

# The impact of herbivory on plant numbers in all life stages of *Cynoglossum officinale* L. and *Senecio jacobaea* L.

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## SUMMARY

Striking differences in herbivory were found between *Cynoglossum officinale* and *Senecio jacobaea*, two common and equally apparent plants. *C. officinale* was only influenced by herbivores during seed stage (maximal seed predation: 31%). *S. jacobaea*, in contrast, suffered severely from herbivory during all life stages. Seed number was strongly reduced by seed predation (65%). Rabbit activity in winter significantly reduced the probability of flowering. In summer, larvae of *Tyria jacobaeae* reduced the seed production to zero. The differences in herbivory between the two plant species are discussed in relation to plant defensive characteristics.

*Key-words:* *Cynoglossum officinale*, herbivory, life stages, plant defence, *Senecio jacobaea*.

## INTRODUCTION

Fitness is determined by all life stages of a plant, as Crawley (1983) stated: 'plant survival must be measured from *seed* to *seeding plant*'. Most studies on herbivory, however, concentrate on only one life stage, usually the most conspicuous one. Consequently, the majority of information available is on leaf damage (Belsky 1986; Verkaar 1988).

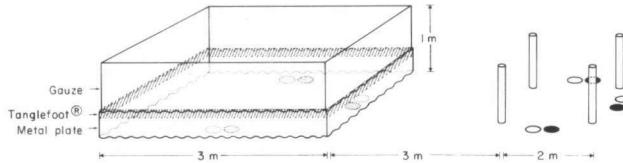
In this study the impact of herbivores on all life stages is compared in two common biennial plant species: *Cynoglossum officinale* and *Senecio jacobaea*. The total life span is subdivided into three stages: 1. seed to seedling, 2. seedling to rosette (establishment) and 3. rosette to flowering plant (probability of flowering and number of seeds).

Intensity of herbivory can be strikingly different between plant species, as Coley (1983, 1987) demonstrated for tropical tree species and van der Meijden *et al.* (1988) demonstrated for biennial plant species in a dune area.

Feeny (1976) and Rhoades & Cates (1976) stress the importance of predictability of plants to be found by herbivores. Plant species that are easily found by herbivores (apparent plants) would have developed expensive quantitative defence. On the other hand, plant species that are not easily detected by herbivores (unapparent plants) would have developed cheaper qualitative defence. These theories are focused strongly on chemical defence.

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**Fig. 1.** Experimental design of the seed-predation experiment. Seeds were sown in one protected or unprotected site. Open circles represent containers with seed, shaded circles represent controls. The cylinders around the unprotected site represent the angular points of this site.

The two plant species examined in this study are equally apparent. They share the same life history, both of them being monocarpic and delaying flowering until several years after germination. They are equally abundant in the area studied. They are of similar size, as a rosette and as flowering plant. Moreover, the most important leaf herbivores are specialists for both species. *S. jacobaea* is attacked by larvae of *Tyria jacobaeae*, a monophagous Lepidopteran species (e.g. van der Meijden 1971; van der Meijden & van der Waals-Kooi 1979). The most important leaf herbivores on *C. officinale* are larvae of *Ethmia bipunctella*, an oligophagous Lepidopteran on Boraginaceae (Prins *et al.* 1987; Prins & Laan 1988). Leaf herbivory by rabbits also occurs in both plant species. They both contain alkaloids that may be important in defence against herbivores (Pedersen 1975; van der Meijden *et al.* 1984).

Therefore, the second objective of this study is to examine if plants with similar characteristics, like *S. jacobaea* and *C. officinale*, suffer equally from herbivores in different life stages. We will examine which defences have been developed in these plant species against herbivores.

## MATERIALS AND METHODS

The experiments were carried out in the coastal sand dune area Meijndel, The Netherlands, from January 1986 to April 1987. *C. officinale* and *S. jacobaea* are abundant species in this dune area.

*C. officinale* and *S. jacobaea* are so called 'biennial' plant species. Biennials grow into a vegetative rosette in their first year and may flower in the second growing season (Harper 1977). Delay of flowering, however, is a common phenomenon for biennial plants (e.g. Werner 1975; van der Meijden & van der Waals-Kooi 1979; de Jong *et al.* 1986, Klinkhamer *et al.* 1987). As flowering is related to plant size, herbivory can cause delay of flowering in biennial plants (van der Meijden & van der Waals-Kooi 1979).

### *Survival of seeds*

Seed predation was studied in pairs of unprotected and protected populations (enclosures), measuring 2 × 2 m (Fig. 1). For protection against herbivores, a metal strip 30 cm high and gauze wire cloth (mesh width 3 cm) up to 1 m formed the enclosure. The top 10 cm of the metal strip was coated with an adhesive (Tanglefoot®) to prevent small herbivores entering the enclosure.

On 2 October 1986 sods were cut and fitted into well-drained polyethylene containers (diameter 10 cm, depth 7 cm). The containers with the sods were replaced in the original hole. The rim of the containers and the vegetation inside and outside the container were all at the same level. Six containers were placed in pairs near each unprotected population

(seven for *C. officinale* (two enclosures were already destroyed since being made in October 1985) and nine for *S. jacobaea*). Another six containers were placed in pairs in enclosures (Fig. 1). Ten seeds of *C. officinale* and 15 seeds of *S. jacobaea* were sown in three out of six containers nearby each unprotected population or in each enclosure. As *C. officinale* seeds are much larger than *S. jacobaea* seeds, we applied less seeds per container for *C. officinale* than for *S. jacobaea*. We do not expect these differences in seed density to have an effect on the level of seed predation.

After 1 month (28 October 1986), after 2 months (8 December 1986), and after 6 months (3 April 1987) one pair of containers with and without seeds was removed from each site. Containers without seeds allowed an estimate of seed input from plants that flowered in previous years. After removal, the containers were placed in a growth cabinet (20°C) and watered daily. Emerging seedlings were counted and non-germinated seed was collected from the containers by sieving afterwards.

### *Seedling establishment*

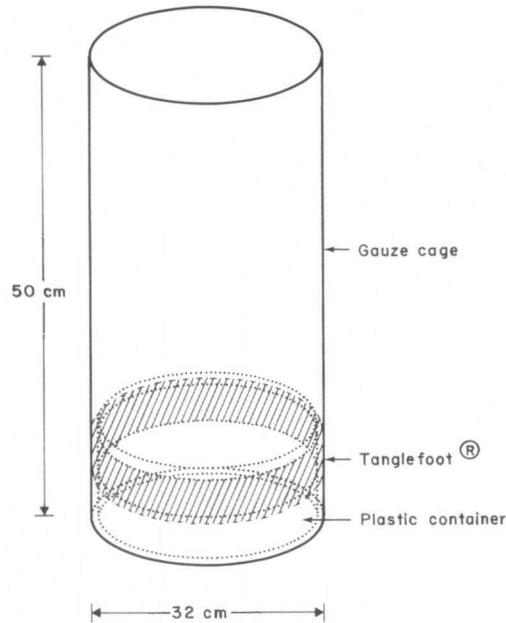
At the end of March 1986 seeds of *C. officinale* and *S. jacobaea* collected in Meijndel in the previous year and stored dry thereafter were germinated in Petri dishes on wet filter paper. *C. officinale* seeds were germinated at 15°C/5°C; 12 h light/12 h darkness (van Breemen 1984) and *S. jacobaea* seeds at 20°C/15°C; 16 h light/8 h darkness. After germination the seedlings were allowed to grow for 1 week in plastic containers filled with sand. Fifty seedlings of *C. officinale* were planted in two rows inside and outside each of nine enclosures on 25 April 1986, giving a total of 900 seedlings. These seedlings were watered during the first week of the experiment until they had become established. Fifty seedlings of *S. jacobaea* were planted on 6 May 1986 inside and outside each of nine enclosures, also giving a total of 900 seedlings. Despite frequent watering and abundant rain, all *S. jacobaea* seedlings died, probably because of the weak roots of the seedlings. The experiment was started again on 16 May 1986 with *S. jacobaea* seedlings naturally occurring in the unprotected populations and enclosures. No significant differences were found in the initial number of seedlings in the unprotected populations or enclosures (Wilcoxon matched-pairs test).

Every 14 days from April to November 1986 seedlings were counted. Differences between the number of seedlings present inside and outside each enclosure were tested for each observation with a Wilcoxon matched-pairs test.

### *Reproduction*

On 22 January 1986 the size of 150 rosettes of *C. officinale* and *S. jacobaea* was determined by measuring root-crown diameter (mean =  $1.17 \pm 0.06$  cm) and rosette diameter (mean =  $13.2 \pm 0.4$  cm), respectively. Large rosettes were selected because these are known to have a high probability of flowering the next summer (van der Meijden & van der Waals-Kooi 1979; de Jong *et al.* 1986). Of each plant species, 100 rosettes were left unprotected and 50 rosettes were protected against herbivores by a gauze cage (50 cm high, diameter 32 cm, mesh width 3 cm). Small plastic containers (10 cm high, diameter 30 cm) were put inside the gauze cages and coated with Tanglefoot® to prevent small herbivores reaching the protected plant (Fig. 2). Every 10–14 days from April 1986, until plants were harvested in July and August 1986, a plastic bag containing a Vapona insecticide strip was placed around each gauze cage for one night.

*C. officinale* plants that had flowered were harvested on 22 July 1986. Number of cymes, number of seeds, seed dry weight, plant dry weight and plant height were measured.



**Fig. 2.** Experimental design of the protection of rosettes and flowering plants. The top of the plastic container was coated with Tanglefoot®.

*S. jacobaea* plants that had flowered were harvested on 15 August 1986. Number of flower-heads, number of seeds of two capitula per plant and plant height were determined.

As we compared two groups (protected vs. unprotected plants) in a number of variables it is appropriate to use a multivariate analysis of variance. To test for all overall difference between the groups we normalized the data and computed Hotelling's  $t$ -value.

## RESULTS

### *Survival of seed*

In enclosures of *C. officinale*, 70–80% of the seeds were retrieved on the three collection days, in enclosures of *S. jacobaea* this was 80–90% (Fig. 3). The level of seed predation is defined as the difference in the number of retrieved seeds inside and outside the enclosures. Seed predation of *S. jacobaea* was highest (65%), only 31% in *C. officinale* (Fig. 3). Seed predation varied from 19% (after the first month) to 31% (after 6 months) in *C. officinale* and from 40% (after the first month) to 65% (after 2 months) in *S. jacobaea*.

### *Seedling establishment*

Inside and outside enclosures half of the planted seedlings of *C. officinale* died during the growing season (April to October 1986) (Fig. 4). Differences in the number of seedlings inside and outside enclosures were never significant (Wilcoxon matched-pairs test).

The attempt to plant seedlings of *S. jacobaea* was not successful, therefore we followed the naturally occurring seedlings in unprotected populations and enclosures. All naturally occurring seedlings in unprotected populations died because of dry weather or were observed to be eaten by the larvae of *T. jacobaeae* at the end of June and the beginning of

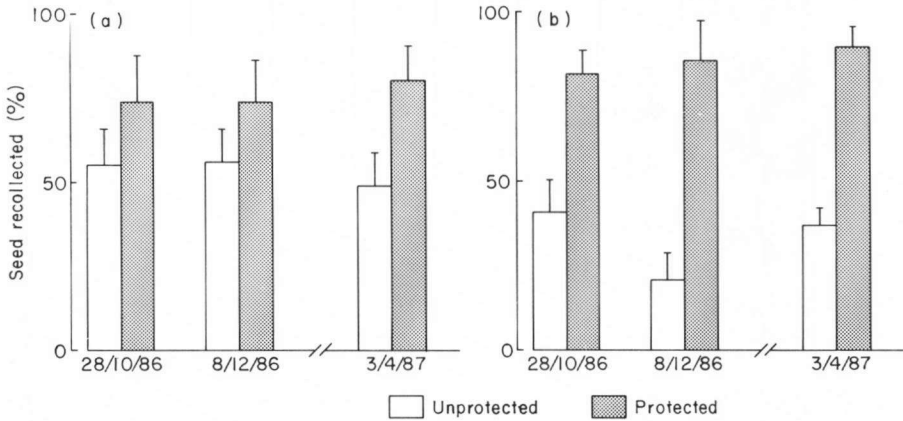


Fig. 3. Percentage of retrieved seed for (a) *Cynoglossum officinale* (seven populations) and (b) *Senecio jacobaea* (nine populations). (Bars represent SE.)

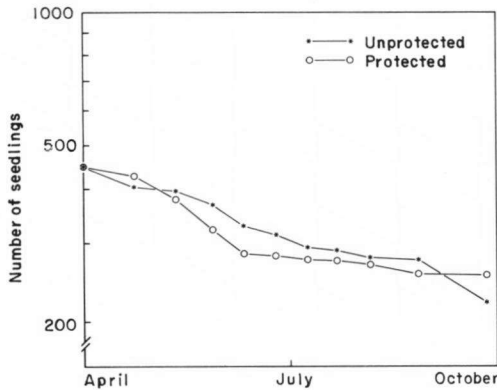


Fig. 4. Seedling survival of *Cynoglossum officinale* during the experiment from April to October 1986.

July (Fig. 5). Mortality of naturally occurring seedlings in enclosures was high because of a very dry period in June and July, but the absence of herbivory in these enclosures still resulted in seedlings which became established during the season (Fig. 5). As vegetation inside and outside enclosures did not differ we do not expect any differences in dessication of the seedlings to have occurred.

The dry period in June and July also accounts for the much higher mortality of protected *S. jacobaea* seedlings over the year (93%) compared to the mortality of protected *C. officinale* seedlings (44%). As *C. officinale* forms a tap root, it is less sensitive to water stress than *S. jacobaea*.

**Reproduction**

In both species survival of large rosettes was very high (100% for *C. officinale* and 98% for *S. jacobaea*). Herbivory on unprotected *C. officinale* was very low (less than 10% leaf area

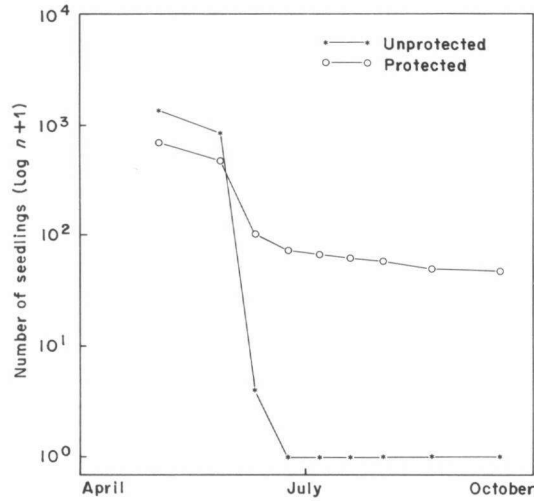


Fig. 5. Survival of natural seedlings of *Senecio jacobaea* which germinated at the beginning of May 1986.

**Table 1.** Influence of herbivory on probability of flowering in *Cynoglossum officinale*

	Unprotected (n = 100)	Protected (n = 50)
Non-flowering	36	23
Flowering	64	27

$\chi^2 = 1.01$ , NS.

**Table 2.** Reproduction of protected and unprotected plants of *Cynoglossum officinale*

	Unprotected (n = 64)	Protected (n = 27)
No. of cymes	18.66 (1.34)	18.63 (1.80)
No. of seeds	218.75 (19.42)	260.19 (47.11)
Total seed weight (g)	3.77 (0.34)	4.36 (0.85)
Weight per seed (g)	0.02 (0.00)	0.02 (0.00)
Height of flowering stem (cm)	70.95 (6.39)	67.57 (5.77)

Values represent means with SE in parentheses.  
Hotellings *t*-value:  $P = 0.65$ .

**Table 3.** Influence of herbivory on probability of flowering in *Senecio jacobaea*

	Unprotected (n = 100)	Protected (n = 47)
Non-flowering	85	0
Flowering	15	47

$\chi^2 = 91.27, P < 0.01.$

**Table 4.** Reproduction of protected and unprotected plants of *Senecio jacobaea*

	Unprotected (n = 15)	Protected (n = 47)
No. of flowering heads	0	397.3 (78.8)
No. of seeds	0	55.5 (6.6)
Height of flowering stem (cm)	0	50.0 (2.4)

Values represent means with SE in parentheses.

eaten) and did not influence the probability of flowering (Table 1). Furthermore, reproduction was not significantly affected by herbivores (Table 2).

*S. jacobaea*, in contrast, was highly affected by herbivores. The probability of flowering was significantly reduced, mainly by rabbits eating leaves and part of the root system during winter (Table 3). Seed production was reduced to zero by larvae of *T. jacobaeae* (Table 4). Unprotected flowering plants were completely defoliated, did not produce seeds and did not form regrowth shoots.

## DISCUSSION

### *Influence of herbivores on different life stages*

In *C. officinale*, 18–31% seed predation was found after 1–6 months exposure in unprotected situations. (Percentage predation = % seeds retrieved in protected populations – % seeds retrieved in unprotected populations.) As we followed the fate of the seeds until germination in spring, summer predation is not included. *C. officinale* does not have a buried seed bank (van Breemen & van Leeuwen 1983), but the seed bank exists of seed on the soil surface and seed on infructescences. Most *C. officinale* seed on the soil surface germinates in spring, so seed predation in summer is not very likely.

In the enclosures, 20–30% of the seeds were not recovered. It is likely that there is no predation inside the enclosures, so this must be the result of horizontal secondary dispersal (van Breemen & van Leeuwen 1983) caused by the wind. The horizontal secondary dispersal is probably larger in the unprotected situations than in the enclosures, so the 18–31% seed predation found in our experiment might even be an overestimation. Moreover, we did not find any traces of predation on retrieved seeds, only intact seeds were found. Our

results are in agreement with the results of van Breemen (1984) who found a maximum of 25% seed loss in *C. officinale*.

Seed predation in *S. jacobaea* was much higher and varied from 42 to 65%. We did find traces of predation on *S. jacobaea* seeds caused by small insects and mice. *S. jacobaea* has a buried seed bank (van der Meijden & van der Waals-Kooi 1979). Seed predation on these seeds may take place in summer.

The establishment of protected and unprotected *C. officinale* seedlings was not significantly different. Half the number of seedlings died between April and October 1986. de Jong & Klinkhamer (1988) found a negative correlation between seedling mortality and percentage cover of trees and shrubs, soil water content and percentage humus between 0 and 10 cm. Soil water content appeared to be the most important determinant for survival in their study. In our study, unprotected populations and enclosures were chosen next to each other in such a way that differences in plant cover were kept as small as possible. The similarity in seedling establishment for protected or unprotected seedlings is in line with the earlier observation that water is the main factor determining seedling survival in *C. officinale*. Intraspecific competition between seedlings during establishment could not have occurred because individuals were placed at a distance of 10 cm apart.

Herbivory on *S. jacobaea* by *T. jacobaeae* can be very important during the seedling stage. Defoliation of *S. jacobaea* by *T. jacobaeae* is a common phenomenon (van der Meijden 1971; van der Meijden & van der Waals-Kooi 1979), although intensity of herbivory differs between years (van der Meijden 1979). In 1986, when the experiments described in this study were carried out, total defoliation occurred. All natural seedlings which did not die because of the drought died by the attack of larvae of *T. jacobaeae* at the end of June and beginning of July. Seeds of *S. jacobaea* may germinate from April to November. In years with a high level of attack by larvae of *T. jacobaeae*, germination after *Tyria* attack is thus important. Germination from the seed bank of at least 1-year old seeds enables populations of *S. jacobaea* to be maintained in the study area.

Reproduction of *C. officinale* was not influenced by herbivores. Leaf herbivory on this species is very low (Prins *et al.* 1987; van der Meijden *et al.* 1988). When the density of *Ethmia bipunctella* is increased experimentally, a negative effect of herbivory on *C. officinale* results (Prins *et al.* 1987). That level of herbivory, however, is not reached in natural situations.

Fecundity of *S. jacobaea* is highly influenced by herbivores. Food availability for rabbits in the coastal dunes in The Netherlands is frequently very low in winter (Wallage-Drees & Deinum 1986). This may cause a high level of herbivory of rabbits on *S. jacobaea*. In this study a significant decrease in probability of flowering was caused by rabbit herbivory in winter. Additionally, seed production of unprotected plants of *S. jacobaea* was totally prevented by attack of *T. jacobaeae* at the end of June and beginning of July. When weather conditions are favourable *S. jacobaea* is able to produce new flowering shoots and seeds after complete defoliation (Cameron 1935; Harris *et al.* 1978; van der Meijden & van der Waals-Kooi 1979; Dempster 1982; Crawley 1983; Islam & Crawley 1983). In 1986, when this study was performed, no regrowth at all was found, probably due to a very dry period following defoliation.

#### *Comparing herbivory of C. officinale and S. jacobaea*

*C. officinale* and *S. jacobaea* seem to be equally apparent (Feeny 1976; Rhoades & Cates 1976), yet they suffer extremely different degrees of herbivory. *C. officinale* is only slightly if at all influenced by herbivores during the seed stage. *S. jacobaea*, in contrast, is



**Table 5.** Defensive plant characteristics of *Cynoglossum officinale* and *Senecio jacobaea*

	<i>C. officinale</i>	<i>S. jacobaea</i>
Hairs/mm <sup>2</sup>	9·30	5·90
Toughness (mg/3·14 mm <sup>2</sup> )	182·30	125·40
Alkaloid concentration (%)	1·03	0·18
Nitrogen concentration (%)	2·52	3·32
Sugar concentration (%)	6·62	6·26
Water concentration (%)	82·50	85·90

Leaf toughness is expressed as the amount of weight needed to punch a hole with a diameter of 2 mm (see Prins & Laan 1988 for methods). Concentration is % of plant dry weight.

influenced by herbivores in all three life stages. Effect of herbivores on *S. jacobaea* in terms of probability of flowering and amount of reproduction is obvious. *C. officinale* and *S. jacobaea* have both a qualitative chemical defence (pyrrolizidine alkaloids, see Harborne 1988). The level of defence, however, is different for both species. *C. officinale* rosettes and flowering plants have a very high level of alkaloids compared to related species (Pedersen 1975) and compared to vegetative and flowering *S. jacobaea* (van der Meijden *et al.* 1984) (Table 5). Alkaloids are thus suspected to be involved in causing the difference found in leaf herbivore pressure. Further studies are required to examine their importance for herbivores.

Other plant defensive characteristics, however, may also be important in determining herbivore pressure. *C. officinale* has other characteristics which probably make the species more defensive against herbivores compared to *S. jacobaea* (Table 5). *C. officinale* leaves contain more hairs, are tougher and have a lower nutritional value (lower concentration of nitrogen and a lower water content) (Table 5). A combination of both these factors and the presence of alkaloids may make *C. officinale* less attractive to herbivores compared to *S. jacobaea*.

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## REFERENCES

- Belsky, A.J. (1986): Does herbivory benefit plants? A review of the evidence. *Am. Nat.* **127**: 870–892.
- Breemen, van, A.M.M. (1984): Comparative germination ecology of three short-lived monocarpic Boraginaceae. *Acta Bot. Neerl.* **33**: 283–305.
- & van Leeuwen, B.H. (1983): The seed bank of three short-lived monocarpic species, *Cirsium vulgare* (Compositae), *Echium vulgare* and *Cynoglossum officinale* (Boraginaceae). *Acta Bot. Neerl.* **32**: 245–246.

- Cameron, E. (1935): A study of natural control of ragwort (*Senecio jacobaea* L.). *J. Ecol.* **23**: 266–322.
- Coley, P.D. (1983): Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Mon.* **53**: 209–229.
- (1987): Interspecific variation in plant anti-herbivore properties: the role of habitat quality and the rate of disturbance. *New Phytol.* **106**: 251–263.
- Crawley, M.J. (1983): *Herbivory, the Dynamics of Animal-Plant Interactions. Studies in Ecology*, **10**. Blackwell Scientific Publications, Oxford.
- Dempster, J.P. (1982): The ecology of the Cinnabar Moth, *Tyria jacobaea* L. (Lepidoptera: Arctiidae). *Adv. Ecol. Res.* **12**: 1–36.
- Feeny, P. P. (1976): Plant apparency and chemical defence. *Rec. Adv. Phytochem.* **10**: 1–40.
- Harborne, J.B. (1988): *Introduction to Ecological Biochemistry*. Academic Press, London.
- Harper, J.L. (1977): *Population Biology of Plants*. Academic Press, London.
- Harris, F., Thomson, L.S., Wilkinson, A.T.S. & Neary, M.E. (1978): Reproductive biology of tansy ragwort, climate and biological control by the cinnabar moth. In: Friedman, I.E. (ed.): *Proc. IV International Symposium on Biological Control of Woods*. 163–173.
- Islam, Z. & Crawley, M.J. (1983): Compensation and regrowth in ragwort (*Senecio jacobaea*) attacked by the cinnabar moth (*Tyria jacobaea*). *J. Ecol.* **71**: 829–843.
- Jong, de, T.J. & Klinkhamer, P.G.L. (1988): Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand dune area: the importance of water for differential survival and growth. *J. Ecol.* **76**: 393–402.
- Jong, de, T.J., Klinkhamer, P.G.L. & Prins, A.H. (1986): Flowering behaviour of the monocarpic perennial *Cynoglossum officinale* L. *New Phytol.* **103**: 219–229.
- Klinkhamer, P.G.L., de Jong, T.J. & Meelis, E. (1987): Life history variation and the control of flowering in short-lived monocarps. *Oikos* **49**: 309–314.
- Meijden, van der, E. (1971): *Senecio* and *Tyria* (Callimorpha) in a Dutch dune area. A study on an interaction between a monophagous consumer and its host plant. In: Boer, den, P.J. and Gradwell, G.R. (eds): *Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations*. 390–404. Pudoc, Wageningen.
- (1979): Herbivore exploitation of a fugitive plant species: local survival and extinction of the cinnabar moth and ragwort in a heterogeneous environment. *Oecologia* **42**: 307–323.
- & van der Waals-Kooi, R.E. (1979): The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *J. Ecol.* **67**: 131–153.
- , van Bemmelen, M., Kooi, R. & Post, B.E. (1984): Nutritional quality and chemical defence in the ragwort-cinnabar moth interaction. *J. Anim. Ecol.* **53**: 443–453.
- , Wijn, M. & Verkaar, H.J. (1988): Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* **51**: 355–363.
- Pedersen, E. (1975): Pyrrolizidine alkaloids in Danish species of the family Boraginaceae. *Arch. Pharm. Chem. Sci. Ed.* **3**: 55–64.
- Prins, A.H., Verboom, B. & Verboom, J. (1987): On the relationship between *Ethmia bipunctella* and its host plant *Cynoglossum officinale*. *Proceedings of the 39th International Congress on Crop Protection*. 1335–1341.
- & Laan, R.M. (1988): Do plant characteristics influence the numbers of *Ethmia bipunctella* on *Cynoglossum officinale*? *Proceedings of the 40th International Congress on Crop Protection*. 1409–1415.
- Rhoades, D.F. & Cates, R.G. (1976): Towards a general theory of plant anti-herbivore chemistry. *Rec. Adv. Phytochem.* **10**: 168–213.
- Verkaar, H.J. (1988): Are defoliators beneficial for their host plants in terrestrial ecosystems?—a review. *Acta Bot. Neerl.* **37**: 137–152.
- Wallage-Drees, J.M. & Deinum, B. (1986): Quality of the diet selected by wild rabbits (*Oryctolagus cuniculus* (L.)) in autumn and winter. *Neth. J. Zool.* **36**: 438–448.
- Werner, P.A. (1975): Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia* **20**: 197–201.