Facilitation and Competition in Alpine Plant Communities

Zaal KIKVIDZE

Laboratory of Ecology, Faculty of Science, Chiba University
1-33 Yayoi-cho, Inage-ku, Chiba, 263-8522 Japan
e-mail: zaal@nature.s.chiba-u.ac.jp

Abstract

Alpine plant communities are very suitable for ecological experiments that study plant-plant interactions. Actually, in mountains we find magnitude of environmental gradients and well-pronounced spatial patterns with strong shifts between competition and facilitation. These advantages were especially useful for the experimental testing of the abiotic stress hypothesis, which states that in a plant community neighboring individuals may have both competitive and facilitative effects on each other, and that the relative importance of facilitation increases with the harshness of the environment. The experimental data obtained from alpine gradients support well this hypothesis, and indicate to a probable balance of competition and facilitation in most plant communities that are moderately stressful. The goal for further experiments may be disclosing the mechanisms of this balance.

Key words: abiotic stress hypothesis, alpine plant communities, ecological experiments, plant-plant interactions

1. Introduction

The abiotic stress hypothesis states that in a plant community neighboring individuals may have both competitive and facilitative effects on each other, and that the relative importance of facilitation increases with the harshness of the environment (Callaway and Bertness, 1994; Brooker and Callaghan, 1998; Callaway and Pugnaire, 1999). An increasing body of data, obtained in harsh environments such as deserts, salt marshes and high elevations, supports this hypothesis. Apparently, the abiotic stress hypothesis has good potential to develop to an ecological theory. For this, three major steps are required. First, all principal predictions of this hypothesis must be experimentally tested: facilitative and competitive

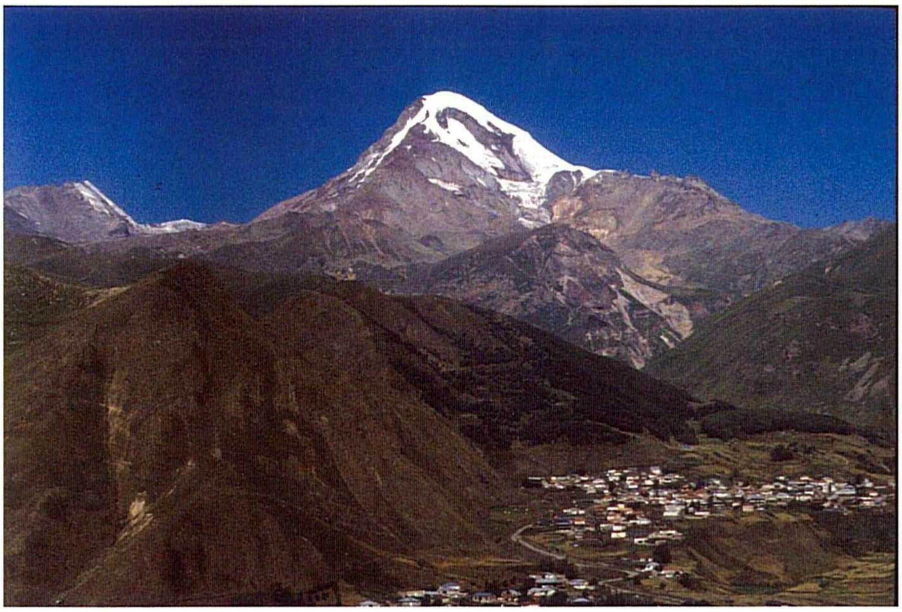

Photo 1 Mt. Kazbegi (5,033 m a.s.l.) in the central Caucasus. "Better than mountains may only be other mountains" (a popular Caucasian slogan).

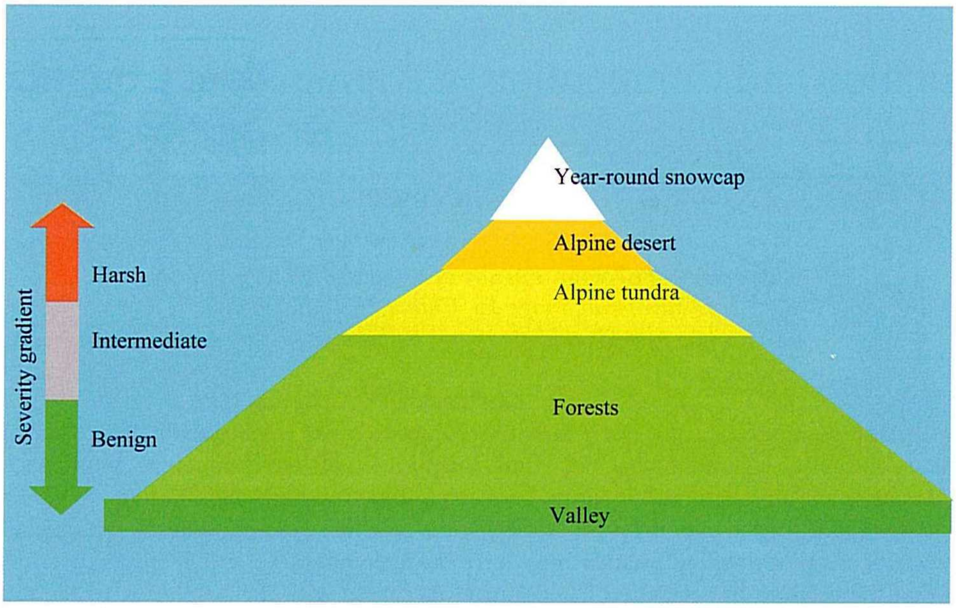

Fig. 1 A hypothetical severity gradient along altitudinal zones in mountains.

interactions must be compared both in harsh and benign communities. Second, the mechanisms that explain how a stress level governs plant-plant interactions must be worked out in details. Third, clear connections must be established with other ecological theories and hypotheses.

An overview of the current literature shows that experimental data nearly fulfill the first requirement and even set outlines for the second and third steps. However, here I will not provide an excessive review, which may be found elsewhere (e.g. see Callaway and Pugnaire, 1999). Rather, I will try to demonstrate that alpine communities are very suitable for studying facilitation and competition along a stress gradient as required by the first step of conversion of the abiotic stress hypothesis into a sound theory. Many famous plant ecologists emphasize the esthetic beauty of mountains (e.g., Braun-Blanquet, 1928; Walter, 1974; Numata, 1987; Ohsawa, 1991, see Photo 1). Yet attractive vistas offer not a single advantage in alpine ecological studies. Actually, in mountains we can find large environmental gradients and well-pronounced spatial patterns, so that strong shifts between competition and facilitation may be expected (Fig. 1).

2. Experimental Approaches to Plant-plant Interactions

In studying plant-plant interactions under field conditions of alpine communities, three major experimental approaches are applied. The first is based on spatial patterns – associations and disassociations between species. Actually, in stressful communities the spatial distribution of species is often clustered; in extreme cases it is visible as patches of vegetation on a matrix of bare ground. Such an aggregated pattern, in the absence of small-scale topographical and microclimatic variability, is usually considered a manifestation of facilitation (Haase, 2001). There have been numerous studies of spatial associations among alpine and arctic plants in which extreme clumping among species has been interpreted as evidence of facilitation (Sohlberg and Bliss, 1984; Alliende and Hoffman, 1985; Kikvidze, 1993, 1996; Aksenova, *et al.*, 1998; Kikvidze and Nakhutsrishvili, 1998; Nuñez *et al.*, 1999). However, even very precise description of the observed patterns does not disclose the mechanisms responsible for them. In particular, the suggested role of plant-plant interactions in producing spatial associations or disassociations needs more direct experimental evidence.

The second approach is a manipulative experiment: a removal of neighbor plants around a target individual (Photo 2 represents an example from a sub-alpine hay meadow in the central Caucasus). Monitoring the development of and measuring the final above-ground biomass of isolated individuals in comparison to controls that are left intact, allow us to judge whether neighbors were beneficial (facilitation) or interfering (competition). Such manipulative experiments on facilitation are fewer than studies of spatial patterns (Sohlberg and Bliss, 1987; Carlsson and Callaghan, 1991; Theodose and Bowman, 1997; Aksenova *et al.*, 1998; Olofsson *et al.*, 1999), although a similar technique was extensively employed to study competition (Goldberg and Burton, 1992; Wilson and Tilman, 1995; Twolan-Strutt and Keddy, 1996; Thomas and Bowman, 1998). A disadvantage of such experiments is that they need a long time (one or several seasons) to reveal the effects of neighbors on individual plants. During this time acclimation of target individuals may attenuate the

Photo 2 Isolated target plant of a manipulative experiment in a sub-alpine hay meadow community (the central Caucasus, elevation 1,850 m a.s.l.).

effects of manipulative isolation, especially in benign environments. This may obscure facilitation and, by this, exaggerate competition. The role of acclimation in such experiments has not yet been examined.

The third approach is direct measurements of plant performance in isolation compared to that in control conditions. Isolation of a target individual is performed as in the previous technique, yet instead of leaving plants for a long time and later checking, the plant's physiological conditions (e.g., leaf temperature, net-photosynthesis rate, etc.) are immediately monitored for one or several days. This method is free from the influence of acclimation, but it is much more laborious and needs expensive tools. This makes handling many species simultaneously difficult, so it is not surprising that such studies are the fewest (Kikvidze and Abdaladze, 1988; Abdaladze and Kikvidze, 1990; Kikvidze, 1996).

Though the results produced by these three and some other technical approaches are not sufficient for final elucidation of plant-plant interactions, they basically compose well with each other and with the predictions of the abiotic stress hypothesis. Most of these studies concern climatic stress and biotic interactions, and fewer works are devoted to other kinds of stresses (e.g., human impact), or to other kinds of processes (e.g., succession). Many studies have found strong spatial associations of plants at very high elevations (alpine desert), where the environment is supposed to be extremely harsh (Kikvidze, 1993, 1998; Kikvidze and Nakhutsrishvili, 1998; Nuñez *et al.*, 1999; Choler *et al.*, 2001). Lower, in alpine and sub-alpine grassland communities where the environment is not as harsh, spatial patterns have not been intensively studied; yet some works indicate to no association (Choler *et al.*, 2001), or to the predominance of disassociations (Kikvidze, 1998). The few experimental data on plant-plant interactions match this spatial pattern: at high elevations interactions were positive (Choler *et al.*, 2001), while at lower elevations interactions were found strongly competitive (Choler *et al.*, 2001; Kikvidze *et al.*, 2001).

3. Abiotic Stress Hypothesis

Recently, a group of authors undertook a most systematic way to test the abiotic stress hypothesis along a severity gradient in mountains (Callaway *et al.*, 2002). In a global experiment conducted in sub-alpine and alpine plant communities with 115 species in 11 different mountain ranges, they found that competition generally, but not exclusively, dominates interactions at lower elevations where conditions are less physically stressful. In contrast, at higher elevations where abiotic stress is high the interactions among plants are predominantly positive. Furthermore, across all high and low experimental sites positive interactions were more important at sites with low temperatures in the early summer, but competition prevailed at warmer sites.

Aside from alpine herbaceous communities, facilitation apparently plays an important part in processes at timberline as shown by Japanese authors (Ohsawa, 1984; Endo Megumi *et al.*, personal communication). These studies found nursing effects of bushes on tree seedlings. A strong shift from facilitation to competition was also found between a leguminous shrub and its associate understorey species along a severity gradient in a semi-arid environment (Pugnaire and Luque, 2001). In this study, changes in environmental severity were measured by a productivity gradient. The authors have found a change in the net balance of the interaction between the shrub and several of its associated species, from clearly positive in a water-stressed, infertile environment to neutral and even negative in a more fertile habitat.

Figure 2 shows a conceptual model that summarizes the abiotic stress hypothesis in its modern interpretation. It is based on the earlier models (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). In this model competition and facilitation prevail, respectively, in benign and harsh environments. It also supposes that at intermediate stress levels the biotic interactions are nearly balanced, yet this suggestion needs a vigorous experimental examination. By this conceptual model, the absolute

Z. KIKVIDZE

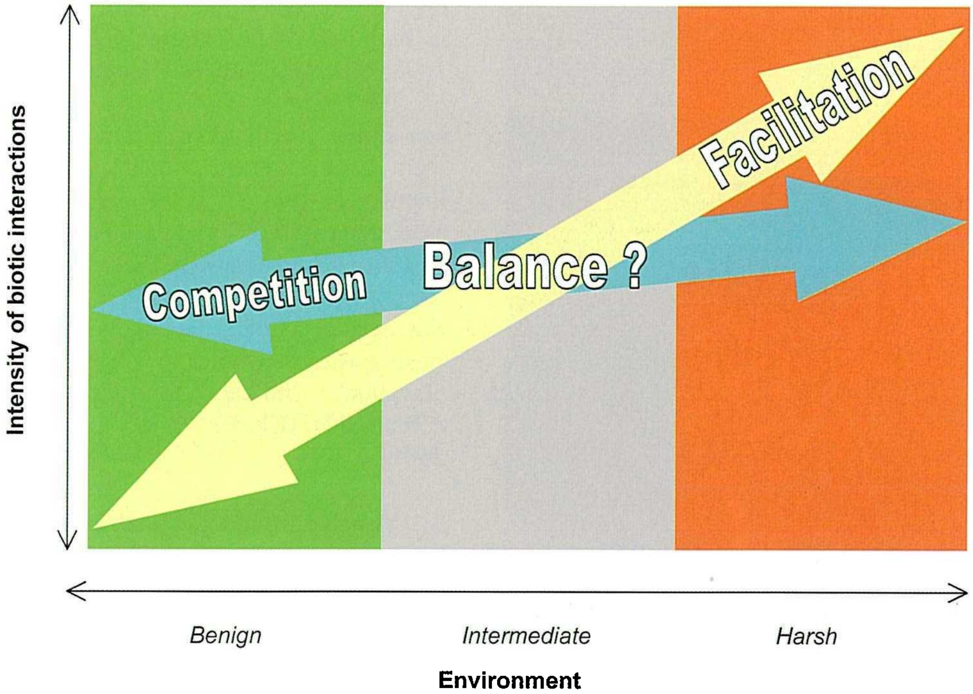

Fig. 2 A conceptual model for the abiotic stress hypothesis.

intensity of competition for the resources may slightly increase in facilitative communities because of the aggregated pattern, yet absolute intensity of facilitation grows much faster along a stress gradient, so that at first it balances and then overwhelms competition. (In relative terms, this means that the importance of competition declines and that of facilitation increases linearly along a severity gradient as suggested in the earlier model – see Brooker and Callaghan, 1998).

4. Plant-plant Interactions under Anthropogenic Disturbances

Very few studies (a single one to my knowledge) examined plant-plant interactions during anthropogenic disturbances, such as overgrazing (Callaway *et al.*, 2000). This study assessed the role of highly unpalatable plants in sub-alpine pastures in the central Caucasus Mountains. Livestock avoids these species because of spines and toxicity, and unpalatable plants have increased dramatically in abundance due to overgrazing. The authors found that plant communities associated with unpalatable plants sharply differed in composition from open pastures. 44% of all species were found only negligibly abundant (less than 1% of cover) in the open pasture, but at significantly higher abundances under unpalatable plants. Communities associated with unpalatable species had 78-128% more species in flower or fruit than open pastures. Overall, these results indicate that unpalatable plants, which are generally indicators of unhealthy rangelands, have the potential to preserve plant diversity in overgrazed pastures.

The abiotic stress hypothesis, though simply stated, implies intricate mechanisms, both visible and invisible. It predicts a strong predominance of facilitation or competition at the extremes of severity gradient, yet it says nothing of what could be expected in the middle. How do facilitation and competition interplay with each other? How do they balance each other under moderately stressful conditions when their importance is nearly similar? These questions have not been studied yet, though a few experimental data give certain clues on this matter.

5. Ambient Physical Conditions and Plant-plant Interactions

Direct measurements of the physiological conditions of target plants immediately after removal shows that even within a single day neighbors may be both competitive and facilitative, depending on weather conditions (Kikvidze, 1996). The experiments were carried out in species-rich sub-alpine pastures and hay meadows in the central Caucasus Mountains, and the results show that neighbor interactions were important for stabilization of environmental relations within the canopy, at least in hay meadows as compared to intensively grazed pastures. Overall, neighbors were beneficial in maintaining optimal conditions for plant life despite a wide variation of environmental factors above the canopy. The main source of variation was a frequent and rapid change of weather conditions from sunny to overcast; these contrasting weather conditions occur with about equal frequency during the days of mass vegetation in the Caucasus.

Specifically, competition for light under overcast was more important and thus neighbor effects were negative, while under direct sun, neighbors protected other plants from heat stress and thus were facilitative. Eventually, although neighbors were competitive during approximately half of the observation time and facilitative during another half, the overall neighbor effect on the net-photosynthesis rate was 30% more positive than negative. However, repeated experiments measuring biomasses at the end of growing seasons did not coincide with these results (Kikvidze *et al.*, 2001). In the same hay meadows it was found that after approximately three month's isolation, the target individuals gained more biomass than controls. This clearly points to the higher importance of competition in this community, contrary to the previous results from direct measurement experiments. However, in this study, facilitation was evident in a general wilting response of plants to neighbor removal; this result suggest that isolated individuals experienced increased stress. Another fascinating finding was that neighbors interfered with vegetative growth in most species but facilitated their reproductive efforts. Probably, in biomass measurement experiments, the water relations of target plants acclimatized to sunnier, warmer conditions over time so that increased vegetative growth occurred later at the expense of reproductive effort. This study reveals the intricate interplay of facilitation and competition in a plant community; simultaneously it states that our knowledge of the effects of biotic and abiotic interactions on plant reproductive strategies is still meager. Accordingly, more studies should be conducted in this field.

6. Conclusions

The experimental data obtained from alpine gradients, as well as from other stressful environments, support well the abiotic stress hypothesis. We may even state, that the first step in conversion of this hypothesis into an ecological theory is nearly completed. The immediate goal for further experimental studies is depicting the mechanisms of interplay of facilitation and competition not only under extremes of severity gradient (harsh versus benign), but also under intermediate conditions. The latter situation seems to be most common for the terrestrial ecosystems of our planet, and the knowledge of interspecific interactions will play an important role in advancing ecological theory, as well as in more successful conservation and restoration activities.

Acknowledgements

This work is part of the project "Facilitation and Competition on alpine elevation gradients: a global experiment on the organization of plant communities" funded by National Science Foundation (U.S.A.) in the form of a grant to collaborate at the National Center for Ecological Synthesis and Analysis (NCEAS).

References

Abdaladze, O. and Z. Kikvidze (1991) Herbage influence upon carbon dioxide absorption intensity in the clover *Trifolium ambiguum* M.B. in subalpine zone of the Central Caucasus. *Ekologiya,* 22: 33-37 (*Soviet J.Ecology*, Engl.Tr. 1992, 22 No.1).

Aksenova, A.A., V.G. Onipchenko and M.S. Blinnikov (1998) Plant interactions in alpine tundra: 13 years of experimental removal of dominant species. *Ecoscience,* 5: 258-270.

Alliende, M.C. and A.J. Hoffman (1985) Plants intruding *Laretia acaulis* (Umbelliferae), a high Andean cushion plant. *Vegetatio,* 80: 151-156.

Bertness, M.D. and R.M. Callaway (1994) Positive interactions in communities. *Trends Ecol.Evol.,* 9: 191-193.

Braun-Blanquet, J. (1928) *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Springer, Berlin (English translation 1932/1951. *Plant Sociology: the Study of Plant Communities*, McGraw-Hill, New York).

Brooker, R. and T.V. Callaghan (1998) The balance between positive and negative interactions and its relationship to environmental gradients: a model. *Oikos,* 81: 196-207.

Callaway, R.M. and F.I. Pugnaire (1999) Facilitation in plant communities. *In*: F.I. Pugnaire and F. Valladares, eds., *Handbook of functional plant ecology*, Marcel Dekker, Inc., New York, Basel, pp. 623-648.

Callaway, R.M., R.W. Brooker, P. Choler, Z. Kikvidze, C.J. Lortie, R. Michalet, L. Paolini, F.I. Pugnaire, B.J. Cook, E. Aschehoug, C. Armas and B. Newingham (2002) Positive interactions among alpine plants increases with stress: a global experiment. *Nature* (in press).

Callaway, R.M., Z. Kikvidze and D. Kikodze (2000) Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus Mountains. *Oikos*, 89: 275-282.

Carlsson, B.A. and T.V. Callaghan 1991. Positive plant interactions in tundra vegetation and the importance of shelter. *J. Ecol.,* 79: 973-983.

Choler, P., R. Michalet and R.M. Callaway (2001) Facilitation and competition on gradients in alpine planrt communities. *Ecology*, 82: 3295-3308.

Goldberg, D.E. and A.M. Burton (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am.Nat.,* 139: 771-801.

Haase, P. 2001. Can isotropy vs. anisotropy in the spatial association of plant species reveal physical vs. biotic facilitation? *J. Veg. Sci.*, 12: 127-136.

Kikvidze, Z. and O. Abdaladze (1988) On temperature relations and CO_2 gas exchange of some alpine succulents of the Caucasus. *In*: G.Nakhutsrishvili, ed., *The Ecology of High Mountains*, Metsniereba, Tbilisi, pp.169-174 (Russ.with Engl.summary).

Kikvidze, Z. (1993) Plant species associations in alpine-subnival vegetation patches in the Central Caucasus. *J. Veg. Sci.*, 4: 297-302.

Kikvidze, Z. (1996) Neighbour interactions and stability in sub-alpine meadow communities. *J. Veg. Sci.,* 4: 297-302.

Kikvidze, Z. (1998) Positive and Negative species associations along altitudinal gradient in the Central Caucasus. *In*: G. Nakhutsrishvili, and O. Abdaladze, eds., *Plant life in high mountains*, Diogen Press, Tbilisi, pp.66-70.

Kikvidze, Z. and G. Nakhutsrishvili (1998) Facilitation in

subnival vegetation patches. *J. Veg. Sci.*, 9: 79-391.
Kikvidze, Z., L. Khetzuriani, D. Kikodze and R.M. Callaway (2001) Facilitation and interference in sub-alpine meadows of the central Caucasus. *J. Veg. Sci.*, 12: 833-838.
Numata, M. (1987) Vegetation, plant industry and nature conservation in Bhutan. *In*: M.Ohsawa, ed., *Life Zone Ecology of the Bhutan Himalaya*,. Chiba University, pp. 133-142.
Nuñez, C.L., M.A. Aizen and C. Ezcurra (1999) Species association and nurse plant effects in patches of high Andean vegetation. *J. Veg. Sci.*, 10: 357-364.
Ohsawa, M. (1984) Differentiation of vegetation zones and species strategies in the sub-alpine region of Mt.Fuji. *Vegetatio*, 57: 15-52.
Ohsawa, M. (1991) Preface. *In*: M. Ohsawa, ed., *Life Zone Ecology of the Bhutan Himalaya*, II. Chiba University.
Olofsson, J., J. Moen and L. Oksanen (1999) On the balance of positive and negative interactions in harsh environments. *Oikos*, 86: 539-543.
Pugnaire, F.I. and M.T. Luque (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos*, 93: 42-49.
Sohlberg, E.H. and L.C. Bliss (1987) Responses of *Ranunculus sabinei* and *Papaver radicatum* to removal of the moss layer in a high arctic meadow. *Can. J. Bot.*, 65: 1224-1228.
Sohlberg, E.H. and L.C Bliss (1984) Microscale pattern of vascular plant distribution in two high arctic plant communities. *Can. J. Bot.*, 62: 14-20.
Theodose, T.A. and W.D. Bowman (1997) The influence of interspecific competition on the distribution of an alpine graminoid: evidence for the importance of plant competition in an extreme environment. *Oikos*, 79: 101-114.
Thomas, B.D. and W.D. Bowman (1998) Influence of N_2-fixing *Trifolium* on plant species composition and biomass production in alpine tundra. *Oecologia*, 115: 26-31.
Twolan-Strutt, L. and P.A. Keddy (1996) Above- and below-ground competition intensity in two contrasting wetland plant communities. *Ecology*, 77: 259-270.
Walter, H. (1974) *Die Vegetation Osteuropas, Nord- und Zentralasiens*. Fischer, Stuttgart.
Wilson, S.D. and D. Tilman (1995) Competitive responses of eight old-field plant species in four environmens. *Ecology*, 76: 1169-1180.

(Received on 19 Mar., 2002, Accepted on 12 Apr., 2002)