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Facilitation and interference in subalpine meadows of the central Caucasus

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Abstract. We studied the effects of neighbours on the biomass of seven randomly chosen species in species-rich sub-alpine meadows in the central Caucasus Mountains by comparing the performance of plants with neighbours removed experimentally to that of paired plants with their neighbours left intact. In most cases the removal of neighbours led to significant increases in vegetative and total above-ground biomass implying the species were limited by competition. However, the neighbour removal led also to an increased leaf wilting for target plants, as well as to strong decline in reproductive effort for some species. We hypothesise that competition may be the prevailing type of interaction in species-rich sub-alpine meadow communities, but competitive effects on vegetative production may be balanced, if not outweighed, by facilitation, at least for some species. Such a balance may enhance species coexistence in communities.

Keywords: Competition; Plant-plant interaction; Species-rich community.

Introduction

Facilitation, or the positive effect of one species on another, plays an important role in determining the structure and dynamics of many plant communities (for a recent review see Callaway & Pugnaire 1999). There have been numerous studies of spatial associations among alpine and arctic plants in which extreme clumping among species has been interpreted as evidence for facilitation (Sohlberg & Bliss 1984; Alliende & Hoffman 1985; Kikvidze 1993, 1996; Aksenova et al. 1998; Kikvidze & Nakhutsrishvili 1998; Nuñez et al. 1999) and a few manipulative experiments that have shown evidence for both competition and facilitation (Sohlberg & Bliss 1987; Carlsson & Callaghan 1991; Theodose & Bowman 1997; Aksenova et al. 1998; Olofsson et al. 1999; Choler et al. in press; Haase 2001). However, most studies are on one member of a community and not on the community as a whole, and few have searched for facilitative effects by manipulating randomly chosen species from communities, as we propose to do. Furthermore, studies of facilitation have generally been conducted in environmentally stressful, species-poor communities rather than species-rich communities.

European sub-alpine meadows in the Alps and the Caucasus that have been managed for hay production for centuries are among the most species-rich plant communities found in temperate climates (Stampfli & Zeiter 1999; Grubb 1985; Nakhutsrishvili 1999). This richness appears to develop because of abundant summer rainfall, high summer temperatures, and predictable intermediate levels of disturbance (*sensu* Connell 1978).

To examine the competitive and facilitative effects of neighbours on target species within a species-rich community, we removed the above-ground vegetation from around individuals of seven different species and compared the final biomass and sexual reproduction of these individuals to those of paired individuals with surrounding vegetation left intact. We also conducted a similar removal experiment and censused leaf wilting for five randomly chosen species in order to assess possible water stress induced by the formation of a gap after neighbour removal.

Methods

We established our study sites in the subalpine belt of the Kazbegi District of the Republic of Georgia, in the central Caucasus Mountains (42° 48' N, 44° 39' E, elevation 1900 - 2000 m). Climate is temperate-humid with cold winters and mild summers. The average annual precipitation is 800 - 1000 mm, with a maximum in spring and a minimum in autumn. The average temperature of the warmest months (July and August) is 14 °C, with maximum values up to 30 °C. The subalpine meadows have dense, fully closed canopies with a maximum height of 100-150 cm. Other details on the climate, soils and vegetation of this area may be found elsewhere (Kikvidze 1996; Nakhutsrishvili 1999).

Species for the experiments were chosen randomly from the 25 most common species (assessed by cover abundance) of the site (for an example relevé see Nakhutsrishvili 1999, p. 38). We assessed the effects of neighbours on seven different species by removing above-ground biomass of all neighbouring plants within approximately 10 cm of a target individual, and comparing target plant performance to that of paired control plants in which neighbours were left intact. There were 12 replicates. Our removals were probably conservative for both facilitative and competitive effects as neighbours outside the 10 cm radius could still have had facilitative effects by ameliorating wind speed, and still could have competed for below-ground resources. Pairs were located as close as possible to each other and within the same apparent micro-environment. Care was taken to choose pairs of individuals that were as similar as possible (same shoot size, same number of leaves). The removal was conducted in May (late spring) and final responses were measured in August. At the end of the experiment we harvested the above-ground parts of the control and experimental plants, separated them into vegetative (stems and leaves) and reproductive (flower buds, flowers and fruits) parts, dried them at 80 °C, and weighed them.

We conducted a second experiment in which we removed neighbours from around five randomly selected species and assessed leaf wilting on all individuals. (Two species happened to be in common in both experiments.) We used a similar experimental design with 12 replicated pairs of plants (treatment and control). We recorded the number of leaves on an individual plant and calculated per cent of leaves visibly wilted. The removal was conducted in mid-July. We monitored plants three times: at the start, two weeks later and at the end of the experiment.

We tested the difference between the observed values (dry weights and numbers of wilted leaves) by a randomization technique. Randomization methods do not require any assumptions on data distribution but generate empirical distribution from the observed sample. This advantage is especially important with small samples so common in ecological studies, and randomization tests increasingly replace standard statistical tests in ecological research (Slade 1999; Fortin & Jacquez 2000). As test statistic, we calculated the difference between the mean values of the control and experimental samples. We repeated the randomizations 10 000 times, calculating the randomized mean differences while the significance level was determined from the number of randomization means equal to or more extreme than that observed.

Results

The response of target species to the removal of neighbouring vegetation was highly variable, but five of seven species (*Alchemilla retinervis, Leontodon hispidus, Trifolium ambiguum, Trifolium pratense*, and *Veronica gentianoides*) were significantly greater in above-ground vegetative mass compared with the control plants when neighbours were removed (Fig. 1). Two species did not respond to neighbour removal (*Hordeum violaceum* and *Ranunculus elegans*). The overall effect of neighbour removal on biomass was highly significant ($p < 0.0001$ by randomization test), indicating that neighbours are in strong competition in this subalpine meadow.

However, neighbour removal showed the opposite effect on the reproduction effort of the examined plants (Fig. 2). These species reproduce sexually except for one apomict, which develops hypanthia (*Alchemilla retinervis,* Rosaceae). In two species (*Alchemilla retinervis* and *Veronica gentianoides*) we were not able to measure their reproductive effort because the control plants completed reproduction and dispersed seeds before the end of the experiment. Simultaneously, a strong effect of neighbours on reproduction of these two species was evident in the fact that the isolated plants did not produce any flowers (hypanthia in *Alchemilla retinervis*) at all. In the other five species the overall effect of neighbours on reproductive effort, though not significant ($p = 0.245$ by randomization test), and highly variable, was still positive. Two species (*Hordeum violaceum* and *Trifolium ambiguum*) decreased strongly in reproductive effort in the removal treatment; two other species (*Leontodon hispidus* and *Trifolium pratense*) increased in reproductive output with neighbour removal, and for one species (*Ranunculus elegans*) there was no effect (Fig. 2).

The overall effect of neighbour removal on wilting occurrence was highly significant ($p < 0.0001$ by randomization test) indicating that water stress increased, at least temporarily, and that neighbours may have a strong protective effect against this stress (facilitation). The removal of neighbouring vegetation produced substantial wilting in target species (effects for four of five species significant, Fig. 3). One exception was *Tragopogon reticulatus*, showing insignificantly less wilting in the removal treatment. This apparently happened because the control plants completed fruiting before the end of the experiment and went into senescence, while the isolated plants were still in a vegetative phase.

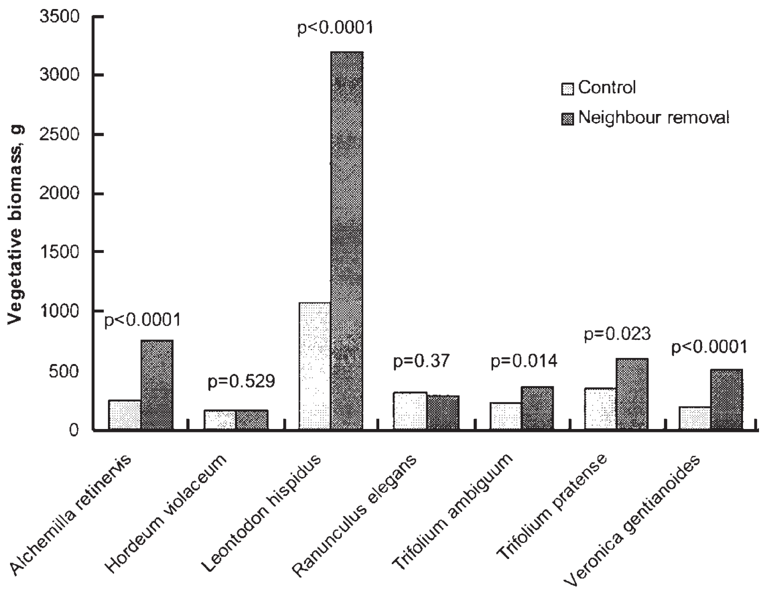

Fig. 1. Effects of removing neighbours on the vegetative biomass of target plants (mean of 12 replicates). *p*-values above means are from randomization tests.

Discussion

Our results correspond with similar experiments in mesic subalpine meadows in the French Alps (Choler et al. in press). Others have shown facilitative effects within herbaceous communities and attributed neighbour effects to the amelioration of microclimate by the vegetation matrix (Ryser 1993; Kikvidze 1996; Sans et al. 1998). In our study facilitation was evident in a general wilting response of plants to neighbour removal; this result suggests that isolated individuals experience increase in stress. Despite this apparent stress, vegetative biomass was greater with neighbour removal in most cases. The water relations of these plants may have acclimatized to sunnier, warmer conditions over time so that the increased growth in these conditions occurred later.

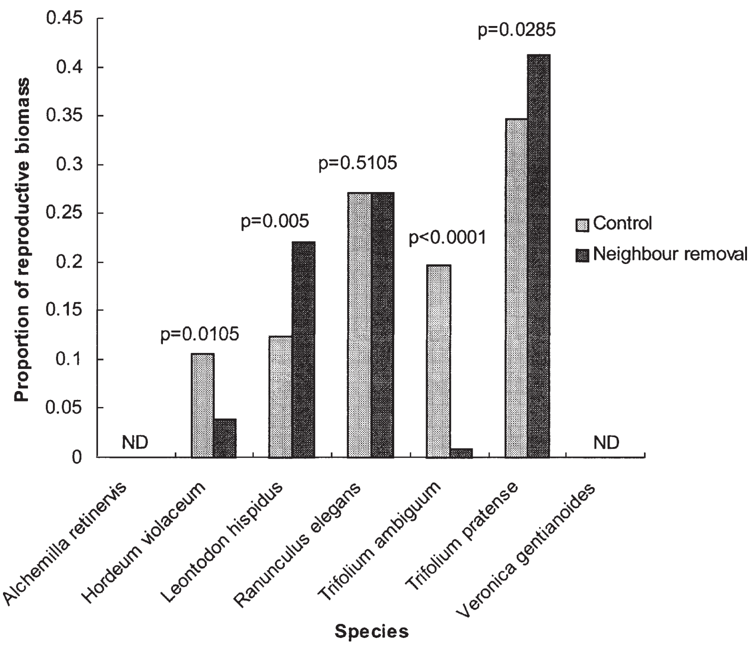

Fig. 2. Effects of removing neighbours on the proportion of biomass allocated to reproduction by target plants (mean of 12 replicates). *p*-values above means are from randomization tests.

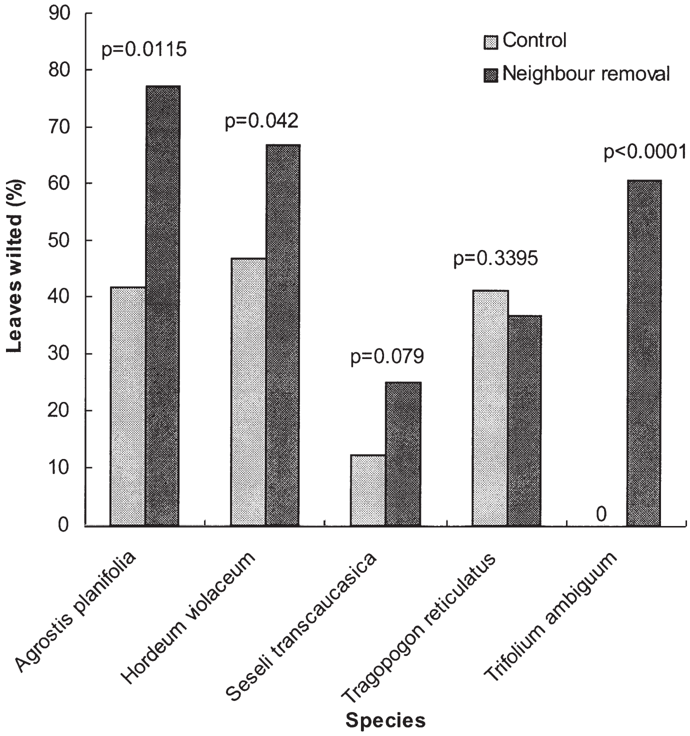

Fig. 3. Effects of removing neighbours on neighbours on wilting of leaves in target plants (mean of 12 replicates). *p*-values above means are from randomization tests.

The available literature on plant reproduction strategies in stressful environments draws a complicated picture. On the one hand, we know about the reproductive-vegetative switch: a water stress even reduces reproductive effort in annuals (Pyke 1989). At our study site plants normally flower every year like annuals; hence, the lower allocation to reproductive organs in isolated individuals may be a response to the water stress induced by neighbour removal. Such an interpretation is also in line with the findings that regeneration by seed is often less successful than vegetative reproduction in subalpine and alpine environments (Larcher 1995; Pickering 2000), as well as in other stressful environments (Kobayashi et al. 1999; Kozlowski & Teriokhin 1999; Juenger & Bergelson 2000). Allocation of biomass to vegetative growth when experiencing stress may be more adaptive than continuing to allocate resources to sexual reproduction in such environments.

On the other hand, there is another body of data that does not fit well to the above view and asks additional explanation. At higher elevations, where the growing season is limited and environmental severity is nearly extreme, assimilation yield is much reduced and plants require several seasons to complete their reproductive cycle; although fewer flowers are produced, a larger proportion of biomass is invested in reproductive organs (Douglas 1981; Kawano & Masuda 1980). Besides, Douglas (1981) has found that in the less stressful environments intraspecific competition may be responsible for the increased allocation to reproductive organs: in the populations of *Mimulus primuloides* growing at different elevations in California the maximum allocation to vegetative growth was found at middle-elevations. This apparently was due to reduced plant density (compared to the density at lower elevations) as confirmed by the controlled environment chamber experiments (Douglas 1981). This points to reduced competition as to another probable cause of the lower reproductive effort in isolated plants in our experiments.

Certainly, we need to know more about the effects of biotic interactions on plant reproduction strategies. Yet, the two above interpretations may not exclude each other. We suspect that both competition and facilitation can contribute to the higher reproduction effort, though with differing importance for different species.

Facilitative processes have been demonstrated in other herbaceous communities (Wilson & Tilman 1995; Hillier 1990; Greenlee & Callaway 1996; Wardle et al. 1999). However, in several empirical studies involving large numbers of species, generally designed to examine competition, the proportion of positive interactions reported was very low (Wilson & Tilman 1995; Twolan-Strutt & Keddy 1996; Thomas & Bowman 1998). A review by Goldberg & Barton (1992) indicated that neighbours promoted the survival or growth of individuals in ca. 10% of experiments; most studies used in their meta-analysis stated that the intent was to study competition, which may have underestimated facilitation.

We tried to measure both competition and facilitation in order to compare their relative importance. Our results suggest that competition may be the prevailing type of interaction in species-rich subalpine meadow communities, but only if the focus is on vegetative biomass. For some species, competitive effects on vegetative production may be balanced, if not outweighed, by facilitation. Such a balance may enhance species coexistence in communities.

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