

Seasonal shifts in competition and facilitation in subalpine plant communities of the central Caucasus

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Abstract

Question: Temporal and spatial shifts in competitive and facilitative interactions among plants have important implications for species coexistence and community diversity. Many studies have focused on inter-seasonal variation in these interactions, but very few have examined short-term intra-seasonal shifts between competition and facilitation. In the central Caucasus Mountains the subalpine climate changes considerably over the season, with a relatively benign (humid and cooler) first part followed by a much more stressful (drier and warmer) second part. We ask: do plant interactions shift from competitive to facilitative during the growing season as environmental conditions change from mesic to dry?

Location: The central Caucasus Mountains, Georgia.

Methods: We experimentally investigated shifts in the balance of positive and negative interactions in plant communities over the course of a single growing season by conducting sequential removal experiments on two co-dominant species.

Results: We found that during the wet and cool first half of the growing season, target plants without neighbours accumulated significantly more biomass than individuals with neighbours, indicating competition. However, in the drier second half of the growing season competitive interactions were shifted to facilitation as individuals without neighbours accumulated significantly less biomass.

Conclusions: In general, these results support the view that competitive and facilitative effects exist in dynamic tension in plant communities with facilitation intensifying as abiotic stress increases, also within a growing season.

Keywords: Environmental stress gradient; Neighbour effects; Plant-plant interactions.

Abbreviation: EP = Effective precipitation.

Nomenclature: Nakhutsrishvili (1999).

Introduction

Competitive and facilitative mechanisms often operate simultaneously in complex and synergistic ways in plant communities (Hunter & Aarssen 1988; Callaway et al. 1991; Callaway 1994, 1995; Bertness & Shumway 1993; Brooker & Callaghan 1998; Holzapfel & Mahall 1999; Levine 1999; Pugnaire & Luque 2001). Bertness & Callaway (1994) hypothesized that positive effects increase in intensity or importance (Brooker et al. 2005) relative to negative effects with the harshness of the abiotic environment. The logic behind this conceptual model is based on the fundamental nature of competition, which by definition is a struggle to pre-empt limiting resources such as light, water, and nutrients that determine rates of carbon acquisition. Under relatively benign abiotic conditions that permit rapid resource acquisition competition may be more important. However, if severe physical conditions restrict resource acquisition, amelioration of severe stress by a neighbour may be more likely to favour growth than competition with the same neighbour is to reduce growth. A large number of empirical studies have supported this 'abiotic stress hypothesis' (Bertness & Hacker 1994; Greenlee & Callaway 1996; Pugnaire & Luque 2001; Choler et al. 2001; Mulder et al. 2001; Tewksbury & Lloyd 2001; Callaway et al. 2002) although there are exceptions (Donovan & Richards 2000; Tielbörger & Kadmon 2000). Virtually all of these studies focused only on the particular spatial gradient thought to generate variation in abiotic stress. Such an approach implies a relatively uniform frequency of stress in a particular place over time and does not explicitly consider temporal gradient of stress. However, uneven frequency of stress is the rule in nature: climatic conditions vary seasonally, during the lifetime of a plant, and physiological measurements taken immediately after neighbour removal have demonstrated that interactions between the same individuals may vary between competitive and

facilitative effects within a single day (Kikvidze 1996).

During a growing season, stress is rarely uniformly distributed over time but variation is often predictable (see Archibold 1995). In the central Caucasus Mountains variation in climate during the growing season creates rather predictable temporal variation in physical stress. The first months of the growing season are relatively wet and mild in temperature, whereas mid-July through September is marked by a significant decline in rainfall and higher temperatures, which leads to a two-fold change in effective precipitation (de Martonne 1927, also see Methods). Stress, in particular at the scale of communities, is difficult to define and quantify (Körner 2003, 2004; Lortie et al. 2004; Marrs 2004; Weiher 2004). Here, we assume that abiotic stress increases during the most xeric (high mean monthly temperature and low precipitation) time period in an otherwise mesic system. By comparing the strength and direction of interactions among dominant plants during the wet early summer with those during drier conditions at the end of the summer we were able to use relatively short-term temporal variation in stress to investigate how stress affects interactions for the same species in the same place. Specifically, we hypothesized that competitive interactions would predominate in the benign early months of the growing season, but as conditions become more xeric facilitation would increase.

To explore this hypothesis we conducted sequential neighbour removal experiments throughout the growing season. We measured accumulated above-ground biomass of a target species. We tested whether neighbours modified biomass accumulation in the mesic early months of the growing season, and whether this effect changed as conditions later become more xeric.

Methods

Our study site was located in the subalpine belt of the Kazbegi District of Georgia, in the central Caucasus Mountains (42°48' N, 44°39' E) near Gudauri (ca. 2000 m a.s.l.). The climate is temperate-humid with cold winters and mild summers, and rainfall has a markedly uneven distribution with a maximum in the spring and a minimum in the autumn. At the Gudauri Meteorological Station (2.2 km from the experimental site) there is a marked increase in aridity from May through August, as rainfall declines and temperature increases (Fig. 1). We studied plant interactions during one season (2003), which was not marked by any climate abnormality (Fig. 1).

We worked in a semi-natural subalpine hay meadow, a community type that develops when meadows are protected from livestock grazing for centuries in order to provide hay for livestock during the winter. These

meadows have dense, fully closed canopies reaching a maximum height of 100 - 150 cm. Other details on the climate, soils and vegetation of this area may be found in Kikvidze (1996) and Nakhutsrishvili (1999). For the experiments we used a meadow dominated by *Hordeum violaceum* and *Trifolium ambiguum*. Cover of these species in our meadow on the Braun-Blanquet scale corresponded to 5 (> 75% cover) and 4 (50-75%), respectively. Other, less abundant but still common, species are *Poa pratensis*, *Agrostis planifolia*, *Phleum pratense*, *Festuca pratensis*, *Trifolium pratense*, *Alchemilla retinervis*, *Leontodon hispidus*, *Veronica gentianoides*, *Tragopogon recticulatus*, *Myosotis alpestris* (Nakhutsrishvili 1999, p. 38). We worked in a fenced area of an old meadow that is hand-mown each year at least for the last 150 years, and restricted our experiments to a central 400 m². The site had a 5° slope facing southwest.

The objective of our experimental design was to examine intra-seasonal temporal patterns in plant-plant interactions focusing on the dominant species. We conducted short-term, three-week experiments from late May to mid-August. An earlier start was not possible because plants could not be clearly identified. The end of the experiments was when the field was mowed, in mid-August. This design resulted in experiments that were conducted through four sequential three-week periods of growing season: first, May 18 to June 8 (referred as May); second, June 8 to July 1 (referred as

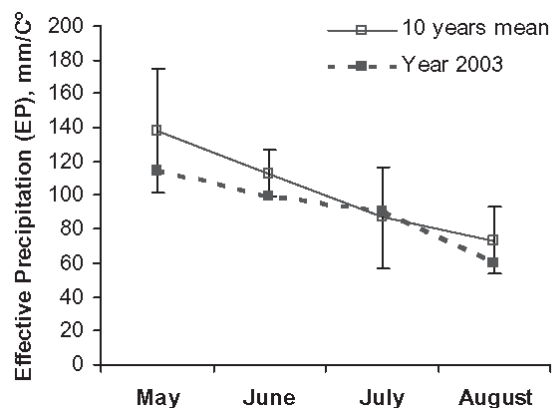


Fig. 1. Change of Effective Precipitation (EP) during the growing season (May to August) in experimental area; data from nearby Gudauri Meteorological Station (2194 m a.s.l., annual precipitation 1513 mm, annual mean temperature 3.1°C). The dotted line shows change of EP during the experiments (growing season of 2003). For a relative comparison of months we used the monthly Effective Precipitation of de Martonne (1927), calculated as: $EP = 12 * P / (T + 10)$, where P is monthly precipitation and T is monthly mean temperature. EP drops with lower P and/or higher T , which is well expressed in the central Caucasus by the end of growing season. Error bars indicate one standard deviation.

June); third, July 2 to July 23 (referred as July); and fourth, July 24 to August 15 (referred as August).

We conducted neighbour removal experiments on two species that dominate our community: *Hordeum violaceum* and *Trifolium ambiguum*. In general, we followed procedures already described (Kikvidze et al. 2001; Callaway et al. 2002). We removed the above-ground biomass of all neighbouring plants within approximately 10 cm radius of a target individual, and compared target plant performance to that of control plants in which neighbours were left intact. We marked 12 pairs of target individuals of each experimental species, selecting them to be as similar as possible (same shoot size, same number of leaves), at the beginning of each of the four experimental periods. From each of these 12 pairs we selected one target and removed neighbours around it, while the remaining one was left as a control. Care was taken to mark individuals of treated-control pairs that were spatially as close as possible, and within the same apparent micro-environment, but apart enough so they were unlikely to influence each other (20 - 40 cm). Our removals were probably conservative as manipulations of both facilitative and competitive effects, as neighbours outside the 10 cm radius could have still ameliorated some wind, light or temperature effects, and still could have competed somewhat for below-ground resources. At the end of the experiment we harvested the above-ground parts of the control and experimental plants, dried to constant dry mass (three days at 80 °C), and weighed them. We used repeated measures ANOVA to test the differences in dry mass accumulation among treated and control individuals, sequential experimental periods, and the species.

We also measured neighbour effects on plant dry masses accumulation during the experimental periods using the index of relative neighbour effect (*RNE*, Markham & Chanway 1996); however, we modified *RNE* after Callaway et al. (2002) to make its interpretation more intuitive:

$$RNE = (C - T) / \max(C, T), \quad (1)$$

where *T* and *C* correspond, respectively, to performance of treated (neighbours removed) and control individuals. *RNE* values that range between 0 and 1 indicate positive neighbour effects (facilitation) and values that range between 0 and -1 indicate negative neighbour effects (competition). We assessed plant performance by accumulated above-ground dry biomass, and calculated *RNE* for each pair. We tested changes in *RNE* values during experimental periods for two species using two-way ANOVA and Tukey comparisons test. All statistical tests were performed using software Statistix8 (Analytical Software, Tallahassee, FL).

Results

The responses of target plants to the removal of neighbours were variable through the experimental periods (Fig. 2). The repeated measures ANOVA have tested that plant growth responded strongly both to neighbour removal ($F = 20.63, p = 0.0105$) and to experimental time ($F = 11.35, p = 0.0200$). These two factors interacted also significantly ($F = 7.66, p = 0.0331$), but species did not differ in their responses. Likewise, comparisons of *RNE* values found that neighbour effects changed significantly over the season ($F = 22.17, p < 0.0001$ by two-way ANOVA), and that species did not differ in their responses. Tukey comparison tests indicated that interactions for both species could be differentiated into two general time period groupings in which the means were significantly ($p < 0.05$) different from one another. Negative neighbour effects were significant in May, June and July, whereas positive neighbour effects were significant in August (Fig. 3). These findings fit well to our initial hypothesis: neighbours had strong competitive effects on above-ground biomass accumulation in experiments conducted early and hence principally during the relatively cool and mesic periods of growing season. Conversely, neighbours had significantly facilitative effects in experiments conducted later, within the last and more xeric period of the growing season.

At the same time, presence of neighbours resulted in long and thin plants and removal of neighbours strongly decreased this etiolation early in the season. This effect of neighbours disappeared later in the season (not shown). This apparent neighbour-driven reduction in etiolation may indicate intense competition for light at the start of the growing season, but waning of this competition after the late season increase in aridity.

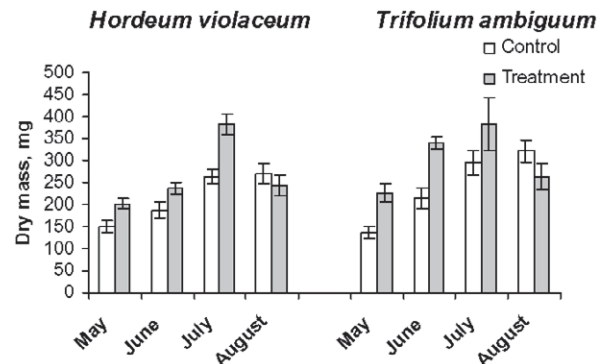


Fig. 2. Different responses of control and treated individuals on neighbour removal during experimental periods of the growing season (left: *Hordeum violaceum*, right: *Trifolium ambiguum*). Error bars indicate 1 SE.

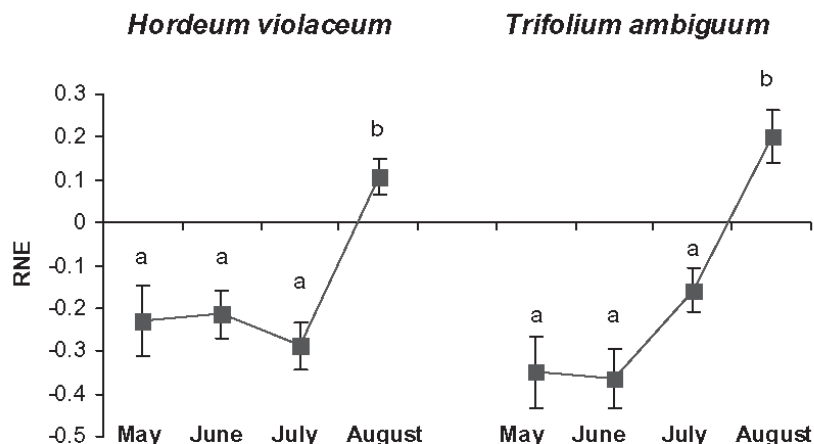


Fig. 3. Effects of neighbours on above-ground dry mass accumulation during the experimental periods of the growing season (left : *Hordeum violaceum*, right: *Trifolium ambiguum*). Error bars indicate 1 SE. Different letters above graph points show statistically significant differences between cases ($p < 0.05$, Tukey comparisons test).

Discussion

The ‘abiotic stress hypothesis’ proposes increases in facilitative interactions relative to competition with increased impact of stress in a given community (Bertness & Callaway 1994). Increasing abiotic stress often shifts the balance of plant interactions from competition to facilitation along spatial and temporal gradients (Choler et al. 2001; Callaway et al. 2002), and at the temporal scales multiple seasons (Greenlee & Callaway 1996; Olofsson et al. 1999; Pugnaire & Luque 2001), and hours (Kikvidze 1996). To our knowledge, shifts in plant-plant interactions with stress (measured as soil water content) during a single growing season have been examined only once before, and in an arid system (Holzapfel & Mahall 1999). Others have considered annual or spatial variability in precipitation (Barchuk et al. 2005; Tielbörger & Kadmon 2000). Some of these results contradict predictions of the ‘abiotic stress hypothesis’ (Maestre & Cortina 2004; Tielbörger & Kadmon 2000). However, these studies were conducted in arid to semi-arid systems, different from our temperate, species-rich and productive subalpine meadows. The aridity gradient is pronounced during a single growing season, but the system is cool-temperate. Soils of subalpine meadows are fertile and not as nutrient-limited as in arid zones or alpine tundra (Soudzilovskaia et al. 2005). Soils can be important mediators of facilitative neighbour effects in arid systems (Escudero et al. 2005; Pugnaire et al. 2004), but in our subalpine meadow moderation of micro-climate is likely to be more important. To our knowledge, the

results presented here are the first to demonstrate that competition may shift to facilitation with increasing abiotic stress within a single growing season.

Competition for light appeared to be a driving factor in our meadow, as the reduction of etiolation was a clear response of individuals with removed neighbours early in the season. Strong competition for light has been documented also in other grasslands (Wilson & Tilman 1993; Leishman & Westoby 1994). However, our results suggest that seasonal weather patterns may alter competition for light.

Overall, our results support a switch from competition to facilitation due to aridity later in the growing season. The dry end to an otherwise mesic season is not unusual in temperate systems (Archibold 1995), and such shifts from competition to facilitation may occur elsewhere. Seasonal shifts in the intensity and direction of plant interactions may be important processes maintaining species richness because consistent growing season conditions may favour competitive exclusion and thus decrease community diversity. Conversely, as stress intensity increases during the growing season, a shift from competition to facilitation may give less competitive species a chance to survive within the community. In fact, the end of growing season drought coincides with a crucial stage in the life cycle of most plants in our meadow – flowering and fruiting (Nakhutsrishvili 1999). Thus, shifts in plant interactions during the growing season may contribute to species coexistence and may help to explain the occurrence of species-rich communities such as those in the subalpine meadows of the central Caucasus.

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