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Leaf Shape, Stomata Density and Photosynthetic Rate of the Common Oak Leaves

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Abstract. Leaf shape and size, stomata dimensions and density, chlorophyll content and photosynthetic rate of the common oak leaves were investigated in shoots of various growth phases (polycyclic growth).

Mean and maximal daily net photosynthetic rates, shoot length, leaf area, stomatal density and chlorophyll contents were significantly higher in shoots of the second growth phase. Intraspecific differences in leaf shape were found within each shoot growth phase.

Oaks are characterized by great intraspecific variability and as loessial woody species they hybridize interspecifically. In consequence, hybridogenous populations make the taxonomic research of this economically important tree species still more difficult. Thus from the taxonomical, physiological and productional aspects it is important to estimate exactly not only the physiological, morphological and anatomical features of leaves, but also the leaf size or leaf area and other quantitative characteristics.

MATERIAL AND METHODS

Four years old saplings of *Q. robur* L. (three samplings) were grown in compensation lysimeters positioned at the experimental station with a permanent meteorological station (Masarovičová *et al.* 1989). Photosynthetically adult leaves of the first (SGP-1) and second (SGP-2) growth phase shoots were used for experiments.

Daily courses of net photosynthetic rate (P_N) and maximal daily net photosynthetic rate ($P_{N,max}$) were measured using an open gas exchange system with a simple assimilation chamber for short time exposure (approximately 5 min). Carbon dioxide concentration was measured with IRGA (Infralyt 4,

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VEB Junkalor Dessau, GDR). Gas exchange was measured on the same leaves during the day (06.00–21.00). Values of $P_{N,max}$ were obtained from daily curves of CO_2 exchange. The time of day and irradiance at which the $P_{N,max}$ values were attained were also determined. Simultaneously with the ecophysiological measurements the basic meteorological factors (air and soil temperature, relative air humidity, wind speed, *etc.*) were recorded. Irradiance and ambient CO_2 concentration were measured separately at every leaf exposure during the whole day (Masarovičová 1989).

For morphological observation leaves of the two SGPs were always sampled from one current year's shoot. Thus they did not represent a set of leaves, but were selected randomly to show only shape differences, but not those of leaf size. However, for leaf area estimation the number of analysed leaves of the SGP-1 and SGP-2 were 45 and 50, respectively (Masarovičová and Požgaj 1988).

Leaf chlorophyll (Chl *a, b* and $a+b$) contents were determined directly in 80 % acetone extracts. Measurements of absorbance were made on a Unicam SP 800 recording spectrophotometer. The chlorophyll contents were calculated according to Vernon (1960). The results were expressed per dry mass and per leaf area units.

The microrelief (replica) method was used for determining density, length and width of stomata in leaves. Oak species have hypostomatical leaves, so the prints were taken only from the abaxial epidermis.

The other quantitative characteristics of the leaves were calculated. For statistical evaluation of the results the standard *t*-test was used.

RESULTS AND DISCUSSION

The growth of current shoots of *Q. robur* consisted of two phases (polycyclic growth). Intraspecific differences of common oak leaf features were ascertained (Fig. 1 and Table 1). On the basis of our previous results (Masarovičová 1985) the growth of SGP-1 leaves is believed to depend on sufficient quantities of supply substances in the root system that were formed in the preceding photosynthetic period with a positive carbon balance. Therefore the role of the photosynthetic activity not only of SGP-1 leaves but also of SGP-2 leaves, namely at the end of the growing season is significant. Nilsson and Ericsson (1986) came to the same conclusion in a willow stand (*Salix viminalis*).

Fig. 1 presents the equation of the regression line, differences in the values of leaf shape and leaf area of the first (SGP-1) and second (SGP-2) growth phase shoots. Leaves of SGP-2 were larger than leaves of SGP-1 and they differed also in their shape. Similar tendency was also found for the beech leaves (Roy *et al.* 1986) as well as for the oak leaves (*Q. cerris, Q. petraea* (Virágh and Précsényi 1985).

Mean daily P_N as well as $P_{N,max}$ of the SGP-2 leaves were significantly higher than those of the SGP-1 (Table 1). Daily course of P_N showed tendency with two peaks for the leaves of SGP-1. Time of day when $P_{N,max}$ was attained ranged from 08.00 to 10.00 h and "midday" depression was manifested in both SGPs. However, P_N decline at midday was more conspicuous in the leaves of SGP-1 than in those of SGP-2 (Fig. 2). Negative balance of the carbon metabolism (prevailing of the respiration processes over photosynthesis) in the leaves of SGP-1 was observed at about 17.00. Leaves of the SGP-2 showed positive carbon metabolism for a longer time (Fig. 2). Shoots of the SGP-2 were longer, their leaf area and leaf dry mass were also larger (Table 1). Higher photosynthetic activity in leaves of SGP-2 than in those of SGP-1 was also confirmed for *Q. cerris* and *Q. petraea* (Virágh and Préscényi 1985) and for *Fagus sylvatica* (Roy *et al.* 1986).

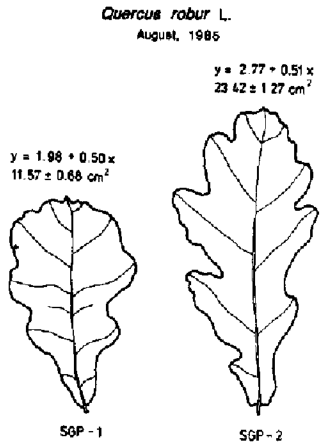

Fig. 1. Leaf morphology and leaf area of the first (SGP-1) and second (SGP-2) growth phase shoots. Leaf area was estimated using the equation to the regression line y = a + bx, where y is the leaf area and x is the product of leaf length and maximum leaf breadth.

A certain analogy in the significance and partitioning of current year and one-year old needles (also developing under various light conditions) for annual carbon gain, may also be seen in coniferous trees. It is generally considered that the photosynthetic activity of current year needles is higher than that of one-year old needles as soon as the current year foliage has reached maturity and that thereafter the capacity will decrease with age (*cf.* Troeng and Linder 1982). The translocation of photosynthates from one-year old foliage to the current year shoot ceases when the current year needles reach about 50 % of their final lenght (Ericsson 1978). Seasonal change in the source-sink relationship between shoots of different age could then also influence the annual carbon gain (*e.g.* Masarovičová 1989).

The leaves of SGP-2 showed a higher stomata density, but no differences within the stomata length and stomata width. Chlorophyll (*a, b, a+b*) content

TABLE 1

Net photosynthetic rate (P_N) and some quantitative leaf characteristics of the first (SGP-1) and second (SGP-2) growing phase shoots in the common oak saplings

Parameter		SGP-1	SGP-2
Mean daily P_N [mg (CO_2) m^{-2} s^{-1}]	July	0.482 ± 0.045	0.678 ± 0.076**
	August	–	0.724 ± 0.077
	Septeber	0.437 ± 0.041	0.567 ± 0.051**
$P_{N,max}$ [mg (CO_2) m^{-2} s^{-1}]	July	0.737 ± 0.042	1.046 ± 0.083**
	August	–	1.196 ± 0.107
	September	0.670 ± 0.025	0.804 ± 0.071**
Leaf area per tree [dm^2]		69.72 ± 14.49 Total 180 ± 0.24	101.31 ± 16.58**
Leaf dry mass per tree [g]		49.93 ± 10.38 Total 116.92	60.32 ± 9.87
Length of shoot [m]		0.22	0.50
Stomata density [mm^{-2}]		384 ± 5	471 ± 4**
Stomata length [µm]		33.48 ± 0.21	33.04 ± 0.17
Stomata width [µm]		22.07 ± 0.15	22.54 ± 0.16
Chl *a* content		0.425 ± 0.004	0.481 ± 0.027
Chl *b* content		0.107 ± 0.005	0.118 ± 0.018
Chl *(a+b)* content [g m^{-2}]		0.533 ± 0.008	0.600 ± 0.033
Chl *a* content		5.938 ± 0.109	8.071 ± 0.233**
Chl *b* content		1.502 ± 0.087	2.002 ± 0.305*
Chl *(a+b)* content [g kg^{-1} (d.m.)]		7.440 ± 0.186	10.073 ± 0.390**
Chl *a:b* ratio		3.97	4.08

mean, ± standard error
*significant differences at P = 0.05
**significant differences at P = 0.01

was higher in the leaves of the SGP-2, too (Table 1). Similar results were found for the beech leaves (Roy *et al.* 1986).

In spite of the fact that in adult forest stand SGP-2 do not currently occur, their existance gains importance when leaves of the SGP-1 are damaged by biotic and abiotic factors. This fact was pointed out also by Virágh (1979) and Virágh with Précsényi (1985), who observed in adult *Q. cerris* and *Q. petraea* fluctuations in leaf area and leaf mass. The cause of these fluctuations is that in summer, after the period of chewing, new young leaves develop in huge number and their sizes differ from the old (spring) leaves. Photosynthetic activity of the new (summer) leaves is higher and their growth rate is faster than in leaves developed in spring (SGP-1). Our results (Table 1 and Fig. 2) are in good agreement with the above mentioned findings.

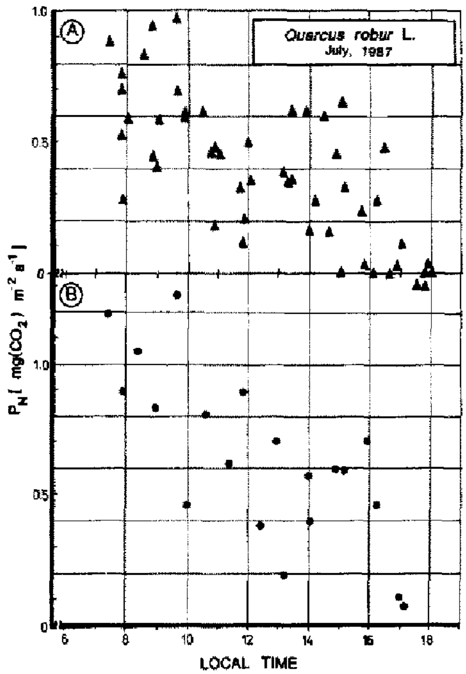

Fig. 2. Daily course of net photosynthetic rate (P_N) in leaves of the first (A) and second (B) growth phase shoots, respectively.

The rather efficient photosynthetic and storage system, and the regenerative power of the trees from epicormic buds and coppice shoots may partly explain oak's extraordinary longevity, promoted also by the strong and durable heartwood and continued cambial activity in the trunk (Longman and Coutts 1974).

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During the XIV International Botanical Congress in July 1987 in Berlin a special Symposium on "The Evolution and Ecophysiology of Vascular Plants as Epiphytes" was organized. Some of speakers were asked by the editor of this monograph to prepare individual chapters. Hence the first comprehensive evaluation of the ecological adaptations in epiphytic plants originated.

General aspects including the taxonomic diversity, the life forms, the biomass production and the economic use are discussed in the opening chapter. The second chapter is devoted to the evolution of epiphytism. The characteristics of the CO_2 concentrating mechanism and the development of CAM as one of the most important physiological adaptations to special growing conditions of these plants are the main items of the third chapter. The following three chapters address in detail special problems of the gas exchange and the water relations and the dependence of these processes on environmental factors in major taxonomic groups (ferns – Chapter 4, bromeliads – Chapter 5, orchids – Chapter 6) separately. The seventh chapter covers the problems concerning the mineral nutrition of epiphytes. Information about the epiphytic associations with ants is provided in the eighth chapter. The book is closed with the overview of all known epiphytes (more than 850 genera) and their systematic distribution.

As is briefly shown above, the book affords the synthesis of the present knowledge of ecophysiology of this specialized plant group. In addition it contributes to the solution of general problems concerning the adaptation of plants to environmental conditions. It is richly illustrated by perfect black-and-white photographs and supplemented with instructive diagrams and tables. The extensive bibliography facilitates getting information about special problems. The high quality of printing should also be mentioned.

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