Contribution to the ecophysiological study of the water relations of forest shrubs

Príspevok k ekofyziologickému štúdiu vodného režimu lesných krov

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Several leaf indexes (the potential leaf tissue hydration, degrees of succulence and consistency, specific leaf area, and development of leaf area), stomata frequency and size, water saturation deficit (WSD), transpiration rate (TR), and stomatal resistance were determined or followed in five shrub species. The study was made in an oak-hornbeam forest in the IBP Research Area at Báb near Nitra, SW. Slovakia, Czechoslovakia. The development of water saturation deficit and rate of water loss were also studied in the same species exposed to field laboratory conditions. Differences were found between the species in leaf indexes, field physiology and water-holding capacity. Three species groups may be distinguished: 1. *Crataegus oxyacantha* and *Cornus mas* with high WSD-maximum values (more than 30 per cent), higher TR, low stomatal resistances and water holding capacity. 2. *Euonymus verrucosa* and *Ligustrum vulgare* with lower maxima of WSD and high water holding capacity. Some leaf indexes in *Euonymus* and *Ligustrum* are closely related to the first and third group, respectively. 3. An evergreen shrub, *Hedera helix*, with the lowest WSD-maxima (about 20 per cent), very low TR and very high water-holding capacity.

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INTRODUCTION

Woodlands are the most complex natural ecosystems with particular vertical structure and high species diversity. Their structure involves the gradient of growth forms as a result of the adaption to the light intensity gradient within a forest canopy (WHITTAKER 1970). Three main growth form groups — trees, shrubs, and herbs — are adapted to different positions in this gradient. They form the three essential forest layers. In order to characterize water relations of plants of a forest ecosystem, it is necessary to investigate the components of all main growth forms and forest layers.

In the Research Area of the International Biological Programme (IBP) at Báb near Nitra, SW. Slovakia, Czechoslovakia, in an oak-hornbeam forest, the water relations were studied in plants growing in the herb layer (cf. e. g. ELIÁŠ 1975), but also in the shrub and tree layers. The present paper gives some results of the ecophysiological study of various parameters of the shrub water relations. They will be useful for characterizing the plant water relations in deciduous broad-leaved woodlands of Central Europe.

In the oak-hornbeam forest at Báb, shrub species have been followed since the beginning of the ecosystem investigations (cf. BISKUPSKÝ 1970). Their aboveground biomass and production were determined and expressed in the units of dry mass (BISKUPSKÝ 1975a, BISKUPSKÝ et OSZLÁ-

NYI 1975, OSZLÁNYI 1974) and energy (VOOKOVÁ 1976). An attempt at a non-destructive age analysis of *Cornus mas* branches was made by VOOKOVÁ et STEINHÜBEL (1976). In *Cornus mas*, *Ligustrum vulgare*, and *Crataegus oxyacantha* leaves, seasonal changes in the contents of some macronutrients were followed (HUZULÁK 1973) as well as of microelements (UHRÍN 1973, HUZULÁK et UHRÍN 1974). DUDA (1975) used the Sachs' gravimetric method for the determination of seasonal dynamics of *Cornus mas* photosynthesis. Quantitative changes of chlorophylls in *Cornus mas* leaves were followed by MASAROVIČOVÁ (1974), and MASAROVIČOVÁ et DUDA (1975). Correlations were found between the amount of chlorophylls and the phenological phases, and several climatic factors. The authors considered neither the soil moisture nor the plant water status, both of which may have affected the amount of photosynthetic pigments in the plant tissues.

MATERIAL AND METHODS

Description of the site and community

The study was carried out in an oak-hornbeam forest in the IBP Forest Research Area at Báb which is situated in SW. Slovakia (48°10′ N., 17°53′ E., altitude 210 m), in the warm climatic region of Czechoslovakia (VESECKÝ et al. 1958). While the annual mean air temperature reaches about 9.3 °C and the annual mean rainfall amounts from 550 to 650 mm, an average rainfall of only 300 (350) mm occurs during the growing period. Rainfall is the only water source in this area. The soil type is chernozem on loess (see PELÍŠEK 1975) which dried out markedly in summer. For more detailed information on this region and on the research area see JURKO et DUDA (1970), BISKUPSKÝ (1975).

The oak-hornbeam forest at Báb is a residual stand within the agricultural land of S. Slovakia. It may be included into the association *Primulae veris-Carpinetum* R. NEUH. et Z. NEUH. 1964, which represents a thermophilous variant of mesophilous oak-hornbeam forests on loess in the rolling country of S. Slovakia. In the tree layer, *Carpinus betulus* predominates; *Acer campestre*, *Quercus cerris* and *Q. petraea* are also represented. The stands is of uneven age, 78 years old on the average and about 20 m high. In the shrub layer, *Cornus mas* and *Crataegus oxyacantha* occur frequently; *Euonymus verrucosa* and *Ligustrum vulgare* are also present. Most of the woody plants (trees and shrubs) are also represented in the herb layer. The species composition of the herb layer and other typological and phytocenological data have been described by KUBÍČEK et BRECHTL (1970).

Plant material

Five species of forest shrubs were studied: *Cornus mas* L., *Crataegus oxyacantha* L., *Euonymus verrucosa* SCOP., *Hedera helix* L. and *Ligustrum vulgare* L. They are winter-deciduous broad-leaved shrubs, only *Hedera helix* is broad-leaved evergreen shrub. Thermophilous species prevail. The centre of their distribution are warmer deciduous woodlands of Central Europe (the class *Querco-Fagetea*). *Cornus mas* and *Euonymus verrucosa* are Mediterranean and Balkan (Central-European) species, respectively. *Ligustrum vulgare* occupies the largest area of distribution of the shrubs investigated. It has been introduced also in North America. The shrub species mentioned above also occur outside forest stands (woodland), forming frequently shrub stands.

Shrub individuals, of which shoots and leaves were sampled, grow within both the shrub and herb layer. Their whole current year's twigs were cut off. In the field or laboratory study, whole twigs were used or their separated leaves (parts of leaf blades) only (see method descriptions). *Hedera helix* leaves were sampled exclusively from individuals creeping on the forest floor. The current year's (young) and previous year's (old) leaves were distinguished in the last species.

Structural characteristics of leaves

The following five leaf indexes were used as ecophysiological characteristics of the leaf tissues:

1. potential leaf hydratation, expressed as leaf water content at saturation in per cent of leaf dry mass;
2. degree of succulence, i.e., the ratio between leaf water content at saturation and leaf surface; the ratio is expressed in mg water content per cm^2 of leaf surface;
3. degree of consistency, i.e., the ratio between dry mass and leaf surface expressed in mg dry matter per cm^2 of leaf tissue; for an alternative name see e.g. PAGANELLI et PAGANELLI CAPPELLETTI (1971);
4. specific leaf area, expressed as leaf area in mm^2 per leaf dry mass in mg;

5. development of leaf area, i.e. the ratio between leaf area and leaf fresh mass, expressed in dm^2 per g.

Discs of leaf tissue 8 mm in diameter cut regularly out from whole area of leaf blades, involving simple lateral veins, were used for the determination of the leaf indexes mentioned above. In order to obtain leaf water content at saturation, the discs were saturated with water for 3 hours, in the same way and under similar conditions as when determining the water saturation deficit. Samples consisting of 20 (30) discs were oven-dried at 95 °C. Only one disc surface was considered in calculations of the leaf indexes.

Stomata density was determined by the microrelief (replica) method (PAZOUREK 1963, SLAVÍK 1974). Replica prints of epidermis were taken on two different dates, each time from 10 leaves of each species investigated. Shrub leaves are hypostomatous, and the prints were taken only from the abaxial (lower) epidermis. Stomata were counted and measured on the screen of a MP-3 microscope with magnification 500×. In each print, stomata were counted on 15 different spots and their frequency was expressed in their absolute number per mm^2 of leaf surface area. The stomata size was determined preliminarily by measuring the lengths of the twenty guard cells and expressed in μm.

Field physiological measurements

The water saturation deficit (WSD) was determined by both Stocker's method (see SLAVÍK 1974) and the disc method (ČATSKÝ 1960). The shoots and discs were saturated in darkness, in a saturated atmosphere, and at laboratory temperature. The time necessary for saturation of the shoots and discs (8 mm in diameter) was 16 to 24, and 3 to 6 hours, respectively. During the daily course study, the first weighing of the shoots took place in the forest environment. In the case of the disc method, the shoots were transferred to the field laboratory in polyethylene bags (the distance was only 25 to 100 m). Here, discs were rapidly cut out from leaf blades and then weighed and saturated.

Transpiration was estimated gravimetrically by the method of short-term weighing of detached plant parts (see SLAVÍK 1974). The detached shoots were exposed at the original height within the forest canopy for 3 minutes. The transpiration rate (TR) was expressed in terms of water loss per unit dry mass [$mg\ g^{-1}\ min^{-1}$]. The measurements were made at approximately 1-hour intervals from 5 to 21 h. In view of the wide random variation in the actual values of transpiration rate, its daily courses were evaluated from gliding averages, each calculated from 3 consecutive actual values. These averages were used for estimating the other characteristics of plant water relations employed. The estimation of the daily total transpiration was made in the same way as described by RYCHNOVSKÁ et al. (1972) or by KVĚT (1975).

The diffusion resistance of leaves to water-vapour loss was measured with a water-vapour diffusion porometer and a horizontal sensor similar to those described by KANEMASU et al. (1969). In course of a day, 3 to 6 leaves of each species were examined at approx. 2-hour intervals in situ from 5 to 21 h. Only the diffusion resistance of the abaxial leaf surface was measured (hypostomatous leaves) and considered as stomatal resistance. If necessary during the measurement, both the porometer cup and the leaf were shaded to maintain isothermal conditions between the sensor and the leaf surface. Calibration of a porometer followed the procedure described by KANEMASU et al. (1969) and recommended by MORROW et SLATYER (1971).

Soil moisture content was always determined on the days of the other field measurements. Samples were taken from five soil layers: 0 to 10, 10 to 20, 30 to 40, 50 to 60, and 70 to 80 cm. Gravimetric method (drying to a constant weight at 105 °C) was used. Soil moisture is expressed in terms of water weight percentage of total fresh mass.

Solar radiation, air temperature and air humidity were measured within the forest canopy at the height of 2 m above soil surface. The shrub individuals investigated grew at a distance 50 m and less from the sensors. The meteorological instruments and devices, data registration and analysis were described by SMOLEN (1970b). The meteorological data given in this paper were obtained from the Meteorological Station of the Geophysical Institute, Slovak Academy of Sciences, at Báb.

Laboratory measurements

Laboratory experiments were conducted with saturated shoots and leaves. Plant material was sampled one day before an experiment (usually at about 18 h). This material was first saturated in dark vessels for 16 hours. After saturation, the shoots were exposed to light for full photoactive opening of stomata.

Tab. 1. — The comparison of several leaf indexes of six shrub species growing in oak-hornbeam forest at Báb. The numbers express mean values

Species		Water content$_{max.}$ (% d. m.)	Degree of succulence (mg_{H_2O} cm^{-2})	Degree of consistency ($mg_{d.m.}$ cm^{-2})	Specific leaf area ($mm^2mg^{-1}{}_{d.m.}$)	Development of leaf area ($dm^2g^{-1}{}_{f.m.}$)
Cornus mas		303.9	6.95	2.55	38.5	1.2
Euonymus verrucosa		326.7 (223.8+)	6.9	2.55	35.6	1.0
Crataegus oxyacantha		226.3	6.94	3.8	29.1	0.95
Euonymus europaea		(283.0+)	9.8	3.5	28.6	0.74
Ligustrum vulgare		332.8	10.1	3.45	29.2	0.73
Hedera helix leaves	old	239.0	13.0	5.5	18.3	0.54
	young	300.0	11.1	3.7	26.9	0.67

+ actual water content

The transpiration rate at full water saturation was measured in the laboratory. It was estimated gravimetrically from the water loss recorded after a 3 minutes' exposure to the laboratory conditions.

The water-loss curves were determined by long-term drying of the detached and saturated shoots (*Hedera helix* leaves only) under standard conditions (see Slavík 1974). During drying, the samples were weighed first at 30 minutes' intervals up to 3 hours, and then only after 4 and 6 hours of drying.

Development of the water saturation deficit in detached shrub shoots and leaves was determined by long-term drying in the same way as the water loss curves (cf., e.g., Květ et Rychnovská 1965).

Tab. 2. — The stomata density and the length of the guard cells of the stomata in the abaxial epidermis of leaves of five shrub species from oak-hornbeam forest at Báb

Species	Month	Stomata density (number per mm²)		Stomata size (μm)	
		mean	range	mean	range
Crataegus oxyacantha	July	93.2	31.8–159.2	24.5	18.9–30.5
	September	83.0	55.7–119.4	21.5	13.7–31.5
Cornus mas	July	94.2	55.7–151.3	27.8	21.3–32.5
	September	66.9	39.8– 95.5	32.3	26.3–35.7
Euonymus verrucosa	August	185.9	119.4–358.3	21.6	14.7–28.4
	September	215.0	135.4–318.4	23.4	19.9–30.5
Ligustrum vulgare	July	154.5	103.5–230.9	26.5	24.2–31.5
	September	182.3	119.4–267.7	28.1	24.2–31.5
Hedera helix	April	143.3	119.4–191.1	35.2	30.5–38.9
	September	147.9	87.6–278.7	33.5	28.4–36.8

RESULTS AND DISCUSSION

1. Structural characteristics of leaves

Leaf indexes determined for six forest shrub species are given in Tab. 1. The highest potential hydratation was found in *Ligustrum vulgare* leaves, while the lowest was in *Crataegus oxyacantha* leaves. In *Hedera helix*, young leaves exhibited higher values than old leaves. These data corresponded with the potential hydratation in the shoots (Fig. 5), although the latter

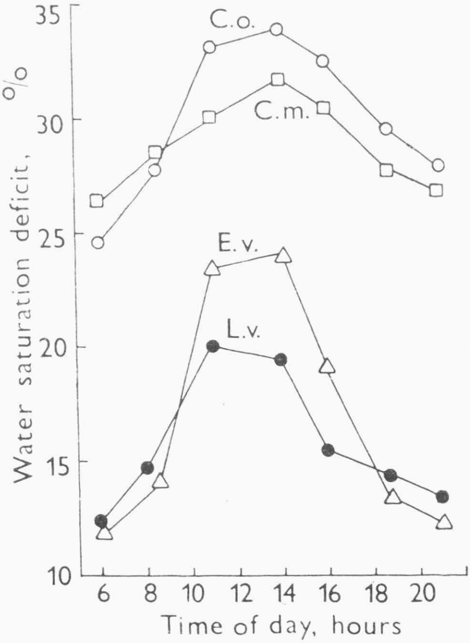

Fig. 1. — Daily courses of water saturation deficits in the leaves of the four species of forest shrubs growing in the oak-hornbeam forest at Báb. Fine, sunny day (July 13). Saturation time of discs: 3 hours; soil moisture content at the depth of 10 to 40 cm: 12.9 per cent. C. o. = *Crataegus oxyacantha*, C. m. = *Cornus mas*, E. v. = *Euonymus verrucosa*, L. v. = *Ligustrum vulgare*.

was somewhat lower. Actual water content was higher in *Euonymus europaea* than in *Euonymus verrucosa* leaves, as it was also found by Goryšina et al. (1961).

The degree of succulence expresses the water content per leaf area. Its values were similar in *Cornus mas*, *Crataegus oxyacantha* and *Euonymus verrucosa*. Higher values found in *Hedera helix*, *Ligustrum vulgare* and *Euonymus europaea* indicate higher succulence of their leaves. They were close to the values found in sun leaves of a mature trees (Huzulák et Eliáš 1975).

The degree of consistency and the specific leaf area are two reciprocal structural characteristics of leaves. In both cases, similar values were found in *Cornus mas* and *Euonymus verrucosa*, and in *Crataegus oxyacantha*, *Ligustrum vulgare* and *Euonymus europaea*. The lowest specific leaf area (the

Tab. 3. — Maximum and minimum values of the leaf water saturation deficit of five shrub species in oak-hornbeam forest at Báb and their differences during the period July—September 1976 (leaf disc method)

Species	Leaf water saturation deficit (%)		
	Maximum	Minimum	Difference
Crataegus oxyacantha	40.0	13.4	26.6
Cornus mas	32.3	3.6	28.7
Euonymus verrucosa	33.5	7.9	25.6
Ligustrum vulgare	28.5	4.0	24.5
Hedera helix	20.2	5.6	14.6

highest degree of consistency) was in *Hedera helix*. High dry matter content in leaves of this species is reflected in low values of the potential leaf tissue hydration related to unit dry mass. This was confirmed by the values of the degree of succulence.

The development of leaf area was also related to the saturation conditions. The values vary between 0.54 $dm^2 g^{-1}$ in *Hedera helix* and 1.24 $dm^2 g^{-1}$ in *Cornus mas*. Pisek et Cartellieri (1939) have shown similar values for several species of forest woody plants.

Stomatal frequency and size are shown in Tab. 2. The highest density and lowest size of stomata were found in *Euonymus verrucosa*, while the lowest stomata density was in *Cornus mas*. In *Hedera helix* leaves, large stomata occur with relatively high frequency. The differences in stomata density

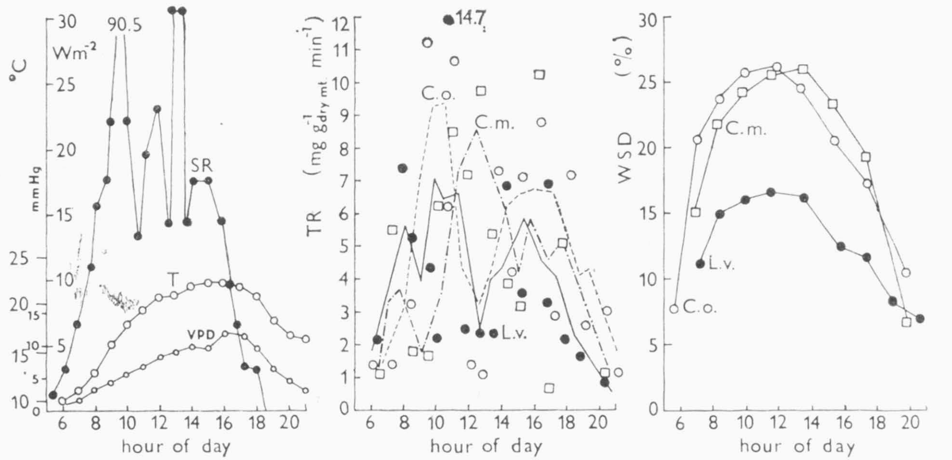

Fig. 2. — Daily courses of several microclimatic and shrub water-relation parameters in the oak-hornbeam forest at Báb (August 24). Left: Solar radiation (SR), air temperature (T) and vapour pressure deficit (VPD) at the height of 2 m within the forest canopy. Middle: Transpiration rate (TR, gliding averages and original data). Right: Water saturation deficit (WSD). Soil moisture content at the depth of 10 to 40 cm: 11.9 per cent. — C. o. = *Crataegus oxyacantha* (○, dotted line), C. m. = *Cornus mas* (□, — . — . —), L. v. = *Ligustrum vulgare* (●, full line)

between sample data may be explained by different light conditions. The values of stomata density given in Tab. 2 lie within the range reported by SALISBURY (1927) for the same species of the woodland flora of the Great Britain. The values obtained in the Báb forest are generally lower than Salisbury's data (*Hedera helix* in the only exception).

2. Field results

Daily courses of the water saturation deficit in the shrub plants are shown in Figs. 1 and 2. Rapid increase of WSD-values is evident in the morning hours. High water deficits were reached at about 10 a.m. During the midday

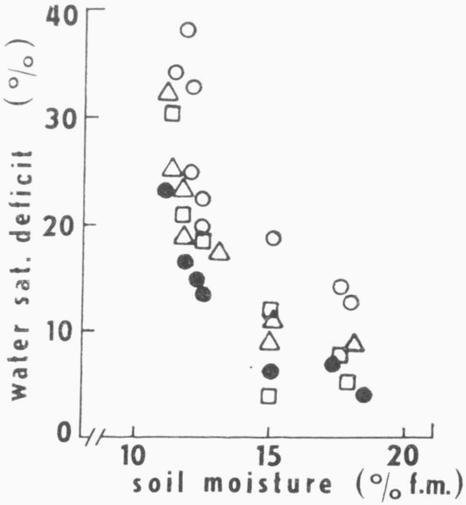

Fig. 3. — Correlation between soil moisture content at the depth of 10 to 40 cm and the water saturation deficit in leaves of four shrub species. Data represent means of the experimental values obtained during the period July—September 1976. — ○ *Crataegus oxyacantha*, △ *Euonymus verrucosa*, □ *Cornus mas*, ● *Ligustrum vulgare*.

they rose only slightly. On both days of measurements, the WSD-values were higher in *Cornus mas* and *Crataegus oxyacantha* than in *Ligustrum vulgare* and *Euonymus verrucosa*.

Fig. 1 illustrates the daily courses of WSD determined by the disc method. On the day of measurement (13th July), soil moisture content was 12.8 per cent at the depth of 10 to 40 cm. The daily percentage variation of WSD (V %), expressing the range of daily fluctuations of WSD (see PAGANELLI et PAGANELLI CAPPELLETTI 1971), was calculated for the species investigated. The highest V % values were obtained in *Euonymus verrucosa* (132.7 %), while the lowest were in *Cornus mas* (33.5 %).

Fig. 2 shows the daily courses of WSD in shoots of three species determined by Stocker's method. On this day (24th August), the transpiration rate was followed simultaneously in the same species. Mean soil moisture content was 11.9 per cent at the depth of 10 to 40 cm. The different positions of the maximum WSD-values in *Cornus mas* and *Crataegus oxyacantha* correspond with the different peaks of the transpiration rate curves. On this day, the maximum WSD-values in *Euonymus verrucosa* were slightly higher than those of the former day (17.8% again 16.5%).

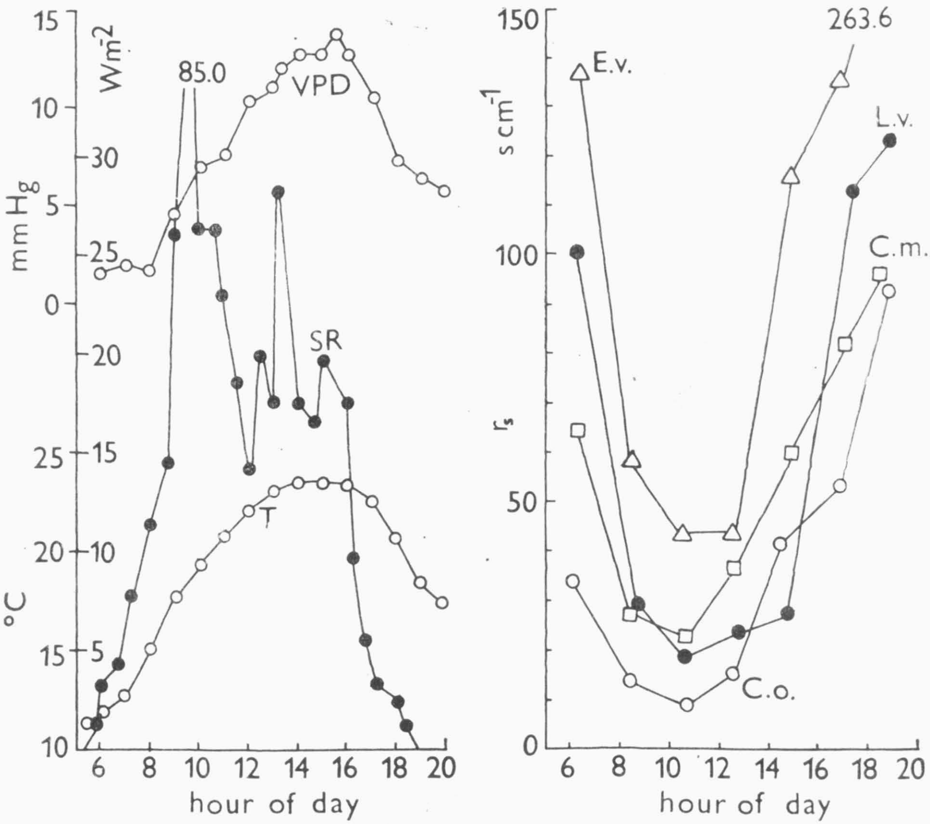

Fig. 4. — Daily courses of stomatal resistance for four species of shrubs growing in the oak-hornbeam forest at Báb (right), and of vapour pressure deficit (VPD), solar radiation (SR) and air temperature (T) at the height of 2 m within the forest canopy (left). (August 25). For legend see Fig. 1.

A comparison of the maximum and minimum WSD-value for the shrub species investigated and of their differences is given in Tab. 3. They were chosen from WSD-values obtained by the disc method during the period of July to September 1976. The highest WSD-maxima were found in *Cornus mas*, the lowest were in *Hedera helix* leaves. In *Cornus mas* and *Euonymus europaea*, growing in dry thermophilous oak-tree forest in the Kodr Mountains (Moldavskaya S.S.R.), Vitko (1975) recorded higher maximum than ours. On the other hand, Jeanrenaud et al. (1965) found lower values of WSD in *Cornus mas*, growing in the mountain region of Rumania. This is in agreement with the results of Gračanin et al. (1970), showing that the same species behaves differently in two different communities.

The difference between the maximum and minimum WSD characterizes the water balance of a plant better than the mere maximum values. This criterion was used for the evaluation of the stability of water balance in the species investigated. The following sequence of species was obtained (Tab. 3,

Tab. 4. — Daily maxima of transpiration rate, daily total transpiration (both parameters for August 24), and minimum stomatal resistance (for August 25) for three shrub species growing in the oak-hornbeam forest at Báb

Species	Daily maximum of transpiration rate [g g^{-1} (d.m.) min^{-1}]	Daily total transpiration [g g^{-1} (d.m.) d^{-1}]	Minimal stomatal resistance [s cm^{-1}]
Crataegus oxyacantha	11.2	5.66	6.7
Ligustrum vulgare	14.7	5.35	10.4
Cornus mas	10.3	4.21	19.5
Euonymus verrucosa	—	—	30.4

from the most to the least stable water balance): *Hedera helix*, *Ligustrum vulgare*, *Euonymus verrucosa*, *Crataegus oxyacantha* and *Cornus mas*.

The relationship between soil moisture content and leaf WSD determined by disc method is shown in Fig. 3. Negative correlation is apparent for all species. The correlation coefficient values ranged between −0.314 and −0.757. The rapid increase of WSD at small changes in soil-moisture content are typical of all species investigated at the low availability of soil water.

The curves illustrating the daily courses of transpiration rate are presented in Fig. 2. The complex light conditions within the forest canopy (moving sunflecks) as well as the heterogeneity of plant material used in the measurements caused a large variation of the values recorded by the gravimetric method. Such variability is also known in plants of other ecosystems (see e.g. Rychnovská et al. 1972, Květ 1975). In *Cornus mas*, the daily course of transpiration rate differed from the two other species investigated. This difference influenced the daily course of WSD in the same species and day.

Table 4 gives a comparison of the amounts of water transpired over the whole day (daily transpiration) and maximum transpiration rates recorded during the study day in the three shrub species. They are similar to the data obtained for forest herbs (Eliáš 1975), but low in comparison with the values recorded by Rychnovská et al. (1972) for several species of grassland

Tab. 5. — The maximum transpiration rate of fully saturated shoots and the rate of water loss of shoots of five forest shrubs for two different time periods during dessication under field laboratory conditions. The rates are expressed in mg g^{-1} dry mass min^{-1}

Species	Maximum rate of transpiration		Water loss rate for 22th July	
	July 1	July 22	0—30 min.	60—120 min.
Crataegus oxyacantha	11.6	5.2	2.3	4.4
Cornus mas	11.8	7.8	4.4	2.7
Ligustrum vulgare	13.1	5.2	1.8	1.2
Euonymus verrucosa	10.3	2.4	1.5	3.1
Hedera helix	5.2	0.9	0.96	0.89

Laboratory conditions: for July 1 27 °C, 46% RH; for July 22 25—26 °C and 66% RH communities or by KVĚT (1975) for seven plant species colonizing a fishpond shore.

The daily course of diffusion resistance of the abaxial epidermis was similar in all species (Fig. 4). On the study day (August 25) mean soil moisture, at the depth of 10 to 40 cm, was 11.9 % and the daily maxima of WSD in *Crataegus*, *Cornus*, *Euonymus*, and *Ligustrum* were 40.0, 21.1, 20.4, and 19.6 per cent, respectively. Stomatal resistance decreased after sunrise as a result of the photoactive opening of stomata, and increased during the

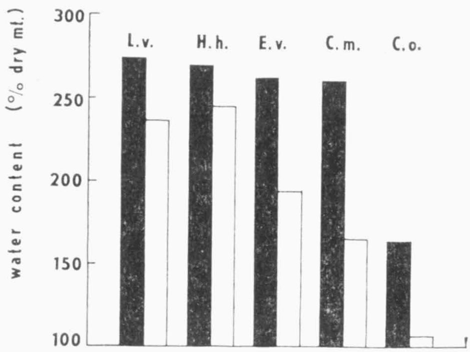

Fig. 5. — The water content in shoots of five species of forest shrubs at full saturation (black columns), and after 6 hours dessication in laboratory (white columns). Drying conditions: temperature 25 to 26 °C, relative air humidity 66 per cent (July 22). — L. v. = *Ligustrum vulgare*, H. h. = *Hedera helix*, E. v. = *Euonymus verrucosa*, C. m. = *Cornus mas*, C. o. = *Crataegus oxyacantha*.

afternoon. Stomata closed afternoon and were fully closed before sunset. High stomatal resistance in the evening indicates this situation. Stomatal closing about midday may be caused by several factors, e.g. low illumination within the forest canopy, high vapour-pressure deficit or high water-saturation deficit (cf. e.g. MOLDAU 1975).

Differences exist between the species in the level of the stomatal resistance values. Of the species studied, *Euonymus verrucosa* showed the highest stomatal resistances (small stomata), while the lowest were those in *Crataegus oxyacantha* (Tab. 4). The maximum transpiration rate values correspond with the minimum stomatal resistance values. Minimum values of stomatal resistance recorded on the day of measurement (Tab. 4) were far higher than those obtained for sun leaves of the mature trees (ELIÁŠ 1976).

3. Laboratory results

The results of the long-term drying of the shoots and leaves of the shrubs, under standard conditions are shown in Tab. 5 and in Figs. 5 and 6.

Fig. 5 shows the water content in shoots at saturation and after 6 hours of drying. At saturation, a low water content (in per cent of dry matter) was found in *Crataegus oxyacantha*. After drying, the highest water content was in *Hedera helix* leaves, the lowest was in *Crataegus oxyacantha* shoots. However, the greatest decrease of water content was found in *Cornus mas*.

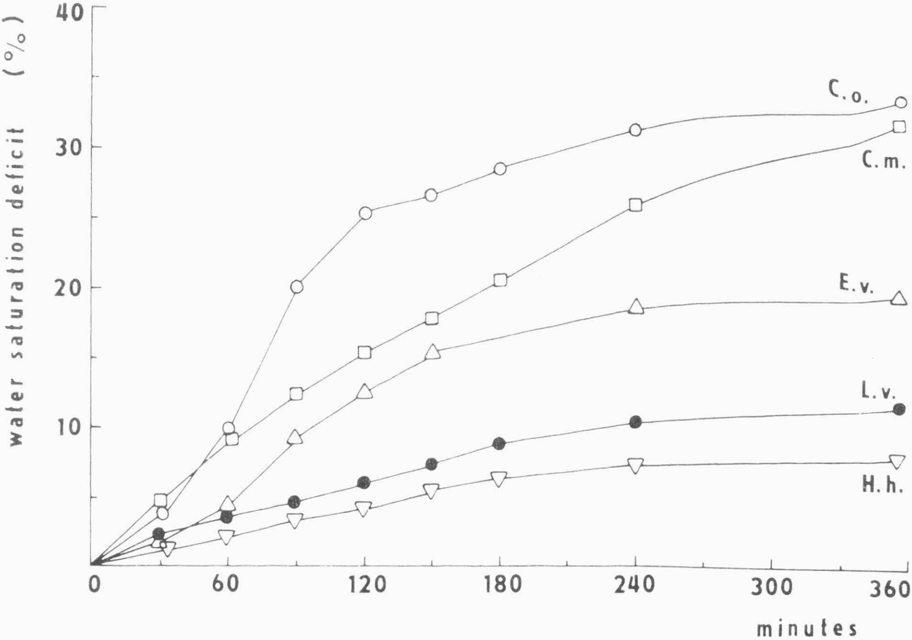

Fig. 6. — Development of the water saturation deficit in detached shoots of five species of forest shrubs during drying under laboratory conditions (Temperature 25 to 26 °C, relative air humidity 66 per cent). (July 22). For legend see Fig. 5.

A comparison of the rates of water loss for two different time period of the long-term drying of shoots is given in Tab. 5. In the first period (0 to 30 minutes from the beginning of drying), the highest rate was found in *Cornus mas*, but in quasilinear phase (60 to 120 minutes) it was in *Crataegus oxyacantha*. *Hedera helix* loses water at the lowest rate. In this species, Cetl (1957) also found similar low values of the rate of water loss over the quasilinear phase.

The development of WSD in shoots of five shrubs under laboratory conditions is shown in Fig. 6. WSD develops most slowly in *Hedera helix* and *Ligustrum vulgare* (in the plants with the highest degree of succulence), and most rapidly in *Cornus mas* and *Crataegus oxyacantha*. These findings are in good agreement with the results of the field measurements.

CONCLUSIONS

In the gradient of growth forms within the forest canopy, the forest shrubs have intermediate position between trees and herbs. They are adapted to lower light intensity than trees and they frequently form a shrub layer. From the point of view ecophysiology they have been followed only extensively.

Differences exist between the shrub species investigated in their leaf indexes, field physiology and water-holding capacity. Similarly, e.g., Jeanrenaud et al. (1963), Eliáš (1975) and others found different responses of several water-relations characteristics of forest plants to the same environmental conditions. RACHMANINA (1970) is of the opinion that the water relations of a plant are primarily determined by its genetically fixed features. Environmental conditions have, in this case, only a secondary importance.

During the experiments with the long-term drying of plant organs under laboratory conditions, the species with a high degree of succulence exhibited a high water-holding capacity as compared with the species with a low degree of succulence. Their resistance to drying appears high. This is in agreement with the results of KVĚT et RYCHNOVSKÁ (1965) who found a high water-retention capacity to characterize succulent and semi-succulent species of herbs. Similarly, CUNNINGHAM et STRAIN (1969) found a positive correlation between the degree of consistency and water-loss rate under laboratory conditions. On the other hand, e. g., SIWECKI et KOZLOWSKI (1973) failed to find a direct correlation between the rate of water loss under standard conditions and structure of leaves of six *Populus* clones.

Hedera helix, an evergreen shrub with a high degree of both succulence and consistency, and with a low specific leaf area, development of leaf area, water saturation deficit and transpiration rate under both field and laboratory conditions, has a special position among the species investigated. RACHMANINA (1970) found the intensity of physiological processes to be in correlation with the length of life duration of leaf tissue: the longer the life span of the leaf apparatus, the slower the processes of water loss and vice versa. POOLE et MILLER (1975) have concluded that evergreen sclerophyllous shrubs possess a higher degree of stomatal control and greater cuticular resistance to water loss than do drought-deciduous shrubs; this aids them in maintaining a favourable leaf-water balance year-round.

SÚHRN

Na výskumnej ploche Medzinárodného biologického programu v Bábe pri Nitre (juhozápadné Slovensko) autor sledoval päť druhov krov, ktoré tu rastú v dubovo-hrabovom lese. Stanovil potenciálnu hydratáciu listového pletiva, stupne sukulencie a konzistencie listov, špecifickú listovú plochu a rozvoj listovej plochy, ako aj hustotu a veľkosť prieduchov. V priebehu niekoľkých letných dní sledoval vodný sýtostný deficit (VSD), intenzitu transpirácie a odpor prieduchov na prirodzenom stanovišti. Vývoj vodného sýtostného deficitu a výdaj vody počas vysušovania výhonkov sa sledoval v podmienkach poľného laboratória. Druhy sa navzájom líšili v sledovaných listových indexoch, v poľnej fyziológii i vo vodnej retenčnej kapacite. Rozlíšili sa tri skupiny druhov: Prvá skupina je charakterizovaná vysokými maximami VSD (viac než 30%), vyššou intenzitou transpirácie, nízkymi odpormi prieduchov a nízkou vodnou retenčnou kapacitou. Patria sem druhy *Crataegus oxyacantha* a *Cornus mas*. Druhá skupina obsahuje *Euonymus verrucosa* a *Ligustrum vulgare* s nižšími maximami VSD a vysokou vodnou retenčnou kapacitou. *Euonymus* sa v niektorých indexoch blíži viac prvej skupine, kým *Ligustrum* tretej. Tretiu skupinu tvorí stálozelený ker *Hedera helix* s najnižšími maximálnymi hodnotami VSD (okolo 20 %), veľmi nízkou intenzitou transpirácie a veľmi vysokou vodnou retenčnou kapacitou. Druhy s vysokým stupňom sukulencie prejavovali vysokú vodnú retenčnú kapacitu oproti rastlinám s nízkym stupňom sukulencie.

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