*Functional Ecology* 1989, **3**, 229-235

# Interactive effects of disturbance and shade upon colonization of grassland: an experiment with *Anthriscus sylvestris* (L.) Hoffm., *Conium maculatum* L., *Daucus carota* L. and *Heracleum sphondylium* L.

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**Abstract.** Seeds of four species of Umbelliferae [*Anthriscus sylvestris* (L.) Hoffm., *Conium maculatum* L. *Daucus carota*, L. and *Heracleum sphondylium* L.] were sown separately into plots of grassland given two types of disturbance treatment, factorially combined with shade in a 4 × 3 × 2 experimental design. All species showed some enhanced recruitment in response to disturbance, the effects of which were still significant 21 months after treatments were applied. The duration of the disturbance, which was different in the two treatments, affected the size and structure of populations at the end of the experiment.

All significant effects of shade (but not disturbance) were accompanied by a first-order interaction. The effect of shade on colonization by the four species in this experiment varied with the occurrence of disturbance and its intensity, and varied significantly between species.

It is suggested that differences between species in their habitat distributions will most often be due to differences in interactions between disturbance and other factors, rather than due to their response to disturbance alone.

*Key-words:* Disturbance, shade, grassland, Umbelliferae

## Introduction

The dependence of recruitment upon disturbance in grasslands has often been investigated experimentally and widely shown to be important (e.g. Platt, 1975; Gross & Werner, 1982; Goldberg & Werner, 1983; Rapp & Rabinowitz, 1985; Rabinowitz & Rapp, 1985a,b). When many species depend upon disturbance for recruitment, interactions between disturbance and other factors are liable to be important to community composition (Collins, 1987). However, such interactions have only rarely been investigated. In this paper we describe an experiment designed to investigate the importance of interactions between disturbance and shade in colonization of grassland by four related dicot species with contrasting life histories.

The species occur in Britain in grasslands and on roadside verges that are often shaded by hedges or trees. We therefore have an *a priori* reason for expecting interactions between disturbance and shade to be important in the distribution of these species. Two levels of disturbance were made in closed turf: (1) by turning the soil over with a garden fork and (2) by applying a non-selective herbicide. Equal areas of bare ground were created by the two treatments, but herbicide created a longer-lasting disturbance than the tillage treatment which was reinvaded by grasses regenerating from buried rootstocks. Disturbance treatments were factorially combined with the shade of a simulated canopy.

## Species and methods

The four species used in the experiment were *Anthriscus sylvestris* (L.) Hoffm., *Conium maculatum* L., *Daucus carota* L. and *Heracleum sphondylium* L. All are Umbelliferae and occur abundantly in Britain in grassland habitats. Their ecology is compared in Table 1. The design of the experiment was a 4 × 2 × 3 factorial with four species, two levels of shade and three levels of disturbance.

In autumn 1983 in an experimental garden at the Open University campus in Milton Keynes, Buckinghamshire, 132 1 m × 1 m plots were marked out in a flat, uniform area of grassland that had been

**Table 1.** Comparative life histories of four umbellifers. Further information may be found in Tutin (1980) and Lovett Doust & Lovett Doust (1982).

| Species | Life history | Seed survival in soil[1] (yr) | Emergence | Weight of 'seed'[2] (mg) |
|---|---|---|---|---|
| *Anthriscus sylvestris* | Perennial, polycarpic | 2 | Spring | 5·18 |
| *Conium maculatum* | Perennial, monocarpic | 5 | Autumn/spring | 2·25 |
| *Daucus carota* | Annual/perennial, monocarpic | ? | Autumn/spring | 0·88 |
| *Heracleum sphondylium* | Perennial, polycarpic | 2 | Spring | 5·52 |

[1] Years to reach <1% of seeds buried in experiments of Roberts (1979).
[2] Data from Grime *et al.* (1981).

plowed and sown with perennial ryegrass *Lolium perenne* L. one year previously. Plots were arranged in rows, two plots wide, with metre-wide pathways between rows. Five treatments and a control for each of the four species were assigned randomly to plots. Treatments were as follows, with the number of replicates shown in parentheses:

(1) entire 1 $m^2$ plot sprayed with the herbicide paraquat, killing all the vegetation (6);
(2) entire 1 $m^2$ plot dug over with a garden fork (6);
(3) plot shaded with a 25 cm high, 1 m × 1 m wooden frame covered in two layers of Rokolene netting, reducing transmitted PAR by 85% (4);
(4) a shade frame placed over a herbicide treatment (6);
(5) a shade frame placed over a tillage treatment (6).

Control plots (five replicates) received no shade or disturbance. Treatments did not receive equal replication because of constraints on space but species were equally represented within treatments. The shade material simulated the effect of a plant canopy on light intensity, but not its effects on light quality.

Seeds of each of the four species were collected in bulk from wild populations in the Milton Keynes area during the summer of 1983, cleaned and broadcast at the rate of 4000 $m^{-2}$ onto plots in November of the same year, after the application of disturbance treatments. To simulate the effect of shade from a deciduous overstorey canopy, shade frames were placed upon the appropriate plots in May 1984, were removed in November 1984 and replaced in May 1985.

From sowing in November, every plot of the experiment was checked frequently for seedling emergence which occurred first for *Conium maculatum*. The considerable space and replication required by the experimental disturbances made it logistically impossible to gather detailed demographic information on plants in all plots. As a compromise, plant abundance was measured by recording presence/absence of rooted individuals in 25 10 cm × 10 cm divisions of a quadrat placed in the central 50 cm × 50 cm area of each plot. This was done once a month from initial seedling emergence to September 1984 and from April to September 1985. Separate counts of seedling and rosette abundance were made in April 1985, which was the only census when these two stages were present and could be clearly differentiated. Plant abundance was arcsine transformed and the results of censuses in April 1985 and September 1985 were analysed by two-way ANOVA for individual species and for the full 4 × 2 × 3 factorial.

## Results

The abundance of each species, at fifteen censuses during the experiment, in herbicide-, tillage- and shade-treated plots is shown in Fig. 1 with abundances in control plots for comparison. The interactions between disturbance and shade treatments are described with the results for individual species below.

### *Anthriscus sylvestris*

Germination took place in spring 1984, fully occupying all treatment and control plots (Fig.

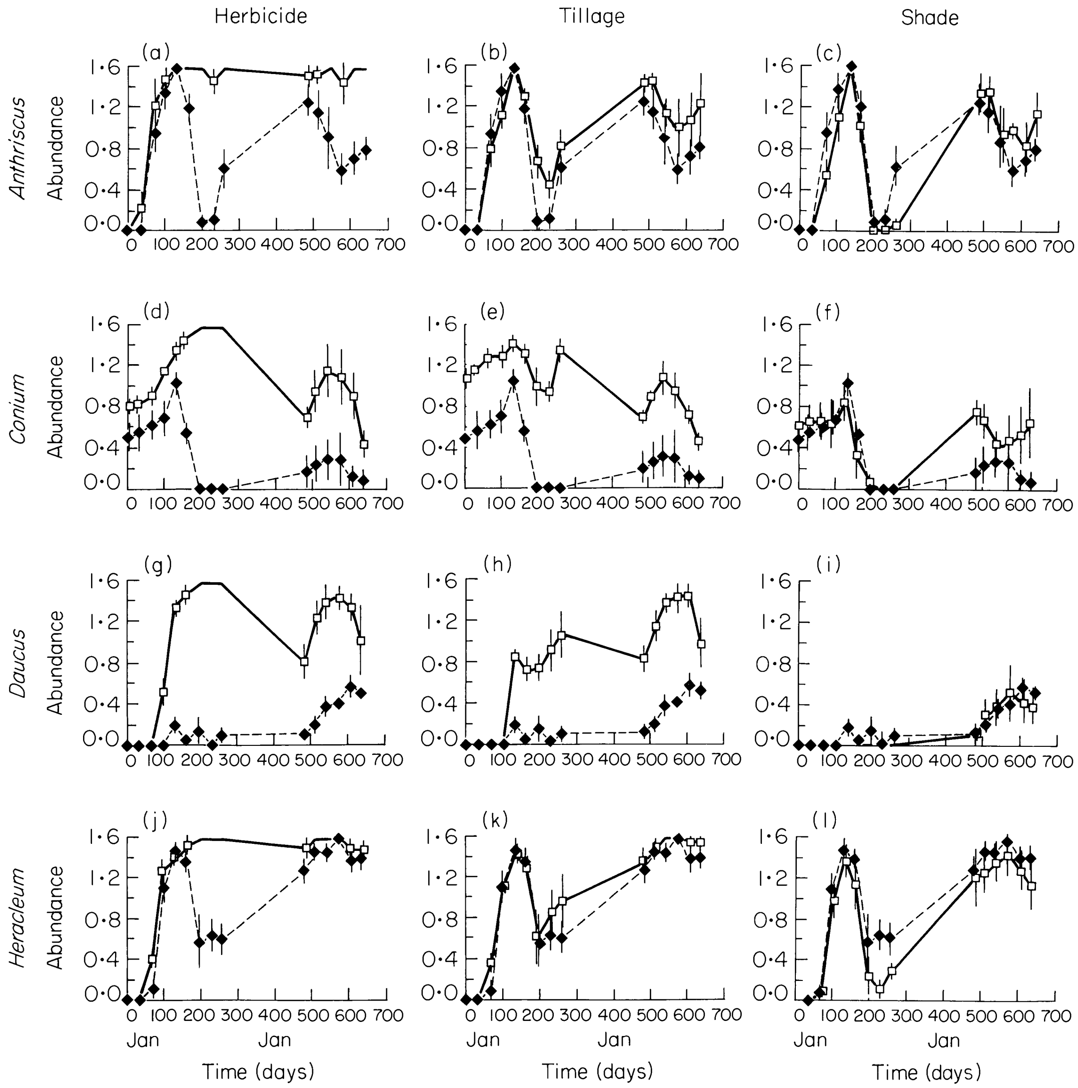


**Fig. 1.** The abundance of four umbellifer species in the experiment between December 1983 and September 1985. Abundance is measured on a scale representing the arcsine transformed proportion of quadrat subdivisions occupied by the species (see text). An abundance value of 1·57 corresponds to a fully occupied plot, with plants rooted in 25 out of 25 subdivisions. Solid lines represent plots receiving the treatment indicated at the head of the appropriate column in the diagram, interrupted lines represent control plots for comparison. Vertical bars indicate standard errors. (a–c) *Anthriscus sylvestris*, (d–f) *Conium maculatum*, (g–i) *Daucus carota*, (j–l) *Heracleum sphondylium*.

1a–c). Heavy seedling mortality occurred in May/June 1984 in tillage and shade, but not in the herbicide treatment. A second wave of germination followed by an episode of seedling mortality occurred in the spring of 1985. In April 1985 shade and disturbance had significant and opposing effects upon rosette abundance (Fig. 2a). A strong shade × disturbance interaction (Table 2a) indicated that disturbance was able to abolish the inhibitory effect of shade upon recruitment. There were considerable differences in population structure between treatments. The shade treatment contained only seedlings (Fig. 2a) but other treatments, including shade/tillage and shade/herbicide, contained rosettes (Fig. 2a). Although there was no significant difference between the disturbance treatments in the abundance of plants in April 1985 (Table 2a), in the herbicide treatment these were all one year old (Fig. 1a) while a proportion of the rosettes in the other treatments were more recent recruits (Fig. 1b,c).

The abundance of plants at the end of the experiment was significantly increased by disturbance, but shade had no significant effect on *total* plant abundance. This measure of abundance, which did not differentiate between

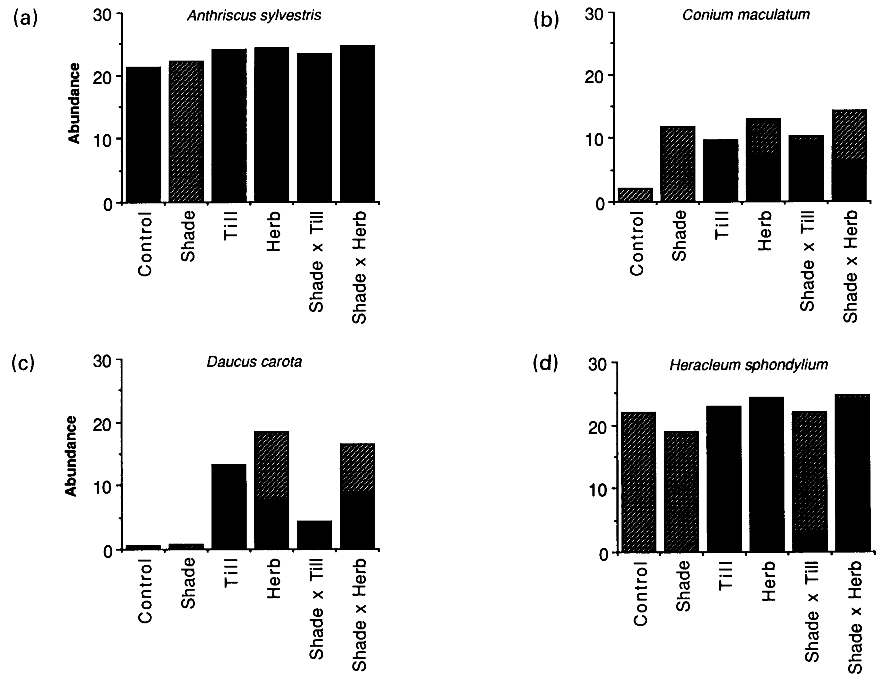


**Fig. 2.** Mean abundance of adults (black) and seedlings (cross-hatched) of (a) *Anthriscus sylvestris*, (b) *Conium maculatum*, (c) *Daucus carota* and (d) *Heracleum sphondylium* in all treatments of the experiment at the end of April 1985.

seedlings and rosettes, showed no significant disturbance × shade interaction (Table 2b).

### *Conium maculatum*

Germination began in November 1983 and continued until July 1984 by which time herbicide treated plots were fully occupied (Fig. 1d). Plant abundance reached a peak earlier and at a lower level in the other treatments and control (Fig. 1e & f). All seedlings in the control and shade treatments were dead by August 1984. Successful recruitment occurred in both types of disturbance treatment. A second wave of germination in spring 1985 was followed by heavy seedling mortality leaving only the plants recruited in 1984 in the disturbed plots. Only disturbance treatments had a significant effect upon the number of rosettes present in April 1985 (Fig. 2b, Table 2a). There was no significant difference between the effects of tillage and herbicide and no interaction of shade and disturbance.

Seedlings from the second wave of germination were present in the shade treatment and control at the last census, showing a significant positive effect of shade and disturbance upon seedling survival (Fig. 1f). There was a significant difference between disturbance treatments and a shade × disturbance interaction (Table 2b). These effects are based upon censuses which did not record the size or age of plants. These were recently emerged seedlings in the shade and control plots but large rosettes in disturbed plots.

### *Daucus carota*

Germination began in spring 1984, filling entire plots only in the tillage treatment (Fig. 1g). A second wave of germination occurred in the late spring of 1985. In the control and shade plots more seedlings appeared in this wave of germination than in the first (Fig. 1i). In April 1985 disturbance had a strong positive effect upon rosette numbers (Table 2a). Herbicide treatments contained many seedlings and tillage treatments contained none (Fig. 2c). Disturbance interacted with shade which had a smaller negative effect upon abundance with disturbance than without, and with herbicide than with tillage (Table 2a, Fig. 2c). By the end of the experiment the shade × disturbance interaction had disappeared, leaving only a significant main effect of disturbance (Table 2b).

**Table 2.** Results of ANOVA for effects of shade and disturbance on the abundance of (a) rosettes in April 1985 and (b) of all plants in September 1985. Individual species effects were derived from a 2 × 3 ANOVA and species × treatment interactions from a 4 × 2 × 3 ANOVA. Differences between disturbance treatments were calculated from cell means in the 2 × 3 ANOVA by a univariate $F$ test. NS = not significant, *$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$.

| | (a) P | (b) P |
|---|---|---|
| *Anthriscus sylvestris* | | |
| Shade | *** | NS |
| Disturbance | *** | ** |
| Shade × disturbance | *** | NS |
| Till and herbicide difference | NS | NS |
| *Conium maculatum* | | |
| Shade | NS | *** |
| Disturbance | *** | ** |
| Shade × disturbance | NS | * |
| Till and herbicide difference | NS | * |
| *Daucus carota* | | |
| Shade | * | NS |
| Disturbance | *** | ** |
| Shade × disturbance | * | NS |
| Till and herbicide difference | NS | NS |
| *Heracleum sphondylium* | | |
| Shade | *** | NS |
| Disturbance | *** | *** |
| Shade × disturbance | *** | * |
| Till and herbicide difference | *** | NS |
| Species × treatment interactions | | |
| Spp. × shade | *** | ** |
| Spp. × disturbance | *** | * |
| Spp. × shade × disturbance | *** | ** |

### *Heracleum sphondylium*

Germination in spring 1984 filled plots only in the herbicide treatment (Fig. 1j) in which the heavy post-germination mortality that occurred in other treatments and the control (Fig. 1k & l) was absent. A second wave of germination occurred in all plots in spring 1985. At this time rosettes were absent from control plots and the shade treatment, with shade showing a strong negative effect and tillage and herbicide showing strong positive, though different, effects upon rosette abundance (Fig. 2d). There was a strong interactive effect between shade and disturbance upon rosette numbers (Table 2a), though the two types of disturbance interacted with shade differently. Herbicide abolished the negative effect of shade upon recruitment in the first season while tillage only slightly ameliorated it (Fig. 2d). This paralleled the difference between the main effects of herbicide and tillage in the first season (Fig. 1j & k). The interaction between shade and disturbance lasted until the end of the experiment in September 1985, though the difference between disturbance treatments did not (Table 2b).

## Discussion

### *Main effects of disturbance and its duration*

All four of the species studied showed significantly enhanced recruitment following disturbance (Table 2a) and this had significant effects upon the final abundance of all species 2 years later (Table 2b). There was a difference between the effects of the two types of disturbance on seedling survival in the first summer (Fig. 1) for the two species with the largest seeds (*Anthriscus* and *Heracleum*, Table 1). Heavy mortality affected *Anthriscus* and *Heracleum* seedlings appearing in control, tillage and shade plots, and *Conium* and *Daucus* in all plots, but did not affect *Anthriscus* and *Heracleum* seedlings appearing in herbicide treatments. The reason for this is not known but desiccation in herbicide-treated plots may have been more severe for small-seeded species (Baker, 1972) and in tilled plots where the grass was also consuming water. In the longer-lasting disturbances created by herbicide, most of the plants of *Anthriscus* and *Heracleum* found in the plots at the end of the experiment originated from recruitment in spring 1984. By contrast, disturbances created by tillage and undisturbed plots with or without shade contained seedlings from later recruitment in 1985. The comparison of recruitment in herbicide and tillage treatments suggests that the duration of the disturbance may influence the age- and size-structure in populations of these two species quite separately from its effects on their abundance, which was the same in the two types of disturbed plot at the end of the experiment (Table 2b).

There were extreme differences in the size as well as in the numbers of plants in different treatments at the end of the experiment. Seedlings of *Conium* and *Daucus* continued to appear in their respective control and shade treatments throughout the experiment though none became established. *Conium* seedlings from the first wave of germination became established in disturbed plots but density-related mortality appears to have thinned their numbers to a few very large rosettes per plot at the end of the experiment. The scenario is one in which *Conium* rapidly colonizes a new disturbance but fails in later recruitment if disturbance does not recur. This coincides with observations in natural populations (Tremlett, Silvertown & Tucker, 1984) which tend to be ephemeral colonists in sites where occasional, large disturbances occur.

*Interactive effects of shade*

All significant effects of shade were accompanied by interactions with disturbance. The effect of shade on colonization by the four species in this experiment varied with the occurrence of disturbance and its intensity, and varied significantly between species, as reflected in significant second-order interactions in April and September 1985 (Table 2). Without disturbance, shade actually raised the abundance of *Anthriscus* seedlings in the second spring (Fig. 2a), maybe as an indirect result of the absence under shade of large *Anthriscus* rosettes that inhibit seedlings. Shade also had a significant favourable effect upon the presence of *Conium* seedlings in the second spring. In this species there were no rosettes present in control plots to account for the lack of seedlings there at the end of the experiment. This suggests that the positive effect of shade was a direct rather than an indirect one in the case of *Conium*. The pattern of plant abundance shown in Fig. 1f is consistent with shade stimulating germination in *Conium*, perhaps by reducing water loss from the soil. There was no lasting effect of shade upon *Daucus*, for which the effect of disturbance and inhibition by a closed turf were the dominant influences upon recruitment.

Shade affected recruitment of *Heracleum* in tillage treatments, but not in herbicide treatments, suggesting that longer-lasting disturbances can abolish shade effects that affect the colonization of disturbances of shorter duration. In *Anthriscus* the two kinds of disturbance alleviated the negative effect of shade equally. Thus, in one species the duration of the disturbance appears to have been important to the shade × disturbance interaction, while in the other it was not. A consequence of this is that *Heracleum* and *Anthriscus* colonizing identical types of disturbance would have the same population structure if the disturbance was of long duration or of short duration and not shaded, but would have different population structures if the disturbance was of short duration (e.g. caused by tillage) and shaded. At a lower seeding rate than was used in the experiment recruitment might not occur at all in the second season and effects which we observed in population structure might be translated into absolute effects determining the presence or absence of species. The greater restriction shade places upon recruitment in *Heracleum* by comparison with *Anthriscus* is consistent with these species' habitat distributions. The reason *Heracleum* tends to be absent from shaded sites where *Anthriscus* can be found may have as much to do with the small size of disturbances in these habitats as the presence of shade *per se*.

Previous studies have tended to examine either the effects of disturbance (e.g. Goldberg & Werner, 1983) *or* the effect of shade (e.g. Cid-Benevento & Werner, 1986) but rarely their interaction. Kawano, Hiratsuka & Hayashi (1982) have documented a correlation between the structure of a population of a woodland perennial and a gradient of light intensity. Our experiment shows that a species' distribution and demographic structure reflects the disturbance history of a site but, even as here when propagule availability does not limit recruitment, subtle interactions between disturbance and other factors (e.g. shade) can determine the outcome. It is highly significant that *all* effects of shade detected in our experiment were interactive. The nature of such interactions can be expected to vary between species, as this study of a set of related grassland species illustrates. It is in unravelling these interactions that we can expect to find explanations of the differences between species in their habitat distributions.

## Acknowledgments

This work was supported by a grant from the Research Committee of the Open University. We thank Ken Hollingshead and the grounds staff at Walton Hall for their help. We are grateful to Jon Lovett Doust, Ken Thompson, Irene Ridge and the late Deborah Rabinowitz for their critical comments on an earlier version of the manuscript and to Kevin McConway for statistical advice.

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*Received 16 June 1988; revised 18 July 1988; accepted 20 July 1988*