BIOLOGIA PLANTARUM (PRAHA)

21(4) : 266—274, 1979

Stomatal Activity within the Crowns of Tall Deciduous Trees under Forest Conditions

P. ELIÁŠ

Institute of Experimental Biology and Ecology, Slovak Academy of Sciences, Bratislava*

Abstract. The variation in stomatal activity within the crowns of *Acer campestre*, *Carpinus betulus* and *Quercus cerris* was measured by vapour exchange porometer on several summer days in an oak-hornbeam forest, in SW Slovakia, Czechoslovakia. Variation resulted from crown position in the forest stand and from leaf position within the canopy. The highest stomatal conductance was in sunlit sun leaves in the upper part of the canopy. Stomatal conductance decreased with increasing depth in the canopy. The steepest decrease was in the upper canopy, in the intermediate zone between fully sunlit and fully shaded leaves, and was caused by the decline in leaf irradiance and in stomatal density. In codominant trees, the conductance in shade leaves at the base of the crown was significantly lower than in the sun leaves at the top of the crown. In a dominant tree, *Q. cerris*, the differences in stomatal conductance were small and most frequently insignificant. Variation in incident light also determined the diurnal variation of stomatal conductance with respect to crown aspect. Differences between sun leaves on the east and west facing aspects of the overstory crown of *Q. cerris* were demonstrated for several days.

The quantitative description of stomatal behaviour is a central problem in models concerning growth, photosynthesis and transpiration of plants and crop surfaces (GOUDRIAAN and VAN LAAR 1978). A knowledge of the stomatal activity within the crowns of trees is expected in the models of the forest canopy.

The aim of this contribution is to describe the variation in stomatal activity within the crowns of tall deciduous trees forming the canopy of an oak-hornbeam forest in SW Slovakia.

MATERIAL AND METHODS

The investigations were made in the I.B.P. Forest Research Site at Báb, SW. Slovakia, Czechoslovakia. The site (see JURKO and DUDA 1970, BISKUPSKÝ 1975) is a natural, deciduous forest representing a typical climate-zonal unit of Central European conditions. The oak-hornbeam forest may be classified as *Primulae veris-Carpinetum* NEUHSL. et NEUHSL. 1964. The mean annual temperature over the period 1931—1960 was 9.3 °C and mean annual

Received 27 September 1978; accepted February 14, 1979

* *Address:* Dúbravská cesta 26, 885 34 Bratislava, Czechoslovakia.

precipitation about 550 mm. The soil is chernozem on loess and dries out markedly during the summer.

The forest stand is formed by *Carpinus betulus* (prevailing species), *Acer campestre*, *Quercus cerris* and *Q. petraea*. It is about 18 m tall and of uneven age (mean about 80 yr). The total leaf area index (woody plants only) is 4 to 6 (Biskupský and Oszlányi 1975, Kubíček 1975). More than 80 % of the leaf area of the trees is accumulated within the layer 10 to 22 m above the forest floor (Oszlányi 1978). The penetration of solar radiation through the canopy varied in individual months; in July, the radiant flux density at heights of 13, 10 and 4 m was 7.3, 10.2 and 3.4 per cent of that at 16 m, respectively (Smolen 1975).

Three sample-trees were chosen for investigation: *Carpinus betulus* L. (approx. 70-year-old, 17 m tall), *Acer campestre* L. (70 yr, 18 m) and *Quercus cerris* L. (80 yr, 21 m). The *Carpinus betulus* and *Acer campestre* sample-trees are classified as codominant trees with relatively well developed crowns constituting, as a rule, the main stand. Their crowns form the main canopy and receive full light from above but little from the sides. The *Quercus cerris* sample-tree is a dominant tree with an extremely strongly developed crown, which projects above the level of the main canopy and receives full light from above and partly from the sides.

Stomatal behaviour was followed at several locations within the crowns of the sample-trees during the clear days in July and August, 1975. A steel tower was installed to provide access to the crown. Sun leaves were measured within the heights 17 to 20 m. Within the canopy, shade leaves were measured at the base of the crowns: in *Carpinus betulus* and *Acer campestre* at 6 m above the ground, but in *Quercus cerris* at 15m (shade intolerant species with short crown). The sun leaves were sampled on south-facing aspects (SE and SW) of the crowns and for *Quercus cerris* also on west and east facing aspects of the crown.

Stomatal activity was measured with a diffusion porometer (Lambda LI-60-S) (Kanemasu *et al.* 1969) in the abaxial epidermis of the hypostomatous leaves and expressed as stomatal conductance in mm s^{-1}. In each location, six leaves were usually measured. In addition, measurements of soil moisture at five depths, solar radiation above and within the canopy, air temperature and vapour pressure were made, see Smolen 1970.

RESULTS

The variation in stomatal activity in relation to crown position within the stand profile, leaf position within the crown as well as to the time of day is illustrated in Fig. 1A for two July days. It is evident that the shade leaves at the bottom of the *Acer campestre* and *Carpinus betulus* crowns exhibit lower stomatal conductance than the sun leaves in the crown tops. These differences were significant in the course of both days. In *Quercus cerris*, a dominant tree, the differences were statistically insignificant throughout the course of the whole day. The stomata of this species were open for the longest time among the species investigated. Fig. 1B shows the spatial and temporal variations in air temperatures, solar radiations and vapour pressure deficits at two different heights within and above the forest stand for the same days as in Fig. 1A. Within the forest canopy (2 m above the ground),

TABLE 1

Vertical gradient of conductance [mm s^{-1}] of abaxial epidermis of leaves within the crown of a codominant *Acer campestre* tree on two different days. $n = 4-6$

Day	Hour of day	Height [m] 16 (sunlit)	Height [m] 16 (shaded)
June 8	12 to 13	1.81 ± 0.14	0.78 ± 0.11
July 8	12 to 13	0.63 ± 0.07	0.47 ± 0.10

air temperature, solar radiation and vapour pressure deficit were much lower than above the canopy (19 or 25 m above the ground).

The vertical variation of stomatal conductance in leaves of the *Acer campestre* codominant tree within the canopy are shown in Table 1 for two

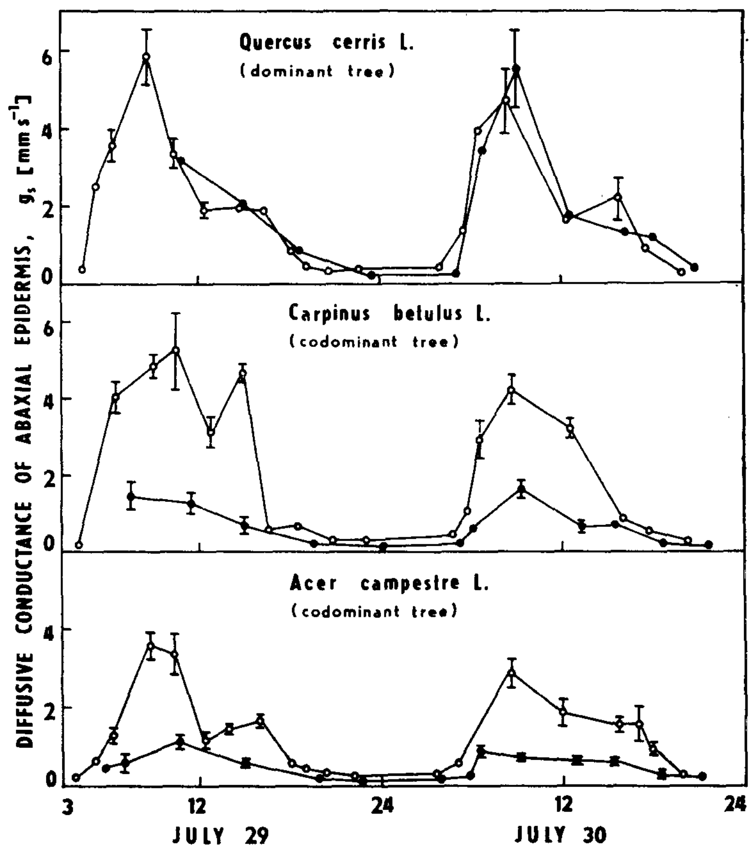

Fig. 1A. Diurnal course of the diffusive conductance of abaxial epidermis in sun (○) and shade (●) leaves of three trees (differing in crown class) in the forest canopy of the oak-hornbeam stand at Báb for two summer days (July 29 and 30, 1975). Means ± one standard error; n = 6.

Height [m]			
14	9	3	2
0.58 ± 0.08	0.41 ± 0.06	0.63 ± 0.09	0.37 ± 0.05*
0.20 ± 0.04	0.11 ± 0.01	0.16 ± 0.03	0.20 ± 0.01

* Seedlings at 0.5 m height.

cloudless summer days. Within the forest canopy, the highest conductances were observed in the upper part of the canopy, *i.e.* in sun leaves exposed to sunlight, while the lowest conductances were in shaded leaves within the

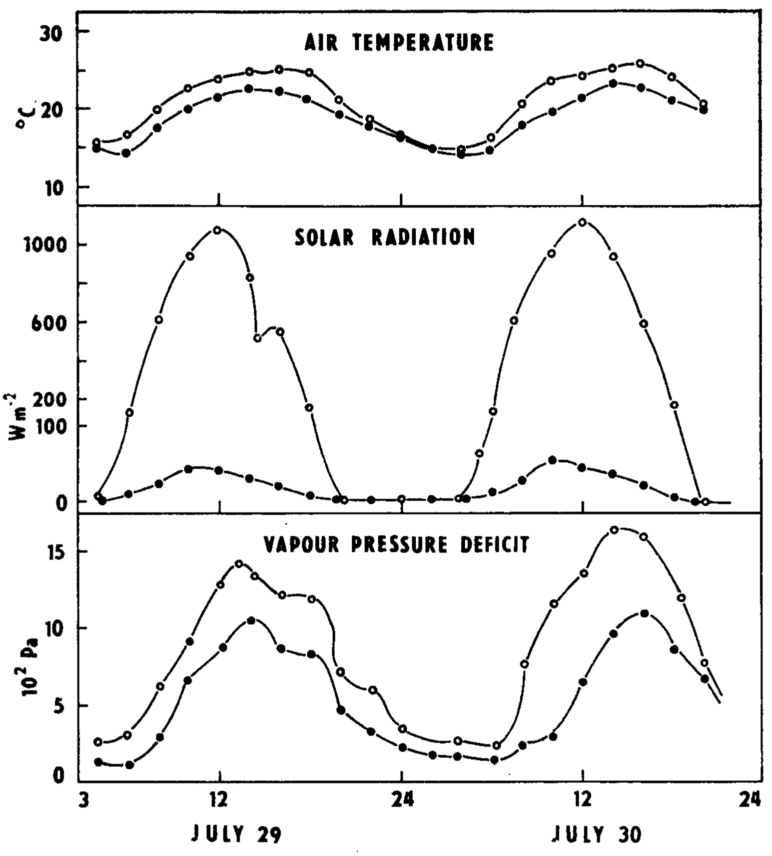

Fig. 1B. Diurnal course of air temperature, solar radiation a. .l vapour pressure deficit at two different heights within (● 2 m above the ground) and above the canopy (○ 19 or 25 m above the ground) for the same days as in Fig. 1A.

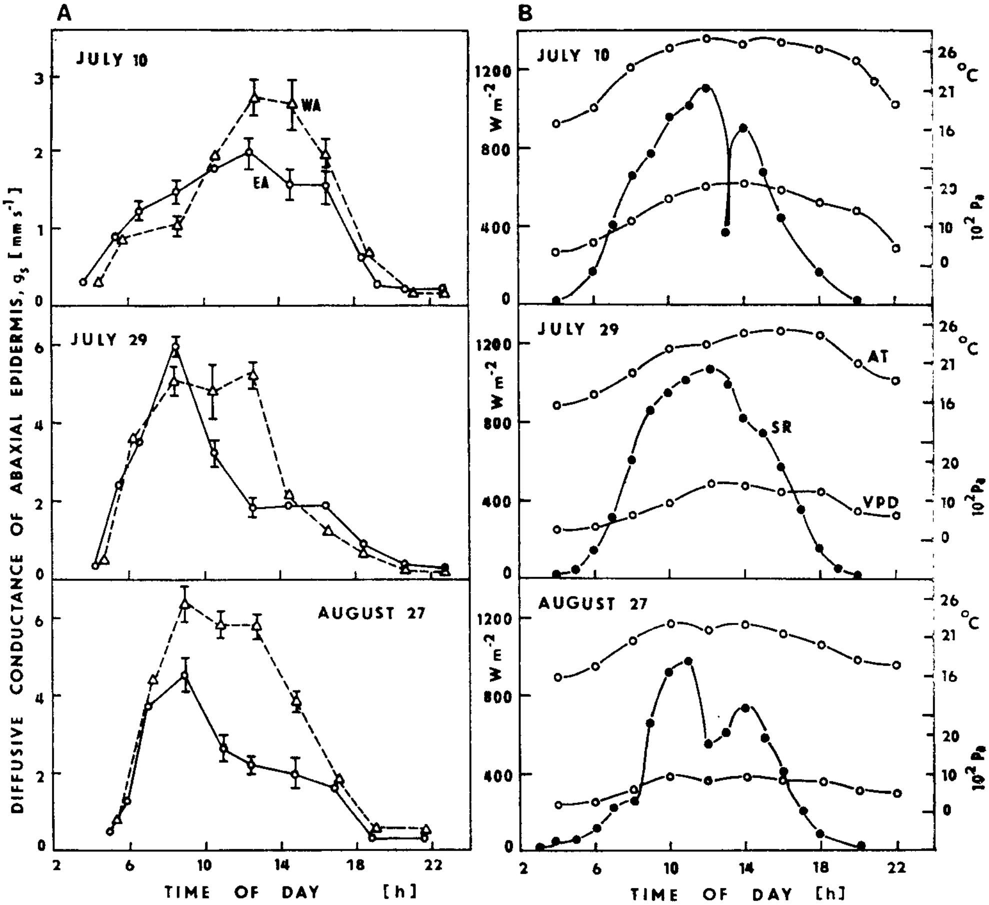

Fig. 2A. Diurnal course of the diffusive conductance of abaxial epidermis in sun leaves situated in the middle part of the overstory *Quercus cerris* crown for two different crown aspects (WA— west-facing, EA — east-facing) in July and August 1975. Means $\pm$ one standard error; $n = 6$. Fig. 2B. Diurnal changes of the air temperature (AT), solar radiation (SR) and vapour pressure deficit (VPD) above the forest canopy during the same days as in Fig. 2A.

lower canopy. The most rapid decrease of the conductance was found in the upper part of the canopy, in the intermediate zone between fully sunlit and fully shaded parts of the crown. Similar results were also obtained for the *Carpinus betulus* codominant tree.

Fig. 2A illustrates the differences in stomatal activity between the foliage on the east and west aspects of the crown of the *Quercus cerris* dominant tree. Stomata on the west side of the crown were opened fully later in the morning, but were open for a long time, and closed frequently later in the afternoon than the stomata on the east side of the same crown. Daily variations in stomatal conductance on both east and west-facing aspects were influenced by the weather and soil moisture content (*cf.* Fig. 2B for meteorological data measured above the canopy). On July 10, a hot sunny day, the stomatal conductance was relatively low (lower than 3 mm s^{-1}) and the vapour pressure deficit was high (noon values about 2.0 kPa). On two other days, July 29 and August 27, the conductance was high, but the vapour pressure deficit was relatively low (see Fig. 2B).

Fig. 3 illustrates the variation in stomatal activity within the crown of the *Quercus cerris* dominant tree. It is evident that at the same time of day there is a relatively large variability in stomatal conductance within a tree crown.

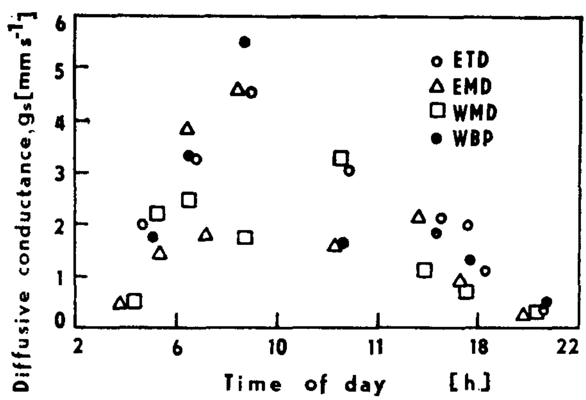

Fig. 3. Diurnal and spatial variations in diffusive conductance of abaxial epidermis in leaves within the crown of dominant *Quercus cerris* sample-tree in an oak-hornbeam forest at Báb (July 30, 1975). For meteorological data see Fig. 1B. Means of six leaves are presented. — E and W — east and west facing side of the crown, T and M — top and middle of the crown, D and P — distal and proximal parts of the limb.

Tables 2 and 3 contain data to illustrate the variation in stomatal conductance in twigs of *Carpinus betulus* and *Acer campestre*. The measurements were made in May and June, 1975 when shoot and leaf growth were still not finished. The differences in diffusive conductance were only significant between the oldest and youngest leaves, *i.e.* between basal and apical leaves of current-year twigs.

DISCUSSION

Previous analysis of the within-crown pattern of ecophysiological features in leaves of mature deciduous trees growing in an oak-hornbeam forest (ELIÁŠ and HUZULÁK 1975, HUZULÁK and ELIÁŠ 1975) have indicated differences in leaf physiological activities. The highest stomatal density was found in the upper parts of the crowns, in sun leaves of the upper canopy, while the lowest stomatal density was in the lower parts of the crowns, in shade leaves of the lower canopy. It is evident that variations in stomatal conductance within the crowns of trees in the forest stand described above are associated with variation in the stomatal density as well as in leaf irradiance within the canopy.

The differences in stomatal resistance between sun and shade needles of *Pinus strobus* growing in forest plantations have been found by WAGGONER and TURNER (1971). Similarly, BEARDSELL *et al.* (1972), WATTS *et al.* (1976)

TABLE 2

The variation in diffusive conductance [mm s^{-1}] of the abaxial epidermis in sun leaves on current-year twigs of *Carpinus betulus* L. The measurements were made with attached leaves in crown-top of the codominant tree (east-facing aspect, 15 m height) on May 11, 1975. $n = 6$

Leaf position on twig (from the base)					
1	2	3	4	5	6
0.56 ± 0.21	0.77 ± 0.12	0.60 ± 0.10	0.63 ± 0.05	0.51 ± 0.09	0.46 ± 0.07

and BEADLE *et al.* (1978) have shown that the highest stomatal conductance is in the upper layer of *Picea sitchensis* stand, while in shaded leaves in the lowest layer the conductance was very low. Similar results for stands of deciduous broad-leaf trees have not been found in any of the literature cited here, except ELIÁŠ (1977, 1978). The author illustrated such differences for *Acer campestre* and other deciduous trees grown in a mixed forest stand. Recently, AUBUCHON *et al.* (1978) published results of their investigation of the leaf conductance within the crown of a dominant white oak (*Quercus alba* L.) in an oak-hickory forest. They showed that the top level of the tree crown experienced higher values for leaf conductance.

The variations observed in stomatal activity within the crowns of the trees, together with the variations in micro-environmental conditions, resulted in variations in transpiration rates. The highest rates were measured in sun leaves at the top of the crowns, and the lowest at the base of the crowns (*cf. e.g.* PARKER 1957, RUTTER 1966). For example, RUTTER (1966) found that the rate of transpiration in the lowest layer of the canopy of *Pinus sylvestris* was about half that in the highest one. In our previous experiments with detached leaves of *Acer campestre* and other forest tree species (see ELIÁŠ 1976), we also found low transpiration rates in shade leaves from the base of the crowns in laboratory conditions. We suggested that high transpiration resistances measured in shade leaves were not only a result of the short term influences of the microclimate, but that they were a fixed property of the leaves.

TABLE 3

The variation in diffusive conductance [mm s^{-1}] of the abaxial epidermis in sun leaves on current-year twigs of *Acer campestre* L. The measurements were made with attached leaves in the upper part of the crown of the codominant tree (south-facing aspect, 16 m height) on May 11, 1975. $n = 4-6$

Leaf	Leaf pair (*a*, *b*) from twig base		
	1	2	3
a	0.34 ± 0.08	0.49 ± 0.08	0.32 ± 0.02
b	0.47 ± 0.13	0.62 ± 0.11	0.31 ± 0.09

In sun leaves in the upper canopy, high net photosynthesis rates have been observed in several coniferous and deciduous trees, *e.g.* by HELMS (1970), WOODMAN (1971), NISHIOKA and NAGANO (*cf.* KIRA 1975), WATTS *et al.* (1976), SCHULZE *et al.* (1977) and AUBUCHON *et al.* (1978) in natural forest conditions. In the oak-hornbeam forest at Báb, OSZLÁNYI (1976) found that the highest proportion of leaf biomass was in the upper third of the crowns of the four main tree species. The values of the specific leaf area in sun leaves of the upper canopy were also high (*cf.* ELIÁŠ 1979). Our results should be supported by these findings. The highest stomatal activity was in the upper canopy where maximum photosynthesis is expected. Similarly, AUBUCHON *et al.* (1978) suggested that photosynthetically-active radiation and leaf conductance are probably most important in causing differing photosynthesis rates in the crown of a dominant white oak in an oak-hickory forest. However, variations in photosynthesis are also associated with many other plant and environmental factors, *e.g.* with the potential of Photosystems I and II to transport electrons (*cf. e.g.* SCHAEDLE 1975, LEWANDOWSKA *et al.* 1977).

Our results indicate that the place of the crown within the forest stand, *i.e.* its vertical position, determines the range of the differences in stomatal activity in various parts of the crown. In codominant trees, the within-crown differences are reinforced by the internal structure of the forest stand. In a dominant tree with the crown projecting above the canopy, the differences are small and most frequently negligible because of a relatively uniform irradiance.

It is suggested that the differences in transpiration and, in some cases, net photosynthesis rates observed by several investigators within the crowns of coniferous and deciduous trees are caused by differences in stomatal activity and leaf or crown microenvironment. In forest conditions, the differences in microenvironment and leaf properties between crown-tops and other crown-parts are more evident than in open-grown trees. These height differences are products of the vertical stratification of the forest ecosystem.

The large variability of physiological activities within the crowns of both open-grown and forest-grown trees is an important feature of this growth form, *viz.* a tree. It should be considered in all samplings, experiments, field measurements as well as in the interpreting of data obtained. The knowledge of the within-crown heterogeneity of any physiological characteristic should be the first and most important requirement of any ecophysiological study of a mature tree. The neglecting of within-crown variations, mainly in large trees, may devaluate experimental results obtained because comparison is impossible.

REFERENCES

AUBUCHON, R. R., THOMPSON, D. R., HINCKLEY, T. M.: Environmental influences on photosynthesis within the crown of a white oak. — Oecologia (Berl.) **35** : 295—306, 1978.

BEADLE, C. L., TURNER, N. C., JARVIS, P. G.: Critical water potential for stomatal closure in Sitka spruce. — Physiol. Plant. **43** : 160—165, 1978.

BEARDSELL, M. F., JARVIS, P. G., DAVIDSON, B.: A null-balance diffusion porometer suitable for use with leaves of many shapes. — J. appl. Ecol. **9** : 677—690, 1972.

BISKUPSKÝ, V. [ed.]: Research Project Báb (IBP), Progress Report II. — Veda, Bratislava 1975.

BISKUPSKÝ, V., OSZLÁNYI, J.: The leaf area index of the timber component of the ecosystem at the research area of the IBP project Báb. — In: BISKUPSKÝ, V. [ed.]: Research Project Báb (IBP), Progr. Rep. II, Pp. 51—60. Veda, Bratislava 1975.

ELIÁŠ, P.: Water-loss rate, transpiration resistances and water saturation deficit of *Acer campestre* leaves during desiccation in the laboratory conditions. — Acta Musei Silesiae, Ser. Dendrol. (Opava) **25** : 107—118, 1976.

ELIÁŠ, P.: Stomatal conductance of *Acer campestre* under forest conditions. — Acta Musei Silesiae, Ser. Dendrol. (Opava) **26** : 9—36, 1977.

ELIÁŠ, P.: Transpiration resistances in leaves of four species of the mature forest trees measured by diffusion porometer in natural forest habitat. — Folia dendrol. **5** : 109—142, 1978.

ELIÁŠ, P.: Some ecophysiological features in leaves of plants in an oak-hornbeam forest. — Folia geobot. phytotax. **14** : 29—42, 1979.

ELIÁŠ, P., HUZULÁK, J.: The density of stomata in the crown of *Acer campestre* L. — Acta Musei Silesiae, Ser. Dendrol. (Opava) **24** : 129—135, 1975.

GOUDRIAAN, J., VAN LAAR, H. H.: Relations between leaf resistance, CO_2-concentration and CO_2-assimilation in maize, beans, lalang grass and sunflower. — Photosynthetica **12** : 241 to 249, 1978.

HELMS, J. A.: Summer net photosynthesis of Ponderosa pine in its natural environment. — Photosynthetica **4** : 243—253, 1970.

HUZULÁK, J., ELIÁŠ, P.: Within-crown pattern of ecophysiological features in leaves of *Acer campestre* and *Carpinus betulus*. — Folia geobot. phytotax. **10** : 337—350, 1975.

JURKO, A., DUDA, M. [ed.]: Research Project Báb (IBP), Progress Report I. — Bot. Inst., Slovak Acad. Sci., Bratislava 1970.

KANEMASU, E. T., THURTELL, G. W., TANNER, C. B.: Design, calibration and field use of a stomatal diffusion porometer. — Plant Physiol. **44** : 881—885, 1969.

KIRA, T.: Primary production of forests. — In: Photosynthesis and Productivity in Different Environment. IBP 3, Pp. 5—40, Cambridge Univ. Press 1975.

KUBÍČEK, F.: Overall organic matter fall in the oak-hornbeam ecosystem. — In: BISKUPSKÝ, V., [ed.]: Research Project Báb (IBP), Progr. Rep. II, Pp. 133—146. Veda, Bratislava 1975.

LEWANDOWSKA, M., HART, J. W., JARVIS, P. G.: Photosynthetic electron transport in shoots of Sitka spruce from different levels in a forest canopy. — Physiol. Plant. **41** : 124—128, 1977.

OSZLÁNYI, J.: The distribution of leaves in the canopy of the oak-hornbeam stand at Báb (I.B.P.). — Oecol. Plant. **11** : 277—289, 1976.

OSZLÁNYI, J.: The distribution of leaf area of trees in an oak-hornbeam forest. — Biologické Práce, Bratislava 1978 (in press).

PARKER, J.: The cut-leaf method and estimation of diurnal trends in transpiration from different heights and sites of an oak and pine. — Bot. Gaz. **119** : 93—101, 1957.

RUTTER, A. J.: Studies in the water relations of *Pinus sylvestris* in plantation conditions. IV. Direct observations on the rates of transpiration, evaporation of intercepted water, and evaporation from the soil. — J. appl. Ecol. **3** : 393—405, 1966.

SCHAEDLE, M.: Tree photosynthesis. — Annu. Rev. Plant Physiol. **26** : 101—115, 1975.

SCHULZE, E.-D., FUCHS, M. I., FUCHS, M.: Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest of Northern Germany. I. Biomass distribution and daily CO_2 uptake in different crown layers. — Oecologia (Berl.) **29** : 43—61, 1977.

SMOLEN, F.: Preparation of meteorological measurements in the plant communities of the Báb Research Site in course of the IBP. — In: JURKO, A., DUDA, M. [ed.]: Research Project Báb (IBP), Progr. Rep. I., Pp. 23—29. Bot. Inst., Slovak Acad. Sci., Bratislava 1970.

SMOLEN, F.: Illumination in the forest stand at the Research Site of Báb. — In: BISKUPSKÝ, V. [ed.]: Research Project Báb (IBP), Progr. Rep. II., Pp. 369—380. Veda, Bratislava 1975.

WAGGONER, P. E., TURNER, N. C.: Transpiration and its control by stomata in a pine forest. — Bull. Connect. agr. exp. Station, New Haven, No. 726, 1971.

WATTS, W. R., NEILSON, R. E., JARVIS, P. G.: Photosynthesis in Sitka spruce [*Picea sitchensis* (BONG.) CARR.]. VII. Measurements of stomatal conductance and $^{14}CO_2$ uptake in a forest canopy. — J. appl. Ecol. **13** : 623—638, 1976.

WOODMAN, J. N.: Variation in net photosynthesis within the crown of a large forest-grown conifer. — Photosynthetica **5** : 50—54, 1971.