

# Photochemical efficiency, content of photosynthetic pigments and phenolic compounds in different pitcher parts of *Sarracenia* hybrids

Martina Tušek<sup>1</sup>, Marcela Curman<sup>2</sup>, Marija Babić<sup>3</sup>, Mirta Tkalec<sup>3\*</sup>

<sup>1</sup> Galovec Začretski 43b, HR-49223 Sveti Križ Začretje, Croatia

<sup>2</sup> Mokrice 72, HR-49243 Oroslavje, Croatia

<sup>3</sup> Sveučilište u Zagrebu, Prirodoslovno-matematički fakultet, Biološki odsjek, Rooseveltov trg 6, HR-10000 Zagreb, Croatia

**Abstract** – *Sarracenia* is a genus of carnivorous plants characterised by leaves modified into pitchers which lure, trap and digest insects. The aim of this study was to analyse the photochemical efficiency and contents of photosynthetic pigments and phenolic compounds in different pitcher parts – operculum, wing, pitcher-tube upper part and pitcher-tube lower part of three morphologically different *Sarracenia* hybrids. The photochemical efficiency of the operculum and the pitcher-tube upper part was lower than that of the pitcher-tube lower part and wing, especially in hybrid B. In all hybrids, the wing had higher amount of chlorophyll *a* than other pitcher parts. In contrast, a higher amount of phenolic compounds, in particular anthocyanins, was measured in the operculum and the pitcher-tube upper part, parts which are red-coloured and participate in luring and trapping insects. Although there were some differences among the hybrids, the results show that amount of phenolic compounds and photosynthetic pigments as well as photochemical efficiency are related to the function of the pitcher part analysed.

**Keywords:** anthocyanins, carnivorous plants, carotenoids, chlorophyll, flavonoids, photosynthesis, *Sarracenia*

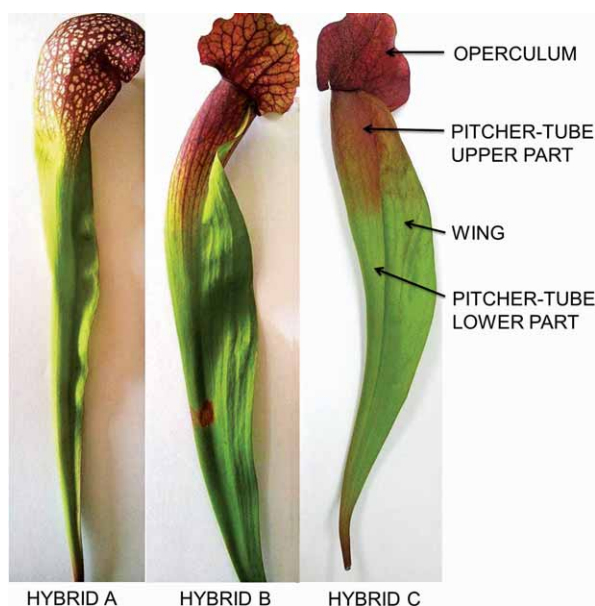
## Introduction

*Sarracenia* is a genus comprising 11 carnivorous species. Those rosette-forming perennials have modified their leaves into pitchers, which perform a dual role – photosynthesis and the capture of insects (Ellison and Gotelli 2002, Pavlović et al. 2007). *Sarracenia* plants attract their insect prey with extrafloral nectaries and the pitchers' colourful patterns (Rodenas 2012). *Sarracenia* species, as well as their numerous hybrids that occur in the wild and cultivation, greatly differ in morphology and the colouration of pitchers (Rice 2006). The pitchers may be erect or decumbent, yellow-green to red and pitcher-tube upper part and hood can have red veins and/or white translucent areolation (Schnell 2002). There are three types of pigments involved in the *Sarracenia* pitcher colouration: chlorophylls, carotenoids and flavonoids. The red of pitchers can be attributed to the presence of flavonoids, in particular anthocyanins (Sheridan and Griesbach 2001, Rodenas 2012). Besides attracting the insects, flavonoids have a significant role in protection from high intensities of visible and UV radiation, as well as being antioxidants (Close and McArthur 2002).

The main pitcher parts (Fig. 1) in *Sarracenia* species are the pitcher tube, pitcher mouth, nectar roll (peristome), lid (operculum) and wing (ala) (Rice 2006). The pitcher mouth is surrounded by a peristome covered with nectar-secreting glands that attract insects into the pitcher tube. Above the pitcher mouth, there is a pitcher operculum which is often coloured red and covered with glands that also secrete nectar and attract prey. Besides preventing rain from filling the pitcher tube, the pitcher lid also serves as a landing platform for flying insects (D'Amato 2013). The wing has nectar trails that lead insects to the pitcher mouth. The pitcher tube can be divided into upper and lower part; the upper part secretes nectar and smooth waxy material, therefore taking a role in attracting insects and preventing their escape (Rice 2006). In lower part of the pitcher there are glands that secrete digestive enzymes enabling digestion of prey and absorption of minerals (Glenn and Bodri 2012).

Since the first Darwin's experiments, it has been assumed that carnivorous plants compensate for the lack of minerals in their natural habitat by capturing and digesting the insect prey. Recent studies have proven the benefit of

\* Corresponding author, e-mail: mtkalec@zg.biol.pmf.hr  
M. Tušek and M. Curman equally contributed to the work



**Fig. 1.** Pitchers of three different *Sarracenia* hybrids (A, B and C) and their main parts used in the study.

carnivory through increased rate of photosynthesis, biomass and fertility (Givnish et al. 1984, Farnsworth and Ellison 2008, Pavlovič et al. 2014). However, carnivory entails also some costs due to energy investment in attracting and trapping the prey (Givnish et al. 1984, Ellison and Farnsworth 2005). Namely, to catch and digest their prey, carnivorous plants have transformed some of their photosynthetic leaves into traps with metabolically active glands, resulting in an overall decrease of photochemical efficiency (Adamec 2010). The recent studies have shown that some *Sarracenia* species have different metabolic activities in wing and pitcher tube, which has more glandular tissue, suggesting that there might be also a difference in photosynthetic activity between different pitcher parts (Adamec 2010). In the genus *Darlingtonia*, which is similar to the genus *Sarracenia*, the pitcher tube contained a higher amount of chlorophyll in regard to the hood-shaped operculum, which is more reddish and has many translucent areoles. Also, pitcher parts with extrafloral nectaries have a lower amount of photosynthetic pigments (Ellison and Farnsworth 2005).

The aim of this study was to analyse content of photosynthetic pigments and phenolic compounds, as well as photochemical efficiency of different pitcher parts in morphologically different hybrids of the genus *Sarracenia*.

## Materials and methods

### Morphological characteristics of hybrids

The research was carried out on three morphologically different hybrids of the genus *Sarracenia* L., named hybrid A, hybrid B and hybrid C (Fig. 1). The plants were grown in plastic pots containing peat, and watered daily with distilled water. There was always 2–3 cm of water in the plates beneath the pots. During spring and summer, the plants were grown outdoors where they were exposed to photo-

synthetically active radiation and UV irradiance of maximum daily levels ca. 2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (quantum sensor Hansatech Quantitherm, UK) and 30  $\text{W m}^{-2}$  (UV meter YX-35UV, Taiwan, China), respectively. The average day/night temperature was  $26/12 \pm 3 \text{ }^\circ\text{C}$ .

In all hybrids, operculum and the upper part of the pitcher tube were red-coloured with numerous red veins, while wing and the pitcher-tube lower part were green. There were some differences between hybrids – in pitcher size, operculum shape as well as in the colouration of operculum and pitcher-tube upper part. Pitchers of hybrid A (ca. 28 cm high) had a reduced wing. The back side of the hood-shaped operculum and upper part of tube had translucent areoles with a network of red veins. The mouth of the pitcher was smaller than in the other two hybrids. Hybrid B (ca. 35 cm high) had undulating operculum and red veins spread all over operculum and pitcher-tube upper part. The space between the veins was more greenish, not white as in hybrid A. The wing was larger than in hybrids A and C. Hybrid C (ca. 23 cm high) had a more reddish operculum than the other two hybrids. The operculum was less undulating than in hybrid B. Although hybrids used in this study are of unknown origin, according to morphological features one of the parents of hybrid A is *S. psittacina* while one of the parents of hybrid B and C is *S. purpurea*.

For each hybrid, three representative and morphologically similar pitchers were used. Four different pitcher parts: pitcher-tube upper part, pitcher-tube lower part, wing and operculum were analysed in the experiment (Fig. 1).

### Photochemical efficiency of PSII

Fluorescence of chlorophyll *a* *in vivo* was measured using fluorometer (Qubit Systems Inc., Canada), with the method described by Lichtenthaler and Babani (2004) and Lichtenthaler et al. (2005). Before measurement, the pitcher samples were kept on well-watered filter paper in the dark for 20 minutes. The dark-adapted pitcher sample was placed on the fluorometer stand, on wet filter paper, and exposed to modulated red light of low intensity ( $1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) to obtain the minimal fluorescence ( $F_0$ ). The sample was then exposed to continuous actinic light of high intensity ( $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ), which resulted in transient increase of the fluorescence signal from  $F_0$  to maximum fluorescence ( $F_m$ ). During five minutes of light exposure, the fluorescence signal decreased, reaching steady-state fluorescence condition ( $F_s$ ). Results were recorded by software Logger Pro 3.2. Recorded data were used for calculation of maximum quantum yield ( $F_v/F_m$ ),  $F_v/F_0$  and fluorescence decrease ratio ( $R_{Fd}$ ) according to Lichtenthaler et al. (2005).

### Photosynthetic pigments

For determination of photosynthetic pigments, 50 mg of samples were homogenised with mortar and pestle in 1.5 mL of cold 80% (v/v) acetone with the addition of calcium carbonate. Homogenates were centrifuged for 10 minutes at 5000 g and 4  $^\circ\text{C}$ . The absorbance of supernatants was measured at 470 nm, 646 nm and 663 nm using a UV/VIS spec-

trophotometer Specord (Analytik Jena). The content of chlorophyll *a*, chlorophyll *b* and total carotenoids was determined according to Lichtenthaler (1987) and Wellburn (1994).

### Total phenolics, flavonoids and anthocyanins

Pitcher samples (50 mg) were homogenised with mortar and pestle in 1.5 mL of cold 50% (v/v) ethanol. After incubation at 60 °C for 30 minutes, the homogenates were centrifuged at 12000 g for 10 minutes. The supernatants were used to measure total phenolics, flavonoids and anthocyanins.

For total phenolics content, a mixture of 1580 µL of distilled water, 20 µL of plant extract, 100 µL of Folin–Ciocalteu reagent and 300 µL of 1.88 M sodium carbonate was prepared. After incubation at 45 °C for 60 minutes, the absorbance at 765 nm was measured using a UV/VIS spectrophotometer (Singleton et al. 1999). The results were expressed as mg of gallic acid equivalents (GAE) per g of fresh weight.

For total flavonoids content, an aliquot of the plant extract (100 µL) was mixed with 20 µL of 10% (w/v) AlCl<sub>3</sub>, 500 µL of 1 M potassium acetate and 380 µL of distilled water. The mixture was incubated at 24 °C for 30 minutes and absorbance at 420 nm was measured using a UV/VIS spectrophotometer (Pourmorad et al. 2006). The results were expressed as mg of quercetin equivalents (QE) per g of fresh weight.

For total anthocyanins content, 500 µL of plant extract was mixed with 500 µL of 50% (v/v) ethanol and 84 µL of 37% HCl. After incubation at 60 °C for 30 minutes, the absorbance was measured at 530 nm using a UV/VIS spectrophotometer (Paiva et al. 2003). Total anthocyanin content was determined using a molar extinction coefficient of 34300 M<sup>-1</sup> cm<sup>-1</sup> and a molecular weight of 449.2 g mol<sup>-1</sup>, and expressed as mg of cyanidin-3-glucoside equivalents (C3GE) per g of fresh weight.

### Statistical analysis

Results were shown as means ± standard errors. Determination of phenolic compounds and photosynthetic pigments content was performed in six replicates. Determination of photochemical efficiency was performed in triplicate. For processing data Microsoft Excel 2007 and Statistica 10 (StatSoft Inc., SAD) were used. The results obtained for different pitcher parts within each hybrid were compared by analysis of variance (ANOVA) and post hoc Tukey's test. Differences between means were considered statistically significant at  $p \leq 0.05$ .

## Results

### Photochemical efficiency of PSII

All pitcher parts of all hybrids had a similar maximum quantum yield of PSII ( $F_v/F_m$ ) with values ranging from 0.72 to 0.78 (Tab. 1). The exceptions were much lower  $F_v/F_m$  values noticed in the pitcher-tube upper part and operculum of hybrid B, the operculum showing an extremely low value (0.37).

The highest value of  $F_v/F_0$  was detected in the wing of all hybrids investigated, while the lowest value was found in the operculum. Analysis of pitcher parts of hybrid A showed a significant decrease of  $F_v/F_0$  in the pitcher-tube upper part and operculum compared to the wing. Amongst hybrids, hybrid B stands out with the lowest  $F_v/F_0$  values measured in the operculum and the pitcher-tube upper part. In hybrid C, there was no significant difference in  $F_v/F_0$  between pitcher parts, though the highest value was observed in the wing (Tab. 1).

In hybrid A, there was no significant difference in  $R_{Fd}$  values among different pitcher parts although a slight decrease was determined in the pitcher-tube lower part. In hybrid B, the highest and the lowest  $R_{Fd}$  values were measured in the wing and operculum, respectively. The operculum of hybrid B had the lowest  $R_{Fd}$  value. There was no significant difference in  $R_{Fd}$  values among the different pitcher parts in hybrid C (Tab. 1).

**Tab 1.** Chlorophyll *a* fluorescence parameters: maximum quantum yield of PSII ( $F_v/F_m$ ), ratio between variable and minimum fluorescence ( $F_v/F_0$ ) and chlorophyll fluorescence decrease ratio ( $R_{Fd}$ ), in three different *Sarracenia* hybrids (A, B and C). Four pitcher parts: pitcher-tube upper part (PU), pitcher-tube lower part (PL), wing (W) and operculum (O) were analysed. The results were expressed as the average of 3 replicates ± standard error. Different letters in each column denote significantly different results ( $p \leq 0.05$ ) among different pitcher parts within each hybrid, ns – not significant.

<i>Sarracenia</i> hybrids	Pitcher part	Fluorescence parameters		
		$F_v/F_m$	$F_v/F_0$	$R_{Fd}$
A	PU	0.74±0.01 <sup>ab</sup>	2.86±0.12 <sup>a</sup>	2.83±0.09 <sup>ns</sup>
	PL	0.77±0.01 <sup>ab</sup>	3.30±0.14 <sup>ab</sup>	2.15±0.22 <sup>ns</sup>
	W	0.78±0.003 <sup>b</sup>	3.62±0.06 <sup>b</sup>	2.66±0.33 <sup>ns</sup>
	O	0.72±0.02 <sup>a</sup>	2.63±0.25 <sup>a</sup>	2.72±0.22 <sup>ns</sup>
B	PU	0.57±0.07 <sup>b</sup>	1.41±0.34 <sup>a</sup>	1.88±0.44 <sup>ab</sup>
	PL	0.77±0.003 <sup>c</sup>	3.36±0.05 <sup>b</sup>	2.43±0.40 <sup>ab</sup>
	W	0.78±0.001 <sup>c</sup>	3.59±0.02 <sup>b</sup>	2.94±0.09 <sup>b</sup>
	O	0.37±0.04 <sup>a</sup>	0.61±0.11 <sup>a</sup>	1.18±0.19 <sup>a</sup>
C	PU	0.75±0.01 <sup>ns</sup>	3.02±0.20 <sup>ns</sup>	3.21±0.07 <sup>ns</sup>
	PL	0.73±0.02 <sup>ns</sup>	2.77±0.25 <sup>ns</sup>	2.83±0.33 <sup>ns</sup>
	W	0.77±0.01 <sup>ns</sup>	3.37±0.13 <sup>ns</sup>	3.06±0.21 <sup>ns</sup>
	O	0.74±0.02 <sup>ns</sup>	2.81±0.24 <sup>ns</sup>	3.76±0.32 <sup>ns</sup>

### Content of photosynthetic pigments

In all three hybrids, the chlorophyll *a* content was significantly higher in the wing than in the other parts of pitchers. The wing of hybrid B had the highest amount of chlorophyll *a*. A high chlorophyll *a* content was also detected in the pitcher-tube lower part of hybrid B. In hybrids A and C, chlorophyll *a* contents in the pitcher-tube upper and lower part as well as operculum did not differ from each other (Fig. 2A).

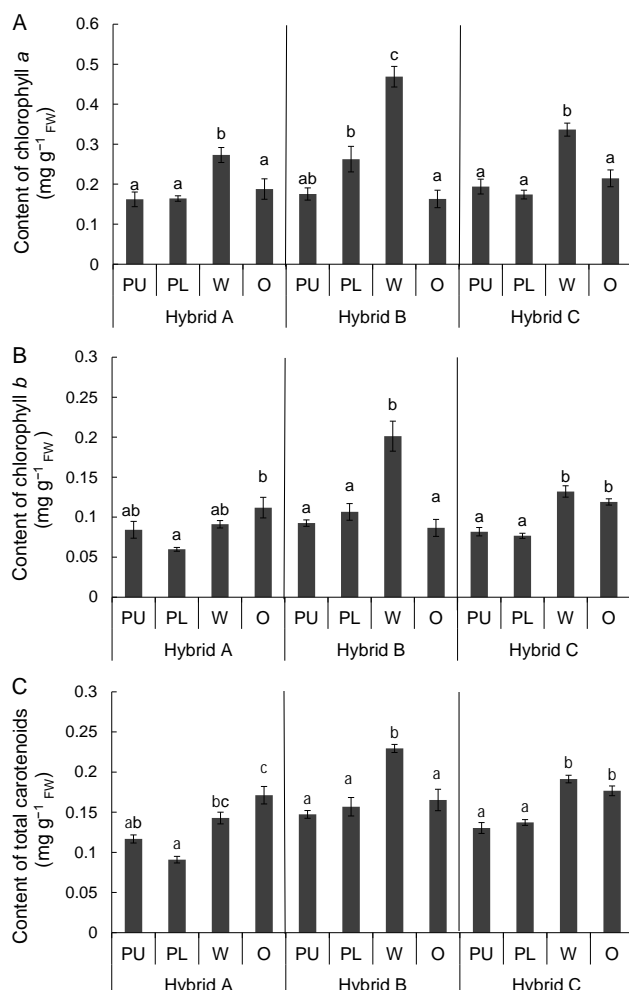
In hybrids B and C, the highest amounts of chlorophyll *b* and total carotenoids were detected in the wing while in hybrid A the highest amount was detected in the operculum.

The wing of hybrid B had the highest amount of chlorophyll *b* and carotenoids. The lowest contents of chlorophyll *b* and carotenoids were observed in the pitcher-tube lower part of hybrid A, as well as in the pitcher-tube lower and upper part of hybrid C when compared to the wing and operculum (Figs. 2B and C).

In hybrids A and B the chlorophyll *a/b* ratio and the chlorophylls/carotenoids ratio were higher in the wing and pitcher-tube lower part than in the other two pitcher parts. In hybrid C the highest values of both ratios were observed in the wing, while the operculum had the lowest chlorophyll *a/b* ratio (Tab. 2).

### Content of phenolic compounds

Among different pitcher parts, the highest amount of total phenolics was detected in the operculum, especially in hybrids A and C. In hybrids A and B, the pitcher-tube lower part and the wing had the lowest amount of total phenolics, while in hybrid C the lowest amount was measured in the pitcher-tube upper part (Fig. 3A).



**Fig. 2.** Content of chlorophyll *a* (A), chlorophyll *b* (B) and total carotenoids (C) in three different *Sarracenia* hybrids. Four pitcher parts: pitcher-tube upper part (PU) and lower part (PL), wing (W) and operculum (O) were analyzed. The results were expressed as the average of 6 replicates ± standard error. Different letters above the bars denote significantly different results (p ≤ 0.05) among different pitcher parts within each hybrid. FW – fresh weight.

**Tab 2.** Chlorophyll *a/b* ratio (chl *a/b*) and chlorophylls/carotenoids ratio (chl/car) in three different *Sarracenia* hybrids (A, B and C). Four pitcher parts: pitcher-tube upper part (PU), pitcher-tube lower part (PL), wing (W) and operculum (O) were analysed. The results were expressed as the average of 6 replicates ± standard error. Different letters in each column denote significantly different results (p ≤ 0.05) among different pitcher parts within each hybrid.

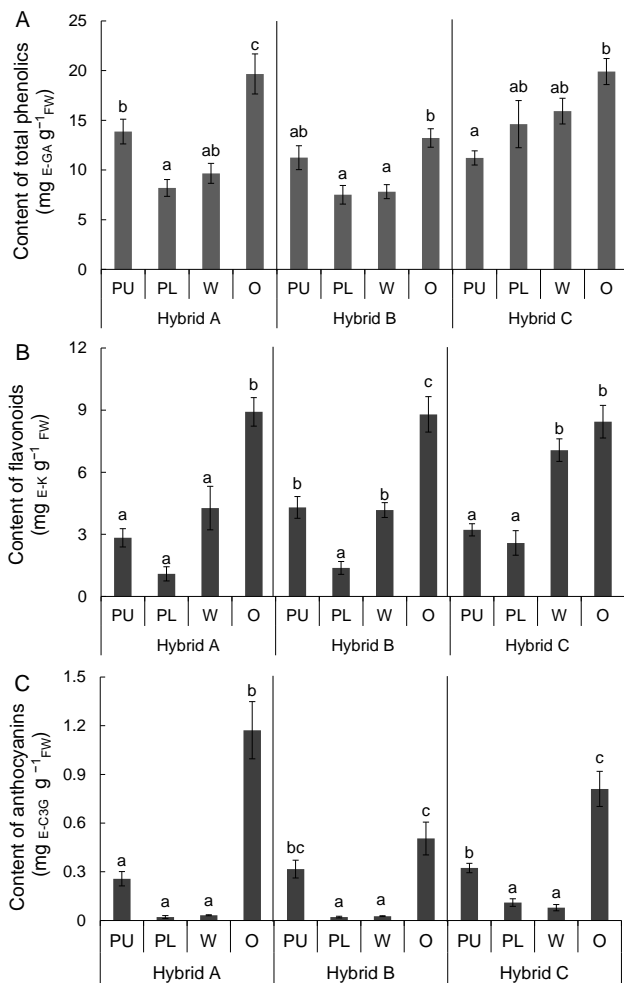
<i>Sarracenia</i> hybrids	Pitcher part	chl <i>a/b</i>	chl/car
A	PU	2.12±0.38 <sup>ab</sup>	2.11±0.12 <sup>b</sup>
	PL	2.75±0.06 <sup>b</sup>	2.47±0.06 <sup>bc</sup>
	W	2.98±0.08 <sup>b</sup>	2.54±0.04 <sup>c</sup>
	O	1.75±0.28 <sup>a</sup>	1.74±0.12 <sup>a</sup>
B	PU	1.91±0.17 <sup>a</sup>	1.83±0.12 <sup>a</sup>
	PL	2.44±0.06 <sup>b</sup>	2.33±0.12 <sup>b</sup>
	W	2.37±0.1 <sup>b</sup>	2.9±0.13 <sup>c</sup>
C	PU	2.35±0.11 <sup>b</sup>	2.11±0.12 <sup>ab</sup>
	PL	2.28±0.16 <sup>ab</sup>	1.82±0.06 <sup>a</sup>
	W	2.58±0.15 <sup>b</sup>	2.45±0.09 <sup>b</sup>
	O	1.8±0.17 <sup>a</sup>	1.89±0.1 <sup>a</sup>

In all analysed hybrids, the operculum showed the highest and the pitcher-tube lower part the lowest content of flavonoids. In hybrid C, the wing also contained a higher amount of flavonoids than the pitcher-tube upper and lower part (Fig. 3B).

The operculum was the pitcher part with the highest amount of anthocyanins, especially in hybrid A. In hybrids B and C, the pitcher-tube upper part also contained a high amount of anthocyanins. In all hybrids, the pitcher-tube lower part and the wing had lower anthocyanin content than the other pitcher parts (Fig. 3C).

### Discussion

The optimal efficiency of PSII ( $F_v/F_m$ ) is an important indicator of photochemical efficiency in plants (Maxwell and Johnson 2000). In all the hybrids investigated, the measured  $F_v/F_m$  values (Tab. 1) were in accordance with theoretical values (0.74 to 0.85) for non-carnivorous plants (Maxwell and Johnson 2000, Lichtenthaler et al. 2005). However,  $F_v/F_0$ , a more sensitive fluorescence parameter (Lichtenthaler et al. 2005), showed values below the critical value of 3.8, indicating a decrease of photochemical efficiency (Chatzistathis et al. 2011) in all pitchers parts (Tab. 1). A lower photochemical efficiency has been often found in carnivorous plants (Bruzzese et al. 2010) and it has been correlated with the costs of carnivory (Adamec 2010) as well as with low foliar nitrogen content and slow growth of carnivorous plants (Ellison and Adamec 2011, Pavlovič and Saganová 2015). The lowest values of both parameters,  $F_v/F_m$  and  $F_v/F_0$  were found mostly in the operculum and upper part of the pitcher tube, which are predominantly red-coloured areas with numerous nectar-secreting glands. Moreover, in these pitcher parts a lower amount of chlorophyll *a* and higher



**Fig. 3.** Content of total phenolics (A), flavonoids (B) and anthocyanins (C) in three different *Sarracenia* hybrids. Four pitcher parts: pitcher-tube upper part (PU) and lower part (PL), wing (W) and operculum (O) were analyzed. The results were expressed as the average of 6 replicates ± standard error. Different letters above the bars denote significantly different results ( $p \leq 0.05$ ) among different pitcher parts within each hybrid. FW – fresh weight.

amount of phenolic compounds were found (Figs. 2 and 3), which is in accordance with higher anthocyanin and lower chlorophyll content found in the traps of *Nepenthes* (Pavlovič and Saganová 2015). On the other hand, the highest photochemical efficiency and chlorophyll content were recorded in the green-coloured wing of *Sarracenia*, a pitcher part that has a role in guiding insects to the pitcher mouth (D'Amato 2013). However, the lower part of the pitcher tube, although green-coloured, had lower photochemical efficiency, probably due to the presence of digestive glands needed for the digestion and absorption of minerals (D'Amato 2013). The lower  $F_v/F_m$  values and photosynthesis rate in the trapping organs of carnivorous plants other than *Sarracenia* have already been described (Pavlovič et al. 2009). We also measured the fluorescence decrease ratio ( $R_{Fd}$ ), a parameter directly related to rate of photosynthesis (Lichtenthaler and Babani 2004). The measured  $R_{Fd}$  values (Tab. 1) were mostly between those of sun-exposed leaves (3 to 5) and those of shade-exposed leaves (1 to 2.5). Higher  $R_{Fd}$  values in sun-exposed leaves reflect their higher pho-

tosynthetic capacity and  $CO_2$  fixation rate (Lichtenthaler et al. 2005). Carnivorous plants grow mostly in sunny habitats (Zamora et al. 1998) suggesting that  $R_{Fd}$  values should be in the range for sun-exposed plants. However, as already mentioned, carnivorous plants mostly have a reduced rate of photosynthesis due to low foliar nitrogen content and nitrogen incorporation into other than photosynthesis-related molecules (chlorophylls, proteins), such as those involved in adjustments for trapping and digesting insects (Ellison and Adamec 2011, Pavlovič and Saganová 2015). Unexpectedly, in hybrid A and C high  $R_{Fd}$  values were observed not only for the green-coloured wings but also for red-coloured pitcher-tube upper part and operculum.

The wing of all hybrids investigated had significantly higher content of chlorophyll *a*, than the operculum and pitcher tube (Fig. 2A). In the genus *Sarracenia*, red-coloured veins with nectar-producing glands (Newell and Nastase 1998) are mostly distributed in the area of operculum, pitcher upper part and peristome (Płachno 2007). Replacement of cells that contain chlorophyll with glands that have an important role in the attraction and digestion of insects is considered to be one of the costs of carnivory (Hájek and Adamec 2010). In the genus *Darlingtonia*, it has been found that pitcher parts that contain more extrafloral nectaries have a lower amount of photosynthetic pigments (Ellison and Farnsworth 2005). Unlike chlorophyll *a*, high values of chlorophyll *b* and carotenoids were found also in the operculum, especially in hybrids A and C (Fig. 2B) which coincided with the high phenolic content (especially anthocyanins, Figs. 3A and C). As anthocyanins could absorb some part of photosynthetically active radiation (Gould et al. 2010), we hypothesize that increased content of chlorophyll *b* and carotenoids could be involved in spectral broadening of light absorbed by the operculum. The relatively high photosynthetic rates observed in hybrids A and C support the idea. Additionally, carotenoids could also have a role in protection from high light stress (Ramel et al. 2012) as the operculum is the pitcher part most exposed to the sunlight. The lower chlorophyll *a/b* ratio found in the operculum may be considered an enlargement of the antenna system of photosystem II while a lower chlorophylls/carotenoids ratio is a typical characteristic of sun-exposed leaves (Lichtenthaler and Buschmann 2001). Similar results were reported by Tkalec et al. (2015) who observed a higher content of anthocyanins as well as a lower chlorophylls/carotenoids ratio in sun-exposed *Drosera rotundifolia* and a lower chlorophyll *a/b* ratio in plants growing in low-light conditions.

The highest content of total phenolic compounds and flavonoids found in the operculum of *Sarracenia* hybrids is probably related to the presence of red-coloured phenolic compounds, like anthocyanins (Sheridan and Griesbach 2001). The operculum is variegated with a lot of red veins that have an important role in luring insects (Newell and Nastase 1998). Furthermore, phenolic compounds with their antioxidant potential can protect the operculum, the pitcher part most exposed to sunlight, from light-induced formation of free radicals (Close and McArthur 2002). Interestingly, in all hybrids the lower part of pitcher tube had

the lowest content of flavonoids, probably because its function is not luring the prey, but digestion of prey trapped in the tube (Glenn and Bodri 2012). By contrast, the content of flavonoids was relatively high in the wing, the green-coloured pitcher part with the highest content of chlorophyll *a* and  $F_v/F_0$ . It is possible that flavonoids protect photosynthetically active tissue from oxidative stress, due to their antioxidant potential and free radical quenching ability (Banasiuk et al. 2012). As already mentioned, anthocyanins are known to be responsible for the red colouration of *Sarracenia* pitchers, so the highest content could be expected to be found in the operculum (Fig. 3C), the most red-coloured part of the pitcher. Besides the operculum, the upper pitcher part had also high content of anthocyanins, pointing to its role in the attraction of insects (Rice 2006). It has been found that some species of the genera *Drosera* and *Dionaea* exposed to mineral deficiency conditions, especially nitrogen, can increase the intensity of red colour to attract more

prey (Ischiishi et al. 1999, Gao et al. 2015). The lowest anthocyanin content was observed in the operculum of hybrid B which had a more greenish tissue between the veins. Interestingly, the operculum of hybrid A which had translucent aureoles showed the highest content of anthocyanins (Figs. 1 and 3C). It is possible that leucoanthocyanins, which are not coloured, contribute to the high content of anthocyanins, but it is yet to be determined.

In conclusion, our results show that variances in photochemical efficiency, content of photosynthetic pigments and phenolic compounds correlate with the function of pitcher part analysed. In all *Sarracenia* hybrids investigated, the green-coloured wing had the highest content of chlorophyll *a* and photochemical efficiency which is connected with its role in photosynthesis. The red-coloured operculum and upper pitcher part, whose role is luring and catching prey, contained more phenolic compounds, especially anthocyanins, which help to attract insects.

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