. Total capsule production is much greater in early succession than in late succession.

In the three successional stages, sward density was measured 3 times during the season. The sward density is only important in the seedling stage of *Rhinanthus angustifolius*. *Rhinanthus angustifolius* establishes itself in relatively open swards in early succession, whereas in late successional stages *Rhinanthus angustifolius* is not dependent on sward density.

1. INTRODUCTION

Secondary succession is induced when there is a sudden change in a long term management regime. Then the existing vegetation is kept intact, but the changing conditions induce succession phenomena (VAN DEN BERGH 1979, BAKKER et al. 1980). However, establishment in an existing vegetation is difficult (FOSTER 1964, CAVERS & HARPER 1977, FENNER 1978, TURKINGTON et al. 1979, GROSS & WERNER 1982).

When in the wet grasslands of the Brookvalley system of the "Drentsche A" the management has changed, the hemi-parasite *Rhinanthus angustifolius* is one of the invading species (HULLU et al. 1985). The former paper suggested that the main factors influencing the size and the density of plants were climate and local environmental factors. One of the differences between succession phases is the potential in host species, this effects seed capsule production and plant size considerably (TER BORG 1972, TER BORG & BASTIAANS 1973, DE HULLU 1984).

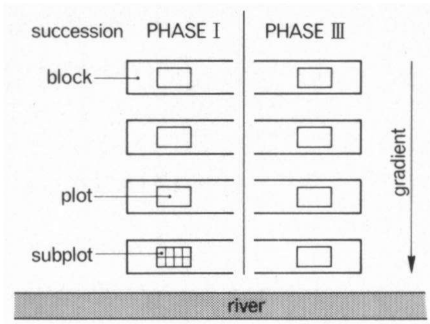

Fig. 1. The experimental design of a split-plot experiment with 4 half-replicates in blocks. The blocks are along a possible gradient towards the river.

This present paper aims to analyse some environmental factors which may influence the population density of *Rhinanthus angustifolius*, following a grassland succession. Special emphasis will be paid to the influence of the sward density.

2. MATERIAL AND METHODS

The study area was just north of the area described in the former paper with the same management regime and the same water tables and soils. Phase I, II and III (DE HULLU et al. 1985) are 4, 9 and 31 years, respectively in the management regime of hay-making once a year without using fertilizers.

2.1. Vegetation pattern

An experiment was designed to determine the ability of *Rhinanthus angustifolius* to establish in different micro-environments during early succession (population establishment) and late succession (population decline). Two neighbouring fields containing *Rhinanthus angustifolius* populations in phase I and III respectively, were selected. Due to the very high density of existing *Rhinanthus angustifolius* populations in phase II artificial seeding was not opportune. Germinated seeds of *Rhinanthus angustifolius* were sown under different conditions. Seeds were collected from a phase II population in the same area. The experiment began in early April 1981, when the natural population of *Rhinanthus angustifolius* was establishing itself. Germinated seeds were sown with a rate of 1 seed/2.5 cm^2. Survival and growth were measured in undisturbed and in cut vegetation. In both vegetation types gaps of 7 cm^2 and 36 cm^2 were created by turning the soil over.

This experiment was carried out in two successional stages. It was designed as a split-plot with four half replicates in blocks. The blocks were introduced to enable correction for a possible gradient from land to river. Within each block were two plots, one in each stage of succession. Each plot consisted of 8 subplots with the different treatment, cuttting, gap creation, gap size and sowing, each with two levels (see *fig. 1*). The half replicates of a 2^4 factoral experiment

Table 1. The overall analysis of variance of the 10 log number of seedlings of *Rhinanthus angustifolius* sown in two successional stages in the field (phase I and phase III) with introduced variables cutting the vegetation (cutting), creating a gap (gap), and different gap size (size). * significant at 5% level, ** significant at 1% level.

Source of variation	DF	SS	VR
Block stratum			
gap, cutting, size	1	0.004	0.17
residual	2	0.052	0.26
Total	3	0.057	0.19
Block, plot stratum			
succession	1	0.055	0.18
succession, gap, cutting, size	1	0.341	0.88
residual	2	0.772	3.79
Total	4	1.168	2.86
Block, plot, unit stratum			
gap	1	0.001	0.01
cutting	1	0.047	0.46
size	1	0.329	3.24
succession, gap	1	0.110	1.08
succession, cutting	1	0.496	4.87*
gap, cutting	1	0.004	0.04
succession, size	1	0.158	1.54
gap, size	1	0.264	2.59
cutting, size	1	0.002	0.02
succession, gap, cutting	1	0.001	0.01
succession, gap, size	1	0.509	4.99*
succession, cutting, size	1	0.317	3.11
residual	12	1.223	
Total	24	3.462	
Grand total	31	4.684	

have the 4 factor interaction confounded between the plots. The replicates were randomized according to the tables of the design (Cochran & Cox 1957).

The analysis (ANOVA) was carried out with the use of GENSTAT (Alvey et al. 1977). The analysis was done for the sown plots only (no plants appeared in the unsown). The data were logtransformed for the analysis and backtransformed for the tables. A missing value procedure was used for the numbers of seed capsules. The measured parameters were number of seedlings established in May and the number of seed capsules of *Rhinanthus angustifolius*.

2.2. Sward density

A survey was made to determine the influence of the sward density on *Rhinanthus angustifolius*. At places with and without *Rhinanthus angustifolius* within each phase of the succession sward density was measured using a point quadrat apparatus with 12 pins. The number of hits every 10 cm above ground level was

Table 2. The overall analysis of variance of the 10 log capsule production of *Rhinanthus angustifolius* sown in two successional stages in the field (phase I and phase III), with introduced variables cutting the surrounding vegetation (cutting), creating a gap (gap) and gap size (size).
* significant at 5% level, ** significant at 1% level.

Source of variation	DF	(MV)	SS	VR
Block stratum				
gap, cutting, size	1		0.167	0.78
residual	2		0.429	7.42
Total	3		0.597	6.87
Blocks, plot stratum				
succession	1		8.181	65.30**
succession, gap, cutting, size	0	(1)	0.039	
residual	2		0.251	4.33
Total	3		8.471	97.62
Block, plot, unit stratum				
gap creation	1		0.149	5.19*
cutting	1		0.421	14.54**
size	1		0.135	4.67
succession, gap	1		1.469	50.81**
succession, cutting	1		0.001	0.03
gap, cutting	1		0.486	16.81**
succession, size	1		0.485	16.78**
gap, size	1		0.001	0.04
cutting, size	1		0.003	0.11
succession, gap, cutting	1		0.002	0.06
succession, gap, size	1		0.008	0.29
succession, cutting, size	1		0.097	3.37
residual	4	(8)	0.116	
Total	16		3.375	
Grand total	22		12.443	

taken as a measure of density. The lowest 2 cm of the vegetation was omitted, because precise measurements were not possible at that level.

Sward density was measured in 6 randomly chosen plots within the *Rhinanthus angustifolius* density ranges. Each of the phases of the succession were measured on three occassions (a) in May, when seedlings had established, (b) in June, when flowering began, and (c) in July when seeds were set.

3. RESULTS

3.1. The influence of the vegetation pattern

The overall analysis of variance of seedling establishment is given in *table 1*. This analysis shows that only two higher order interactions are significant at 5% level. The third order interaction is omitted. *Table 3* shows a closer analysis of the second order interaction.

Table 3. The capsule production of *Rhinanthus angustifolius* sown in two successional stages in the field (phase I and phase III). The significant differences and interaction of the introduced variables cutting, gap, and size are shown. Geometric means and 95% confidence intervals are given.

Number of seedlings		
cutting	not cut	cut
succession		
Phase I	3.4 (1.9– 6.7)	5.3 (3.1– 8.7)
Phase III	5.2 (3.0– 8.7)	2.2 (1.2– 3.8)
Number of seed capsules per plant		
creating a gap	no gap	gap
succession		
Phase I	29.3 (22.4–38.2)	14.9 (11.5–19.5)
Phase III	1.1 (1.0– 1.4)	3.9 (3.0– 5.0)
cutting	not cut	cut
creating a gap		
No gap	6.0 (4.8– 6.7)	5.5 (4.6– 6.4)
Gap	4.4 (3.8– 5.2)	13.2 (11.2–15.6)
size	7 cm²	36 cm²
succession		
Phase I	32.3 (24.7–42.2)	13.6 (9.9–17.7)
Phase III	1.8 (1.4– 2.3)	2.3 (1.8– 3.0)

Seedling establishment of *Rhinanthus angustifolius* was influenced by cutting of the vegetation and varied between early and late stages of the succession, however, the differences are relatively small (*table 3*).

At the beginning of the succession the number of seedlings is not affected by cutting, but at the end of the succession plots which are not cut have significantly more seedlings than the cut plots. The not cut plots have an average of 5.2; the cut plots have an average of 2.2 seedlings. However, these differences in plant numbers had disappeared by the time of harvest.

The overall analysis of variance of the capsule production is given in *table 2*. This analysis shows that differences occur between the two analysed succession stages, and that differences occur between the treatments gap creation, gap size and cutting. *Table 3* shows the pairwise comparison of the higher order interactions.

Considerable differences in seed capsule production occur depending on the treatment (*table 3*). Analysing the effect of a gap detailed, shows that 36 cm² gaps have a considerable lower seed capsule production than the 7 cm² gaps in phase I. The effect of gap size varies according to the succession stage. In

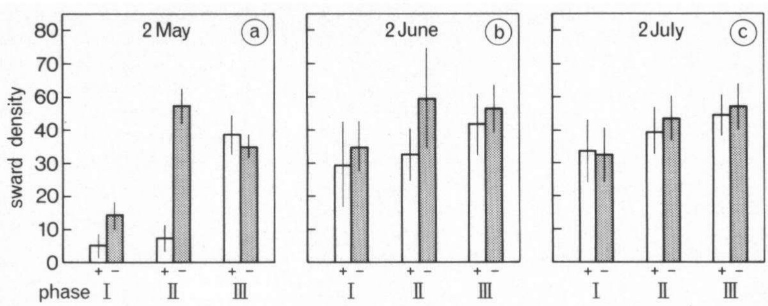

Fig. 2. The relationship between season-dependent sward density (number of hits) and the number of *Rhinanthus angustifolius* plants. Time scale is indicated by a, b, c. Phase I, II and III represent 3 succession stages.
+ indicates *Rhinanthus angustifolius* is present with a mean plot density of 120 plants per m^2.
— indicates absence of *Rhinanthus angustifolius* in the plot.

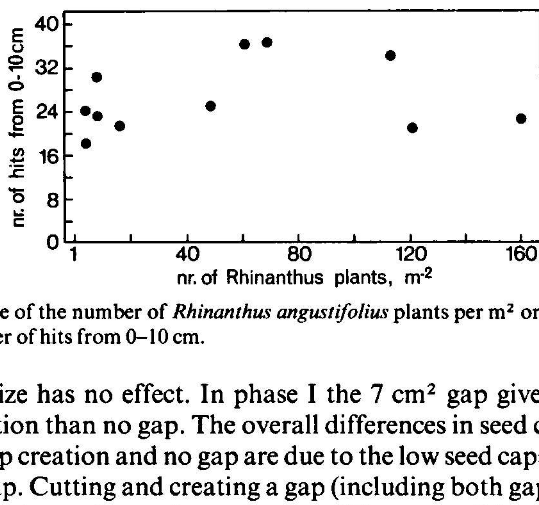

Fig. 3. The influence of the number of *Rhinanthus angustifolius* plants per m^2 on the sward density. Shown is the number of hits from 0–10 cm.

phase III gap size has no effect. In phase I the 7 cm^2 gap gives a higher seed capsule production than no gap. The overall differences in seed capsule production between gap creation and no gap are due to the low seed capsule production of the 36 cm^2 gap. Cutting and creating a gap (including both gap sizes) simultaneously increase the seed capsule production. When one of these is applied seed capsule production is not affected.
The most striking effect is that the overall seed capsule production in phase I is considerably higher than in phase III. This indicates that other factors may be relatively more important, e.g. sward density and host quality.

3.2. The effects of the sward density

To compare the different stages of succession only data from the most dense 10 cm of the vegetation have been analysed (see *fig. 2*). In May this was the layer at 2–10 cm, but in June and July it was at 10–20 cm. *Rhinanthus angustifolius* was present with 120 ± 26 plants m^{-2} (± 95% confidence interval) in May and 92 ± 34 plants m^{-2} during harvest. There are large difference in seedling numbers both between and within the different stages of the succession.

In May and June differences in sward density exist between places with and without *Rhinanthus angustifolius* in phase II, indicating that *Rhinanthus angustifolius* becomes established with high numbers in microhabitats with the lowest sward density. In phase I the differences in sward density are less obvious in places with and without *Rhinanthus angustifolius*, but show the same tendency as in phase II. Within phase III no differences occur. In this phase the places are not different and the density is intermediate, both significantly different from the density in phase I and in phase II without *Rhinanthus angustifolius.*

The possibility exists that *Rhinanthus angustifolius* influences the structure of the vegetation instead of the structure influencing *Rhinanthus angustifolius.* This might be due to its hemi-parasitic life form. However, when *Rhinanthus angustifolius* influences the structure this influence must be stronger when the plant numbers are increasing. *Fig. 3* shows that the sward density remains constant, up to a *Rhinanthus angustifolius* density of 160 m^{-2}.

From this survey we concluded that sward density may be an important factor in the seedling stage of *Rhinanthus angustifolius* (phase I and II) but is not likely to be an important factor in late stages of plant development.

4. DISCUSSION

The better survival of *Rhinanthus angustifolius* seedlings, which occurred in the open vegetation (*table 3*) artificially made by cutting, small gaps or also naturally occurring, is only apparent in the beginning of the succession. This is in agreement with PEMADASA & LOVELL (1974), WERNER (1976), FENNER (1978), TURKINGTON et al. (1979), GROSS & WERNER (1982) and GOLDBERG & WERNER (1983). In phase II *Rhinanthus angustifolius* ɔecomes established in the relatively low density micro-habitats of the sward (*fig. 2*). At the later stages (phase III) however the vegetation density does not seem the main factor for seedling establishment. Cutting the vegetation even decreases the seedling survival (*table 3*).

Sward density therefore is not responsible for population decline. A possible cause for redûced establishment as succession proceeds could be due to changes in the micro-climate (HEINRICHER 1910). TER BORG (1972) states that frost damage can occur in an open environment, but this cannot explain the differences between the phases as they were closely adjacent. *Rhinanthus angustifolius* has a very high evaporation (KLAREN 1975), but this is not likely to have been catastrophic, because these peat soils have a high degree of moisture. The litter and moss layer which accumulates during succession may produce physical, pathogenic and allelopathic effects (RABOTNOV 1969, MILES 1973, GRIME 1979, BAKKER et al. 1980, GOLDBERG & WERNER 1983), which could be responsible for the reduced establishment of *Rhinanthus angustifolius.* These factors have been eliminated by gap creation, which in phase III did not result in a reduced seedling survival. Therefore these effects cannot be responsible for population decline.

The reduced survival in dense vegetation in phase I, shown in this paper, does not show in the demographic data, there survival in phase I is high (DE HULLU et al. 1985). This is probably due to a difference in germination time in the different phases (unpublished data), which is not taken into account in this paper.

4.1. Seed capsule production

The big differences in capsule production of *Rhinanthus angustifolius* at the three successional stages can be due to differences in hosts or differences in nutrient availability in the soil. As shown (DE HULLU 1984), different hosts can cause big differences in capsule production. The big differences in capsule production between the 7 cm^2 and 36 cm^2 gap in phase I can be caused by a possible delay in growth. The time taken to reach a host root will be longer in 36 cm^2 gaps (cf. WILKINS 1963 with *Euphrasia*). This may result in a decreased production for *Rhinanthus angustifolius*, a retarding in the early stages of development can influence production considerably (PEMADASA & LOVELL 1974, ROSS & HARPER 1972, FOWLER 1984). The small gap-size corresponds well with the niche description by GRUBB (1977). Production differences between gap sizes in *Rhinanthus angustifolius* does not show up in phase III because other limiting growth factors are probably coming into play.

These experiments show some indication how the population size of *Rhinanthus angustifolius* may change during a grassland succession. The availability and dispersal of seeds are probably critical factors in phase I. The sward density survey shows that places without *Rhinanthus angustifolius* in phase I have an intermediate number of hits, i.e. very dense and more open patches. Thus some of the places will be suitable for seedling establishment, certainly when seeds germinate earlier than in other succession phases. In phase II places without *Rhinanthus angustifolius* are very scarce. It seems only absent from places where the vegetation density is very high. Seed production is not likely to be limiting in this phase because of the high number of plants. Seed production per plant is very high in phase I, therefore a fast increase in population is likely, if enough suitable sites are available.

Densities up to 160 plants m^{-2} *Rhinanthus angustifolius* do not influence the sward density of the field (*fig. 3*), however, when densities increase *Rhinanthus angustifolius* can reduce biomass production of a hayfield (MIZIANTY 1975). Reduction of the biomass of the host with consequent increase in the amount of light will favour the establishment and development of *Rhinanthus angustifolius*.

In phase III the vegetation is relatively open, but plant numbers decrease considerably. This is probably caused by other limiting factors. *Rhinanthus angustifolius* can complete its life cycle on a variety of hosts and even without a host (KLAREN 1975, WEBER 1981), but big differences in capsule production occur (DE HULLU 1984). This qualitative host specificity means that change in species composition can be an important aspect for the population dynamics of *Rhinanthus angustifolius*.

This study reveals that a detailed analysis of the effects of host quality, sward density and micro-climate may further explain the population dynamics of *Rhinanthus angustifolius* in a grassland succession. These points will be discussed separately in a next series of papers.

ACKNOWLEDGEMENTS

I wish to thank Dr. D. M. Pegtel, Prof. Dr. J. van Andel, Dr. S. J. ter Borg and Dr. M. M. Kwak for stimulating discussion and critical comments on the manuscript. Drs. C. J. F. ter Braak for statistical help and advice. Staatsbosbeheer Drenthe for permission to study the Nature Reserve Stroomdallandschap Drentsche Aa. The investigations were supported by the Foundation for Fundamental Biological Research (BION) which is subsidized by the Netherlands Organization for the Advancement of Pure Research (ZWO).

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