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Population dynamics of monocarpic perennials in a coastal sand dune area.

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Synopsis

The population dynamics of the monocarpic perennials *Cirsium vulgare* (Ten) Savi, *Cynoglossum officinale* L. and *Senecio jacobaea* L. were studied in a coastal sand dune area in the Netherlands. Long term field observations and experiments showed that periods of drought and herbivory by *Tyria jacobaeae* L. were correlated with population fluctuations of *S. jacobaea*. Recruitment of seedlings in *C. vulgare* and *C. officinale* is low due to a small seedbank. Disturbances increased the number of seedlings in sown plots compared to undisturbed sown plots. In all three species seedling mortality was high during periods of drought. Post dispersal seed predation and herbivory on flowering plants had a large impact on the number of seeds of *C. vulgare* and *S. jacobaea*. The population dynamics of *C. officinale* is probably also influenced by restricted seed dispersal and the absence of a seedbank. Different factors were therefore important in the population dynamics of the three species studied.

population dynamics, herbivory, pre–dispersal seed predation, post–dispersal seed predation, drought stress, disturbances, Cirsium vulgare, Cynoglossum officinale, Senecio jacobaea

1. Introduction

To study the fluctuations in population density we followed the percentage cover of *Senecio jacobaea* L. and the number of *Cynoglossum officinale* L. plants for several years in permanent quadrats (2 x 2m) in the coastal sand dunes of Meijendel near The Hague (DE JONG & KLINKHAMER 1988a, VAN DER MEIJDEN 1989). Percentage cover of *S. jacobaea* varied about a factor 100 between the extremes (Fig. 1). The fluctuations in *C. officinale* were less, but the difference between the lowest and highest number of plants is still a factor 8. Moreover it is clear from figure 1 that there is a constant extinction and recolonization of the different quadrats. Which factors cause these fluctuations? For *S. jacobaea*, its main herbivore *Tyria jacobaeae* L. is expected to play an important role as populations in the study area are on average once in two years completely defoliated by the larvae of this moth (VAN DER MEIJDEN 1979, PRINS 1990, SOLDAAT 1991). For *S. jacobaea* and *C. officinale* drought stress during summer is observed; many plants wilt. Furthermore the habitats of monocarpic perennial species are characterized by irregular disturbances. Perhaps the frequency of disturbances is limiting the number of seedlings. Because data on the number of egg batches of *T. jacobaeae* are recorded and data on average rainfall during the summer months are available from a nearby wheather station, these can be correlated with the fluctuations in population density. We also have a relative estimate of the number of rabbits present in the area for several years(1973–1980) through the number of rabbits shot by the guards of the area (WALLAGE 1988). It is expected that increased rabbit density will increase the number of disturbances.

Rainfall and egg load of the moth do correlate with population fluctuation as expected. Instead of a positive effect of the number of rabbits on the cover of *S. jacobaea* a negative trend is observed. This is probably caused by herbivory of rabbits on the root crown during the winter period (Tab. 1).

No correlation is found between the population density of *S. jacobaea* and *C. officinale*. Because correlations do not imply causal relationships, we must use an experimental approach to show that certain factors indeed play a role in the population dynamics of these species.

We therefore investigated three factors (effects of disturbances, drought stress and herbivory) to see whether they had an impact on survival and seed output of three monocarpic species in the dunes.

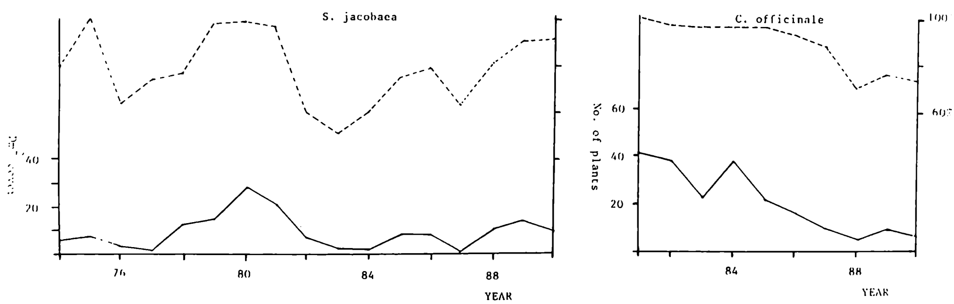

Fig. 1: Average variation in cover of *S. jacobaea* in May (left) and number of plants of *C. officinale* in September (right) in respectively 98 and 95 permanent quadrats in Meijendel (solid line). The broken line gives the percentage of quadrats in which the species is present.

Tab. 1: Pearson correlation coefficients between density of *S. jacobaea* (cover in May) and *C. officinale* (number of plants in September) and rainfall in June, July and August, number of egg batches of *T. jacobaeae* in the previous year and the number of rabbits in the previous year in Meijendel. n between parentheses. Average rainfall was 187 mm with a range from 40 mm to 320 mm.

	Cover of *S. jacobaea* in year n+1 (May)		No. plants of *C. officinale* in year n (September)	
Cover of *S. jacobaea* in year n	---		0.08	(10)
Rainfall in year n	0.51 *	(15) [1]	-0.35	(9)
No. egg batches in year n	-0.46 *	(15) [1]	---	
No. rabbits in year n	-0.50	(8)	---	

* $p<0.05$, [1] VAN DER MEIJDEN 1989

2. Effect of disturbances

KLINKHAMER & DE JONG (1988) investigated the effect of disturbances on germination and survival of *C. officinale* and *C. vulgare*. In the vicinity of the 95 permanent quadrats of each species they chose four plots (0.3x0.3m) which received four different treatments: 1) disturbed, 100 seeds sown, 2) undisturbed, 100 seeds sown, 3) disturbed, no seeds sown, 4) undisturbed, no seeds sown. In the disturbed plots all vegetation was cleared and the soil was stirred with a rake. Figure 2 shows that addition of seeds had a significant impact on seedling emergence in both species. This experiment shows that in the natural situation number of seeds are limiting recruitment indicating that the seedbank is small and hence not all safe sites are occupied. Disturbance in the unsown plots did not increase the number of seedlings significantly although disturbance increased the number of seedlings in sown plots (Fig. 2). Similar results were found by VAN DER MEIJDEN & al. (1979) for *S. jacobaea.*

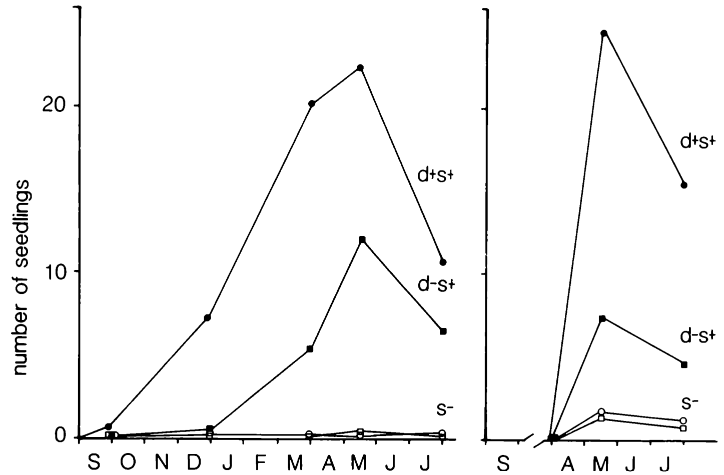

Fig. 2: The mean number of seedlings of *C. vulgare* (left) and *C. officinale* (right) in plots with seeds sown (solid symbols) or without seeds sown (open symbols) that were disturbed (circles) or not disturbed (squares). After KLINKHAMER & DE JONG 1988.

3. Effects of drought

Adult plants wilt during the day in summers with long periods of drought. Seedlings which do not have a well developed root system are therefore expected to suffer severely from such periods of drought. DE JONG & KLINKHAMER (1988b) followed plots with introduced seedlings of *C. officinale* and *C. vulgare* in the natural vegetation. Percentage mortality in the plots was correlated with the top soil water content on 6 June. In both species mortality declined with increasing soil water content (*C. officinale* $r=-0.67$, $n=20$, $p<0.01$, *C. vulgare* $r=-0.65$, $n=11$, $p<0.025$). Additional experiments showed that extra supply of water to plots of *C. officinale* and *C. vulgare* increased survival compared to controls and plots to which nutrients were added in solid form (Fig. 3). In this experiment watered plants were also larger indicating that growth of the plants was positively influenced by water supply. Although no experimental evidence is present for seedlings of *S. jacobaea* it was observed by PRINS & NELL (1990b) that seedling mortality increased severely during dry periods in the summer.

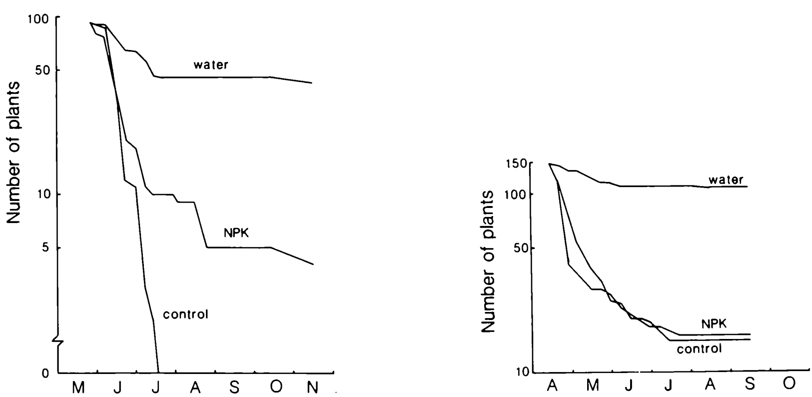

Fig. 3: The effects of watering (three times a week) and a single fertilizer application (solid form, N:P:K=6:5:9, 200 kgN/ha) on seedling survival in *C. vulgare* (left) and *C. officinale* (right) in open vegetation types. After DE JONG & KLINKHAMER 1988b.

4. Effect of herbivores

The effect of herbivores on plants can be divided into direct and indirect effects. Indirect effects are reduced competition between plants as a result of herbivory and an increase in safe sites caused by disturbances. The direct effects of herbivores on plants consists of the loss of biomass due to herbivory. In this paragraph we will discuss the direct effects.

4.1 Effects of herbivory on flowering plants

The effect of herbivory on adult plants was examined as the loss in potential seed production. For *C. officinale* the loss due to herbivory is lowest (Tab. 2). *C. vulgare* stems were mainly attacked by rabbits and the stem-borer *Cheilosia grossa* (Fallèn). Herbivory on *S. jacobaea* is primarily caused by the larvae of *T. jacobaeae*. Both in *C. vulgare* and *S. jacobaea* herbivory differs considerably between years (KLINKHAMER & al. 1988, PRINS & NELL 1990a, VRIELING 1991a).

4.2 Pre–dispersal seed predation

In all three species seed predation on the plant is relatively small (Tab. 2). Although we have no exact data on *C. officinale*, seed predation must be less than 15% as this is the combined reduction in seed number between plants protected against herbivores and controls (PRINS & NELL 1990b).

Tab. 2: Summarized data on *C. vulgare, C. officinale* and *S. jacobaea.*

	C.vulgare	C. officinale	S. jacobaea
Seed production per plant	40 – 2100[1]	5 – 500[2,3]	100–30000[4,5]
Seed weight (mg)	±3[1]	±25[2]	±0.25
Seed dispersal further than 1 m	30 – 50%[4, 6]	<5%[6]	>75%[1, 6]
Seedbank present	±[1, 6, 7]	–[7, 8]	+[4]
Fraction of flowering plants/year	0.39[9]	0.15[10, 11]	0.20[6]
Reduction of potential fecundity due to herbivory	15 – 80%[1]	±15%[3]	0 – 100%[3, 12]
Pre–dispersal seed predation	3 – 17%[1]	<15%[3]	<5%[12]
Post–dispersal seed predation	50 – 70%[1]	25 – 40%[3]	50 – 75%[3]
All safe sites occupied	no[13]	no[13]	no[4]
Effect of extra disturbances	small[13]	small[13]	small[4]
Mortality of seedlings due to drought	60 – 100%[14]	50 – 85%[14]	effect upto 100%[15]

[1] KLINKHAMER & AL 1988, [2] KLINKHAMER & DE JONG 1987, [3]PRINS & NELL 1990a, [4] VAN DER MEIJDEN & VAN DER WAALS-KOOI 1979, [5] VRIELING 1991b, [6] VAN DER MEIJDEN & AL 1985, [7] VAN BREEMEN & VAN LEEUWEN 1983, [8] VAN BREEMEN 1984, [9] KLINKHAMER & AL 1987, [10] KLINKHAMER & DE JONG 1983, [13] DE JONG & AL 1986, [12] VRIELING 1991a, [13] KLINKHAMER & DE JONG 1988, [14] DE JONG AND KLINKHAMER 1988b, [15] PRINS & NELL 1990b.

4.3 Post–dispersal seed predation

Post–dispersal seed predation in *C. vulgare* was examined by KLINKHAMER & al. (1988) and by PRINS & NELL (1990a) in *C. officinale* and *S. jacobaea*. The same experimental approach was used in both studies. Sods were cut out, placed in well–drained plastic tubes and put back in their original place. The same number of seeds were sown in all tubes and half of the tubes were protected with gauze against seed predators. After different periods of time the tubes were harvested and the remaining seeds counted. Post–dispersal seed predation was high in all species, ranging from 25–40% in *C. officinale* and 50–75% in *C. vulgare* and *S. jacobaea* (Tab. 3). For *C. vulgare* and *C. officinale* it was shown that predation was due to voles and mice and not to birds (KLINKHAMER & al. 1988).

Tab. 3: Perecentage post–dispersal seed predation calculated as the number of seeds retrieved from tubes filled with suds of three monocarpic perennial species in their natural habitat in protected and unprotected areas.

	C. vulgare[1] 10 or 20 seeds/tube					*C. officinale*[2] 10 seeds/tube			*S. jacobaea*[2] 15 seeds/tube		
Collection after month:	1	2	3	4	5	1	2	6	1	2	6
Protected	11	7	7	5	2	26	26	20	18	14	9
Unprotected	52	51	76	70	68	45	44	51	59	79	62

[1] KLINKHAMER & al 1988, [2] PRINS & NELL 1990a

4.4 Combining effects of all herbivores

Herbivory decreased the number of seeds produced largely. If all effects are combined (herbivory on adult plant, pre– and post–dispersal seedpredation) the number of seeds is reduced to 5–41% in *C. vulgare,* to 51-64% in *C. officinale* and to 0–47% in *S. jacobaea* which would have been produced in the absence of herbivores. In contrast to *C. vulgare* and *S. jacobaea* the reduction in the number of seeds due to herbivory is fairly constant over the years in *C. officinale.*

5. Discussion

We did not find a positive correlation between population density *S. jacobaea* and number of rabbits (Tab. 1) although natural disturbances consist mainly of rabbit scrapes and the number of scrapes ranges from 0.67–1.60 scrapes/m^2 in May in our study area (BURGGRAAF–VAN NIEROP & VAN DER MEIJDEN 1984). Experimental disturbances on average doubled the number of seedlings in *C. vulgare* and *C. officinale* in plots with seeds added compared to undisturbed plots with seeds added. Unfortunately it is not clear how important disturbances are in the unsown plots as the numbers of seedlings were to small to be significantly different. The number of plots in which seedlings emerged (no seeds added) approximately doubled in both species although the total number of seedlings in all plots did not increase significantly (Fig. 2). Both disturbances and the number of seeds in the seedbank seem to limit recruitment of seedlings although the effect of disturbances is probaly small at low seed densities.

Drought stress decreased seedling survival in all three species studied. Drought furthermore affects each species in different ways in other life–stages e. g. seed production in *C. vulgare* (DE JONG & KLINKHAMER 1988b), fraction of flowering plants in *C. officinale* (DE JONG & al. 1986) and regrowth after defoliation by *T. jacobaeae* in *S. jacobaea* (PRINS 1990) are positevly affected by rainfall.

The effects of herbivores are very important in the population dynamics because they can potentially act in a density–dependent way. Especially in *C. vulgare* and *S. jacobaea* density–dependent regulation could play a role as the effect of herbivores varies considerably between years (Tab. 2).

We did not find a positive correlation between population density of *C. officinale* and *S. jacobaea* (Tab. 1). It can however not be concluded that the population dynamics of these species are (partly) under the control of other factor(s). From the experiments it is clear that in both species seedling survival is affected by drought stress. The exact impact of drought on each species is not known (does a mild drought stress affect both species in the same way as a severe drought stress?), as it is not known whether the population dynamics of the two species are in phase and how large stochastic effects are. These effects all can render correlations in population density between two species obsolete, regardless of the fact that the population density is not measured on the same scale (cover and number of plants). Moreover, the correlation will be strongly weakened if other factors like drought stress in other life stages, seed dispersal and (density–dependent) herbivory affect species differently.

From the overview (Tab. 2) we can conclude that the population dynamics of *C. vulgare* is affected by a small seedbank, herbivory and seedling mortality due to drought, *C. officinale* is affected by the absence of a seedbank, a low seed dispersal, herbivory and seedling mortality due to drought and *S. jacobaea* herbivory and seedling mortality due to drought.

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