ACTA
PHYSIOLOGIAE
PLANTARUM
Vol. 19. No. 3. 1997: 285-293

Response of CO_2 uptake, chlorophyll content, and some productional features of forest herb *Smyrnium perfoliatum* L. (*Apiaceae*) to different light conditions

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Key words: *Smyrnium*, understory herb, CO_2 uptake, chlorophylls, sunflecks, canopy gaps, growth

Abstract

Smyrnium perfoliatum L. (*Apiaceae*), an endangered summer forest herb grown in the understory of dominant oak-hornbeam stands in Devinska Kobyla, Little Carpathians region in SW Slovakia, is considered to form at least five leaf types of different physiological and anatomical quality. These observation are based upon the estimated differences of photosynthetic carbon dioxide uptake, chlorophyll content, leaf anatomy, and several quantitative parameters of growth analysis. There is a further attempt to establish, to what extent the daily changing environment, especially the excess of light of fast-moving sunflecks by the photosynthetic apparatus within any leaf type, according to its dominant shade adaptation could be effectively used.

Introduction

The mechanism and the extent, by which plants adapt to a changing environment is considered to enable one of the crucial requirements - survival. Moreover, in terms of photosynthesis it is classified as the key process to provide optimal light absorption, and thus energy conversion, and photoassimilation of CO_2 as well (see overview of Bolhár-Nordenkampf 1993, Lawlor 1995). According to various light conditions, plants possess several mechanism wherby they may build a photosynthetic apparatus suited for either high or low light conditions. Aside from the genetical adaptation of plants to specific light condition, this trend may occur within plants of any species, however with further adequate limitation with regard to their ontogenetical stage. Accordingly, while a re-arrangement in leaf tissue of fully developed leaves is not feasible, a further modification within the photosynthetic apparatus is described only within a few levels based upon changes within photosystems, chloroplast architecture and pigment composition (Lichtenthaler *et al.* 1981, 1982b, Masarovičová and Štefančík 1990, Bolhár-Nordenkampf 1993). Comparative studies of the photosynthetic response, generally accompanied by changes in the structure, morphology, physiology, and biochemistry on any level of the photosynthetic apparatus provided, however, further crucial insights into the significance of several leaf-level traits seen in plants adapted to sunny v. shady conditions (Boardman 1977, Björkman 1981, see also overview of Givnish 1988). Nevertheless, it is also known that many traits that vary in response to irradiance level also respond to other environmental factors, many of which are themselves correlated with irradiance level (Collins *et al.* 1985, Givnish 1988).

In this paper our attempt was focused on establishing differences among physiological, biochemical, and several productional features of five leaf types described previously by Oláh and Masarovičová (1996a, 1996b). With regard to the photosynthetic CO_2 uptake, we attempt to further resolve the question to what extent the daily changing environment could be effectively used, especially the excess of light of fast moving sunflecks by the photosynthetic apparatus within any mentioned leaf type, according to its dominant shade adaptation. Furthermore, it remains to be resolved in future research, whether the observed patterns of photosynthesis may also be accompanied by an inherent mechanism that protects *Smyrnium perfoliatum* L. against damage under conditions frequently encountered by plants, *e.g.* photoinhibition, photooxidation (see review of Powles 1984, Demmig 1987, Demmig-Adams 1990, Demmig-Adams and Adams 1992, 1993, Pfündel and Bilger 1994, Demmig-Adams *et al.* 1995).

Materials and Methods

Smyrnium perfoliatum L. (*Apiaceae*) is an endangered, fast growing summer forest herb, previously described from many aspects such as root anatomy (Deutschmann 1969, Lux *et al.* 1995), root respiration (Lux *et al.* 1995; Oláh and Masarovičová 1996b), growth rate (Kobelová 1994, Masarovičová *et al.* 1994), phytochemistry (Gren and Ulubelen 1987), photosynthesis (Oláh and Masarovičová 1996a), *etc. Smyrnium perfoliatum* L. plants were sampled from the previously described plant population, grown in the understory of dominant oak-hornbeam stands in Devinska Kobyla, Little Carpathians region in SW Slovakia (Fig. 1e, Lux *et al.* 1995, Oláh and Masarovičová 1996a, 1996b). The individuals, together with their soil monolith (not to disturb water supply), were transfered in the early morning into the garden of the Faculty of Natural Sciences, Comenius University in Bratislava. They were planted in pots, supplied with original forest soil and grown outdoors. Daily course of the net photosynthetic rate (P_N), as well as maximal daily P_N ($P_{N\,max}$) were measured during a few days of April and May 1994, when all mentioned leaf types became fully developed (Fig. 1a-d), using an open gas exchange system with simple assimilation chamber for short time exposure (approximately 5 - 10 min). Carbon dioxide concentration was measured by IRGA (Infralyt 4, VEB Junkalor Dessau, Germany). The used measurements and equipments were described in detail by Masarovičová (1996), Masarovičová and Eliáš (1985). According to Bauer (1988), Masarovičová and Eliáš (1985), Masarovičová and Štefančík (1990), the measurements of photosynthetic CO_2 uptake were conducted within the same leaves of each leaf type during sunny days (07.00 - 19.00 h) under sunflecks and partial shade conditions. Values of $P_{N\,max}$ were obtained from daily curves of CO_2 exchange. The time of day and photon flux density (PFD) at which $P_{N\,max}$ value was attained

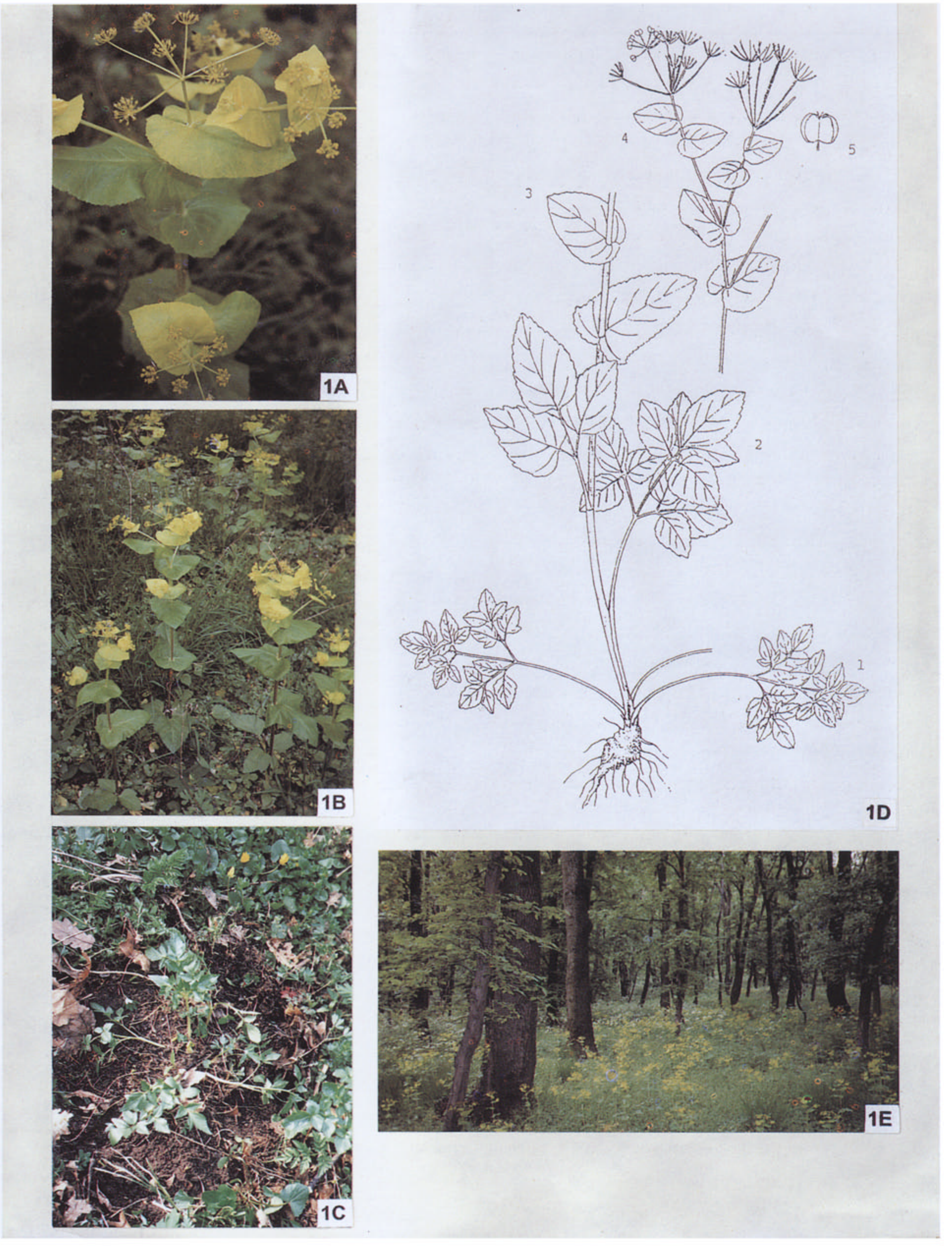

Fig. 1. *Smyrnium perfoliatum* L, grown in the understory of the oak-hornbeam stands in Devínska Kobyla (Little Carpathians region, SW Slovakia, Fig. 1e). During the growing season, the taxon formed five leaf types of different morphological, anatomical, and physiological features described as: (1) compound leaves of the rosette (CLR, Fig. 1c, d); (2) first basal compound leaves (1BC, Fig. 1b,d); (3) second basal compound leaves (2BC, Fig. 1b,d); (4) simple amplexicaul leaves (SAL, Fig. 1 b,d); and bracts (BRA, 1a,b,d,e).

were also determined. The boundary line method as desribed in Webb (1972), Dean *et al.* (1982), and Masarovičová and Eliáš (1986), were used to establish the response curves for CO_2 uptake to irradiance in field conditions. Simultaneously with the ecophysiological measurements, data about the basic meteorological factors (air temperature, global radiation, and relative air humidity) were obtained from ambulant measurements of micrometeorological factors, and the permanent meteorological station situated in the Slovak Institute of Hydrometeorology in Bratislava-Koliba during the whole growing season of 1994, when *Smyrnium perfoliatum* L. occured, and the days when measurements were carried out, respectively (Fig. 2 a, b). Leaf chlorophyll contents (chl [a], [b], [a+b]) were determined in acetone extract (80 % acetone, p.a.). Measurements of absorbance were made on a SPEKOL 20 (K. Zeiss, Jena, Germany). The chlorophyll contents were calculated according to Lichtenthaler (1987) and were expressed per both leaf dry mass and leaf area unit. The specific leaf area (SLA), and specific leaf mass (SLW), and the assimilation number (AN) were estimated from the whole leaves. For statistical evaluation of the differences established within any leaf type, the student's t - test was used.

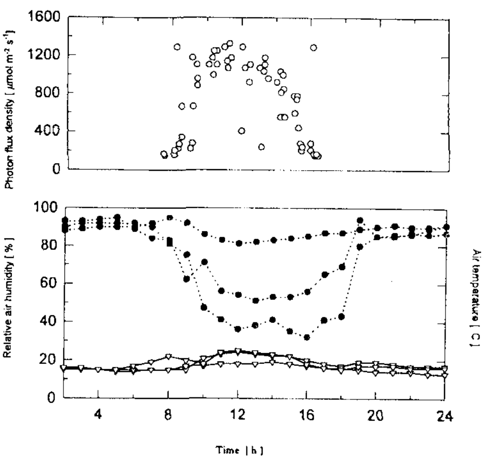

Fig. 2a-b. Daily course of photon flux density (PFD, open circle), relative air humidity (RH, filled circle), and air temperature (T_A, open triangle), established simultaneously with the CO_2 exchange measurements of *Smyrnium perfoliatum* L.

Results

Meteorological factors

The days when the measurements were carried out could be classified as typical days with anticyclonic weather. The highest photon flux density (PFD) (850 - 1300 mol·m^{-2}·s^{-1}) was measured about midday (Fig. 2a).The mean daily air temperature (T_A) ranged from 16 to 18 °C (maximal T_A 19 - 24 °C) and mean daily relative air humidity (RH) ranged from 69 to 88 % (minimal RH 35 - 51 %). As shown in Fig. 2b, the curves of T_A and RH in a 24 hour's cycle possessed the usual course with a maximum for T_A between 11.30 and 14.00 and a minimum for RH between 13.00 and 16.00.

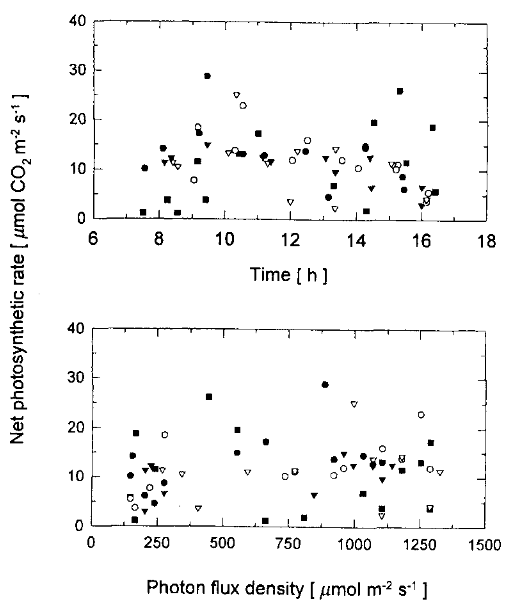

Fig. 3a-b. Daily course of net photosynthetic rate (P_N) plotted against the time (T) or photon flux density (PFD). The values were established for compound leaves of the rosette (CLR - filled circle), first and second basal compound leaves (1BC - filled triangle, 2BC - open triangle), upper simple amplexicaul leaves (SAL - open circle), and bracts (BRA - filled columns) of *Smyrnium perfoliatum* L.

Light CO_2 gas exchange rates (CER)

Fully developed compound leaves of the rosette (CLR, Fig. 1c-d) exhibited the highest photosynthetic activity throughout the whole growing season. The highest values of mean daily net photosynthetic rate (P_N) as well as the maximum net photosynthetic rate ($P_{N\ max}$) under exposure of high irradiance in which the CLR grown, argued the heliophytic character of the mentioned ones (Table 2, Fig. 3a-b). As shown in Table 2, there is considered a relative constant level without statistical meaning within the values of mean daily P_N and maximum daily P_N, when *Smyrnium perfoliatum* L. passed through the further phenophases of the distingly leaf types (Fig. 1a-d). The differences in light CER of any leaf type became substantial, when the val-

Table 1. Photosynthetic activity of compound leaves of the rosette (CLR), first and second basal compound leaves (1BC, 2BC), upper simple amplexicaul leaves (SAL), and bracts (BRA), established by measuring of mean daily net photosynthetic rate (P_N), maximum daily net photosynthetic rate (P_N max) of *Smyrnium perfoliatum* L.

Phenophase	Mean daily net photosynthetic rate, P_N [μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$]	Maximum daily net photosynthetic rate, P_N max [μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$]	Time of day [h]	PFD [μmol $m^{-2} \cdot s^{-1}$]
Compound leaf of the rosette	13.202±6.190	23.999±6.228 *	9.20 - 9.45	660 - 880
1st basal compound leaf	10.334±3.536	12.897±1.812	9.45 - 11.40	950 - 1170
2nd basal compound leaf	11.057±6.034	18.339±6.133	10.10 - 10.35	990 - 1110
Upper simple amplexicaul leaf	11.961±5.372	17.456±4.822	10.35 - 10.55	1170 - 1250
Bracts	10.175±7.967	22.968±3.304	14.50 - 15.30	440 - 550

* significant differences at $P = 0.05$

** significant differences at $P = 0.01$

Table 2. Mean values of assimilation number (AN), specific leaf area (SLA), and specific leaf mass (SLM), established within compound leaves of the rosette (CLR), first and second basal compound leaves (1BC, 2BC), upper simple amplexicaul leaves (SAL), and bracts (BRA) of *Smyrnium perfoliatum* L

Phenophase	AN [mg $CO_2 \cdot g^{-1}$ (chl a+b)$\cdot s^{-1}$]	SLA [$dm^2 \cdot g^{-1}$]	SLM [$g \cdot dm^{-2}$]
Compound leaf of the rosette	1.653 (for 1) 3.005 (for 2)	4.556±0.713	0.224±0.032 **
1st basal compound leaf	1.619 (for 1) 2.020 (for 2)	6.594±0.883 **	0.153±0.019
2nd basal compound leaf	1.773 (for 1) 2.939 (for 2)	6.767±2.189	0.158±0.041
Upper simple amplexicaul leaf	1.839 (for 1) 2.684 (for 2)	5.006± 0.408 **	0.201±0.017
Bracts	2.369 (for 1) 5.348 (for 2)	3.925±0.271	0.256±0.017 **

for 1 ≈ see Table 2

for 2 ≈ see Table 2

* For explanation see Table 1

ues of $P_{N\,max}$ were compared among any leaf type, however with further regard to the time of day and values of PFD, in which the leaves reached the highest level (Table 1, Fig. 3a-b). During the day the leaves of any phenophase, except of bracts (BRA), reached maximum P_N in the morning hours (before 11 a.m.). Exposure to high PFD could involve limitation of photosynthetic activity within BRA, as such they possess according to their dominant shade character, the efficiency to utilize the energy of lower light (Table 1, Fig. 3b). The leaves of any phenophase, however have also indicated a conspicious midday depression of photosynthesis (11.00 - 14.00), associated with high values of both T_A and PFD, as well as low RH values (Fig. 1a-b; 2a). Furthermore, substantially high values of assimilation number (AN) were established within any leaf type (Table 2).

Table 3. Mean values of chlorophyll content ([a], [b], [a+b]) and chlorophyll [a:b] ratio, expressed per leaf area and dry mass, established for compound leaves of the rosette (CLR), first and second basal compound leaves (1BC, 2BC), upper simple amplexicaul leaves (SAL), and bracts (BRA) of *Smyrnium perfoliatum* L.

Phenophase	[a]	[b]	[a + b]	[a : b]
compound leaf of	0.272±0.021* [g·m^{-2}]	0.094±0.010*	0.352±0.024*	2.925±0.317
the rosette	12.123±0.869 [mg·g^{-1} d.m.]	4.187±0.555	16.310±1.288	2.925±0.316
1st basal	0.192±0.011	0.060±0.005	0.281±0.069	3.188±0.181*
compound leaf	12.266±0.431	3.859±0.311	16.126±0.718	3.188±0.182
2nd basal	0.200±0.003	0.075±0.008*	0.275±0.010	2.703±0.258
compound leaf	13.104±0.589*	4.891±0.655*	17.995±1.209*	2.702±0.258
upper simple	0.214±0.012*	0.073±0.009*	0.287±0.020*	2.944±0.188
amplexicaul leaf	10.433±0.199*	3.559±0.305*	13.992±0.502*	2.943±0.189
bracts	0.146±0.021	0.043±0.009	0.189±0.028	3.407±0.431
	6.974±0.766	2.129±0.393	9.103±1.142	3.311±0.285*

For explanation see Table 1

Chlorophyll content

In the middle of March, when the physiologicaly adult compound leaves of the rosette (CLR) had grown as the first of the five distinguishable leaf types, they exhibited the highest values of chlorophyll [a+b] content expressed per leaf area. As shown in Table 3, the chlorophyll [a+b] content per leaf area significantly decreased during further phases of plant ontogenesis - when the first basal compound leaves (1BC) appeared. When the second basal compound leaves (2BC) and simple amplexicaul leaves (SAL) appeared, the chlorophyll [a+b] content per leaf area persisted relatively constant, while during the phenophase of bracts (BRA) a significantly shift downwards was observed (Table 3). Significant differences within the values of chl [a] content per leaf area were evaluated only between phenophases of CLR and 1BC, as well as SAL and BRA (Table 3). Table 3 presents significant differences of chl [b] content per leaf area in comparison to phenophases of CLR and 1BC, 1BC and 2BL, as well as SAL and BRA.

On the other hand, the values of chl [a+b] content per dry mass were constant during the growing season, except for the significant higher chl [a+b] content within the 2BC and SAL. The values of chl [a] and chl [b] content per dry mass within any leaf type exhibited a coincidental pattern. The highest values of chl [a:b] ratio in terms of leaf area were estimated in bracts, however without statistical meaning. However, the bracts indicated the significant highest values of chl [a:b] ratio in terms of dry mass (Table 3).

Growth analysis

Smyrnium perfoliatum L. exhibited the significant highest values of specific leaf mass (SLM) during the phenophase of bracts as well as the compound leaves of the rosette (CLR), while the 1BC, 2BC, and SAL indicated relatively constant values of SLM (Table 2). On the contrary, the lowest values of specific leaf area (SLA) were established during the phenophase of CLR and BRA (Table 2).

Discussion

The response of plants, especially forest herbs grown in natural conditions to different environmental conditions (light, nutrients, water, *etc.*) was well documented many decades ago. Moreover, according to Collins *et al.* (1985) field as well as controlled laboratory conditions have that forest herbs are capable of shifts in metabolism and life history in response to differing environments. As such *Smyrnium perfoliatum* L. belongs to one by Sparling (1967), Taylor and Pearcy (1976), and Collins *et al.* (1985) described plant categories with regard to the photosynthetic response to varying light environments: light-flexible herbs. Accordingly, *Smyrnium perfoliatum* L. is a temporally flexible herb, being characterized of photosynthetically plastic over a range of light intensities. Such plants are thought to emerge usually early in spring, mature with canopy closure, and senesce in early summer. The plants indicate a characteristic shift from sun to shade photosynthetic physiology with canopy development. Since the growing of the taxon in conditions of deep shade, *Smyrnium perfoliatum* L. also indicates a strong non-steady-state behaviour resulting in the daily dynamics of the penetration of solar radiation through forest canopies. The capability of the taxon to also utilize, apart from the incident light conditions during the growing season, the excess of light in the form of sunflecks, could play a role in the explanation of the relative high level of photosynthetic activity during the day. According to Pearcy and Calkin (1983), Pearcy (1988, 1990) we supposed that the taxon in spite of dominant shade adaptation received substantial amounts of irradiance in the form of sunflecks or patches, and whereby the obtained high values of mean daily P_N and maximum daily P_N accounted for a large (40 - 60 %) fraction of the daily carbon gain. High values of daily photosynthetic assimilation are also thought to be neccesary to receive sufficient balance of generally high respiration rates of leaves and roots. On the above mentioned basis *Smyrnium perfoliatum* L. was classified as a fast growing species (see Lux *et al.* 1995). However, in our field measurements, the dark respiration rates exhibited considerable inhibition due to relatively low temperature at the time of measuring (17.30 - 18.00 h), insofar they did not reflect the true dissimilation traits. *Smyrnium perfoliatum* L. Always reached the daily maxima for P_N, except for the fully developed bracts in the phenophase of flowering, in the morning before 11.00 h. A coincidental tendency was observed within two summer herb species, perennial *Aegopodium podagraria* L., and annual *Impatients parviflora* (see Masarovičová and Eliáš 1986), within ten herbaceous perennials described by Eliáš (1979), and within a understory species *Arnica cordifolia* (Young and Smith 1980, 1982). High amounts of P_N are thought to correlate even with a high chlorophyll content within the five leaf types during the growing season in terms of leaf area and dry mass. The highest values of chl [a+b] per leaf area and dry mass were evaluated always in spring, when the growing season started, while the lowest ones were observed in the summer, when the bracts reached maximum development and the onthogenesis of *S. perfoliatum* was finished. However, as described previously by Goryshina (1978, 1979), substantial shade adaptation of individual leaves, which have higher leaf area and thereby lower area concentration of chlorophylls, could be compensated by higher assimilation number. Insofar, a comparative analysis of the AN between leaves of *Smyrnium perfoliatum* L. and sun and shade leaves of *Fagus sylvatica* L. (Masarovičová and Štefančík 1990) have shown substantial higher pattern in bracts of *Smyrnium perfoliatum* L.. Substantial differences in the morphological adaptation of the five leaf types to different light conditions were also evident according to different values of SLM and SLA. The unexpected high values of SLM within bracts in spite of their dominant shade adaptation could be sustained by the so-called regreening effect appearing two weeks before the mentioned leaf type reach the point of no return - the leaf senscence (for more details see Oláh and Masarovičová 1996a).

Today we have, apart from general information about the distribution and phenology, insufficient knowledge about the ecology and ecophysiology of this forest herb. Indeed, insights of the herb response to light condition alone have to be sustained by other comparative studies regarding different environmental factors, many of which are themselves correlated with irradiance level.

Acknowledgment

The authors would like to express their gratitude to Dr. Timotej Ješko, Institute of Botany, Slovak Academy of Sciences for critical reading of the manuscript. Furthermore, we acknowledge technical help of Mrs. E. Khandlová, Mrs. J. Kovaríková, and Dr. L. Vidličková. The research project was financially supported by the grant of the Slovak Grant Agency No. 1 / 76 / 92.

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Received October 29, 1996; accepted 02 June 1997