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Water Relations Pattern of Understorey Species Influenced by Sunflecks

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Abstract. Water relations of plant cenopopulations of understorey species (7 herbaceous perennials, 1 shrub, and 1 tree seedling) growing in an oak-hornbeam forest in SW. Slovakia is markedly influenced by natural sunflecks moving on the forest floor, where stomatal conductance and transpiration rate are significantly higher than in shade areas. In the course of a day, the leaf stomatal conductance fluctuates, following irradiance of the leaf, from minimum in full shade to maximum in sunflecks, including intermediate values in transient conditions. Therefore, there is also a large variability in water saturation deficit and transpiration rate within the cenopopulations of the understorey species. These variations should be considered in modelling the physiology of woodland understorey species.

Irradiance (I) in a plant community is characterized by very large temporal and spatial variability (*cf.* Ross 1980). Complex character of the I on a soil surface in a forest stand is known (*e.g.* Evans 1956, Anderson *et al.* 1969, Alekseev 1975, Hutchison and Matt 1977), namely the uneven distribution of I on a horizontal plane, due to penetration of direct beam radiation through canopy openings (occurrence of sunflecks). The penetration of the solar radiation is strongly controlled by the interaction of solar elevation and canopy density variation with angular elevation (Alekseev 1975, Hutchison and Matt 1977).

In natural environment of a forest floor, understorey plants are exposed to changed I. In the course of a cloudless day, they are subjected to the conditions of full shade and of sunflecks differing by their I, durations, sizes and frequencies. These conditions are reflected in physiology of understorey plants. Pisek and Cartellieri (1932) demonstrated a large increase in transpiration rate of shade-living forest herbs in sunflecks. Young and Smith (1979) and Smith (1981) showed influence of sunflecks on temperature and water relation of subalpine understorey species in subalpine coniferous forests. Eliáš (1979a) reported that within sunfleck conditions in the herbaceous layer of an oak-hornbeam forest lower stomatal-resistance values were more frequently

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measured in some herbaceous species than in sunlit leaves in the upper layer of the tree canopy, but only under non-stress conditions.

This contribution completes our previous report by the data on influence of natural sunflecks on water relations of understorey species.

MATERIAL AND METHODS

The research site was the I.B.P. Forest Research Area at Báb near Nitra, SW. Slovakia, represented by an oak-hornbeam woodland (*Carpinus betulus* L., *Acer campestre* L., *Quercus cerris* L. and *Q. petraea* LIEBL.). For details see: JURKO and DUDA (1970), BISKUPSKÝ (1975), ELIÁŠ (1978, 1979b).

The *I* in the ground layer (at forest floor) varied in the course of a day as well as during the growing period; *e.g.* *I* in the herb layer was 32.4% of the total *I* (a free area) in March, but only 2% in June. In the course of a day, most solar radiation penetrates to the herb layer at 11.00 (9.9% in yearly average) and the least at 15.00 (6.8%). Thus variation in *I* on a horizontal plane is complex, as was demonstrated by DUDA (1975).

The understorey species used in this study were all perennials, and included the herbs: *Pulmonaria officinalis* L., *Mercurialis perennis* L., *Galeobdolon luteum* HUDS., *Glechoma hirsuta* W. *et* K., *Geum urbanum* L., *Viola mirabilis* L., and *Polygonatum latifolium* (JACQ.) DESF., the shrub: *Cornus mas* L., and the tree seedling: *Acer campestre* L.

Two groups of plant individuals were chosen from cenopopulations of the understorey species, growing in two similar micro-habitats no more than 3 m apart within the woodland. In the course of sampling days we registered natural dynamics of sunfleck occurrence in both micro-habitats as well as their influence on characteristics of plant water relations.

Stomatal conductance to water vapour diffusion were estimated by Lambda Instruments Corp. diffusion porometer (Model LI-60). All species investigated exhibit hypostomatous leaves (*cf.* ELIÁŠ 1979b), therefore, diffusive conductance of abaxial epidermis only was estimated. Transpiration rate in sunlit and shaded plants, and water saturation deficit were determined gravimetrically in leaves or plants detached and discs cut, respectively (*cf.* SLAVÍK 1974). Microclimatic data (air and soil temperature, vapour pressure deficit and solar radiation) were systematically registered by the UM-10 type data logging system (SMOLEN 1970). Soil moisture content was obtained by the thermogravimetric method.

RESULTS

In the deciduous woodland in summer period (shade phase), *I* at soil surface is low (about 3% of the total *I*), also in the course of a cloudless, sunny day (Fig. 1), and there is a large variability in the *I* within the stand during a day (Fig. 2). *I* was usually lower than 30 W m^{-2}, but in sunflecks it exceeded the values by one or two orders of magnitude. In the sampling day we registered at a point sensor five peaks of *I*: two high between 9.30 and 11.00 and then three in the afternoon (at 12.30 and between 14.00 and 15.00) (Fig. 2).

Daily variability in stomatal conductance is large in understorey species (Fig. 3). The highest values were evidently recorded always in bright sunflecks, neglecting inter-species differences in absolute values. In the early morning and late afternoon, the conductance was relatively low. Daily maxima were estimated in the morning, between 9.00 and 11.00, in sunlit leaves. [The *Galeobdolon luteum* plants with daily maximum in the afternoon (at 12.57) form an exception]. They ranged from 1.477 in *Polygonatum latifolium* to 2.762×10^{-3} m s^{-1} in *Pulmonaria officinalis*. Maximum values of stomatal conductance reaching in various individual sunflecks during a day varied from one sunfleck to another in the same leaves.

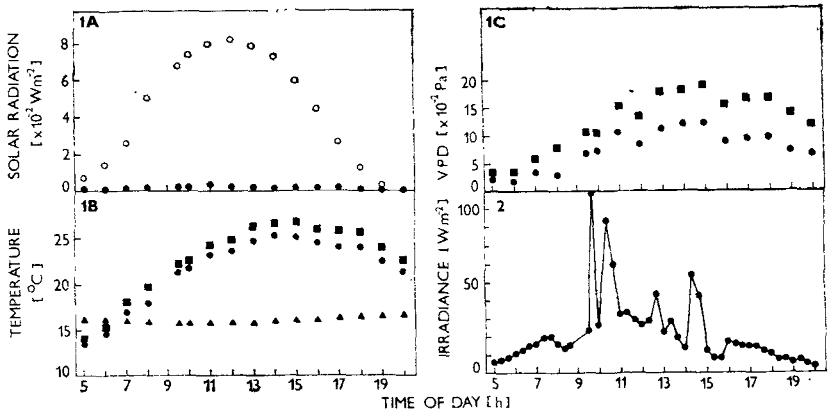

Fig. 1. Diurnal courses of solar radiation (A), air and soil temperature (B), and vapour pressure deficit (C) in a woodland at Báb. — Open symbols: above the stand (height 25 m above soil surface), closed symbols: within the stand (circles — 2.0 m, squares — 0.5 m, triangles — 0.2 m). Measured by point sensors. Datum: July 13, 1977.

Fig. 2. Variation in irradiance at point sensor situated in the forest stand (2 meters above soil surface) in course of a day (July 13, 1977).

In the course of a day, stomatal conductance of a leaf oscillated between the lowest value in full shade to the highest one in bright sunfleck. In the morning, the leaf was frequently sunlit by moving sunflecks and its stomatal conductance, therefore, was close to daily maxima. In the afternoon, the

TABLE 1

Maximum and extreme values of transpiration rate in selected understorey species estimated in course of a day (August 24, 1976) in an oak-hornbeam forest. Daily maxima of plant water saturation deficit are also given

Species	Transpiration rate [g g^{-1} d.m. s^{-1}]		WSD [%]
	Daily maximum	Extreme values in sunflecks	Daily maximum
Pulmonaria officinalis	0.237	0.620	35.6
Geum urbanum	0.187	1.201	20.1
Mercurialis perennis	0.175		37.4
Galeobdolon luteum	0.142	0.730	36.6
Glechoma hirsuta	0.127	0.585	23.8
Polygonatum latifolium	0.098	0.178	18.3

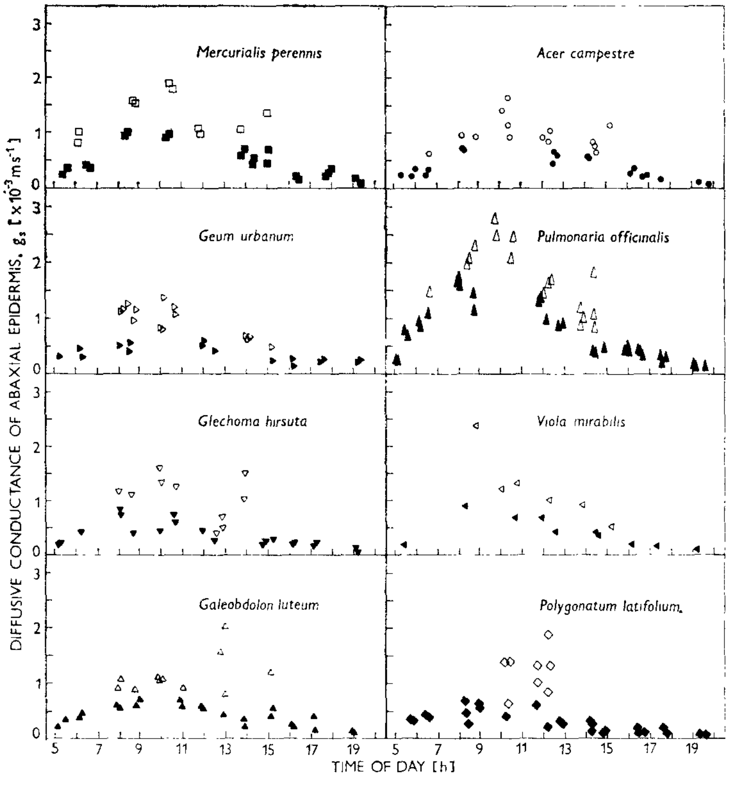

Fig. 3. Variation in stomatal conductance of 7 herbaceous understorey species and 1 tree seedling during a day (July 13, 1977). Open and closed symbols represent sunlit and shaded conditions, respectively.

I intensity of moving sunflecks decreased and stomatal conductance of the leaf was, therefore, usually close to semi-shaded and shaded leaves.

In sunflecks, transpiration rate of the understorey species is extremely high, in comparison with that in shade areas (Table 1). The frequency of sunflecks was high in the morning, therefore, water saturation deficit of the plants rapidly increased from morning to noon and reached maxima in the afternoon (Fig. 4).

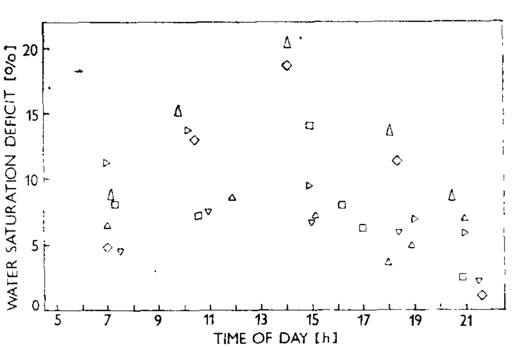

Fig. 4. Variation in leaf water saturation deficit of the understorey species in a woodland at Báb (July 13, 1977). For species legend see Fig. 3.

DISCUSSION

Stomatal conductance and water relations of understorey species are strongly affected by moving sunflecks on forest floor, in cloudless, sunny days. In the sunlight conditions, higher transpiration rate, higher stomatal conductance and lower leaf water potential as well as higher leaf temperature were found, in comparison with shade conditions (PISEK and CARTELLIERI 1932, ELLENBERG 1963, HADFIELD 1975, RACKHAM 1975, ELIÁŠ 1979a, YOUNGH and SMITH 1979, WOODWARD 1980, SMITH 1981). On the contrary, MOLDAU (1975) reported higher leaf resistances in understorey herbs in large sunflecks than in those occurring in shaded areas. However, the large and small sunflecks as well as short-term and long-term sunflecks must evidently be distinguished in the studies on physiological effects of natural sunflecks.

Stomatal conductance of a leaf fluctuates in the course of a day according to the leaf *I*. It rapidly changes during the passage of a sunfleck, being also influenced some time after the passage (post-sunfleck effects). During leaf exposure to sunfleck, leaf temperature and conductance increase rapidly, along with corresponding increase in transpiration and decrease in water potentials. However, plant responses to *I* during the passage of natural sunflecks, as well as post-sunfleck effects are known insufficiently. WOODWARD (1980). demonstrated changes of microclimate and plant responses during the passage of a 7 minute sunfleck. It is evident from his data that duration of the sunlit conditions for a leaf or a plant (*viz.* time interval from the sunfleck start) is important in ecological evaluations of sunflecks in woodland. Post-sunfleck effects must also be considered.

Daily maximum values of stomatal conductance were obtained between 9.00 and 11.00 (*cf.* also ELIÁŠ 1979a), *i.e.* in the period of the highest *I* in the woodland. In the daily period, the highest *I* values at forest floor were also found during seasonal investigation (*cf.* DUDA 1975). This fact resulted from sun position in space: frequency and intensity of sunflecks increase with increasing sun elevation during a day (ALEKSEEV 1975).

Our results showed that the inter-species variations in stomatal conductance of understorey species are complicated by complex *I* conditions within the forest stand, evidently at the floor. Cenopopulations of understorey species are subjected, during a day, to different *I*, including spectral composition of direct and diffuse *I* (ROSS 1980). At the same moment, some individuals of a cenopopulation are exposed to full shade, other ones to bright sunflecks, further to penumbra, un-bright sunflecks, semi-shade areas *etc.* The un-bright sunflecks and semi-shade areas dominate in a forest stand (*cf.* ALEKSEEV 1975). Duration, range and frequency of these different conditions within a cenopopulation are not simple to determine. Therefore, there is a lack of knowledge of the variation of physiological features within a cenopopulation on a horizontal plane. It may be an important limit for correct modelling of the physiology within a plant stand.

Our data also showed the large variability in stomatal conductance within a cenopopulation as well as among cenopopulations of understorey species limited to the use of simple data for models of transpiration of the understorey canopy. It will be necessary to determine or estimate the areas occupied by individual cenopopulations which are affected by sunflecks during a large part of a day and to respect these in considerations and formula. The contribution of forest undergrowth to the total evapotranspiration of a forest stand appears to be larger than is usually assumed (*cf.* TAN and BLACK 1976. ROBERTS *et al.* 1980, ELIÁŠ 1981).

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BOOK REVIEWS

PALTI, J.: CULTURAL PRACTICES AND INFECTIOUS CROP DISEASES. — Springer Verlag, Berlin—Heidelberg 1981. 243 pp. Cloth DM 98.—; approx. US $ 45.70.

This is a modern well arranged book. The author looks at plant diseases from a broader point of view and analyses all accessible factors capable of influencing relations between the plant and the disease. Special attention is paid to the influence of agrotechnical measures on the distribution of agriculturally important plant diseases. The interest is aimed not only at a special agricultural sphere but it also embraces the tropical and subtropical regions. Though it is not possible to cover all agrotechnical measures in individual agroclimatic zones, the author nevertheless completed all the data in a very outstanding way and deduced generally valid principles. This relates especially to the questions of variety composition, physiological changes, plant protection, crop rotation, effect of weeds, nutrition and irrigation. At the same time he pays attention to some basic factors influencing crops, *e.g.* to climate, soil conditions, stress, *etc.* The conclusions show the possibility of harmonizing the mutual relations between agronomical practices, resistance breeding and the use of chemical preparations. This concerns not only new agricultural regions but also regions where an integrated plant protection could intensify agricultural production.

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SILL, W. H., JR.: PLANT PROTECTION — AN INTEGRATED INTERDISCIPLINARY APPROACH. — The Iowa State University Press, Ames., Iowa 1982. 297 pp. US $ 23.95.

The author, professor of biology at the University in South Dakota, U.S.A. presents a new look on the plant protection dealing with it from several points of view. He takes into account the views of the breeder as well as social and economical questions. He deals with the problems of plant protection on all plant breeding levels, beginning with seeds, plant rearing and preparation of plant material till storage and sale of finished products. Attention is also paid to the use of pesticides in all forms. This is connected with a number of further questions *e.g.* with the resistance of plant pests, diseases and weeds to the pesticides and herbicides, the phytotoxicity, the residues of preparations, *etc.* The author also mentions the danger existing in system analysis executed by means of computers. It is therefore necessary to pay attention to feromons and other attractants and to the sterilization of male pests if need be. An integral part of plant protection is an additional set of provisions aimed at the breeding of healthy plants, which concern crop rotations, irrigation, nutrition and other agrotechnical measures. Examples of combined provisions and of an integrated plant protection are also given. In the conclusion the author states that the plant protection is above all an interdisciplinary matter. One of the merits of the book is the fact that it summarizes the ideas and opinions of individual authors concerning plant protection problems. The book can be recommended to workers dealing with integrated plant protection.

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