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Water deficit of plants in an oak-hornbeam forest

Vodný deficit rastlín v dubo-hrabovom lese

Pavol Eliáš

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The water deficit of four tree species, five shrub species, seven vernal ephemeroids and sixteen summer herbs was studied in the natural environment of an oak-hornbeam forest in the IBP research area of Báb (southern Slovakia, Czechoslovakia). The water deficit was established as a water saturation deficit (w.s.d.) and expressed in terms of percentage difference from water content at full saturation. Use was made of both Stocker's method of saturating whole plant organs and of Čatský's leaf disc method. The vernal ephemeroids that grew under conditions of sufficient water supply in the entire soil profile attained low maximal w.s.d. values. In summer, during the dry period of the year, the highest w.s.d. maxima were found in herbs; they were lower in shrubs and lowest in adult trees. The vertical gradient of the water deficit in the forest-plant leaves, prevailing under stress conditions, corresponds with the reversed distribution gradient of the root systems of plants and of soil moisture. In the tree species the maximal w.s.d. values of the leaves increase from the sun-facing leaves of adult trees through the shade leaves of adult trees, shrub leaves as far as down to the leaves of seedlings. The response of the individual species to the same level of soil moisture was different. The water balance of plants (expressed as the amplitude of extreme w.s.d. values) is most stable in adult trees and least stable in herbs.

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INTRODUCTION

The water deficit of a plant is characteristic of a situation in which cells and tissues are not fully turgescent (Kramer 1969). It is an indication of the state of water balance of the plant. Quantitatively it may be expressed by diverse parameters such as the water saturation deficit, relative water content, water potential, or osmotic potential. It reflects the hydration level of plant tissues (cf. e.g. Slatyer 1967, Kozlowski 1968, Hsiao 1973).

The water deficit of plants may be used to appraise the water balance of the plant community. Gračanin et al. (1970) reports "that (a) the two communities have their own range of water deficit values, (b) the water deficit values are dependent on the capability of the species to regulate their water regime, (c) the same species behave differently within the two communities, (d) the water deficit of leaves can be used as an indication of the water status of the site and plants, and consequently may have a significant place in the synecology and synchorology of plant communities". As a matter of fact, these authors studied only woody species.

Previous investigations of the water relations of forest plants concerned only individual components of the forest ecosystem: herbs (e.g. ELIÁŠ 1972, 1975a, b), shrubs (ELIÁŠ 1978) and trees (HUZULÁK et ELIÁŠ 1975a, b, c, 1976, ELIÁŠ 1976a, b). This paper presents data on the water deficit of herbs, shrubs and trees in an oak-hornbeam forest. The aim of these determinations was to ascertain:

1. the naturally occurring range of water deficit in the investigated community;
2. the influence of the different vertical distribution of root systems in forest plants on the water deficit and water balance in the plants;
3. the behaviour of individuals of tree species of different age (seedlings, shrubs and adult trees);
4. the response of the species to different levels of soil moisture as far as water deficit is concerned;
5. the response of the species to soil dryness in the summer season of the year.

MATERIAL AND METHODS

The experiments were made in the oak-hornbeam forest of the IBP Forest Research Area at Báb near Nitra, SW. Slovakia, Czechoslovakia (48°10′ N. lat., 17°53′ E. long., 210 m alt.). The annual average air temperature and precipitation is 9.3 °C and 570 mm, respectively. The soil type is chernozems on loess (PELÍŠEK 1975) drying-out markedly in summer. The only water source is rain water.

The oak-hornbeam forest at Báb is classified as belonging to *Primulae veris-Carpinetum* NEUHÄUSLOVÁ et NEUHÄUSL 1964, a thermophilic variant of mesophilic oak-hornbeam forests in the loessal rolling country of southern Slovakia. The Báb forest is a relic forest stand (mean age 78 years, mean height 20 m) situated in an agricultural landscape under intensive tillage. *Carpinus betulus* along with *Quercus petraea*, *Q. cerris* and *Acer campestre* dominate in the tree layer. The shrub layer includes *Cornus mas*, *Crataegus oxyacantha*, *Euonymus verrucosa*, *Ligustrum vulgare*, *Euonymus europaea* and other species. The ground layer is rich in *Asperula odorata*, *Melica uniflora*, *Mercurialis perennis*, *Pulmonaria officinalis*, *Viola* sp. div., *Galeobdolon luteum*, *Glechoma hirsuta*, *Geum urbanum*. The other species comprise *Polygonatum latifolium* and *P. multiflorum*, *Convallaria majalis*, *Sanicula europaea* and *Hedera helix*. The vernal synusium is rich in *Corydalis solida*, *Anemone ranunculoides*, *Isopyrum thalictroides*, *Ficaria verna*, *Pulmonaria officinalis* (vernal shoots), locally *Gagea lutea* and *Lathyrus vernus*. The experiments were made with the species listed above.

Four tree species, five shrub species and twenty-three herb species (seven of them in the vernal synusium) were selected for estimating the water deficit of the plant community. Water deficit was established as water saturation deficit. Two methods were used: Stocker's method of the saturation of parts of plants (SLAVÍK 1974) and the method of saturating discs of leaf tissue in polyurethane foam (ČATSKÝ 1960). In both cases, the water saturation deficit was calculated according to the formula

$$\text{w.s.d.} = \frac{\text{saturated weight} - \text{initial (fresh) weight}}{\text{saturated weight} - \text{dry weight}} \times 100\ (\%)$$

In the first method whole plants (herbs) or current year's twigs (woody plants) were saturated for 16–24 hours, in the second case the discs were saturated for 3–6 hours, always in three- to sixfold replicate. Twenty discs of 8 mm in diameter were cut from leaves of six to ten plants or twigs and saturated in twenty disc samples. The saturation was acheived in darkness, in an atmosphere saturated with water vapour at laboratory temperature. Since mature leaves were treated, the growth error was not considered. The samples were oven-dried at 95 °C for 24 hours.

The actual water deficit in the plant community was estimated in the afternoon hours, at the time of the diurnal maximum, within a short time interval (not exceeding two hours), in a representative number of tree, shrub and herb species. The upper sun-facing leaves from the crown tops of adult trees (from a height of 18–20 m) and the shade leaves from the crown bottoms (from a height of 3 m) were particularly studied. The cut-off plants or twigs were transported in plastic bags to a nearby field laboratory (at a distance of 25—50—100 m), where the disc were cut and all the other operations done. The number of the samples was chosen so as to ensure that the processing would not exceed 20 minutes.

The daily dynamics of the water deficit of leaves was followed from early morning until late evening on three consecutive days in July. The samples were taken at 2 to 3 hourly intervals.

The water saturation deficit was established on the following dates: April 28 (species of vernal synusia), July 1, 5—8, 13, 15, 20, 22, 27 and 28; August 3, 10, 18 and 25, and September 8. On the same dates, the soil-moisture content was determined at five different depths: 0—10, 10—20, 30—40, 50—60 and 70—80 cm. The soil moisture content was determined gravimetrically: the soil was oven-dried at a temperature of 105 °C for 24 hours and the soil moisture content was expressed in terms of fresh weight percentage.

Air temperature and humidity on the testing days were recorded with thermohydrographs placed at three different heights: at 15 m, 3 m and 0.1 m. Further data on air temperature, global radiation and vapour pressure deficit were taken over or calculated from the data of the Meteorological observatory of the Geophysical Institute of the Slovak Academy of Sciences at Báb near Nitra, taken with sensors mounted at heights of 0.5 m, 2 m and 19 or 25 m above the soil surface, within or above the forest stand.

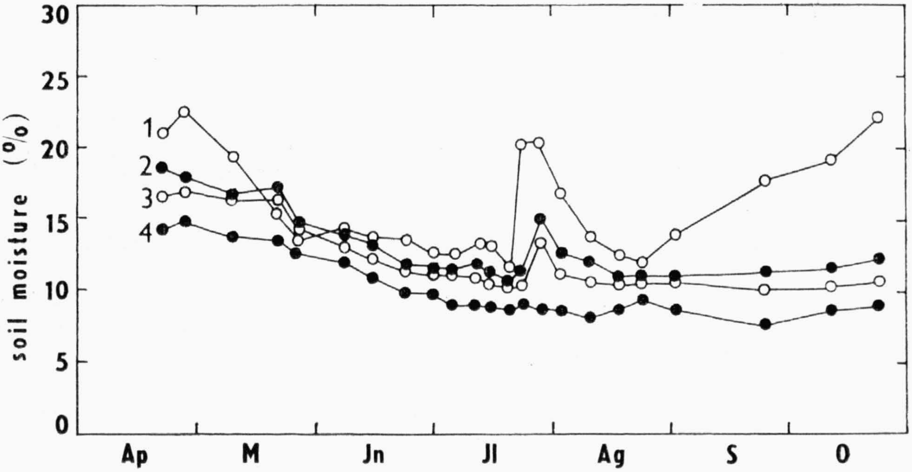

Fig. 1. — Dynamics of soil moisture (in % of fresh weight) at four different depths under oak-hornbeam forest at Báb during growing period of 1976. Soil depth: 1 — 0.10 to 0.20 m, 2 — 0.30 to 0.40 m, 3 — 0.50 to 0.60 m, 4 — 0.70 to 0.80 m.

RESULTS

Soil moisture in the oak-hornbeam forest

Figure 1 illustrates the dynamics of soil moisture at four different depths of the soil in the oak-hornbeam forest at Báb during the growing period of 1976. The high soil moisture in the entire soil profile in April is in strong contrast with the low soil moisture in June and July. Even heavy rains in the summer months did not saturate the entire soil profile and the deeper soil horizons continued to be dry (Fig. 2). In the course of the subsequent rainy months, the water supply in the soil is replenished approximately to the vernal level. The soil moisture content is most variable in the uppermost soil horizons.

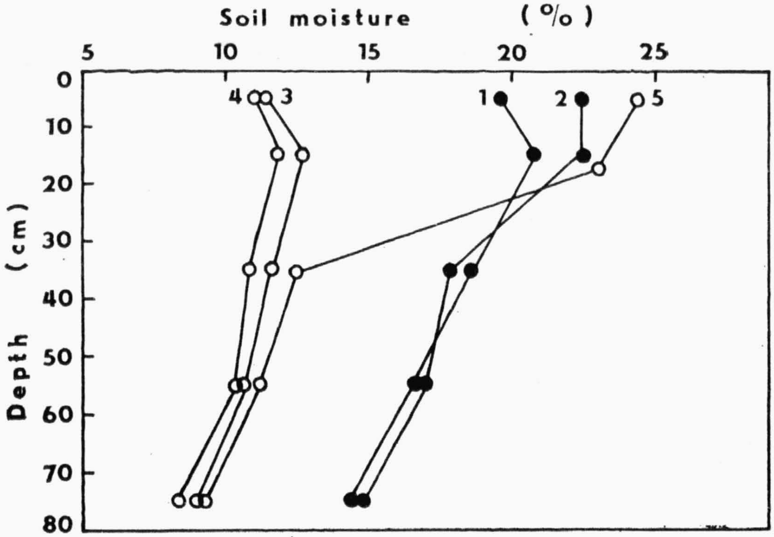

Fig. 2. — Soil moisture gradient in soil of oak-hornbeam forest at Báb for selected days of 1976. Soil moisture content is in % of fresh weight. Open symbols express summer days, closed ones spring days. Dates: 1 — April 22, 2 — April 28, 3 — July 6, 4 — July 20, 5 — July 23.

Afternoon patterns of water deficit in the forest plants

The water deficit of plants in the oak-hornbeam forest was estimated in two different periods: during the dry summer period under a soil water stress, and during the wet period with a higher soil moisture (especially in the upper horizons).

The results of estimating the actual water deficit of plants by Stocker's method in the early afternoon hours during the dry summer period are presented in Fig. 3. The highest values were found in the herbs, namely from 20.4 per cent in *Sanicula europaea* up to 42.6 per cent in *Glechoma hirsuta*. Lower w.s.d. values were ascertained in the shrubs: from 15.5 per cent in *Carpinus betulus* up to 22.4 per cent in *Euonymus verrucosa*, and the lowest values were in trees (10.9 to 23.0 per cent). Tree seedlings exhibited values closer to those of herbs (23.3 per cent in *Quercus cerris* and 29.2 per cent in *Acer campestre*). A particular position among shrubs was held by *Hedera helix* and, among herbs, by *Polygonatum latifolium* which exhibited very low w.s.d. values.

The determination of the water saturation deficit of leaves by Čatský's disc method a few days later (July 5) revealed similar conditions, only the w.s.d. values were generally higher (Fig. 4). Again, the highest w.s.d. values were found in the herbs (31.5 to 61.1 per cent, save *Polygonatum latifolium*), they were lower in the tree seedlings (28.0 to 33.6 per cent) and in the hrubs (20.1 to 38.3 per cent, except *Hedera helix*), and the lowest in the trees (11.3 to 22.0 per cent). The water deficit was higher in shade leaves from the lower parts of the canopy than in the sun-facing leaves from its upper portions.

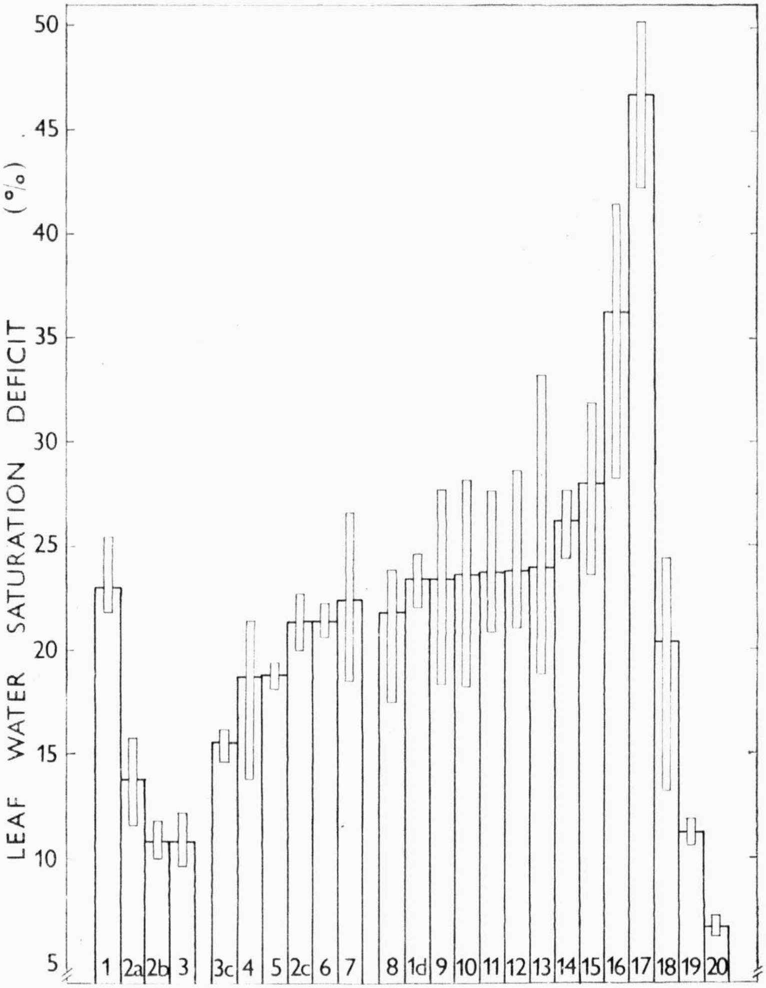

Fig. 3. — Afternoon pattern of water saturation deficits in whole plants (herbs) or current year's twigs (woody plants) of 20 forest species (July 1, 1976). Stocker's method, saturation time 16 hours. The columns indicate mean values, small rectangles on their tops ranges of values in sample series. — Adult trees: 1 *Quercus cerris*, 2 *Acer campestre*, 3 *Carpinus betulus*, a — sun leaves from top of crown, b — shade leaves from bottom of crown. Shrub layer species: 2c *Acer campestre*, 3c *Carpinus betulus*, 4 *Ligustrum vulgare*, 5 *Cornus mas*, 6 *Crataegus oxyacantha*, 7 *Euonymus verrucosa*. Herb layer species: 1d *Quercus cerris* seedlings, 2d *Acer campestre* seedlings, 8 *Geum urbanum*, 9 *Pulmonaria officinalis*, 10 *Galeobdolon luteum*, 11 *Brachypodium silvaticum*, 12 *Dactylis polygama*, 13 *Viola mirabilis*, 14 *Mercurialis perennis*, 15 *Fragaria moschata*, 16 *Asperula odorata*, 17 *Glechoma hirsuta*, 18 *Sanicula europaea*, 19 *Polygonatum latifolium*, 20 *Hedera helix*.

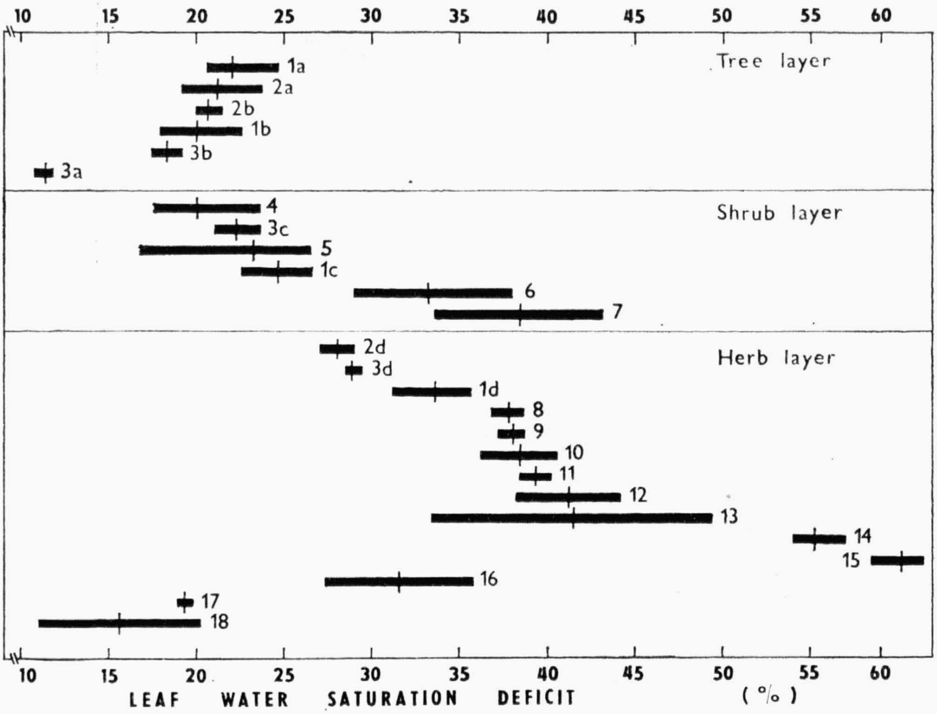

Fig. 4. — Afternoon pattern of water saturation deficits of leaves of 18 forest plant species o oak-hornbeam forest at Báb in drought summer period (July 6, 1976). Leaf-disc method, satuf ration time 6 hours. — Adult trees: 1 *Acer campestre*, 2 *Quercus cerris*, 3 *Carpinus betulus*,- a — sun leaves from crown top, b — shade leaves from crown bottom. Shrub layer species: 1c *Acer campestre*, 3c *Carpinum betulus*, 4 *Cornus mas*, 5 *Ligustrum vulgare*, 6 *Crataegus oxyacantha*, 7 *Euonymus verrucosa*. Herb layer species: 1d *Acer campestre* seedlings, 2d *Quercus cerris* seedlings, 3d *Carpinus betulus* seedlings, 8 *Viola mirabilis*, 9 *Pulmonaria officinalis*, 10 *Geum urbanum*, 11 *Mercurialis perennis*, 12 *Fragaria moschata*, 13 *Galeobdolon luteum*, 14 *Glechoma hirsuta*, 15 *Asperula odorata*, 16 *Sanicula europea*, 17 *Polygonatum latifolium*, 18 *Hedera helix*.

Different conditions were encountered in the wet summer period, after a heavy rainfall (37.7 mm on July 21) as illustrated in Fig. 5 for August 3. The lowest values were found in herbs, higher values in shrubs and the highest ones in tree leaves. Now, the w.s.d. values were higher in the sun leaves of the upper part of the tree crowns than in shade leaves of the lower parts.

Daily patterns of the leaf water-deficit

Fig. 6 shows the daily course of the water saturation deficit in leaves of six herb species, one seedlings, six shrub species and three adult tree species, established by the disc method on three consecutive days of July. Vertical air-temperature gradients in the forest during the day, as recorded by thermographs, are shown in Fig. 7.

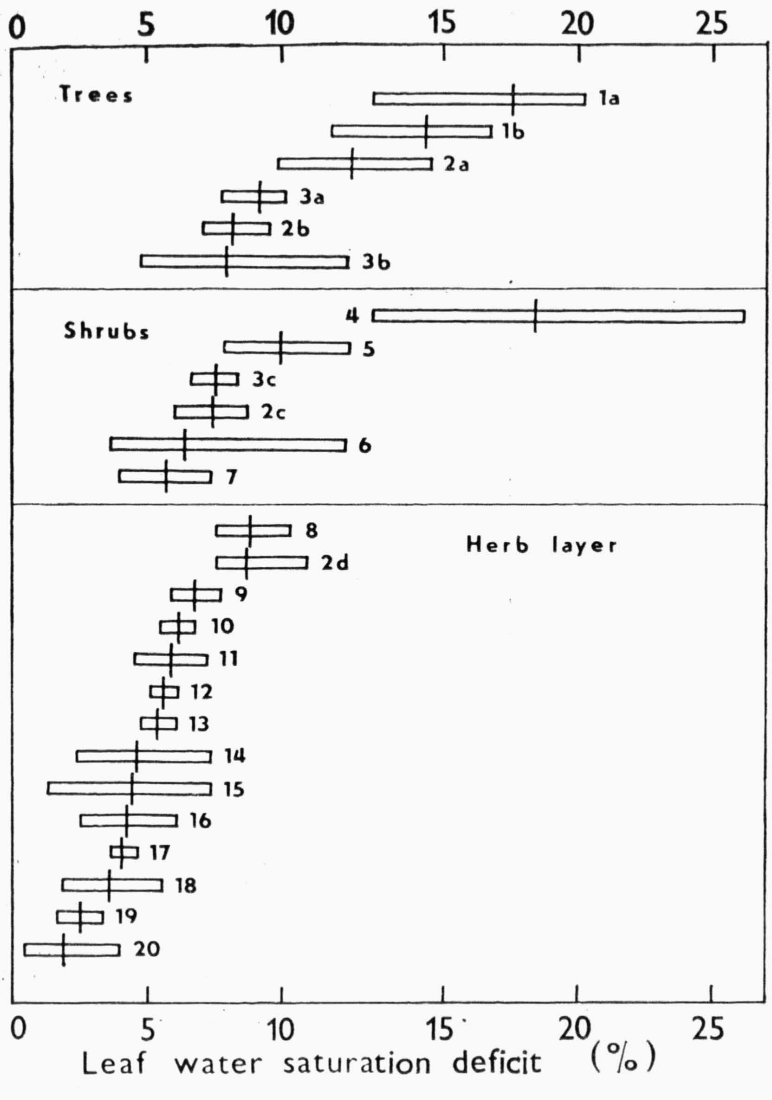

Fig. 5. — Afternoon pattern of water saturation deficits in leaves of 20 forest plant species of the oak-hornbeam forest at Báb in the moist period of summer (August 3, 1976). Leaf disc method. Adult trees: 1 *Quercus cerris*, 2 *Acer campestre*, 3 *Carpinus betulus*, a — sun leaves from top of crown, b — shade leaves from bottom of crown. Shrub layer species: 2c *Acer campestre*, 3c *Carpinus betulus*, 4 *Crataegus oxyacantha*, 5 *Euonymus verrucosa*, 6 *Cornus mas*, 7 *Ligustrum vulgare*. Herb layer species: 2d *Acer campestre* seedlings, 8 *Lathyrus vernus*, 9 *Fragaria moschata*, 10 *Hedera helix*, 11 *Pulmonaria officinalis*, 12 *Geum urbanum*, 13 *Viola mirabilis*, 14 *Galeobdolon luteum*, 15 *Glechoma hirsuta*, 16 *Sanicula europea*, 17 *Convallaria majalis*, 18 *Mercurialis perennis*, 19 *Asperula odorata*, 20 *Polygonatum latifolium*.

These measurements confirmed the findings reported above. Differences in w.s.d. between the trees, shrubs and herbs are encountered not only in the afternoon, i.e. in the absolute daily maxima, but also in the daily course of w.s.d., in the position of the daily maxima and in the variation of the w.s.d. values.

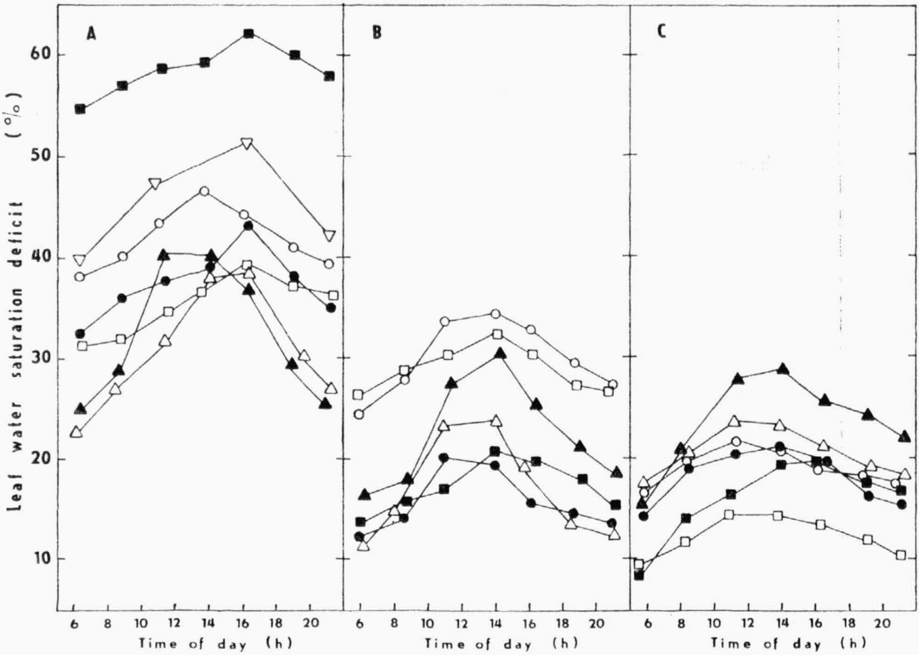

Fig. 6. — Daily courses of leaf water-saturation deficits for herb, shrub and tree species in oak-hornbeam forest at Báb during a dry period in July 1976. (A) Herb layer species (July 16): *Glechoma hirsuta* (■), *Lathyrus vernus* (▽), *Mercurialis perennis* (○), *Pulmonaria officinalis* (●), *Galeobdolon luteum* (△), *Viola mirabilis* (□), *Acer campestre* seedlings (▲). (B) Shrub layer species (July 13): *Cornus mas* (□), *Crataegus oxycantha* (○), *Euonymus verrucosa* (△), *Acer campestre* (▲), *Ligustrum vulgare* (●), *Carpinus betulus* (■). (C) Adult trees (July 15): *Acer campestre* (△), *Quercus cerris* (○), *Carpinus betulus* (□). Closed symbols indicate shade leaves from bottom of crown, open symbols sun leaves from top of crown.

The relation between soil moisture and water saturation deficit

The relation between soil moisture and the water saturation deficit in leaves of the forest herbs, shrubs and trees (sun-facing leaves), estimated by the disc method, is expressed diagrammatically in Fig. 8 for the period July—August. The different response of the individual species to the same level of soil moisture is obvious.

In interpreting this relation, the distribution of the root systems of the plants in the soil profile has also been taken into account. The water deficit was correlated with the soil moisture content at 0.0 to 0.1 m depth for herbs, 0.1 to 0.4 m for shrubs and 0.1 to 0.6 m for trees. At these depths, the closest correlations were found. In the herbs, the correlation coefficients varied be-

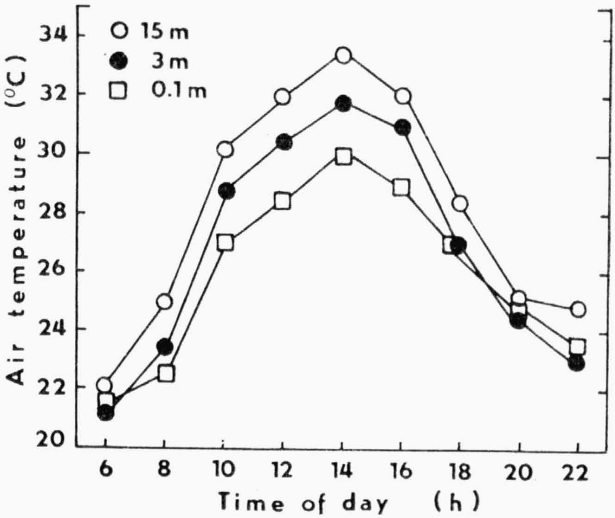

Fig. 7. — Daily course of air temperature at three different levels in the oak-hornbeam forest stand at Báb (July 20, 1976). Measured with thermographs.

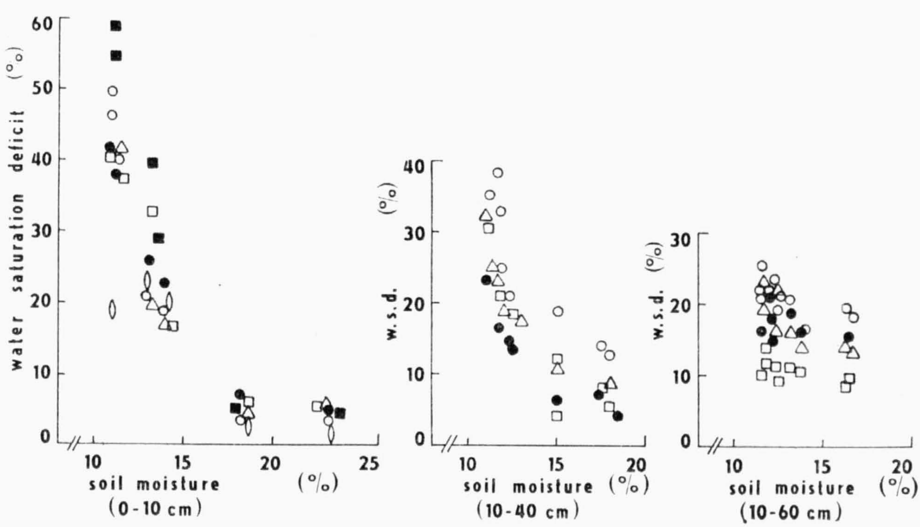

Fig. 8. — The relationship between the water saturation deficit in leaves of forest plants (in per cent) and soil moisture of different depths (in per cent of fresh weight). Herbs (left): *Glechoma hirsuta* (■), *Mercurialis perennis* (○), *Pulmonaria officinalis* (●), *Galeobdolon luteum* (△), *Viola mirabilis* (□), *Polygonatum latifolium* (○), Shrubs (middle): *Crataegus oxyacantha* (○), *Euonymus verrucosa* (△), *Cornus mas* (□), *Ligustrum vulgare* (●). Adult trees (right): *Acer campestre* (△), *Quercus cerris* (●), *Q. petraea* (○), *Carpinus betulus* (□).

tween −0.853 and −0.918, in shrubs between −0.314 and −0.757, and in trees between −0.329 and −0.743. The diagram shows that the response to soil moisture is most pronounced in the herbs, less so in the shrubs and insignificant in trees.

Vernal forest ephemeroids are mostly growing under conditions of sufficient water supply in the soil and hence do not exhibit marked water deficits. Tab. 1 presents w.s.d. values estimated by Stocker's method, by saturating whole plants, for April 28. The average maximum daily values from 2.7 up to 7.3 per cent are in strong contrast to the w.s.d. values of the summer-herb leaves during the dry summer season.

Tab. 1. — Maximum daily values of water saturation deficits in spring forest ephemeroids measured by Stocker's method (April 28, 1976).

Species	Water saturation deficit (%) Mean	Range
Corydalis solida	2.7	0.3−5.0
Isopyrum thalictroides	3.5	3.1−4.2
Pulmonaria officinalis (spring stem)	4.4	3.8−4.7
Lathyrus vernus	4.6	1.2−8.1
Gagea lutea	4.8	3.8−5.6
Anemone ranunculoides	4.8	4.0−5.5
Ficaria verna	7.3	5.7−9.96

The water balance of the plants

The water balance of the forest plants is evaluated according to the differences between the maximum and minimum leaf w.s.d. values for the entire sampling period. Use has been made only of values obtained by the disc method for the period of July-August (Tab. 2).

The widest amplitude of sublethal w.s.d. values of leaves was found in herbs: from 33.2 per cent up to 61.2 per cent. A narrower amplitude occurred only in *Convallaria majalis* and *Polygonatum latifolium* (24.0 and 19.0 per cent, respectively). The water balance of the shrubs is more stabilized. The ascertained differences varied between 22.5 and 28.7 per cent. An exception is *Hedera helix* with a very narrow amplitude (14.7 per cent only). The water balance of the trees is most stable (differences between 10.6 and 21.5 per cent). Here, the sun-facing leaves exhibited a smaller variation than the shade leaves. Young individuals of the trees species lag behind adult individuals in the stability of water balance, the shrubby individuals being more stable in this respect than seedlings.

Plant response to soil drought

The response of the plants to severe drought was investigated in the summer of 1976. No distinct visual changes were observed in trees. Only *Carpinus betulus* shed more leaves than normally in August. In the shrubs, the wilting of the leaves was visible in *Ligustrum vulgare* and indistinct in *Euonymus verrucosa* and *Cornus mas*. The herbs responded to water shortage in the soil (especially in the upper horizons) by wilting of their entire aerial shoots,

Tab. 2. — Maximum and minimum values of water saturation deficit in leaves of 20 forest plant species and its differences during mid-day hours in the period July—August 1976. Leaf-disc method.

Species	Water saturation deficit (%) Maximum	Minimum	Difference
Tree species:			
Acer campestre (sun-facing leaves)	24.7	9.9	14.8
— (shade leaves)	28.6	7.1	21.5
— (shrubs)	31.0	6.3	24.7
— (seedlings)	35.6	7.7	27.9
Carpinus betulus (sun-facing leaves)	15.1	1.3	13.8
— (shade leaves)	22.8	4.8	18.0
— (shrubs)	22.0	6.8	15.3
Quercus cerris (sun-facing leaves)	26.0	13.7	12.3
— (shade leaves)	22.5	12.0	10.5
Shrub species:			
Crataegus oxyacantha	40.0	13.4	26.6
Euonymus verrucosa	33.5	7.9	25.6
Cornus mas	32.3	3.6	28.7
Ligustrum vulgare	26.5	4.0	22.5
Hedera helix	20.2	5.6	14.6
Herb species:			
Glechoma hirsuta	62.5	1.3	61.2
Asperula odorata	62.4	2.3	60.1
Lathyrus vernus	52.2	7.6	44.6
Mercurialis perennis	49.6	1.9	47.7
Galeobdolon luteum	49.4	2.3	47.1
Pulmonaria officinalis	46.6	4.5	42.1
Viola mirabilis	45.6	4.8	40.8
Fragaria moschata	44.1	5.9	38.2
Geum urbanum	40.5	5.1	35.4
Sanicula europaea	35.7	2.5	33.2
Convallaria majalis	27.8	3.7	24.1
Polygonatum latifolium	19.4	0.4	19.0

mainly of leaves. Only plants with somewhat succulent leaves (*Polygonatum*, *Convallaria*) wilted rather indistinctly.

Following a protracted drought, brown patches of dead tissues showed up on leaves of several species (*Pulmonaria officinalis*) or whole basal leaves withered away (*Glechoma hirsuta*, *Asperula odorata*). Flowers, flower buds or whole flowering shoots of certain species (*Geum urbanum*) dried up. The formation of new above ground organs was not observed.

Sufficient water supply after the heavy rainfall at the end of July renewed the turgor of the majority of plants and the growth of new leaves was observed in several species (*Pulmonaria officinalis*, *Glechoma hirsuta*, *Galeobdolon luteum*), occasionally accompanied by that of whole flowering shoots (*Geum urbanum*). Many individuals of several species that had reached a sub-lethal or lethal water deficit in the preceding dry period (*Polygonatum latifolium*, older leaves of *Pulmonaria officinalis*) did not renew their turgor and dried up.

DISCUSSION

Forest ecosystems are characterized by a particular vertical structure in both the aboveground and underground part. The vertical structure of the forest is the result of the competition of coenobionts for light and water. In the aboveground part, the vertical gradient of irradiance determines the gradient of plant growth forms — of trees, shrubs, herbs, mosses — that are adapted to diverse positions within this gradient. In the underground sphere, the primary factor is the root competition of the plants for water and mineral nutrients.

The vertical structure of the forest includes, in addition to the main gradient of growth forms, also vertical gradients of anatomical and morphological features. Together with the gradient of microclimatic elements, they form vertical gradients of the physiological properties of the plants and their organs.

In the forest ecosystem, a certain water deficit gradient in the plant leaves reflects primarily the vertical gradient of soil moisture content and the vertical distribution of the plant root systems. This vertical gradient of the water deficit is most distinct under stress conditions. Under conditions of drought, the highest water deficit develops in forest herbs rooted in the surface soil layers which mostly dry up during the summer months. (An exception are only species with leaves succulent to a high degree and with a high water retention capacity). The underground organs of the majority of herbs of the deciduous forest penetrate through the surface layer of the soil to a depth of 0.15 m; the maximum concentration of the roots occurs in the 0.05 m thick top soil layer (PLAŠILOVÁ 1970). According to ŠIMONOVIČ (personal information) 96.1 per cent of the herb root biomass is concentrated at a depth of 0.15 m in the oak-hornbeam forest of Báb, up to 75.5 per cent at a depth of 0.05 m. Only 16.2 per cent or 2.6 per cent, respectively, of the biomass of the tree roots (not counting the trunk) may be found at the same depths.

The highest water deficits were found in shallow-rooted herbs. The rhizomes of *Asperula odorata* and *Glechoma hirsuta* creep on the soil surface or in the uppermost layer of the humus layer which is subject to the greatest fluctuations in soil moisture content and mostly dries up. Lesser water deficits were ascertained in somewhat deeper-rooted species, i.e. plants with most of their roots down to 0.15 m depth (PLAŠILOVÁ 1970). Similarly, SLAVÍKOVÁ (1965) encountered a greater root suction force in shallow-rooted species of a community subject to drought, and the highest at all in *Calamintha clinopodium* whose root system very much resembles that of *Asperula* or *Glechoma*.

Lower maximum water deficits were found in shrubs and the smallest in adult trees whose root systems penetrate much deeper than those of herbs (at Báb to a depth of 1.3 m and more) and their horizontal spread is also much larger. This enables them, along with effective water-loss control (PISEK et CARTELLIERI 1939, ELIÁŠ 1976a, b) to maintain their water balance at an equilibrium. In the deeper soil horizons, however, the changes in soil moisture are smoother and fluctuations smaller.

In their competition for water, herbs are in a disadvantage against trees. In beech forests with a poor herb layer (*Fagetum nudum*), the shallow roots of the beech dry up the upper soil profile so that herbs cannot grow there (SLAVÍKOVÁ 1958). In a natural habitat, the tree roots have no stronger suction force than the herb roots (SLAVÍKOVÁ 1966) but the more voluminous root system provides them with sufficient water. Only if their root system is restricted (e.g. in a pot) does the maximal root suction force of trees outstrip that of herbs. The artificial removal of the root competition of trees results in an increased soil moisture content and a better growth of seedlings and herb layer species was observed by virtue of the improvement of their water balance and mineral nutrition (Karpov 1955, Slavíková 1958, Bannikova 1967, Abražko 1969, 1970, Titov 1970 and others). By intensive water absorption the roots of adult trees dry up the soil horizons and thus indirectly check the growth and development of other synusia in forest communities.

Vitko (1966, 1972) found similar relations between maximal values of the leaf water deficit in herbs, shrubs and trees, in a deciduous oak forest in Moldavia (U.S.S.R.). In comparison with herbs, the trees of dry oak forests are characterized by smoother changes of water deficit in the course of the growing period and the daily fluctuations of their water deficit are small; their absolute w.s.d. values are lower on an average. The author observed only a moderate dependence of the water deficit in tree leaves on soil moisture and microclimatic conditions. This testifies to a good water balance control in trees in comparison with herbs.

It is interesting to note the difference between young and adult individuals of tree species (*Acer*, *Quercus*, *Carpinus*). The seedlings of these species growing amidst the herb layer exhibit the highest water deficits, though somewhat lower than herbs. This is obviously due to their mesomorphous character (Serebrjakov 1952), by which they come near to herbs. They also have a low stomatal density, but their water loss under laboratory conditions places them nearer to the sun-facing leaves of adult trees (Eliáš 1976b). Smaller water deficits may be found in shrubby individuals with deeper root systems and the lowest deficit occur in leaves of adult trees.

Sun-facing leaves of adult trees have a more stabilized water balance than the shade leaves. This has also been pointed out by Paganelli et Paganelli Cappelletti (1971). Huzulák et Eliáš (1975b) also made similar findings in investigating the relative saturation deficit of trees. The shade leaves, however, have higher stomatal resistances (Eliáš 1976a) and a high water retention capacity (Eliáš 1976b). Higher water deficit values in shade leaves during the dry period of summer may be explained by preferential water supply to the physiologically more active leaves in the upper portion of the crown. In the lateral limbs of the lower part of the crown, a series of resistances obviously put a brake upon water flow towards the shade leaves.

Differences exist in the response of individual plant species to the dry summer period. The intense shedding of leaves in *Carpinus betulus* in August (see also Kubíček 1974) appears to be the result of an unfavourable water balance of the plant. *Carpinus*, with its shallower root system than those of both dominant tree species (Jeník 1957), reduces its transpiration by reducing the leaf area and by rising the transpiration resistances in the leaves (the author's unpublished data). *Carpinus* thus exhibits the lowest water deficit out of all the species investigated in their natural habitats. But the highest w.s.d. values occur in *Carpinus* during the desiccation of its detached leaves under laboratory conditions (Eliáš 1976b).

The leaves of forest herbst lose their turgor rapidly. During the summer drought they were predominantly in the stage of wilting. Long-standing droughts bring about actual water deficits approaching or reaching the sublethal water deficit. Leaf necroses as observed in the dry summer of 1971 (Eliáš 1972, 1975b) are not rare. The growth processes are stopped under such conditions. But as soon as the water balance improves, new assimilatory organs frequently substitute the old and dying ones.

The most interesting feature in the water relations of summer herbs in an oak forest is seen by Goryšina (1975b) in their ability to survive a long and strong wilting that sets in quickly in periods of long-lasting summer droughts. These plants lack xeromorphic adaptations and, nonetheless, survive. They are tolerant towards high water deficits. Underground organs with the storage of reserves obviously play an important role here: the herbs of deciduous forests are predominantly classified as rhizocaulophytes and caulophytes (PLAŠILOVÁ 1970). The storage of reserves in the rhizome enables the rapid formation of new replacement assimilatory organs.

Two of the species investigated, *Hedera helix* and *Polygonatum latifolium*, are particularly noteworthy. Both of them exhibited very low leaf water deficit values even during the dry summer period. These species have a high water retention capacity and their leaves are succulent to a high degree. *Hedera helix* is an evergreen shrub with a very stable water balance (ELIÁŠ 1978). *Polygonatum latifolium* is a caulophyte and behaves similarly also in dry oak forests in Moldavia (VITKO 1966, 1972). Despite the low values of the water saturation deficit in the leaves, however, its whole above-ground parts yellowed and died as a consequence of long-standing drought. This is due to the very low sublethal water saturation deficit in this species (VITKO 1972).

CONCLUSIONS

Individual plant growth forms that make up the basic structure of the forest ecosystem (trees, shrubs, herbs) mutually differ also by the maximum water deficits they exhibit in their natural environment and, generally, by the character of their water balance. The ascertained differences are considered to be due to the diversified distribution of root systems along the vertical gradient of soil moisture and to the corresponding specific maximum root suction forces.

Herbs rooted in the soil layer subject to most extensive changes in soil moisture respond markedly to these changes by altering their water deficit. Hence their water balance is considerably unstable. Shrubs and trees are rooted in deeper layers subject to lesser changes in soil moisture, the changes themselves being much smoother. The active surface of the tree crown is exposed to direct solar radiation. To maintain such a stable water balance the trees must be provided with certain control mechanisms especially in water loss.

Individuals of trees of the same species but of different age behave differently. Seedlings approach herbs by their mesomorphous character and by high water deficits. Shrubby individuals behave like shrubs. Differences are also found between the sun-facing leaves in the upper part of the crown, and the shade leaves in the lower part of adult tree crowns. Sun-facing leaves exhibit a more stable water balance than shade leaves.

Differences also exist among the various groups of plant growth forms in the absolute daily maxima of the water saturation deficit, in the daily course of w.s.d., in the position of its daily maxima and in the relative variation of w.s.d. values. Within the frame of each group of growth forms, certain interspecific differences are found.

SUMMARY

The water deficit was followed in four tree species, five shrub species and 23 herb species (seven of them in the vernal synusium) in their natural habitats in an oak-hornbeam forest at the IBP Research Area at Báb, SW. Slovakia). The water deficit was determined as the water saturation deficit (w.s.d.) and expressed in terms of percentage difference from water content at full saturation. Two methods were used: Stocker's method of saturating whole aboveground plant

organs, and Čatský's leaf disc method. Both provided similar results but the w.s.d. values estimated by the leaf disc method were somewhat higher.

Spring ephemeroids growing under conditions of sufficient water supply in the entire soil profile (soil moisture content at a depth of 0.1 to 0.6 m was higher than 16 per cent of fresh weight) attained low maximal w.s.d. values (less than 10 per cent). In summer, during the dry period of the year (soil moisture content at a depth of 0.1 to 0.6 m was less than 12 per cent of fresh weight) the highest maximum w.s.d. values were found in herbs (35.7 to 62.5 per cent, disc method), lower in shrubs (26.5 to 40.0 per cent) and the lowest in adult trees (22.5 to 28.6 per cent). An exception were only species with a high degree of succulence in their leaves and with a high water retention capacity (*Hedera helix*, *Polygonatum latifolium*, *Convallaria majalis*) which, under similar conditions, reached w.s.d. values essentially lower than the other species in the corresponding layer. The vertical gradient of the leaf water deficit in the forest plants prevailing under stress conditions corresponds with the reversed gradient of the root-system distribution in the soil and of soil moisture.

In tree species the maximal w.s.d. value of leaves increased as follows: sun-facing leaves of adult trees (15.1 to 26.0 per cent), shade leaves of adult trees (22.5 to 28.6 per cent), leaves of shrubs (22.0 to 31.0 per cent), leaves of seedlings (more than 30 per cent).

The individual species responded to the same level of soil moisture in a different way. Soil drought provoked leaf shedding only in *Carpinus betulus*; the wilting of above-ground plant organs was observed in certain shrubs and in all herb species.

The water balance of the plants (expressed as the amplitude of extreme w.s.d. values ascertained in the natural habitats) is most stable in trees (amplitudes 10.5 to 21.5 per cent), less stable in shrubs (22.5 to 28.7 per cent) and least stable in herbs (33.2 to 61.2 per cent).

SÚHRN

Vodný deficit štyroch druhov stromov, piatich druhov krov a 23 druhov bylín (z toho 7 z jarnej synúzie) bol sledovaný na prirodzenom stanovišti dubo-hrabového lesa na výskumnej ploche MBP pri Bábe (JZ Slovensko). Vodný deficit bol stanovený ako vodný sýtostný deficit (VSD) a vyjadrený v % obsahu vody pri plnom nasýtení. Použili sa dve metódy: Stockerova metóda sýtenia celých nadzemných orgánov a Čatského terčíková metóda. Jarné efemeroidy, ktoré rástli v podmienkach dostatočnej zásoby vody v celom profile pôdy, dosahovali nízke maximálne hodnoty VSD (menšie než 10 %). V lete, v suchom období roka (vlhkosť pôdy v hĺbke 10—60 cm bola nižšia než 12 % čerstvej váhy), sa zistili najvyššie maximá VSD pri bylinách (35,7 až 62,5 %, terčíková metóda), nižšie pri kríkoch (26,5 až 40,0 %) a najnižšie pri dospelých stromoch (22,5 až 28,6 %). Výnimku tvorili len druhy s vysokým stupňom sukulencie listov a s vysokou vodnou retenčnou kapacitou (*Hedera helix*, *Polygonatum latifolium* a *Convallaria majalis*), ktoré dosahovali aj v týchto podmienkach podstatne nižšie hodnoty ako ostatné druhy v príslušnej vrstve. Vertikálny gradient vodného deficitu listov rastlín v lese, existujúci v stresových podmienkach, odpovedá obrátenému gradientu distribúcie koreňového systému raslín pozdĺž gradientu vlhkosti pôdy. Pri stromových druhoch stúpala maximálna hodnota VSD listov v smere: výslnné listy dospelých stromov (15,1 až 26,0 %), tieňové listy dospelých stromov (22,5 až 28,6 %), listy krovitých jedincov (22,0 až 31 %), listy semenáčikov (viac ako 30 %). Jednotlivé druhy reagovali rozdielne na rovnakú úroveň vlhkosti pôdy. Pôdne sucho vyvolalo opad listov len pri *Carpinus betulus;* vädnutie nadzemných orgánov rastlín bolo pozorované pri niektorých krikoch a pri všetkých druhoch bylín. Vodná bilancia rastlín (vyjadrená ako amplitúda krajných hodnôt VSD zistených na prirodzenom stanovišti) je najstabilnejšia pri stromoch (amplitúdy od 10,5 do 21,5 %), menej stabilná pri kríkoch (od 22.5 do 28,7 %) a najmenej stabilná pri bylinách (od 33,2 do 61,2 %).

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