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On the balance between positive and negative plant interactions in harsh environments

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Positive interactions between plants typically occur where the presence of a species ameliorates the abiotic environment for another. However, there is also a potential for resource competition to act at the same time, which creates a situation where the net outcome is a balance between positive and negative interactions. We present data from a nine-year study in two extreme high alpine habitats that was designed to test whether the effects of established *Ranunculus glacialis* individuals on germination and growth of *Oxyria digyna* are primarily positive or negative at the altitudinal limit of vascular plants. We show net effects ranging from neutral to negative, but no positive effects were detected. We also argue that close associations between plants in these harsh environments may both ameliorate and deteriorate the abiotic environment, and that experimental manipulations are necessary to tell the difference.

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Recently, there has been a wealth of papers reexamining the role of positive interactions in plant communities. Several review papers have collected descriptions of instances where positive interactions have a strong effect on community processes (e.g. Bertness and Callaway 1994, Callaway 1995, Jones et al. 1997), and today most scientists would agree that these interactions are important in some communities. Positive interactions typically occur where the presence of a species ameliorates the abiotic environment for another (Bertness and Shumway 1993, Bertness and Hacker 1994, Berkowitz et al. 1995). For instance, shading by marsh plants may limit surface evaporation and thus the accumulation of salt which relieves osmotic stress (Bertness and Hacker 1994), and tree seedling survival may be enhanced through the protection of heat and desiccation stress by intact vegetation (Berkowitz et al. 1995). The mechanisms of these positive interactions necessarily mean that plants have to grow in close proximity of each other, and there is thus the potential for resource competition to act at the same time as the amelioration of the abiotic environment (Callaway et al. 1991, Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997).

Brooker and Callaghan (1998) presented a graphical model of the balance between positive and negative interactions where they proposed that a positive net effect is more likely to be seen in disturbed (or stressful; Bertness 1998) environments while negative net effects would be more likely in undisturbed environments (see also Bertness and Callaway 1994 and Callaway and Walker 1997). The reasoning is that harsh environments may restrict plants from acquiring resources, and any amelioration of these conditions will favour growth to the extent that it outweighs the negative, competitive impacts of growing in close associations, whereas in less harsh environments amelioration of environmental conditions has a minimal impact and the balance is tipped towards negative effects. Brooker and Callaghan (1998) also conclude that the Arctic is particularly suited for studies of positive interactions since Arctic environments contain a wide variety of stress and disturbance factors and because the severity of the abiotic environment is the primary limitation on plant growth.

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We do not doubt the importance of positive interactions in some plant communities (including the Arctic), nor do we doubt that net positive effects are more likely to be seen in harsh environments. However, we would like to caution against interpreting this to mean that plant communities in harsh Arctic environments will be dominated by positive interactions as suggested by Callaghan and Emanuelsson (1985) and Callaghan (1987). We will present data from a nine-year study in two extreme high alpine habitats that was designed to test whether the effects of established *Ranunculus glacialis* individuals on germination and growth of *Oxyria digyna* are primarily positive or negative at the altitudinal limit of vascular plants. The two chosen species are common in Fennoscandian block fields, and were thus good candidates for experimental manipulations. These high alpine plant communities are characterised by a lack of closed vegetation, with scattered solitary individuals spread out in a matrix of stones and gravel and should qualify as extreme physical environments where the benefits of growing in close associations should be strong. We will show net effects ranging from neutral to negative, but no positive effects were detected. We will argue that close associations between plants in these harsh environments may both ameliorate and deteriorate the abiotic environment, and that experimental manipulations are necessary to tell the difference.

Study area and methods

The experiment was carried out on Vuorasnjarháldi (69°56′N, 22°55′E), about 15 km west of Alta, in northernmost Norway (see Moen 1993 for details on study species and study area). The study area is a cirque-like depression at altitudes of 850–1100 m (500–800 m above the timberline and above the limit of continuous vegetation). Two populations with scattered individuals of *Ranunculus glacialis* were selected in the latest melting part of the area around a lake, at altitudes of about 850 m. One population, consisting of 45 individuals, occurred on a block field facing the lake (exposition south-west). The density of vascular plants in this subarea was in the order of one shoot per 10 m^2. All plants grew in troughs between stones. The second population was encountered on an almost horizontal terrace on a north facing slope with fine-grained substrate, annually disturbed by melt water. Here the density of vascular plants was in the order of one shoot per 3 m^2, and there were also some small mosses and lichens scattered in the area. No visible differences between microsites with or without vascular plants in any of the two habitats were obvious (e.g. no patterned ground or desiccation cracks).

In August 1988, 45 solitary *R. glacialis* individuals in the block field and 60 individuals on the terrace were selected (see Moen 1993 for more details). There were no vascular plants or cryptogams growing closer than ca 30 cm from any of the chosen individuals and there was no litter layer at all, and we thus regard it as unlikely that these individuals were influenced by other plants either above or below ground. Half of the individuals were randomly assigned to be removed, while the other half were left intact. (Out of the 45 block field individuals, 22 were assigned to be removed and 23 were left as controls. We will henceforth call the point where an individual is growing or where an individual has been removed for a microsite.) In the removal treatments, the resident *R. glacialis* individual was carefully removed with a pair of tweezers, resulting in all of the above-ground and most of the below-ground biomass being removed while still causing minimal disturbance to the "soil" (some small roots were impossible to remove which could have influenced the nutrient conditions of those microsites). The same kind of soil disturbance as in the removal treatment was created in the control microsites, i.e. within one cm of the erect stem of the resident *R. glacialis* individuals. 10 seeds of *Oxyria digyna* were sown in each microsite from where the individuals had been removed and also to the disturbed spot under each intact individual. To investigate variations in seed germination between years, 100 new terrace microsites were selected in 1989 and treated in the same way. The few *R. glacialis* leaves that regrew from root fragments in removal microsites were removed.

The area was revisited every year between 27 July and 11 August (later in years with late snowmelt) from 1989 to 1997, and the presence of *O. digyna* in each microsite was recorded. All microsites where the markers could be found were checked. We initially also counted the number of seedlings, but this soon became impossible as the rhizomes of the seedlings started to intermingle (see Moen 1993). In 1997, we also counted all leaves on each microsite and measured the diameter of each leaf at the point of attachment of the petiole in a right angle against the longitudinal axis of the leaf. On the basis of these data, we estimated leaf areas of *O. digyna* per microsite in 1997, assuming that leaves had circular shapes. Differences between presence of *O. digyna* in control and removal microsites in each habitat were tested on the actual numbers (not proportions) for the first and last year with Fisher's exact test. Differences between leaf areas of *O. digyna* in control and removal microsites in each habitat were tested with Mann-Whitney tests.

Results

The over-all effect of *R. glacialis* on the germination, growth, and survival of *O. digyna* was consistently negative. In habitats sown in 1988, germination rates were initially significantly higher in removal microsites than in controls (Fig. 1; block field: $\chi^2 = 6.42$, $p = 0.017$; terrace-88: $\chi^2 = 10.4$, $p = 0.002$; see also Moen 1993). This effect persisted in the block field for the entire experiment ($\chi^2 = 10.1$, $p = 0.002$). In the part of the terrace sown in 1988, the initial significant difference had completely disappeared by 1992, as *O. digyna* germinated in many initially empty control microsites. In the part of the terrace sown in 1989, no initial treatment effect was observed ($\chi^2 = 0.92$, $p = 0.52$), but by 1997 there were more microsites with *O. digyna* in the removal treatment ($\chi^2 = 15.8$, $p < 0.001$).

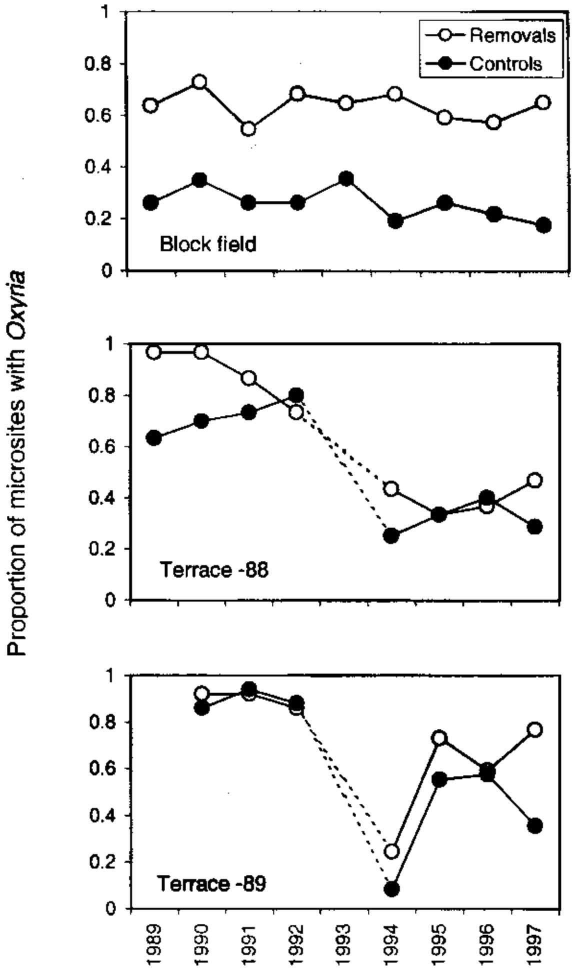

Fig. 1. The proportion of microsites with *Oxyria digyna* seedlings. In 1993, several of the marked microsites could not be located due to late snowmelt and this year is therefore excluded. Removal microsites refer to microsites where an established *Ranunculus glacialis* individual has been removed, and control microsites to microsites where the individual has been left intact.

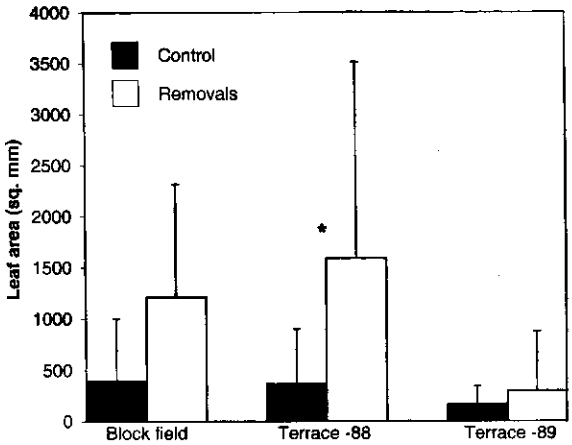

Fig. 2. Leaf areas per microsite in control and removal treatments (mean + sd). The star indicates a significant difference from Mann-Whitney U-test ($p = 0.032$)

The proportion of microsites with *O. digyna* in the different habitats (Fig. 1) did not indicate any treatment effects on survival, whereas there was a clear between-habitat difference in survival patterns. In the block field, almost all microsites where the seeds had germinated in 1989 remained colonized until 1997 (although in some years, some seedlings remained below ground when the site was visited). On the terrace, the seedling populations were decimated after the extremely stressful summer of 1993 when persistent snow covered much of the area. Especially in the part of the terrace sown in 1989, however, small seedlings were again observed in many microsites which had been recorded as empty in 1994, indicating that seedlings of *O. digyna* can work themselves back to the surface even after having been covered by snow or sediments for two consecutive growing seasons.

The negative impact of established *R. glacialis* individuals on the growth of *O. digyna* was especially pronounced on the part of the terrace sown in 1988, where the mean leaf area of *O. digyna* was significantly larger in removal microsites than in controls (Fig. 2, $U = 13.0$, $p = 0.032$). For the two other habitats, corresponding significant treatment effects could not be demonstrated, but the differences were consistently in the same direction, even in the part of the terrace sown in 1989 where almost all *O. digyna* seedlings were small and where the difference in average leaf areas between removal and control microsites was not visually obvious (Fig. 2).

Discussion

The over-all impact of established *R. glacialis* individuals on the germination and growth of *O. digyna* in these extreme high alpine environments was negative. This conforms with the observation of Järvinen (1989) that the local distribution of *O. digyna* is negatively correlated with the distribution of *R. glacialis*. The main impact was retardation of growth rates, which is a typical way in which competition expresses itself in all kinds of herbaceous vegetation (Ellenberg 1954, Wilson and Tilman 1991, Campbell and Grime 1992, Goldberg and Barton 1992). In the block field, where plants grew in troughs between boulders, there appeared to be pre-emptive competition for suitable microsites, as proposed by Oksanen (1980). Some troughs were entirely covered by the leaves of the resident *R. glacialis* individual, and the seeds of *O. digyna* sown in these microsites failed to germinate. In habitats of this type, germination is clearly favoured by the death of established *R. glacialis*. Regeneration of plants thus resembles the gap-dependent regeneration of trees encountered in many temperate forests (Fenner 1985).

The main proximate mechanism causing pre-emptive competition of microsites may be a lowering of ground surface temperature by shading. Moen (1993) measured the surface temperatures during twelve days in 1990 under nine established *R. glacialis* individuals and on nine microsites where the established individual had been removed. The data showed a significantly lower temperature under the established individuals, and Moen (1993) concluded that (1) the lower temperature likely inhibited germination in *O. digyna*, and (2) the magnitude of this effect was dependent on average air temperatures during the growing season which could explain why the repetition of the experiment on the terrace in 1989 failed to produce negative interactions. However, even here the growth rates of *O. digyna* tended to be lower under the established individuals as shown by the leaf areas, and the long-term outcome is likely to be the same as in the block field. It is thus possible that plants growing in close associations in highly stressful and disturbed environments may actually depress growth through a deterioration of the abiotic environment.

A similar mechanism has been proposed for high Arctic *Ranunculus sabinei* individuals growing in moss turfs (Sohlberg and Bliss 1987). This species shows an interesting case of the balance between positive and negative effects where seeds germinating in moss turfs have a higher chance of surviving to maturity due to the water-holding capacity of the mosses, while at the same time the mosses lower the soil temperature which leads to a reduction in nutrient turnover and a reduction in growth in established *Ranunculus* individuals as shown in removal experiments. Another case where changes in soil temperature in high arctic/alpine environments influences plant interactions is suggested in habitats dominated by cushion plants or mosses with corresponding morphology. In these habitats, many non-cushion species establish inside cushions (Griggs 1956, Sohlberg and Bliss 1984, Alliende and Hoffman 1985), apparently exploiting higher local temperatures and nutrient concentrations created by these plants (Wilson 1952, Aleksandrova 1983, Gauslaa 1984). However, the evidence for the supposed advantages of growing inside cushions is at best correlative and has, to our knowledge, not been substantiated by removal experiments.

These examples, together with the data in this paper, illustrate that positive and negative interactions tend to be species- and/or habitat-specific (Callaway 1997, 1998): *Ranunculus glacialis* and high Arctic moss turfs influence germination and growth of other species through a reduction in soil temperature, while cushion plants may do the same through an increase in soil temperature. The difference in response on the terrace between the 1988 and 1989 sowing treatments also shows that the strength of the interspecific interaction varies over time (see also Goldberg and Barton 1992, Callaway 1997). This makes it absolutely necessary to conduct critical experimental manipulations in order to determine the type of interaction present. An example of this is the particularly intriguing study on positive plant-plant interactions in a middle alpine ridge habitat in northern Scandinavia conducted by Carlsson and Callaghan (1991). The authors found that *Carex bigelowii* grew more rapidly when associated with *Cassiope tetragona* than when growing alone. Moreover, the authors showed experimentally that artificial shelters also increased the growth rates of *C. bigelowii* shoots. From these two results, they inferred that plants of alpine ridges help each other by providing shelter against winds. In windy habitats, there might indeed be some optimum density of vegetation, which rhizomatous single-shoot graminoids cannot produce alone. However, the critical experiment – to study the impact of removal or transplantation of *C. tetragona* on the performance of *C. bigelowii* – was not conducted. Hence, differences in microsite conditions might account for the observed correlation between the relatively high growth rate of *C. bigelowii* and the presence of *C. tetragona* as was also suggested by Carlsson and Callaghan (1991; see also Billings and Bliss 1959, Mölgard 1982).

To conclude, plant-plant interactions mediated through alterations of the abiotic environment may even in harsh environments range from positive to negative. As these alterations of the environment are expected to occur simultaneously with resource competition, we advocate against assuming any type of interaction from patterns of species associations. The only way to determine mechanisms behind patterns is through field experimentation.

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