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Neighbour interaction and stability in subalpine meadow communities

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Abstract. The ability of a plant community to maintain favourable conditions within its canopy was examined by means of removing the vegetation around individual plants (radius ca. 1 m) and measuring light and temperature relations and rates of net photosynthesis in both isolated and sward plants. The results suggest that neighbour interactions are important for the stabilization of environmental relations within the canopy, at least in hay meadows as compared to intensively grazed pastures. The canopy may maintain optimal conditions for plant life within a wider variation of environmental factors. At the same time, plants have to adapt to contrasting (sunny vs. cloudy) weather conditions occurring with about equal frequency during the vegetation period in the central Caucasus.

Keywords: Caucasus; Environmental relation; Function; Photosynthesis; Structure.

Nomenclature: Sakhokia & Khutsishvili (1975).

Introduction

Neighbour interactions between plants may play an important part in plant community organization. One approach in the study of such interactions is to determine species associations in a spatial and temporal context (e.g. Aarssen et al. 1979; Gitay & Agnew 1989; Wilson et al. 1992; Kikvidze 1993; Wilson & Watkins 1994). Plant communities may behave as entities showing a certain resistance to environmental stress, an ability to regulate water and temperature relations and a specific microclimate within the canopy (Stoutjesdijk & Barkman 1992). There is evidence of 'self-favouring' in plant communities (Ipatov & Kirikova 1989), 'positive feedback' between vegetation and environment, or 'switch' (Wilson & Agnew 1992), 'nursing effect' and other kinds of positive plant-plant interactions, mostly in stressful environments: deserts (Franco & Nobel 1989; Valiente-Banuet et al. 1991; Franco-Pizaña et al. 1995), arctic tundra (Carlsson & Callaghan 1991), high mountains (Holtmaier & Broll 1992; Kikvidze 1993), marshes (Bertness & Hacker 1994), savannas (e.g. Belsky 1994).

Another way to study interspecific relations is to examine the physical effects of neighbouring plants upon each other by means of measurements and/or experiments. The present work describes an example of the latter approach to subalpine meadows in the central Caucasus, dealing with possible effects of plant neighbours on temperature and light conditions in the canopy.

Material and Methods

Study area

Experiments were carried out in the subalpine belt of the Kazbegi District in the Central Caucasus (42°48'N, 44°39'E), in the valley of the River Tergi (Terek). This region is characterized by a temperate humid climate with cold winters and cool summers. The average annual precipitation is ca. 800 mm, with a maximum in spring. The average temperature of the (uniform) warmest months (July and August) is ca. 14 °C, with maximum values up to 30 °C.

The following plant communities on the northeastern slope of Mt. Kuro were selected for this study:
- *Deschampsietum* (1800 m a.s.l.). Hay meadow on wet soil near the river. *Deschampsia caespitosa* and *Equisetum palustre* are dominant; *Phragmites australis* forms distinct patches.
- *Hordeetum* (1850 m). Yearly mown species-rich meadow (> 50 species), dominated by *Hordeum violaceum*, *Anthriscus nemorosa* and *Trifolium ambiguum*.
- *Pulsatilletum* (2000 m). Overgrazed pasture dominated by *Pulsatilla violacea* and *Carex buschiorum*.

The canopy of the *Pulsatilletum* is open because of intensive grazing by sheep (cover 80%, height ca. 20 cm). The *Deschampsietum* and *Hordeetum* have a dense canopy with a well-developed structure (cover 100%, height 50 cm and 120 cm, respectively). For details, see Gamkrelidze & Chiboshvili (1990) and Tappeiner et al. (1988/1989).

Experimental design and measurements

The ability of a plant community to keep stable conditions for plant functioning within the canopy was studied by isolating individual plants in meadows, i.e. by clipping and removing the vegetation around one target plant (radius ca. 1 m). Plant communities on level ground were selected with an apparently uniform cover and species composition. Suitable sites for the experiments were chosen subjectively. Control plants in the sward were selected not nearer than 2 m from the edge of the clipped area around the isolated plant; this distance was considered sufficient to ignore the impact of clipping on the control plants.

Then physiological characteristics of both isolated and sward plants were measured simultaneously. Measurements started immediately after isolation between 8.00 and 9.00 a.m. and ended between 20.00 and 21.00 p.m. Instruments were read every 15 min. Most experiments were carried out in July and August 1987-1988. Each experiment was repeated at least three times.

For further experiments, the next target plant was selected at least 10 m from the previous one in order to prevent influences of experimental sites on each other; no specific measures were taken to ensure a random distribution of target plants.

Temperature measurements were carried out by means of a channel electric thermometer (Cer-Thermo, Innsbruck, Austria) with 0.13 mm diameter copper vs. constantane thermocouples (SWG 48, Dural-NSW, Australia). The same electric equipment was connected to a photon sensor (Lambda Instruments, Lincoln, NE, USA) to measure PAR as quantum flux density. For comparisons of light relations, PAR measurements were conducted at five additional sites situated at different altitudes (from 1600 m to 3000 m a.s.l.) in the same area. Records were taken during at least three days.

Net photosynthetic rate (CO_2 uptake) was measured by IRGA (Leybold-Heraeus GmbH, Hanau, Germany) with the assistance of O. Abdaladze using standard methods (Kreeb 1990; see also Abdaladze 1988; Abdaladze & Kikvidze 1991). These measurements were conducted with one species (*Trifolium ambiguum*) of the *Hordeetum* community.

Results

Temperature relations

Isolation had no or very little effect in the *Pulsatilletum* (Table 1). Average leaf temperature was high and varied considerably (from 10 to 40 °C) as indicated by high values of SD. In the *Deschampsietum* and *Hordeetum* average temperatures and deviations were, on the contrary, much lower (range only from 14 to 28 °C). At the same time experimental and control plants differed strongly in their temperature relations: average leaf temperature of isolated plants was 3 - 4 °C higher, with a standard deviation 2 - 3 × larger. Hence, the dense canopies of *Deschampsietum* and *Hordeetum* could stabilize temperature relations of plants, whereas the open sward of *Pulsatilletum* failed to do so.

Light relations

A preliminary study of light relations revealed a pronounced bimodality in the frequency distribution of PAR values (Fig. 1A-C), confirmed by additional measurements at other sites (Fig. 1D-H). The bimodality seems to reflect the contrasting weather conditions with low and high PAR values following each other quite often, the transitions between them being short. In other words, the frequency of 'intermediary' conditions with 'medium' PAR values were low. Actually, shading by clouds, a typical situation in the mountains of the central Caucasus, may be responsible for such a bimodality. On mostly cloudy, or on mostly sunny days, or on days when clouds varied largely in 'transmittance' (Fig. 1E-G), the bimodality still occurred. In total, 'cloudy' conditions with PAR < 1400 micromol photons $m^{-2}s^{-1}$ scored 46 % and 'sunny' conditions with PAR > 1600 micromol photons $m^{-2}s^{-1}$ scored 49 %. An intermediate 'boundary band' of PAR of 1400 - 1600 micromol photons $m^{-2}s^{-1}$ occurred with a frequency of occurrence of 5 %.

Photosynthetic rate

The dependence on PAR level of the net photosynthetic rate (CO_2 uptake) in *Trifolium ambiguum* differs between plants within the sward and those in isolation (Fig. 2, Table 2). During sunny weather the net photosynthetic rate in sward plants was on average 50 % higher than in isolated plants. The difference in PAR values was also considerable, but these values lie above the photosynthetic saturation level (not shown). On the other hand, high values of PAR imply intensive solar radiation which may cause overheating of leaves, particularly those unprotected by the canopy. Actually, the

Table 1. Effect of isolation on temperature relations of plants: average leaf temperature (°C) ± SD.

Communities and species	Sward plant	Isolated plant
Deschampsietum		
Ranunculus oreophilus	14.8 ± 0.71	19.4 ± 1.39
Equisetum palustre	16.8 ± 1.29	22.3 ± 3.14
Blysmus compressus	19.9 ± 1.73	19.1 ± 2.68
Phragmites australis	15.8 ± 0.88	19.8 ± 2.38
Hordeetum		
Trifolium ambiguum	19.9 ± 3.94	21.8 ± 5.36
Pulsatilletum		
Ranunculus oreophilus	25.5 ± 5.63	28.5 ± 4.90
Leontodon hispidus	26.3 ± 5.85	28.9 ± 6.23
Pulsatilla violacea	26.8 ± 4.33	27.4 ± 6.44
Alchemilla sericata	27.1 ± 7.16	26.1 ± 6.62

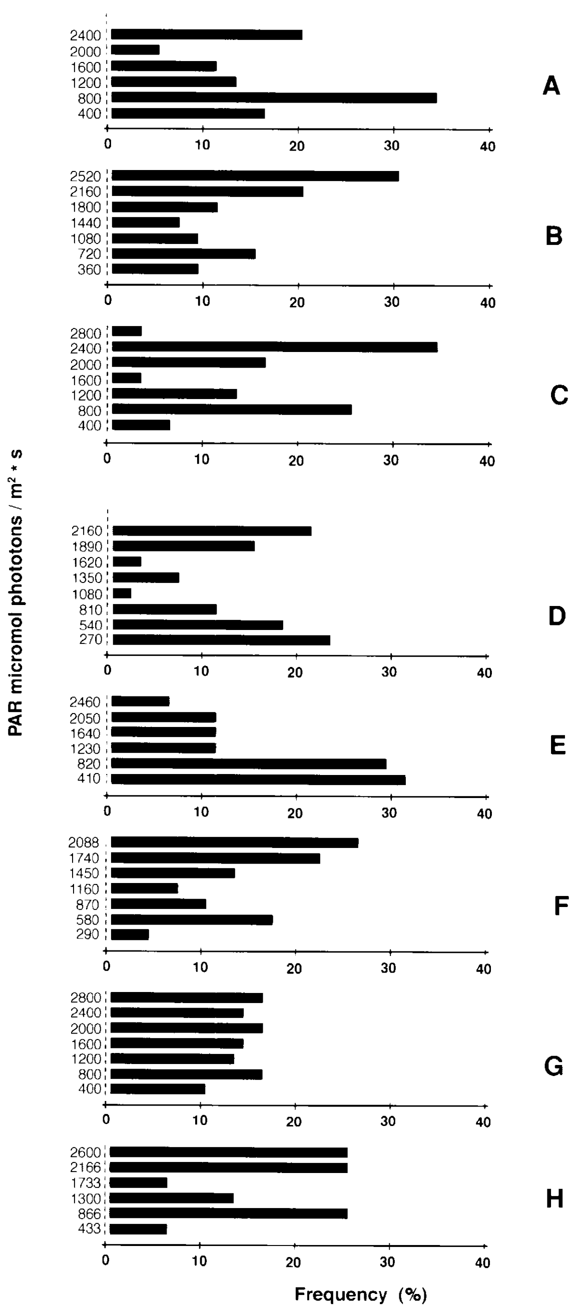

Fig. 1. Frequency distribution of PAR values during the day in three plant communities and five additional sites: A = *Pulsatilletum*; B = *Deschampsietum*; C = *Hordeetum*; D at 1600m; E at 2200m; F at 2300m; G at 2500m; H at 3000m.

Table 2. Effect of isolation on net photosynthetic rate as CO_2 uptake ($mg\,m^{-2}\,h^{-1}$) by *Trifolium ambiguum* under contrasting weather conditions (community *Hordeetum*).

	Sward plant	Isolated plant
Sunny weather	18.0 ± 1.8	12.0 ± 4.5
Cloudy weather	6.4 ± 4.4	8.6 ± 3.5
Total	13.0 ± 6.6	10.0 ± 4.3

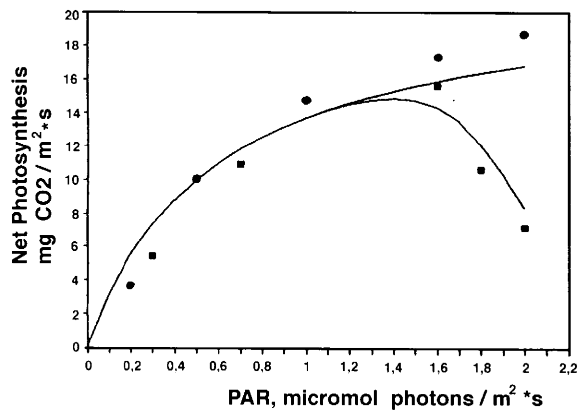

Fig. 2. Net photosynthetic rate on PAR in *Trifolium ambiguum*: ■ = isolated plants (experimental); ● = sward plants (control).

leaf temperature of the isolated plants was on average 3 °C higher and more variable (see above). Naturally, this affected the CO_2 assimilation rate and at PAR levels exceeding 1500 micromol photons $m^{-2}\,s^{-1}$, photosynthesis in isolated plants was strongly reduced (Fig. 2). It should be noted that the air temperature near the plant, as well as the CO_2 concentration in the air, hardly varied as a result of isolation (not shown).

Under overcast the difference between control and experimental plants in the temperature relations disappear. The intensity of PAR in the sward diminished in comparison to the open air by 42 % on average (figures not shown); these values of PAR are below the photosynthetic saturation level; hence these less favourable light relations in the sward will have caused the lower rate of net photosynthesis (Table 2).

Discussion

The results suggest that neighbour interactions may be very important for the stabilization of microclimate factors within the sward, in any case in hay meadows with a well-developed canopy structure. Intensive grazing seems to change the canopy to the extent that this effect on neighbour relations disappears. In the open canopy of the overgrazed *Pulsatilletum* a microclimate with specific light, water and temperature conditions is found (Gamkrelidze & Chiboshvili 1990; Tappeiner et al. 1988/89), but removal of neighbours had no specific effect on the temperature relations of the experimental plants (Table 1).

Light conditions cannot be regulated by plants as they cannot accumulate light and re-utilize it. However, the present study revealed that plants have to adapt to contrasting weather conditions which occur with almost equal frequency during the optimal growing season

(Fig. 1). Accordingly, it seems reasonable to analyse net photosynthesis, under such contrasting conditions (Table 2). Under cloudy conditions, in the absence of neighbours, the experimental plants showed a 26 % higher net photosynthetic rate. Thus plant growth may be larger for isolated plants under overcast. On the other hand, neighbours appeared to be beneficial under sunny conditions: the average net photosynthetic rate was 50 % higher in control plants as compared to those in isolation, so that eventually the total net photosynthetic rate was 30 % higher in the sward than in isolated plants. That is, in a sward the costs of competition with neighbours for resource uptake may be well compensated by the benefits of the stabilization of environmental relations. Actually, isolation did not alter the maximum values of net photosynthetic rates very much. However, the occurrence frequency of values close to the maximum of isolated plants, decreased significantly (2.5 ×) in comparison to sward plants. This points to the ability of a well developed canopy to maintain optimal conditions for plant function within a considerably wider variation of environmental factors. Gamkrelidze (1988) found that in a *Hordeetum* stand a fairly constant water vapour pressure is maintained compared to open air. Hence, the canopy may promote stable air humidity and temperature which, together with soil humidity, may create favourable conditions for plant life.

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References

Aarssen, L.W., Turkington, R.A. & Cavers, P.B. 1979. Neighbour relationships in grass-legume communities. II. Temporal stability and community evolution. *Can. J. Bot.* 57: 2695-2703.

Abdaladze, O. 1988. On field research of plant CO_2 gas exchange in high mountains of the Caucasus. In: Nakhutsrishvili, G. (ed.) The Ecology of High Mountains, pp. 63-75. Metsniereba, Tbilisi. (In Russian with English abstract.)

Abdaladze, O. & Kikvidze, Z. 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. (In Russian; English translation in *Sov. J. Ecol.* Vol. 22, No.1).

Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients and tree-grass competition. *Ecology* 75: 927-932.

Bertness, M.D. & Hacker, S.D. 1994. Physical stress and positive associations among marsh plants. *Am. Nat.* 144: 363-372.

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

Franco, A.C. & Nobel, P.S. 1989. Effect of nurse plants on the microhabitat and growth of cacti. *J. Ecol.* 77: 870-886.

Franco-Pizaña, J., Fulbright, T.E. & Gardiner, D.T. 1995. Spatial relations between shrubs and *Prosopis glandulosa* canopies. *J. Veg. Sci.* 6: 73-78.

Gamkrelidze, T.A. 1988. Phytoclimate and energy budget of subalpine meadows in the Central Caucasus. In: Nakhutsrishvili, G. (ed.) *The Ecology of High Mountains*, pp. 109-125. Metsniereba, Tbilisi. (In Russian with English abstract.)

Gamkrelidze, T.A. & Chiboshvili, M. 1990. Microclimate and the energy balance of meadow vegetation in the Central Caucasus. In: Nakhutsrishvili, G. (ed.) *Ecological and Geobotanical Studies at the Kazbegi High Mountain Station*, pp. 30-38. Institute of Botany of the Georgian Academy of Sciences, Tbilisi.

Gitay, H. & Agnew, A.D.Q. 1989. Plant community structure, connectance, niche limitation and species guilds within a dune slack grassland. *Vegetatio* 83: 241-248.

Holtmaier, F.K. & Broll, G. 1992. The influence of tree islands and microtopography on pedological conditions in the forest alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. *Arct. Alp. Res.* 24: 216-228.

Ipatov, V.S. & Kirikova, L.A. 1989. Self-favouring in plant communities. *Bot. Zh.* 74: 14-21. (In Russian with English abstract.)

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

Kreeb, K.-H. 1990. *Methoden der Pflanzenokologie*. Fischer, Jena.

Sakhokia, M.F. & Khutsishvili, E.J. 1975. *Synopsis of the flora of higher plants of Khevi (Kazbegi District of the Georgian SSR). Pterodophyta-Spermatophyta*. Academy of Sciences of the Georgian SSR Press, Tbilisi.

Stoutjesdijk, P. & Barkman, J.J. 1992. *Microclimate, vegetation and fauna*. Opulus Press, Uppsala.

Tappeiner, U., Cernusca, A. & Nakhutsrishvil, G.S. 1988/1989. *Bestandesstruktur und Lichtklima ausgewählter Pflanzenbestande der subalpinen Stufe des Zentralkaukasus. Österr. Akad. Wiss. Math. Naturw. Kl. Sitzungsber. Abt.* I, 197 (5-10): 395-421.

Valiente-Banuet, A., Vite, F. & Zavala-Hurtado, J.A. 1991. Interaction between the cactus *Neubuxbaumia tetetzo* and the nurse shrub *Mimosa luisiana*. *J. Veg. Sci.* 2: 11-14.

Wilson, J.B. & Agnew, A.D.Q. 1992. Positive-feedback switches in plant communities. *Adv. Ecol. Res.* 23: 263-336.

Wilson, J.B. & Watkins, A.J. 1994. Guilds and assembly rules in lawn communities. *J. Veg. Sci.* 5: 591-600.

Wilson, J.B., Roxburg, S.H. & Watkins, A.J. 1992. Limitations to plant species coexistance at a point: a study in a New Zealand lawn. *J. Veg. Sci.* 3: 711-714.

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