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Leaf Diffusion Resistance Pattern in an Oak-Hornbeam Forest

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Abstract. Four tree, five shrub, and ten herbaceous species growing naturally in an oak-hornbeam forest were used for simultaneous study of the leaf diffusive resistances in the course of several summer days. Absolute minima of the stomatal resistance in the sun tree, the shrub, and the herbaceous species leaves were 1.7 to 6.2 s cm^{-1}, 6.1 to 10.8 s cm^{-1}, and 4.8 to 9.7 (17.3 in *Convallaria majalis* leaves) s cm^{-1}, respectively. Minimum daily leaf resistances in the course of a day were noted earlier in the morning in sun leaves of large trees than in shade leaves of other species. Stomata were fully opened later in the morning and they began to close sooner in the afternoon in usual shade leaves of the plants in the interior of the forest canopy than those in sun leaves in active surfaces of the canopy (tops of tree crowns). The relatively large differences in leaf resistances found among investigated species may be explained by differences in leaf anatomy (stomata frequency and size) and in ambient leaf or plant environment caused by leaf (plant) position in different vertical layers.

Leaf diffusion resistances are important in regulating gas-exchanges between plant and ambient atmosphere. Rates of two gas-exchange processes, photosynthesis and transpiration, may play a major role in determining the outcome of competition among plant species, and, hence, species composition of plant communities (WUENSHER and KOZLOWSKI 1971). Variation among species in stomatal and mesophyll resistances may largely determine species differences in photosynthesis and transpiration under various environmental conditions (HOLMGREN *et al.* 1965).

At the present time we have not a sufficient idea of the level and variability of the leaf diffusion resistance values within plant communities growing in natural habitats. Quantitative data are scarce or absent. However, it is necessary to understand and quantify relationships between plant processes and environment, but also to develop and construct plant community (ecosystem) models.

Within the ecological investigations in an oak-hornbeam forest in I.B.P. Forest Research Area at Báb near Nitra, SW. Slovakia, Czechoslovakia (see JURKO and DUDA 1970, BISKUPSKÝ 1975), the variability in leaf diffusion resistances to transpiration was studied in many plant species growing in different vertical layers with respect to several sources of variability (*cf.* ELIÁŠ 1977a).

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In summer 1976 an attempt was made to measure simultaneously the leaf diffusion resistances in several plant species which occupied different vertical positions in an oak-hornbeam forest. Measurements were conducted in the field on intact naturally growing forest plants. Some of these results will be presented in this paper.

Material and Methods

The nineteen species listed in Table 1 were followed in the course of several days in summer 1976. In porometer measurements mature leaves attached to plants growing in different vertical strata in the oak-hornbeam forest were used. The vegetation and environment of the oak-hornbeam woodland at Báb have been described in preceding papers (JURKO and DUDA 1970, BISKUPSKÝ 1975, ELIÁŠ 1978, 1979).

Leaf resistance to water vapour diffusion out of leaves (r_l) was measured with water vapour diffusion porometer Lambda LI-60 and a horizontal sensor LI-20S, similar to that described by KANEMASU *et al.* (1969). Calibrations were performed using perforated plates at several temperatures covering the range experienced in the field.

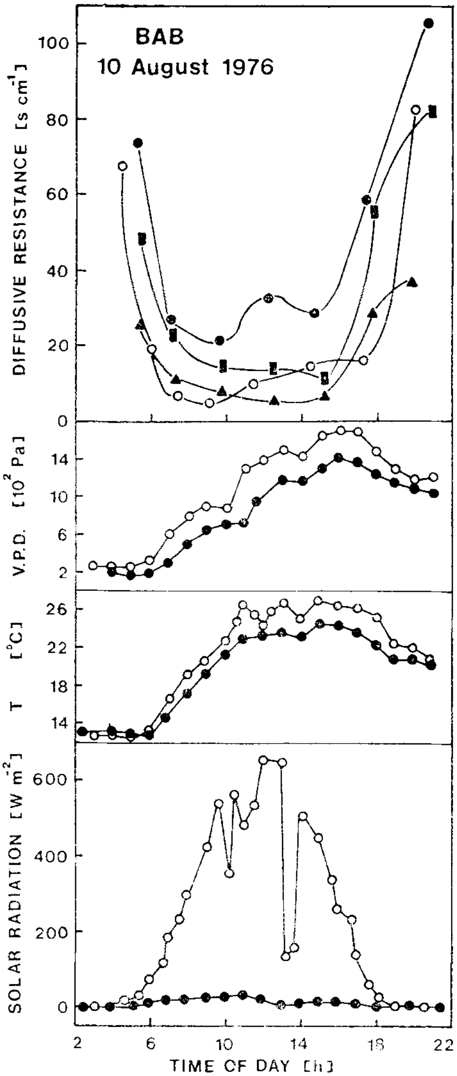
Diffusion resistance of the abaxial surfaces of the leaves were measured only because all the studied species have stomata in the abaxial epidermis only (hypostomatic leaves). This leaf resistance is usually considered as "a stomatal resistance". The approach described above was sufficient to obtain a diurnal course and minimal values of leaf resistance.

Porometer readings were made at four different levels within the forest canopy. Tree leaves were reached from a 20-m-high steel tower within the closed forest stand. Sun leaves were measured at the tops of the tree crowns in the upper layer of the canopy (heights 16 to 20 m), shade leaves at the bottom of the crowns in the lower part of tree layer (heights 6 or 3 m). Shrub leaves were reached from a 2-m-high portable stand; they were measured in a shrub layer up to 2.5 m height. Herbaceous species leaves data were collected in a herb layer up to 0.3 m. Four to six leaves were sampled separately at each time and location.

The water saturation deficit was measured gravimetrically by the leaf disc method (ČATSKÝ 1960, ELIÁŠ 1978). Noon values are presented only. Soil moisture content was obtained by the thermogravimetric method for five different soil horizons and expressed in dry mass percentages. Micrometeorological data were systematically registered by the UM-10 type data logging system (SMOLEN 1960) in the meteorological station at Báb.

Results

Fig. 1 illustrates diurnal changes of stomatal resistances in the sun and shade leaves of a large *Acer campestre* tree, in leaves of *Acer campestre* seedlings and in a herbaceous species leaves (*Pulmonaria officinalis*). In the morning, stomata in sun leaves of the large tree were fully opened earlier than those in other leaves. Stomata open fully later and begin to close earlier in the course of a day in the leaves of the plants growing in the interior of the forest canopy than stomata in sun leaves of large trees on active surfaces of the canopy (see Figs. 2A and 3). In sun tree leaves, minimum daily r_l-values



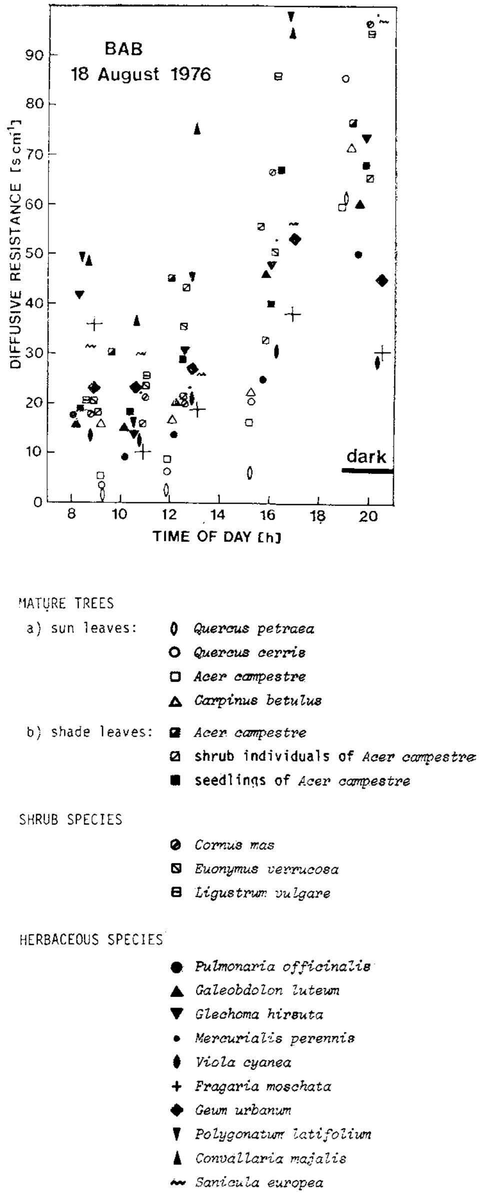


Fig. 1. Daily course of stomatal resistance in leaves of forest plants growing in different vertical layers in the forest stand and of solar radiation, air temperature and vapour pressure deficit at two heights: above the forest stand, 19 or 25 m (open signs) and within the forest stand, 2 m (full signs).
○ sun leaves and ● shade leaves of large *Acer campestre* tree, ▩ leaves of *Acer campestre* seedlings. ▲ leaves of *Pulmonaria officinalis*, a herbaceous species.

Fig. 3. Diurnal pattern of diffusion resistance of the abaxial surfaces of the leaves of plants growing in oak-hornbeam forest. Summer 1976, moderate stress conditions (for leaf water saturation deficits see Table 1). Each point represents the mean of four leaves at least.

were usually noted before 09.00 h, while in shade leaves of trees and in leaves of other species growing within the canopy they were measured most frequently after 09.00 h (*cf.* also Table 1). The lowest stomatal resistances were recorded in sun leaves of the mature trees, the highest in shade leaves at the bottoms of the crowns of *Acer campestre* and *Carpinus betulus*. As Fig. 2A shows, diffusion resistance in shrub leaves was usually higher than in the sun leaves of large trees in the course of a whole day. Within sunfleck conditions in the herbaceous layer lower r_s values were more frequently measured in some herbaceous species than in sun leaves in the upper layer of the canopy, but under non-stress conditions only. However, sunflecks are movable and duration of this condition for the same plant is short.

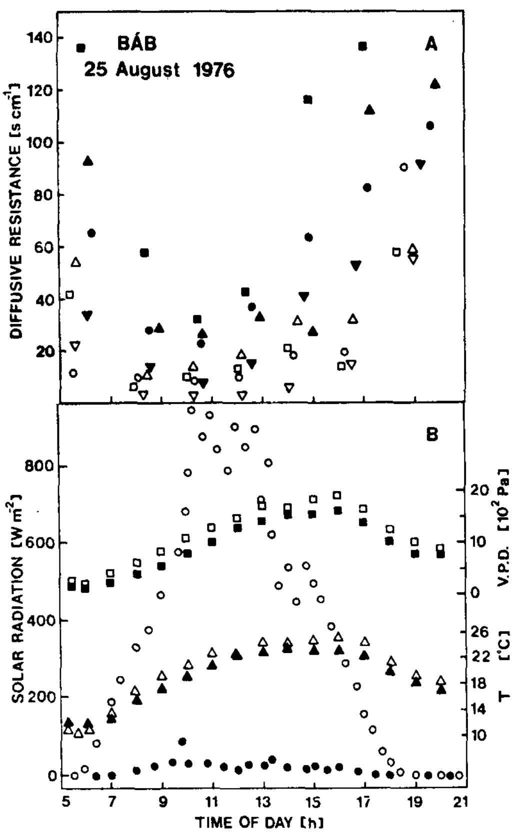


Fig. 2A. Diurnal variations in stomatal resistances in sun leaves of large trees (open signs) and in leaves of shrubs (full signs) growing in the oak-hornbeam forest at Báb collected on 25th August 1976. For soil moisture content see Table 2. Trees: □ *Acer campestre*, ○ *Quercus cerris*, △ *Carpinus betulus*, ▽ *Quercus petraea*. Shrubs: ■ *Euonymus verrucosa*, ● *Cornus mas*, ▲ *Ligustrum vulgare*, ▼ *Crataegus oxyacantha*.

Fig. 2B. Diurnal variations in solar radiation (SR, cycles), air temperature (T, triangles) and vapour pressure deficits (v.p.d., squares) at two different heights: above the forest canopy, 19 or 25 m (open signs) and within the forest canopy, 2 m (full signs). 25th August 1976.

The variations in leaf diffusion resistance in nineteen forest species occupying different strata in the natural oak-hornbeam forest stand are shown in Fig. 3 for one summer day. Maxima of global radiation, air temperature, and vapour pressure deficit above the forest (heights 19 or 25 m) and at 2 m within the forest canopy for the studied day were 810 and 100 W m^{-2}, 24.05 and 23.05 °C, and 17.35 and 15.07 mbar, respectively. Large variation in stomatal resistance in this natural plant community is evident. The lowest

TABLE 1

Minimum means and absolute minimal values (in parentheses) of stomatal diffusion resistance with time of day measured in course of three summer days in an oak-hornbeam forest and noon leaf water saturation deficits on 18 August 1976 for nineteen forest species. Mean values of number of stomata per mm² in abaxial epidermis and their range are also introduced

Leaves	12 August 1976 r_s [s cm^{-1}]	12 August 1976 time of day	13 August 1976 r_s [s cm^{-1}]	13 August 1976 time of day	18 August 1976 r_s [s cm^{-1}]	18 August 1976 time of day	18 August 1976 w.s.d. [%]	Stomata number per mm^{2}*
Herbaceous species								
Pulmonaria officinalis	5.1	11.50	5.4	10.00	9.6	10.20	24.2	67.1
	(5.07)		(4.88)		(8.73)			52–84
Mercurialis perennis	9.0	9.20	6.1	10.00	23.3	12.40	18.1	74.8
	(5.58)		(5.42)		(21.5)			31–135
Galeobdolon luteum	7.3	9.00	5.6	10.10	15.3	10.20	17.0	116.2
	(5.05)		(4.95)		(13.1)			63–191
Glechoma hirsuta	11.0	12.00	10.9	10.25	14.6	10.25	41.7	143.4
	(6.38)		(7.75)		(8.26)			95–255
Viola cyanea	5.7	9.40	6.0	10.50	13.4	10.45	16.9	123.3
	(4.89)		(6.0)		(12.2)			95–191
Polygonatum latifolium	10.6	9.20	10.9	10.30	17.8	10.30	19.5	84.5
	(7.45)		(9.74)		(13.1)			47–112
Convallaria majalis	19.2	9.30	23.0	10.30	36.7	10.35	18.2	40.8
	(18.9)		(17.3)		(31.3)			23–56
Sanicula europea	6.4	9.35	7.5	10.40	26.8	12.50		103.0
	(4.77)		(5.37)		(21.4)			63–143
Geum urbanum	(7.63)	9.40	(9.56)	10.50	(23.5)	10.50		123.1
								79–175
Fragaria moschata	13.0	9.40	16.8	10.50				
	(9.6)		(15.7)					
Shrub species								
Cornus mas	12.1	9.50	16.0	11.00	18.6	9.00	18.9	94.2
	(10.7)		(14.7)		(18.1)			55–151
Euonymus verrucosa	7.1	9.50	7.3	10.55	20.8	8.50	17.8	185.9
	(6.22)		(6.1)		(17.1)			119–358
Ligustrum vulgare	(7.55)	12.40	(6.1)	10.50	(20.8)	8.50	14.5	154.5
								104–231
Crataegus oxyacantha			7.9	11.10				93.2
			(6.17)					31–159
Hedera helix			11.6	11.10				143.3
			(9.83)					119–191
Tree species								
a) sun leaves								
Quercus petraea			7.0	9.30	1.8	9.20	17.9	578.4
			(6.98)		(1.44)			417–892
Quercus cerris			13.9	9.20	3.9	9.20	22.5	
			(12.5)		(3.69)			
Acer campestre			14.1	9.20	5.4	9.20	19.9	387.8
			(10.8)		(4.97)			297–412
Carpinus betulus			8.0	9.30	16.2	9.20	11.6	174.9
			(6.18)		(10.8)			159–183
b) shade leaves								
Acer campestre			17.6	9.50	30.7	9.40	27.0	189.0
			(15.4)		(28.6)			180–220
c) shrub individuals								
Acer campestre	9.4	9.50	9.8	11.00	16.1	10.55	17.9	246.8
	(8.65)		(8.78)		(11.1)			127–350
d) seedlings								
Acer campestre	5.5	9.10	5.2	10.20	19.9	10.30	20.7	167.8
	(4.81)		(4.28)		(10.7)			150–180

* Data from ELIÁŠ 1979.

resistances were again measured in sun leaves of large trees as mentioned above.

Data in Table 1 show the lowest r_s-values measured in the course of three different days in August 1976 for many investigated forest plants. Soil moisture content in various horizons for August 11, 18 and 24 is given in Table 2. Under non-stress conditions (August 12 and 13) daily minima were lower in herbaceous species than in sun leaves of mature trees. But they were reversed under drought-conditions. The lowest absolute minima of stomatal resistance were in sun tree leaves. During drying cycles stomatal resistance increased more rapidly in herbaceous species than in sun leaves of tree species (see Table 1). Within each layer and species group the differences were found between separate species.

TABLE 2

Soil moisture content expressed in terms of percentages of both fresh weight [% f.w.] and dry weight [% d.w.] recorded in five different soil layers on three summer days

Depth	11 August 1976		18 August 1976		24 August 1976	
[m]	[% f.w.]	[% d.w.]	[% f.w.]	[% d.w.]	[% f.w.]	[% d.w.]
0.0–0.1	17.00	17.05	14.01	16.29	13.13	15.12
0.1–0.2	13.99	16.28	12.65	14.49	12.07	13.72
0.3–0.4	12.26	13.98	11.32	12.89	11.81	13.39
0.5–0.6	10.59	11.85	11.08	12.45	11.89	13.44
0.7–0.8	7.99	8.69	9.06	9.96	10.80	12.10

Discussion

There is a relatively large variation in leaf diffusion resistances of plants in an oak-hornbeam forest. These might be associated with variation sources in the plants alone (genetically controlled variation) and in environmental variables.

Woodland ecosystems included several groups of plant growth forms. Within these groups, sun and shade plant species, and sun and shade leaves occur. There are great differences *e.g.* in stomata density and size between plants in a forest. In the oak-hornbeam forest at Báb, the highest stomata density was found in sun tree leaves, the lowest in shade leaves of some herbaceous species (see ELIÁŠ 1979, Table 1). The changes in stomatal frequency and therefore the maximum stomatal pore area per unit area of leaf correlated with the maximum stomatal conductance (BOARDMAN 1977). The highest maximum stomatal conductance (reciprocal of resistance) was obtained in sun leaves of *Quercus petraea* with the highest stomata density (417 to 892 stomata per mm^2), while the lowest maximum were found in shade leaves of *Convallaria majalis*. Stomata density in *Convallaria majalis* leaves was twice or three times lower as compared with that in other herbaceous species growing in the same oak-hornbeam forest (*cf.* ELIÁŠ 1979, Table 1). The increases in the stomatal conductance in plants grown at high light intensity appear to be a direct consequence of the altered leaf morphology, correlating with the greater stomatal frequency (BOARDMAN 1977).

The differences between species in stomatal resistance do not necessarily depend on differences in the frequency or structure of the stomata but may also depend on differences in the relation between stomatal aperture and environmental conditions (HOLMGREN *et al.* 1965). Within the forest stand there are large differences in environmental conditions between different vertical layers, most remarkably between the active surface of a canopy and the forest floor (see Fig. 1 and 2B for solar radiation, air temperature and vapour pressure deficit). They influenced both stomata density and stomata behaviour in individual vertical layers.

Differences also exist in depth of the rooting among plant species. Rooting depth strongly influenced plant water status, namely maxima of water deficit in plants. Together with vertical gradients of soil moisture content in soil profile, it caused a vertical gradient of leaf water deficit within the forest ecosystem (ELIÁŠ 1978). This gradient was the most contrasted under drought-stress conditions. Herbaceous species are rooted at a depth of a few centimetres only because of their water balance is strongly affected by soil moisture. Therefore the leaf diffusion resistance increased more rapidly in shallow-rooted plants than in large trees during drying cycles. MOLDAU (1975) introduced a similar explanation. He explains the rapid increase of stomatal resistance of ground flora species by the depletion of water storage in the rooting zone of these species.

The differences in light conditions and diurnal cycles between the active surface of the forest canopy and forest floor appear to cause different behaviour of stomata in sun leaves of large trees as compared with those in shade leaves of herbs. ELIÁŠ (1977a, b) found that stomata of plants in the interior of the forest canopy (ground flora) opened later and closed sooner than the stomata in the leaves on the active surface of the canopy in the course of a day. Similar differences in stomata behaviour were observed by THOMPSON and HINCKLEY (1977) for two understory species as compared with the overstory white oak (*Quercus alba*). These include delayed completion of photoactive opening and earlier evening photoactive stomatal closure and increases in leaf resistance.

Minimal stomatal resistances of a number of farm crops, herbaceous plants and trees have been listed and discussed by many authors, *e.g.* HOLMGREN *et al.* (1965), WHITEMAN and KOLLER (1967), RUTTER (1968, 1976), COWAN and MILTHORPE (1968), TURNER (1974), JARVIS *et al.* (1976). There is an appreciable overlap between the groups of herbaceous plants and trees, but high values of r_l were found in trees. In conifers they are somewhat larger than minimal values for deciduous trees and other plant species. The lowest minima appear to be in crop species. Leaf resistances reported in this study for shade forest herbs are higher than published estimates for sun herbaceous species (*cf.* WHITEMAN and KOLLER 1967). Our data for sun tree leaves are within the range of resistance values reported in recent literature (*cf.* FEDERER and GEE 1976).

This paper is an attempt to illustrate the variability in leaf resistance within a mixed plant community occurring naturally in the field. Our present knowledge of actual values of leaf resistance over a wide range of field conditions is still meagre. There is a real need for much further investigation of many species naturally forming plant communities. It will be necessary to investigate the responses of species to environmental factors. In ecosystem modelling these responses and variations should be considered if ecosystem or community models are to be correct, accurate and meaningful.

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