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Gradients of Several Leaf Characteristics on Stems of Two Forest Herbs

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Abstract. The plants of two herbaceous species, namely *Pulmonaria officinalis* L. and *Symphytum tuberosum* L., growing in two deciduous forests in SW. Slovakia, were used for analysis of anatomic-physiological gradients along the insertion level of individual leaves. The gradients were established for six leaf characteristics. Specific leaf area and development of leaf area increased, while leaf tissue hydration, degrees of succulence and consistency decreased with height of insertion of leaves upon the stems. The gradients indicate the decreasing of the leaf water content and dry mass with height of the leaf on the stem. Stomatal resistance was usually the lowest in basal leaves and the highest in apical leaves of the plant. The anatomic-physiological heterogeneity of leaves of a plant is large and cannot be neglected in any anatomical or physiological investigations.

Anatomical and physiological heterogeneity of leaves of the same plant has been known, in general, and frequently interpreted as ZALENSKIĬ's Law (*cf.* MAXIMOV 1929). It considers the heterogeneity as a function of the distance of a leaf from a root system.

The heterogeneity investigations were predominantly concentrated on the study of the anatomical heterogeneity of leaves, namely stomatal apparatus. Very little attention has been devoted to the study of the physiological heterogeneity of the leaves of a plant (*cf.* FARKAS and RAJHÁTHY 1955, WILSON 1977). Recently, it was demonstrated in *Phragmites communis* by RYCHNOVSKÁ (1967) in an excellent form. The analysis of the heterogeneity of leaf sets of a single plant is an important methodological step which affects all sorts of eco-physiological analysis of the plant as well as correct interpretation of the results obtained.

The variations of values used for characterising leaf variation with insertion level can be well expressed as gradients according to the definition of PRAT (1948): "A gradient is a progressive variation of a factor in function of the position." The aim of this contribution is to demonstrate the gradients of six eco-physiological leaf characteristics along the insertion level of individual leaves on the stems of two forest herbs.

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TABLE 1

Five leaf indices determined for six successive leaves of flowering shoots of *Pulmonaria officinalis* L. growing in an oak-hornbeam forest at Báb (April 22, 1976). Means and ranges of absolute values are given

	Leaf number from shoot apex	Leaf tissue hydration [% d.m.]	Degree of succulence [$mg_{w.c.}$ cm^{-2}]	Specific leaf area [mm^2 $mg_{d.m.}^{-1}$]	Degree of consistency [$mg_{d.m.}$ cm^{-2}]	Development of leaf area [cm^2 $mg_{f.m.}^{-1}$]
Leaves of shoot	I.	613.7	12.57	49.08	2.04	6.90
		592.8—634.6	11.4—13.7	46.4—51.8	1.93—2.2	6.3—7.5
	II.	614.0	12.54	49.04	2.035	6.88
		596.9—631.1	11.7—13.3	47.4—50.7	1.97—2.1	6.4—7.3
	III.	636.9	13.29	48.02	2.08	6.52
		622.8—651.2	12.5—14.1	46.3—49.7	2.01—2.15	6.1—6.9
	IV.	637.7	13.91	45.88	2.17	6.22
		620.7—654.7	13.4—14.4	45.5—46.3	2.10—2.2	6.0—6.4
	V.	681.5	14.96	45.60	2.20	5.84
		672.6—690.4	14.3—15.6	43.2—48.1	2.08—2.31	5.5—6.1
	VI.	717.03 *	17.54 *	40.90 *	2.45 *	5.00 *
Leaves of rosette	youngest	582.05	13.89	41.9	2.39	6.14
	oldest	552.3	14.28	45.7	2.18	6.07

* Lower number of measurements.

MATERIAL AND METHODS

Two forest herbaceous species, namely *Pulmonaria officinalis* L. and *Symphytum tuberosum* L., were chosen for the analysis. In the spring period, they form 20 to 30 cm high flowering shoots with 4 to 6 leaves. The first species also has a ground rosette with 3 to 5 large leaves. In April 1976, the plants were collected from spring synusia on the forest floor in two different localities:

A) an oak-hornbeam forest at the village of Báb near Nitra in SW. Slovakia, which formed one of the research areas of the International Biological Programme in Czechoslovakia (*cf.* JURKO and DUDA 1970).

B) an oak-hornbeam forest at Bratislava-Železná Studienka in SW. Slovakia situated in the southern part of the Little Carpathian Mountains, which have been included into Project No. 2 of the programme Man and Biosphere as one of the Czechoslovak national projects (UNESCO, Project No. 90).

Twenty discs with a diameter of 8 mm were cut off from each leaf blade of ten plants of each species. The following leaf characteristics were calculated from the disc area, mass as well as water content values:

1) leaf tissue hydration, expressed as leaf water content in percentages of leaf dry mass;
2) degree of succulence (leaf water content/leaf area);
3) specific leaf area (leaf area/leaf dry mass);
4) degree of consistency (leaf dry mass/leaf area);
5) development of leaf area (leaf area/leaf fresh mass).

For further data see ELIÁŠ (1979). In Tables 1 to 3 actual values are presented, while in Figs. 1 and 2 gradients are expressed graphically in relative values as percentages of the maximum and of total variation above the minimum. The latter values were calculated in the same way as in MIGAHID and ABU RAYA (1952) and PAZOUREK (1966).

Diffusive resistance of stomata was determined by a Lambda LI-60 S diffusive resistance meter with horizontal sensor in the intact plants growing in natural conditions of forest stands.

Light conditions within the deciduous forests were favourable because leaves were not yet present on trees and shrubs. Soil moisture content in upper horizons was close to maximum capillary capacity.

RESULTS AND DISCUSSION

Absolute values of leaf characteristics determined for *Pulmonaria officinalis* are given in Tables 1 and 2. Specific leaf area and development of leaf area increased while other leaf characteristics (leaf tissue hydration, degree of succulence and degree of consistency) decreased with height of the leaf on the stem. The leaves of the ground rosette also differed: the oldest (and largest) leaf exhibited, in comparison with the youngest one, lower leaf tissue hydration, development of leaf area as well as degree of consistency, but it has a higher degree of succulence and specific leaf area (*cf.* Table 1, plants from Báb forest). In other determinations of the leaf characteristics (see Table 2) similar tendencies were obtained. Gradients of relative values of the characteristics are graphically expressed in Figs. 1 and 2.

TABLE 2

Five leaf indices determined for three different groups of leaves of *Pulmonaria officinalis* plants growing in two oak-hornbeam forests in SW. Slovakia. Means and ranges of absolute values are given

Leaves	Leaf tissue hydration [% d.m.]	Degree of succulence [$mg_{w.c.}$ cm^{-2}]	Specific leaf area [mm^2 $mg_{d.m.}^{-1}$]	Degree of consistency [$mg_{d.m.}$ cm^{-2}]	Development of leaf area [cm^2 $mg_{f.m.}^{-1}$]
			Báb (April 29, 1976)		
Two highest	626.0 611.8—640.3	13.23 12.7—13.7	48.44 48.0—48.8	2.06 2.08—2.04	6.68 6.6—6.8
Two lowest	712.75 93.6—731.9	15.98 15.5—16.4	44.62 44.5—44.7	2.24 *	5.49 5.3—5.6
Ground rosette	525.99 527.2—524.8	11.95 *	43.88 43.6—44.1	2.27 2.26—2.28	7.01 6.9—7.1
			Železná Studienka (April 27, 1976)		
Two highest	529.3 525.6—533.1	12.35 11.8—12.7	42.96 40.8—45.1	2.27 2.2—2.3	6.83 6.5—7.1
Two lowest	605.95 *	15.92 *	38.06 *	2.63 *	5.39 *
Ground rosette	489.29 *	12.55 *	38.99 *	2.56 *	6.62 *

* Lower number of measurements.

In *Symphytum tuberosum* the gradients of the leaf characteristics were similar as in *Pulmonaria officinalis*, except for leaf tissue hydration and degree of consistency (*cf.* Table 3).

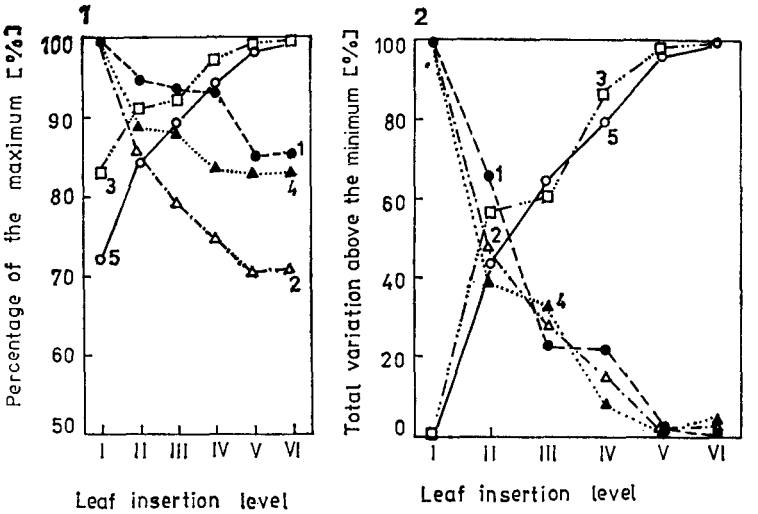

Fig. 1. Gradients of the mean values of five leaf characteristics in six successive leaves of the flowering shoots of *Pulmonaria officinalis* L. The characteristics are given as percentage of the maximum (maximal values = 100 %). Ordinate: percentage of the maximum, abscissa: leaf insertion level (from base to apex of shoot). — 1 (●) — leaf tissue hydration; 2 (△) — degree of succulence; 3 (□) — specific leaf area; 4 (▲) — degree of consistency; 5 (○) — development of leaf area.

Fig. 2. The same gradients as are shown in Fig. 1, given in total variation above the minimum (minimum = 0 %, maximum = 100 %). For legend see Fig. 1, except ordinate (= percentages of total variation above the minimum).

Higher water content in leaves (in % of dry matter as well as per area) inserted lower upon a stem, in comparison with those inserted higher, corresponded with gradient of water deficit in plant tissues (*cf. e.g.* POSPÍŠILOVÁ 1974). This is a result of friction resistances (*see* RICHTER 1973) and occurs also in plants with stable water balance as well as under the conditions

TABLE 3
Five leaf indices in successive leaves of flowering shoots of *Symphytum tuberosum* L. growing 1976). Means and ranges of absolute values are given

Leaf numbered from shoot apex	Leaf tissue hydration [% d.m.]	Degree of succulence [$mg_{w.c.}$ cm^{-2}]
I.	548.75	14.93
	527.7—569.9	13.6—16.2
II.	534.9	15.43
	515.5—554.3	15.2—15.7
III.	525.6	15.90
	513.6—537.7	15.3—16.5
IV.	580.1	18.32
	555.7—604.6	16.7—20.0

of sufficient water supply, *e.g.* in plants growing in a fishpond and its littoral zones (*cf. e.g.* RYCHNOVSKÁ 1967).

KRASNOSEL'SKAYA-MAKSIMOVA (1917) was the first to discover that leaf water content diminished with leaf height on stem. Her results were confirmed later by YAPP and MASON (1932), MIGAHID and ABU RAYA (1952), FARKAS and RAJHÁTHY (1955) and many other investigators.

The same character of the gradients, both the degree of succulence and leaf tissue hydration, supported the facts discussed above. It indicates that the gradient of leaf tissue hydration was not a result of the differences in dry matter content in successive leaves on the stem. Similarly, FARKAS and RAJHÁTHY (1955) found a higher degree of succulence in lower leaves compared with upper ones.

The dry mass of leaves decreases with the increasing leaf insertion height as is indicated by gradients of degree of consistency. Leaves at the stem base contains more dry mass than leaves at the stem apex. The increasing of the values of specific leaf area with height of leaf insertion confirmed the results introduced above. FARKAS and RAJHÁTHY (1955) did not find significant differences in degree of consistency ("Hartlaubcharakter") between the upper and lower leaves.

Our results are not in absolute agreement with the statements of ZALENSKIĬ's Law. The large development of both transport and mechanical tissues in upper leaves, as it assumes, should be shown in higher dry matter of these leaves and, hence, also in higher values of degree of consistency and lower values of specific leaf area. But our results did not show the gradients of those characters. The character of the anatomical-physiological gradients along the insertion height of individual leaves appear to depend both on species and environmental conditions. This assumption is supported by our present results as well as the results of many other investigators, *e.g.* RYCHNOVSKÁ (1967), PAZOUREK (1970, 1973), ELIÁŠ and KOZINKA (1976), WILSON (1977).

Our porometric measurements of diffusive resistance of abaxial epidermes in successive leaves of *Pulmonaria officinalis* and *Symphytum tuberosum* shoots did not show simple, one-direction gradients of stomatal resistance (*cf.* Table 4). However, the lowest stomatal resistance was most frequently found in the basal leaves of the shoots. Resistance of adaxial epidermis was

in spring synuzium of an oak-hornbeam forest at Bratislava—Železná Studienka (April 27,

Specific leaf area [$mm^2\ mg_{d.m.}^{-1}$]	Degree of consistency [$mg_{d.m.}\ cm^{-2}$]	Development of leaf area [$cm^2\ mg_{f.m.}^{-1}$]
36.91	2.72	5.70
35.1—38.7	2.6—2.9	5.2—6.1
34.66	2.89	5.46
33.9—35.4	2.8—3.0	5.4—5.5
33.66	2.82	5.31
32.5—34.8	2.8—2.9	5.1—5.5
32.04	3.18	4.71
27.8—36.3	2.7—3.6	4.2—5.2

TABLE 4

Diffusive resistances of abaxial epidermes of four successive leaves on the flowering shoots of two forest herbaceous species. Porometric measurements were made during midday hours on April 14, 1976 in an oak-hornbeam forest at Bratislava—Železná Studienka. Absolute values in s cm^{-1} are given for three individual plants of each species investigated

Plant	Leaf insertion level (from shoot apex)			
	I.	II.	III.	IV.
		Pulmonaria officinalis		
A.	4.69	4.84	6.36	3.41
B.	4.60	4.09	3.66	5.57
C.	3.46	3.04	3.41	2.92
Mean	4.25	3.99	4.45	3.96
		Symphytum tuberosum		
A.	2.18	1.97	1.32	0.74
B.	1.87	0.77	0.98	0.06
C.	2.85	1.63	2.20	2.11
Mean	2.30	1.46	1.50	0.97

in both species higher than of abaxial epidermis with stomata, *e.g.* in *Symphytum tuberosum*, the same leaves exhibited in adaxial and abaxial epidermis 12.62 (range 9—16) s cm^{-1} and 2.73 (1.3—3.6) s cm^{-1}, respectively. In *Pulmonaria officinalis*, lower stomatal resistance was determined in leaves of ground rosette as compared with that in leaves of flowering shoots. In the same group of leaves, resistance of adaxial and abaxial epidermes of rosette leaves was 86.43 (range 50-115) and 2.39 (1.6-3.2) s cm^{-1}, respectively. But in the other, large group of rosette leaves, the latter was 3.04 (range 1.6 to 5.6) s cm^{-1}.

As ZALENSKIĬ's Law states the leaves inserted higher on the stem exhibit a higher number and smaller size of stomata than leaves inserted lower. Then, lower stomatal resistances will be expected in apical leaves of the plant. However, the correlation between both stomata density and size and stomatal resistance is not simple, *viz.* linear. This fact was demonstrated *e.g.* by HEICHEL (1971) and JONES (1977) for crop plants or by DAVIES and KOZLOWSKI (1974), DAVIES *et al.* (1974), KOZLOWSKI *et al.* (1974) and PEREIRA and KOZLOWSKI (1976) for seedlings of several coniferous and deciduous tree species. Transpiration rates of species investigated were not consistently related to stomatal frequency, pore size, or relative pore area. Other factors must be considered in the interpretation of the differences observed by the authors, *e.g.* leaf cuticle and external cuticular waxes (KOZLOWSKI *et al.* 1974).

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