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Effects of herbivory and competition on an introduced plant in decline

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Abstract *Anthemis cotula* was introduced to Denmark 500 years ago, and its distribution is presently limited and in decline. A manipulative field experiment was performed to investigate the effects of native plant competitors and native invertebrate herbivores on its performance. Generally, both herbivory and competition treatments had great impact, and when both factors were operating, the effects were additive for all variables except plant height. Although *A. cotula* showed plasticity in growth, resource allocation and flowering timing, it was unable to adjust to competition and compensate for losses due to herbivory sufficiently to ensure and restore its achene production. This vulnerability, combined with improved cereal cleaning techniques and thus fewer reintroductions of *A. cotula* seeds, may be the cause of its current decline. *A. cotula* responded to herbivory by prolonging its flowering period, a "bet-hedging" strategy. In Denmark this strategy is unreliable since risks of suboptimal conditions are much greater in August–October.

Key words Invasion barrier · Interspecific competition · Invertebrate herbivory · Compensation · *Anthemis cotula*

Introduction

Most investigations of plant invaders have focused on successful invasions. Although the causes of invasion failures have long been debated, the discussion has primarily been based on qualitative observations due to a lack of quantitative field investigations and experiments. However, it is important to investigate life histories and population dynamics of plants experiencing invasion failure in order to provide guidelines for the management of natural communities. With a detailed knowledge of natural barriers to invasion, invasion rates can be reduced by strengthening the barriers or by reducing their debilitation.

Interspecific competition and herbivory by generalists are two community parameters that may act as barriers to invasion (Crawley 1987). Shared requirements for limited resources can affect key life history traits of competing plants. Biomass may be reduced (Fowler and Rausher 1985), and nutrient stress may increases root/shoot ratios (Wilson 1988). High density of neighbours may reduce plant height (Harper 1977), and time of flowering may be changed (Thébaud et al. 1996). Studies have produced strong or highly suggestive evidence that the competitiveness of established invaders is correlated with their distribution (Weiss and Noble 1984). Competitive interactions between native and introduced species may thus affect both plant performance and population dynamics.

Invertebrate herbivory can likewise affect plant growth, biomass allocation and reproduction (Harper 1977; Crawley 1983). The net effect of herbivory depends on the absolute loss to herbivores and the capacity and copportunity for compensatory regrowth, which varies from negative to positive according to interactions with environmental factors (Maschinsky and Whitham 1989; Louda et al. 1990). Biological control projects offer clear evidence that imported herbivores can not only modify the expression of traits of successful plant invaders but can also change their abundance and distribution (Crawley 1996). In contrast, native herbivores often have only small effects on the fitness of successful invaders (Weiss and Milton 1984; Schierenbeck et al. 1994; Thébaud et al. 1996).

The aims of this study are to estimate the effects of two hypothesised invasion barriers, invertebrate herbi-

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vory and interspecific competition, on plant performance of an unsuccessful invader. The field experiment was designed to investigate these two factors and their interaction. *Anthemis cotula* L. was chosen as the test plant since its distribution in Denmark is limited and in decline.

Methods

Study plant

A. cotula (Asteraceae) is a 25- to 50-cm-tall annual herb with branched stems (Baagoee and Tind 1988). Capitula are 15–30 mm in diameter and contain white neuter ray florets and 70–200 yellow hermaphroditic disc florets (Kay 1971). *A. cotula* is strongly self-incompatible and pollinated by syrphids and other Diptera (Kay 1971). In Denmark *A. cotula* has a summer annual lifecycle, and flowering occurs from June to September (Baagoee and Tind 1988). The species grows on loamy disturbed soil near waste ground, harbours, built-up areas and ponds (Pedersen 1961; Baagoee and Tind 1988). In Britain *A. cotula* is most abundant where the July temperature exceeds 15.6°C, and the annual rainfall is less than 880 mm (Kay 1971).

A. cotula is native to southern Europe-west Siberia but is presently considered to be cosmopolitan (Pedersen 1961). It has spread to most parts of Europe northwards to Finland, Norway and Sweden and southwards to the Atlas mountains (Pedersen 1961). *A. cotula* was brought to Denmark in the 16th century, most likely as impurities of cereals (Pedersen 1961). The species was commoner by the end of the 19th century than it is presently (Lange 1864; Baagoee and Tind 1988). This pattern is also observed in Ireland and is presumably caused by improved seed cleaning (Kay 1971).

Study site

The experiment was conducted from May to November 1996 on a loamy field at the Danish research station Paaskehojgaard. The climate is temperate with an average annual rainfall of 648 mm and a mean July temperature of 15.8°C (The Danish Meteorological Institute, personal communication). Prior to the experiment, the field had lain fallow for 4 years. Its vegetation was dominated by *Tripleurospermum inodorum*, *Taraxacum* spp., *Sonchus oleraceus*, *Epilobium montanum*, *Festuca rubra*, *Lolium perenne* and *Elytrigia repens*. The experimental area was exposed to a potential soil water gradient caused by a slight slope, and the experimental design was chosen and set up with respect to this influence.

Field experiment

Seeds from the Botanical Garden, Copenhagen, were sown on 2 May in trays in an unheated greenhouse, and seedlings were transferred to pots.

A randomised complete block design was selected to make allowance for gradient effects and spatial heterogeneity of the area. Ten 5 × 45 m blocks were set up in the direction of the water gradient and separated by 1-m-wide walkways to allow access to the plants. The treatments consisted of three levels of competition and two levels of herbivory and accordingly a total of six factorial treatment combinations. Each block was divided into 12 subblocks, and each treatment combination was assigned to two randomly selected subblocks. Each subblock contained one row with 14 plants 1 m apart. On 1–3 June, 1680 seedlings with six to eight leaves longer than 1 cm were transplanted into the experimental plot and watered with 0.6 l of water per plant to minimise any transplantation shock. Only three of the seedlings were clearly affected by the transplantation, and they were replaced within the first 5 days.

To estimate the competitive ability of *A. cotula*, three levels of competitive pressure from the surrounding vegetation were established: a high competitive pressure (HC) by conserving the undisturbed vegetation, and a medium (MC) and a low (LC) competitive pressure by hand-weeding all plant material within circles of 20 and 40 cm in diameter, respectively, around the appropriate *A. cotula* plants. During the season regrowth was carefully hand-weeded, and branches or leaves projecting from the surrounding vegetation into the circles were pruned.

To estimate the ability of *A. cotula* to resist herbivory, two levels of herbivory were established. The low herbivory treatment (LH) was imposed by application of three insecticides. Immediately after the transplantation, 1.3 g of pellets of the molluscicide PLK-metaldehyde 5 G (G.F. Agro A/S) were applied to the soil around each LH plant. Foliar insecticide Sumi alpha (Du Pont de Nemours A/S) was applied to *A. cotula* at a concentration of 25 mg l^{-1} four times during the season. Twice during the season, 1.0 g of the soil insecticide Curaterr (Bayer Danmark A/S) was applied to the soil at the base of the LH plants. The pellets were watered down with 0.6 l of water per plant. The control plants (high herbivory, HH) were sprayed and watered with equivalent amounts of pure water to the LH plants.

Herbivory by sap-feeding and/or chewing invertebrates was regularly recorded as present or absent. Plant height from ground surface to shoot apex was measured on 11, 18 and 25 June and on 2 and 16 July. In each block one of the two subblocks sharing the same treatment was randomly selected, and the plants were harvested on 2–5 August. The plants were divided into their shoot and root components and oven-dried at 70°C for 24 h followed by 105°C for 24 h, after which dry weight was determined. Initiation of flowering was recorded for each plant. Termination of flowering was recorded for all individuals that had not previously died due to herbivory, competition or harvesting. From August to November, capitula with mature achenes were collected one to three times a week and numbers of capitula and seeds per plant were counted. Capitula that failed to develop seeds were excluded.

Greenhouse experiment

To test the effects of the insecticides on plant performance, a control experiment was conducted in an unheated greenhouse: 40 control plants were only watered, and 25 plants were treated with the insecticides. Sumi alpha was applied three times in a dose equivalent to the dose applied in the field experiment. Curaterr and PLK-Metaldehyde were applied once, and the doses were only one-third of the amount applied in the field to take into account the small volume of pot soil. Shoot length and dry weight of the above-ground biomass were determined.

Statistical analyses

Among-treatment differences were analysed using the mixed models approach of factorial analysis of variance using the PROC MIXED procedure of SAS (Littell et al. 1996). Variance components for random effects were estimated by restricted maximum likelihood (REML) which takes account of the degrees of freedom used for estimating fixed effects (Searle et al. 1992). Random effects were tested using the PROC GLM procedure of SAS (SAS Institute 1990). Herbivory and competition were fixed factors, and blocking was a random factor effect. The analyses were carried out for plant height on 16 July (onset of achene maturation), shoot and root dry weight, root/shoot ratio and achene and capitula number. All independent variables except plant height were transformed to attain normality and improve homogeneity of data. To test for significant differences between means, appropriate unplanned multiple comparison procedures were carried out on all possible pairs of means for each of the variables (Day and Quinn 1989). Means of plant size and reproductive output were compared by Games-Howell's test at a 5% experiment-wise level of significance (Sokal and Rohlf 1981). Means of flowering timing were compared by the non-parametric Mann-Whitney U-test with significance levels adjusted according to the Dunn-Sidák method to keep the experiment-wise type I error rate below 5% (Sokal and Rohlf 1981). To estimate the efficiency of the insecticides, the percentage of plants with damage caused by sap-feeding and/or chewing invertebrates was computed.

Results

Herbivory

The above-ground herbivores were dominated by aphids (Aphidae), spittlebugs (Cercopidae), bugs (Heteroptera), moths, and slugs and snails. During June and July sucking insects were numerous on *A. cotula*. They fed on all parts of the shoot. Heavily attacked plants produced secondary shoots in September and were later killed by low temperatures while still flowering. Mollusc damage was only observed during the first 3 weeks of the study. This damage induced compensatory regrowth resulting in a lower and more compact plant form. Lepidopteran larvae used the apical meristem and its enveloping leaves in their cocoon construction. Since they are still present at the onset of plant reproduction they may have greater net effects than the molluscs. No damage from vertebrates was observed.

Differences in herbivore attack between *A. cotula* plants were clearly influenced by insecticide applications. Of the untreated plants (HH) 64% were damaged, but only 3% of the treated plants (LH). Sucking and chewing insects attacked 58 and 24% of the HH plants respectively. Although insecticides were very effective against the herbivores, they did not affect plant height ($F = 0.721$, $df = 1, 63$, $P = 0.721$) or above-ground biomass ($F = 0.118$, $df = 1, 63$, $P = 0.056$) in the greenhouse experiment.

Plant size

Growth rates and final height of plants were greatly reduced by herbivory, while competition only caused relatively small differences (Fig. 1, Table 1). The plants treated with insecticides were 74–80% taller. For LH plants height was significantly increased by competition, while the effect of competition upon HH plants was significant but not consistent. There was a significant interaction between herbivory and competition in their effect on plant height.

Herbivory and competition significantly reduced root and shoot weight and increased root/shoot ratio (Fig. 2A–C, Table 1). Interaction effects were non-significant (Table 1). Comparisons of plants under naturally prevailing conditions (HH-HC) with treated plants (LH-LC) showed that under natural conditions root weight was reduced by 58%, shoot weight was reduced by 79%, and root/shoot ratio was increased by 96%.

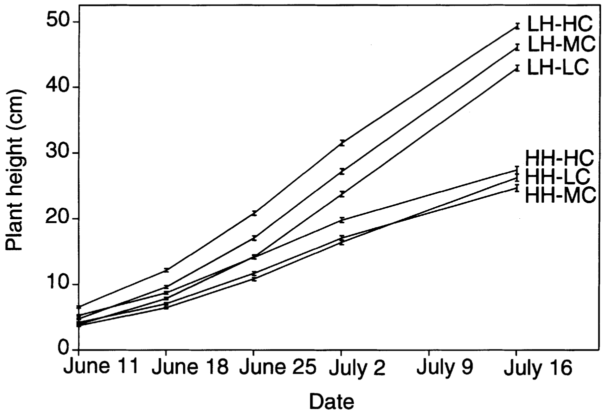

Fig. 1 Mean plant height ±1 SE as a function of time for six combinations of herbivory and competition ($n = 280$). All mean final heights (cm) differ from each other according to Games-Howell's test ($P_{\mathrm{exp}} < 0.05$) (*HC* high competition, *MC* medium competition, *LC* low competition, *HH* high herbivory, *LH* low herbivory). Results of ANOVA in Table 1

Flowering timing

The time from transplantation to the field to onset of flowering was approximately the same for all treatments whereas flowering termination was significantly affected by herbivory and competition (Fig. 3). The flowering periods of HC plants were 17 and 18 days shorter than those of LC plants under HH and LH conditions respectively. HC and MC plants terminated flowering 8 and 12 days later, respectively, when herbivory was high than when it was low. Herbivory did not affect flowering termination of LC plants. The mean upper threshold to the time of flowering termination was mid-September, i.e. 98–103 days after transplantation. Later in the season plants were affected by low temperatures.

Reproductive output

Herbivory and competition affected lifetime achene and capitula production significantly, and their interaction was non-significant (Table 1). Numbers of achenes and capitula of plants under naturally prevailing conditions (HH-HC) were 94% and 82% lower than those of treated plants (LH-LC) (Fig. 4A, B). LH plants produced approximately 3 times as many achenes per capitulum as HH plants (Fig. 4C). Competition caused only small differences in achene number per capitulum.

Discussion

Plant size

Under the naturally prevailing conditions root and shoot biomass were reduced by competition, suggesting that soil resources and/or light were factors limiting growth. This was supported by the root/shoot invest-

Table 1 Analysis of variance for the effects of herbivory (*H*), competition (*C*) and block (*B*) on six variables

Source of variation	SS	*df*	MS	*F*
Plant height by 16 July (untransformed)				
H	168532.42	1	168532.42	317.80***
C	4454.10	2	2227.05	18.07***
B	11132.50	9	1236.94	2.53 NS
H × C	2445.54	2	1222.77	9.92**
H × B	4772.72	9	530.30	3.70**
C × B	1854.72	18	103.04	0.72 NS
H × C × B	2582.51	18	143.47	2.39**
Within	97018.26	1617	59.89	
Total	292792.77	1676	174.70	
Root dry weight (log-transformed)				
H	4.05	1	4.05	10.62*
C	68.68	2	34.34	90.06***
B	7.20	8	0.90	2.66 NS
H × C	2.40	2	1.20	3.15 NS
H × B	3.05	8	0.38	0.95 NS
C × B	5.77	16	0.36	0.90 NS
H × C × B	6.44	16	0.40	3.33***
Within	78.19	648	0.12	
Total	175.78	701	0.25	
Shoot dry weight (log-transformed)				
H	48.28	1	48.28	34.57***
C	143.67	2	71.83	73.27***
B	12.08	8	1.51	0.79 NS
H × C	1.70	2	0.85	1.30 NS
H × B	12.29	8	1.54	2.40 NS
C × B	16.24	16	1.01	1.59 NS
H × C × B	10.22	16	0.64	3.89***
Within	106.36	648	0.16	
Total	350.84	701	0.50	
Root/shoot ratio (log-transformed)				
H	24.36	1	24.36	23.61**
C	14.61	2	7.30	15.51***
B	17.53	8	2.19	1.90 NS
H × C	1.54	2	0.77	2.21 NS
H × B	8.25	8	1.03	2.96*
C × B	7.53	16	0.47	1.35 NS
H × C × B	5.58	16	0.35	2.65***
Within	85.24	648	0.13	
Total	164.65	701	0.23	
Achenes per plant (square-root-transformed)				
H	101023.77	1	101023.77	106.33***
C	58264.24	2	29132.12	41.98***
B	8808.48	9	978.72	1.06 NS
H × C	2424.41	2	1212.20	1.75 NS
H × B	8551.28	9	950.14	1.34 NS
C × B	12228.47	18	679.36	0.96 NS
H × C × B	12743.90	18	707.99	4.51***
Within	122466.41	780	157.01	
Total	326510.96	839	389.17	
Capitula per plant (square-root-transformed)				
H	116.42	1	116.42	8.41**
C	1000.18	2	500.09	40.06***
B	136.78	9	15.20	1.00 NS
H × C	0.64	2	0.32	0.03 NS
H × B	124.63	9	13.85	1.24 NS
C × B	224.72	18	12.48	1.12 NS
H × C × B	201.15	18	11.17	5.31***
Within	1642.11	780	2.11	
Total	3446.63	839	4.11	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, *NS* non-significant

ment strategy of *A. cotula*: under increased competitive conditions more was invested in roots, presumably improving uptake of water and nutrients. Competition induced small but significant increases in mean plant height. This – combined with a reduced total biomass – resulted in unbranched, tall and often fragile plants with

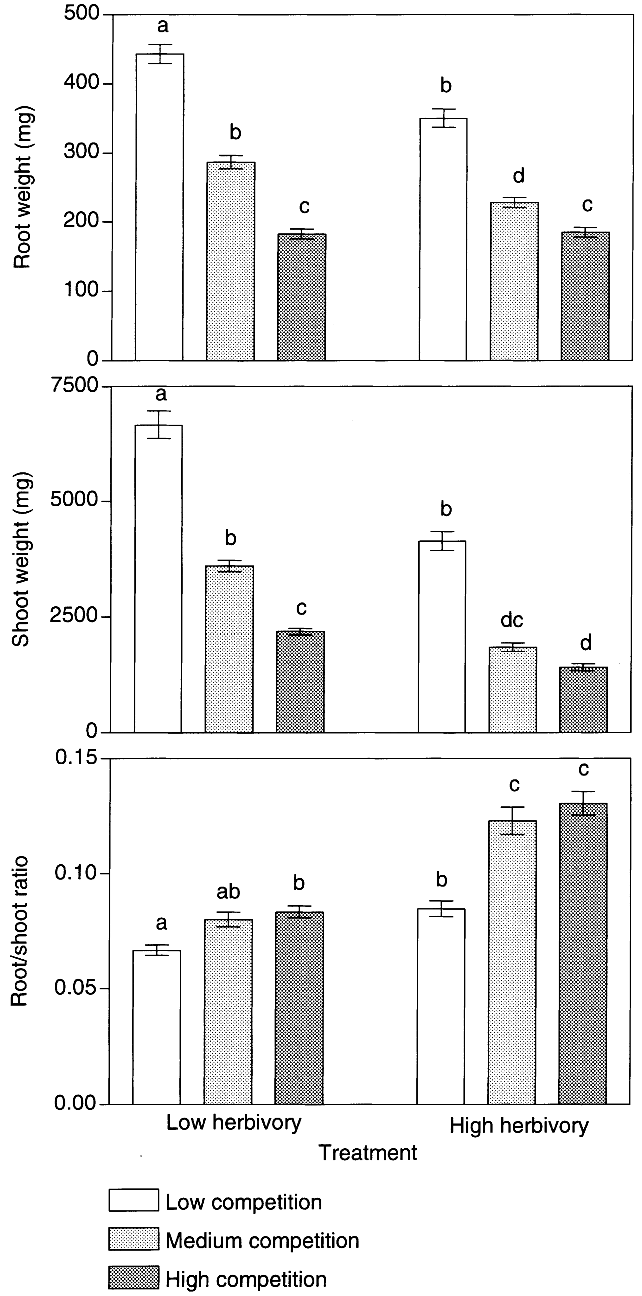

Fig. 2A–C Mean biomass allocation ± 1 SE for six combinations of herbivory and competition. **A** Mean root dry weight per plant (mg). **B** Mean shoot dry weight per plant (mg). **C** Mean root/shoot ratio per plant (n = 117). Games Howell's tests of means are performed on square-root-transformed variates. *Columns* with the same *letters* do not differ from each other ($P_{\mathrm{exp}} < 0.05$). Means and SEs are backtransformed. Results of ANOVA in Table 1

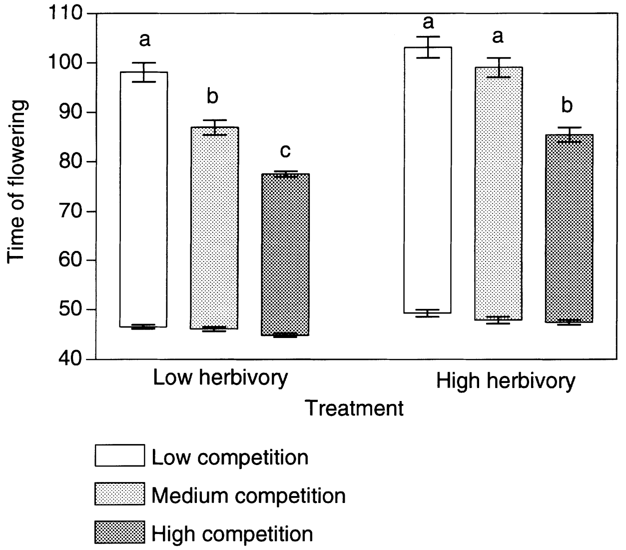

Fig. 3 Mean flowering timing ± 1 SE at six combinations of herbivory and competition. *Bars* indicate the flowering period as the time interval between flowering initiation and termination measured in mean number of days from transplantation (n = 108 for HH-HC, 110 for HH-MC), 106 for HH-LC, 137 for LH-HC, 128 for LH-MC and 119 for LH-LC; abbreviations as in Fig. 1). Mann-Whitney U-tests on means are performed on variates transformed to reciprocals. *Bars* with the same *letters* do not differ from each other in flowering termination ($P_{\mathrm{exp}} < 0.05$). Flowering initiations are similar for all treatment comparisons with the exceptions of: HH-HC and LH-HC, HH-LC and LH-HC, HH-LC and LH-MC. Means and SEs are backtransformed

greatly increased vulnerability to wind and heavy rain in order to reach increased light intensities.

Plants with reduced exposure to herbivory grew twice as high as plants exposed to high herbivory. Herbivory also reduced shoot dry weight, reflecting the inability of the plants to compensate fully for losses through production of replacement tissue. Root biomass was reduced by herbivory under conditions of medium and low competition, indicating that the plants allocated resources from the roots to the shoot or that the root system was damaged by below-ground herbivores. However, inspection of roots at harvest did not reveal any damage. Caldwell et al. (1981) have stressed the importance of flexibility in resource allocation in invasion success of plants. It is thus notable that *A. cotula* was unable to restore the root/shoot ratio under the naturally prevailing herbivore level.

There was no interaction between herbivory and competition in their effects on biomass allocation, but plant height was affected by an interaction between the two factors which indicated that the negative impact of herbivory on plant height was greater when competition was high than when it was low.

Flowering timing

Flowering initiation of *A. cotula* was not affected by competition. This stands sharply in contrast to the results of a study on successfully established invasive *Conyza* species (Thébaud et al. 1996). Likewise, in contrast to *Conyza*, *A. cotula* plants reduced their flowering period in response to increased competition. This may be an effect of a shortened plant lifetime. If a plant is exposed to shading from neighbouring plants, this may negatively affect its physiology (Woledge 1978) and accelerate scenescence (McNaughton 1983). Thébaud et al. (1996) interpreted the prolongation of the flowering

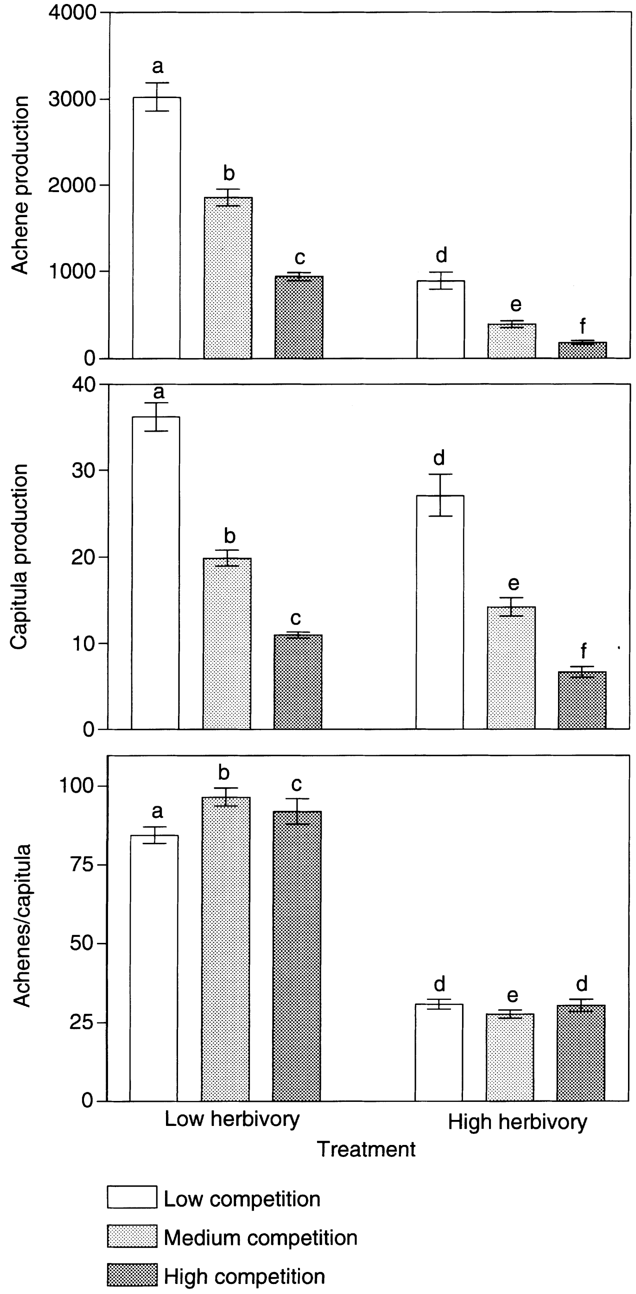

Fig. 4A–C Mean reproductive success ± 1 SE at six combinations of herbivory and competition. **A** Mean number of achenes per plant (n = 140). **B** Mean number of capitula per plant (n = 140). **C** Mean number of achenes per capitulum per plant (n = 110 for HH-HC, 129 for HH-MC, 130 for HH-LC, 139 for LH-HC, 140 for LH-MC and 140 for LH-LC. Games-Howell's test of means are performed on square-root-transformed variates. *Columns* with the same *letters* do not differ from each other ($P_{\mathrm{exp}} < 0.05$). Means and SEs are backtransformed. Results of ANOVA in Table 1

period of *Conyza* by competition as an advantage, allowing more time for seed development if soil resources are scarce. It seems plausible that the opposing effects of competition on *Conyza* and *A. cotula* is because *Conyza* is mainly limited by low soil resources and *A. cotula* by low light intensities.

Herbivory had likewise no, or only small, effects on flowering initiation of *A. cotula*, but it delayed flowering termination and increased flowering period. Considering the many herbivores present in the first month of flowering, this bet-hedging strategy might maximise plant fitness. However, bet-hedging is unreliable since reproduction becomes dependent on the highly unstable climatic conditions during August–October.

Reproductive output

Removal of competitors and herbivores led to a large increase in reproductive output, which demonstrated that compensation was only partial and low. Reduced seed set does not necessarily have an adverse impact on plant abundance and distribution, if the number of seeds lost to herbivory and competition would later have failed to develop further for other reasons. A demographic study including e.g. estimations of germination and establishment success, seed dormancy, seed bank size and seed influx is needed to demonstrate the conditions under which *A. cotula* can maintain itself. This study provides only some of the parameters needed for modelling the dynamics of invaders (e.g. Turelli 1981; Crawley 1986), but it forms the basis of speculations. When herbivory and competition are reduced, *A. cotula* has a high fecundity, and although the seed bank is not particularly long-lived (6% germination after 11 years of burial in sterilised soil: Kay 1971), the intensity of herbivory and competition has to be both strong and persistent over several generations in order to empty the seed bank. The densities of various herbivore species are known to vary considerably over time, but considering that *A. cotula* is damaged by a great array of generalist herbivore species, it seems plausible that the overall herbivore intensity is more and less constant. The strength and persistence of competition may be more variable, as *A. cotula* is found in habitats that are highly influenced by humans. Such habitats are exposed to many physical disturbances varying in frequency and extent and thus in their effects on plant density and species composition.

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