Responses of photosynthetic parameters of *Mikania micrantha* and *Chromolaena odorata* to contrasting irradiance and soil moisture

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Abstract

Photosynthetic parameters were measured in two invasive weeds, *Mikania micrantha* and *Chromolaena odorata*, grown in soil under full, medium, and low irradiance and full, medium, and low water supply. Both species showed significantly higher net photosynthetic rate, quantum yield of PS 2 photochemistry and photochemical quenching coefficient under high than low irradiance. For *M. micrantha*, low irradiance caused decreased chlorophyll content (Chl), Chl *a*/*b* ratio and maximum photochemical efficiency of PS 2 (F_v/F_m), while drought decreased Chl content and F_v/F_m and increased nonphotochemical quenching (NPQ). However, these parameters were much less affected in *C. odorata* except that Chl content and NPQ slightly increased under drought and high irradiance. High irradiance increased xanthophyll pools in both species, especially *M. micrantha* under combination with drought.

Additional key words: chlorophyll fluorescence, invasive weeds, net photosynthetic rate, photosystem 2, xanthophyll cycle.

Introduction

Irradiation is essential for photosynthesis but it becomes harmful to plant photosynthetic capacity when absorbed in excess, creating high irradiance stress which may result in photoinhibition and photodamage (Golan *et al*. 2006). Water stress may lead to photosynthesis reduction through stomatal closure and decreased CO_2 supply may also result in photoinhibition (Gimenez *et al*. 1992, Lu *et al*. 2003). Irradiation and/or water stress damage not only the oxygen-evolving complex of PS 2 but also the PS 2 reaction centres (Giardi *et al*. 1996).

Xanthophyll cycle is involved in protection of photosynthetic apparatus (Adams *et al*. 1999). Xanthophyll cycle can harmlessly dissipate excess excitation energy in the antennae complexes of PS 2 as heat through the formation of zeaxanthin (Z) by de-epoxidation of violaxanthin (V) *via* the intermediate antheraxanthin (A) (Demmig-Adams and Adams 1992, Qiu *et al*. 2003). Other carotenoids (Car) such as β-carotene or lutein also play an important role in PS 2 protection (Pogson *et al*. 1998).

Mikania micrantha Kunth and *Chromolaena odorata* L. are two of the most invasive weeds in southern China. Both species belong to the *Asteraceae* family. *M. micrantha* is a perennial herbaceous vine, native to tropical Central and South America, whereas *C. odorata* is a perennial herbaceous shrub, native to Mexico, South America and West India (Holm *et al*. 1977). Our previous study found that the growth of both species favoured high irradiance, while differing in that *M. micrantha* was most efficient at full soil water regime and *C. odorata* at moderate soil water condition, but the relevant underlying mechanisms are not clear (Zhang and Wen 2009). In this study, we aim to determine the species-dependent differences of PS 2 photochemistry, photoinhibition and photoprotection of the two weeds in response to combined irradiance and soil moisture conditions, and elucidate the respective role of the xanthophyll cycle in photoprotection of the two species.

Received 12 November 2008, *accepted* 27 July 2009.

Abbreviations: A - antheraxanthin; FC - field water capacity; FI - full irradiance; F_v/F_m - maximum photochemical efficiency of PS 2; FW - full water; LI - low irradiance; LW - low water; MI - medium irradiance; MW - medium water; NPQ - nonphotochemical quenching coefficient; P_N - net photosynthetic rate; qP - photochemical quenching coefficient; V - violaxanthin; Z - zeaxanthin; Φ_{PS2} - quantum yield of PS 2 photochemistry.

Acknowledgements: We thank Prof. Zhi-Fang Lin, Prof. Han-Hui Kuang, and two anonymous reviewers for critical comments on earlier version of this manuscript. The study was funded by National Natural Science Foundation of China (No. 30630015) and the Pear River Delta Urban Forest and the Environment Research Program of SCBG (200603).

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Materials and methods

Research was conducted in two rows of equal-sized plots (1.5 m length × 1.2 m width) within three glasshouses located in South China Botanical Garden, Guangzhou (23°08′ N，113°17′ E). Air temperature ranged from 28 to 36 °C, and air relative humidity ranged from 50 to 85 % inside the glasshouses. The maximum photosynthetic photon flux density (PPFD) outside the glasshouse was 1500 μmol m^{-2} s^{-1}.

On April 23, 2006, seeds of *Mikania micrantha* Kunth. and *Chromolaena odorata* L. were separately sown in pots (2.5-dm^3 volume) filled with forest soil. In early July, 30 seedlings of about 90 cm height for *M. micrantha* and 25 cm height for *C. odorata* were transferred to each plot and two weeks later they were subjected to different irradiance and soil water treatments. Irradiance levels were full (FI, 100 % radiation inside the glasshouse, about 1 300 μmol m^{-2} s^{-1} at midday), medium (MI, 25 - 35 % of available radiation) and low (LI, 3 - 5 % of available radiation) irradiance, which were controlled by different layers of nylon-net shade. The soil water treatments were full (FW, 70 - 90 % of field water capacity, FC), medium (MW, 35 - 55 % FC) and low (LW, stopped receiving water) water supply (for detail see Zhang and Wen 2009).

All measurements were made on attached uppermost fully expanded sun leaves during sunny days. Seven weeks after the experiment treatment began, net photosynthetic rate (P_N) was determined with a portable photosynthesis system (*LI-6400*, *LI-COR,* Logan, USA) at irradiance of 1200 μmol $m^{-2}s^{-1}$ (PAR) and ambient CO_2 concentration. At least six leaves of six individual plants for each plot and per species were tested.

Diurnal changes in chlorophyll (Chl) fluorescence parameters were made on the same leaves that were used for P_N measurements with a portable Chl fluorometer (*PAM 2100*, *Walz*, Effeltrich, Germany). The procedure of measurements is described in detail in Melgar *et al*. (2008). The leaf temperature was ascertained using the sensors integrated into the leaf clip holder of the *PAM-2100* unit, and irradiance in the glasshouse was measured with a photometer (*LI-185B, LI-COR,* Lincoln, NE, USA). Prior to measurement, the leaves were kept under leaf clamps for 30 min dark adaptation. The maximum photochemical efficiency of PS 2 (F_v/F_m), quantum yield of PS 2 photochemistry (Φ_{PS2}), photochemical quenching coefficient (qP) and non-photochemical quenching coefficient (NPQ) were calculated as described by Van Kooten and Snel (1990) and Souza *et al*. (2004).

Followed P_N and Chl fluorescence measurements, ten leaf disks (6 mm in diameter) from five leaves of one individual plant were collected. One half of the leaf disks were extracted with 80 % acetone and the extract was used for Chl content measurement according to Lin *et al*. (1984). The other half were immediately frozen in liquid nitrogen and then were extracted with ice-cold 100 % acetone; the extract was used for Car determination by using the high performance liquid chromatography (HPLC) procedure of Gilmore and Yamamoto (1991). Each treatment per species had three sample replicates. The data were subjected to one way *ANOVA* and means were compared using the appropriate Fisher's protected LSD.

Results and discussion

The leaf P_N for both species decreased significantly from FI to LI, and LW had a significant effect on *M. micrantha* under FI and MI and on *C. odorata* under FI and LI (Table 1). Irrespective of water treatment, the average P_N under FI was 5.7 and 9.3 folds of that under LI for *M. micrantha* and *C. odorata*, respectively.

During the Chl fluorescence measurement, incident irradiance and leaf temperature revealed diurnal variations with peaks at noon under FI and MI, while the irradiance in LI was lower than 40 μmol m^{-2} s^{-1} and maintained somewhat stable during the day (data not shown). Under FI, the midday Φ_{PS2} in LW were depressed by 70.4 and 24.8 % as compared to that under FW for *M. micrantha* and *C. odorata*, respectively (Fig. 1). Furthermore, LI significantly decreased Φ_{PS2} of both species ($P < 0.05$). In *M. micrantha*, F_v/F_m showed significant midday depression under FI and MI, and recovered at different extents as PPFD decreased in the afternoon; under LI, however, all the measured F_v/F_m were below 0.80 (Fig. 1*G*,*H*,*I*). In contrast, the F_v/F_m in *C. odorata* decreased slightly only at midday in all treatments and almost completely restored in the afternoon (Fig. 1 *G*,*H*,*I*). Throughout the day, *M. micrantha* under FI showed considerably higher NPQ and lower qP in LW than in FW and MW, with the highest NPQ of 8.7 and the low qP of 0.67 occurred at midday (Fig. 1*D*,*J*). In *C. odorata*, LW slightly increased NPQ under FI and water treatment had minor effect on qP (Fig. 1*D*,*J*). However, LI did not cause significant reductions of NPQ but resulted in significant decreases of qP in both species (Fig. 1*F*,*L*).

Chl (*a*+*b*) content and Chl *a*/*b* ratio in *M. micrantha* decreased significantly with irradiance reduction, and Chl (*a*+*b*) content in LW were lower than in MW under FI and MI (Table 1). Chl (*a*+*b*) content in *C. odorata* slightly decreased from FI to LI and no significant differences were observed between different soil water treatments ($P > 0.05$), though Chl content showed an increasing trend with reduced soil water conditions under FI. Chl *a*/*b* ratio in *C. odorata* was much stable and the significant difference between water treatments was only presented in LI.

On a Chl basis, the highest content of total Car appeared in FI-LW for *M. micrantha* and in FI-FW for

Table 1. Net photosynthetic rate, P_N [μmol CO_2 m^{-2} s^{-1}], chlorophyll content [μg cm^{-2}], neoxanthin, Neo, lutein, Lut, violaxanthin, V, antheraxanthin, A, zeaxanthin, Z, and total carotenoid content [mmol mol^{-1}(Chl)] in *M. micrantha* and *C. odorata* under full (FI), medium (MI), and low irradiance (LI) and full (FW), medium (MW), and low water (LW) supply. Values are mean ± SE (n = 6 for P_N, and n = 3 for other parameters). Different capital letters indicate the statistical difference between soil water treatments within the same irradiance level, and different small letters indicate the statistical difference between irradiance treatments within the same soil water condition at the confidence level of $P < 0.05$ according to Fisher's protected LSD test.

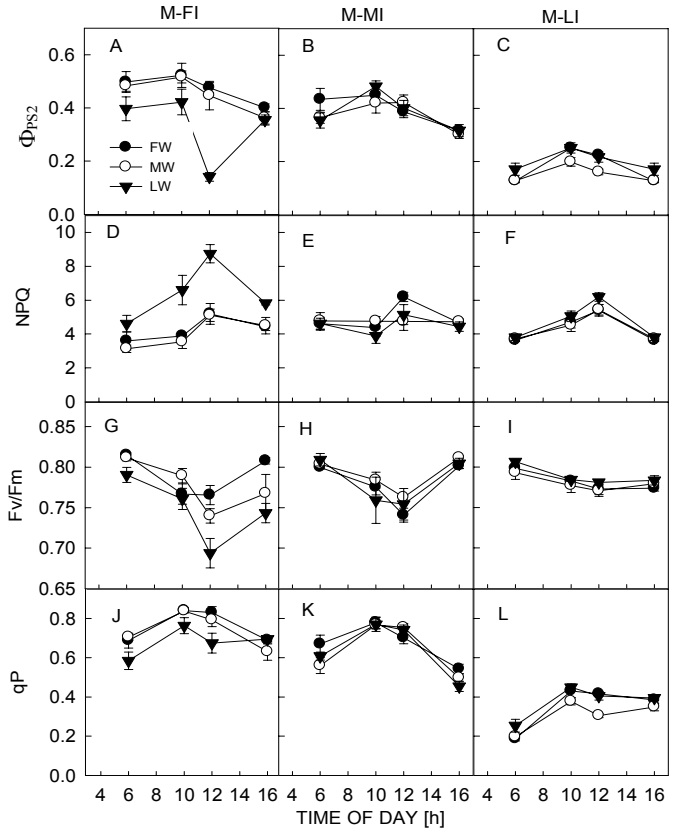
	FI			MI			LI		
	FW	MW	LW	FW	MW	LW	FW	MW	LW
M. micrantha									
P_N	21.2±1.7^{Aa}	20.0±2.3^{Aa}	15.2±4.0^{Ba}	13.2±2.3^{Ab}	12.2±1.3^{Ab}	9.2±1.7^{Bb}	2.9±0.7^{Ac}	3.1±0.6^{Ac}	3.8±0.9^{Ac}
Chl (*a*+*b*)	22.8±1.2^{Aa}	27.1±0.8^{Aa}	24.6±1.6^{Aa}	13.9±0.8^{Ab}	19.4±0.2^{Bb}	17.4±1.3^{Bb}	12.3±0.1^{Ab}	12.9±0.6^{Ac}	13.2±1.1^{Ab}
Chl *a*/*b*	2.3±0.0^{Aa}	2.4±0.0^{Aa}	2.0±0.1^{Ba}	2.0±0.0^{Ab}	1.9±0.0^{Bb}	1.9±0.0^{Ba}	1.6±0.0^{ABc}	1.5±0.0^{Bc}	1.7±0.0^{Ab}
Neo	74.7±0.6^{Aa}	81.2±3.2^{Aab}	115.7±5.4^{Ba}	76.2±1.4^{Aa}	76.8±0.3^{Aa}	89.8±4.1^{Bb}	78.2±1.7^{Aa}	87.6±0.5^{Bb}	82.7±4.3^{ABb}
Lut	257.6±0.0^{Aa}	274.3±6.8^{Aa}	344.5±12.1^{Ba}	274.7±0.4^{Aa}	278.3±0.5^{Aa}	302.2±13^{Bab}	259.5±22^{Aa}	313.7±1.7^{Bb}	290.6±12^{ABb}
V	116.2±2.0^{Aa}	129.1±2.6^{Aa}	188.4±7.5^{Ba}	109.9±0.3^{Ab}	106.4±0.8^{Ab}	109.1±1.6^{Ab}	86.3±0.7^{Ac}	82.5±0.7^{Bc}	107.2±1.4^{Cb}
A	8.6±0.2^{Aa}	9.4±0.5^{Aa}	15.5±0.9^{Ba}	3.0±0.3^{Ab}	2.7±0.2^{Ab}	7.5±1.2^{Bab}	4.4±0.2^{Ac}	0.0±0.0^{Bc}	0.0±0.0^{Bc}
Z	11.1±0.2^{Aa}	9.6±0.3^{Ba}	7.1±0.4^{Ca}	9.8±0.1^{Aa}	9.5±0.4^{Aa}	9.8±0.5^{Ab}	7.5±1.9^{Aa}	5.2±0.1^{Ab}	0.0±0.0^{Bc}
β-car	251.8±0.4^{Aa}	264.8±6.7^{Aa}	294.0±8.4^{Ba}	241.9±0.1^{ABb}	233.8±0.7^{Ab}	248.6±5.8^{Bb}	235.8±0.4^{Ac}	243.4±3.0^{Ab}	247.7±7.2^{Ab}
A+Z+V	135.9±1.6^{Aa}	148.1±3.4^{Aa}	211.1±7.9^{Ba}	122.7±0.1^{ABb}	118.6±1.0^{Ab}	126.5±3.4^{Bb}	98.2±2.5^{Ac}	87.8±0.6^{Bc}	107.2±1.4^{Cc}
Total Car	720.0±0.8^{Aa}	768.5±20^{Aa}	965.4±33.8^{Ba}	715.5±2.0^{Aa}	707.5±2.5^{Ab}	767.0±20^{Bb}	671.7±26^{Aa}	732.4±5.7^{Aab}	728.2±22.2^{Ab}
C. odorata									
P_N	18.6±1.3^{Aa}	19.6±1.2^{Aa}	16.7±1.1^{Ba}	10.7±1.5^{Ab}	10.2±1.7^{Ab}	9.2±1.3^{Ab}	1.5±0.5^{Ac}	1.7±0.5^{Ac}	2.7±0.6^{Bc}
Chl (*a*+*b*)	26.0±0.6^{Aa}	26.6±1.2^{Aa}	27.2±0.2^{Aa}	22.7±1.1^{Ab}	20.5±0.5^{Ab}	23.1±0.3^{Ab}	21.4±0.4^{Ab}	21.7±0.4^{Ab}	23.7±1.1^{Ab}
Chl *a*/*b*	2.4±0.0^{Aa}	2.3±0.2^{Aa}	2.4±0.0^{Aa}	2.4±0.1^{Aa}	2.4±0.0^{Aa}	2.3±0.1^{Ab}	2.3±0.0^{Aa}	2.2±0.0^{ABa}	2.2±0.0^{Bc}
Neo	87.2±3.0^{Aa}	78.1±2.9^{Ba}	91.6±0.1^{Aa}	80.1±1.0^{Ab}	80.5±1.7^{Aa}	90.3±4.2^{Ba}	89.8±0.9^{Aa}	91.5±1.2^{Ab}	97.0±3.4^{Aa}
Lut	283.5±4.4^{Aab}	266.9±1.6^{Ba}	282.1±0.2^{Aa}	246.4±20.9^{Aa}	284.9±3^{ABb}	292.1±7.2^{Ba}	303.9±0.4^{ABb}	306.7±1.2^{Ac}	292.3±6.2^{Ba}
V	127.6±3.6^{Aa}	136.8±1.1^{Ba}	146.1±0.1^{Ca}	113.5±3.3^{ABb}	106.6±1.0^{Ab}	118.7±2.6^{Bb}	98.4±0.3^{Ac}	90.0±1.2^{Bc}	69.2±0.0^{Cc}
A	8.9±2.2^{Aa}	6.9±1.9^{Aa}	6.5±3.1^{Aa}	3.9±0.1^{Aa}	2.0±0.0^{Bb}	1.8±0.1^{Ba}	9.7±3.2^{Aa}	3.6±0.2^{ABab}	2.2±0.3^{Ba}
Z	9.4±1.4^{Aa}	10.1±0.5^{Aa}	9.9±0.0^{Aa}	6.9±0.3^{Ab}	7.7±0.5^{Ab}	7.5±0.9^{Aab}	6.0±0.4^{Ab}	6.5±0.4^{Ac}	4.3±2.9^{Ab}
β-car	282.8±5.6^{Aa}	257.0±3.6^{Ba}	255.9±0.4^{Ba}	249.3±14.3^{Ab}	267.0±3.1^{Ab}	273.9±8.6^{Ab}	271.7±1^{Aab}	265.2±1.3^{Bab}	266.5±0.8^{Bab}
A+Z+V	145.9±5.0^{Aa}	153.8±2.6^{Aa}	162.5±3.0^{Ba}	124.3±3.6^{ABb}	116.3±0.6^{Ab}	128.0±1.9^{Aab}	114.1±3.2^{Ab}	100.1±1.6^{Bc}	75.7±2.0^{Cc}
Total Car	799.3±17.9^{Aa}	755.8±10.6^{Ba}	792.1±2.5^{ABa}	700.1±35.6^{Ab}	748.7±8.1^{Aa}	784.4±21.9^{Aa}	779.6±3^{Aab}	763.5±2.2^{Ba}	731.5±1.5^{Cb}

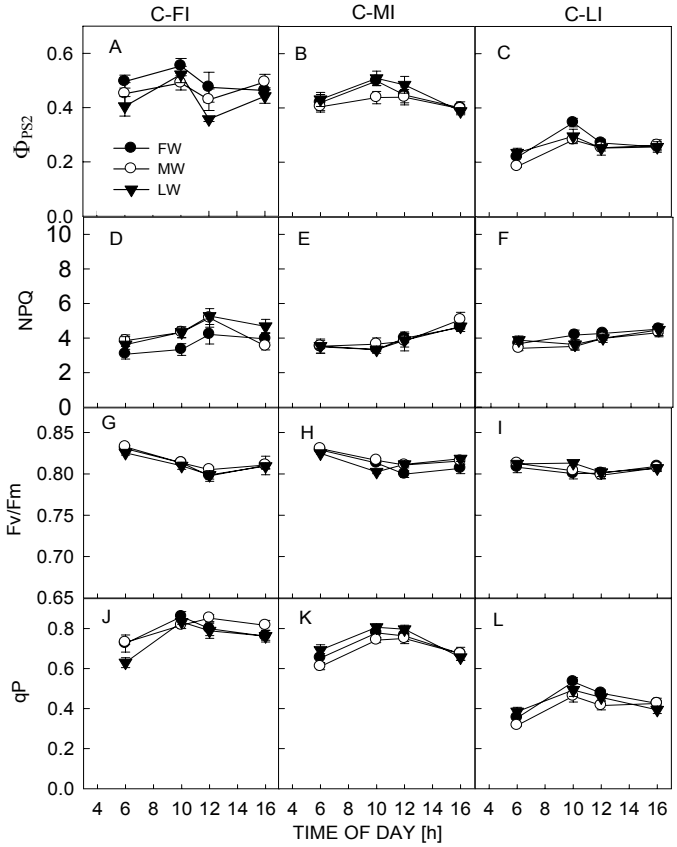
C. odorata. Total Car content increased with increasing irradiance combined with drought in *M. micrantha*, which were mainly due to the increase in the predominant components of Car, lutein and xanthophyll cycle pigments (V + A + Z), although both neoxanthin and β-carotene also increased under these environmental conditions (Table 1). In *C. odorata*, the order of xanthophyll pool size under different irradiance was FI > MI > LI, but lutein and β-carotene contents of this species were relatively unaffected by irradiance and soil water treatments.

Our study showed that LI led to substantial reduction of P_N in leaves of both species, which agreed with previous studies (Liao *et al*. 2003, Wang *et al*. 2003). Decreases in P_N could be related with the reduction of Φ_{PS2} and qP in both species, in addition with the decreases of F_v/F_m and Chl content in *M. micrantha* (Table 1, Fig. 1). By contrast, most of the measured parameters of pigments and photochemistry in *C. odorata* were less affected by different soil water conditions under all irradiance levels, except Chl and Car content and NPQ that were slightly higher under LW of FI (Table 1 and Fig. 1). The results indicated that drought accelerated the high irradiance impact on *M. micrantha*, while did much less effect on *C. odorata* except under high irradiance. Moreover, significantly higher P_N of both species under FI than LI suggested they had high saturated irradiance. The high P_N allows the two species a large pool of available carbon to allocate into growth, reproduction and powerful seeds, which make conditions for their invasion.

Despite higher Chl content, the observed higher Chl *a*/*b* ratio in FI than in LI for *M. micrantha* suggested that this species had smaller light-harvesting complex (LHC 2) but had a larger reaction center (Schiefthaler *et al*. 1997) under high than low irradiance (Lichtenthaler *et al*. 1981). *C. odorata*, however, maintained relatively stable Chl *a*/*b* ratio among most of irradiance and soil water combinations, suggesting that LHC 2 and the reaction center were less sensitive to the changing irradiance and soil moisture.

The midday decline of Φ_{PS2} for both species under FI-LW allowed an improved radiationless de-excitation of PS 2 (Adams *et al*. 1999), which could limit further damage of photosynthetic apparatus (Yu *et al*. 2009). The observed diurnal reversible changes in F_v/F_m in


M-FI
M-MI
M-LI
A
B
C
D
E
F
G
H
I
J
K
L
Φ_{PS2}
NPQ
Fv/Fm
qP
FW
MW
LW
TIME OF DAY [h]


C-FI
C-MI
C-LI
A
B
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D
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F
G
H
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K
L
Φ_{PS2}
NPQ
Fv/Fm
qP
FW
MW
LW
TIME OF DAY [h]

Fig. 1. Diurnal changes of quantum yield of PS 2 photochemistry, Φ_{PS2} (*A*,*B*,*C*), nonphotochemical quenching coefficient, NPQ (*D*,*E*,*F*), maximum photochemical efficiency of PS 2, F_v/F_m (*G*,*H*,*I*), photochemical quenching coefficient, qP (*J*,*K*,*L*) in *M. micrantha* (*above*) and *C. odorata* (*below*) under full (FI), medium (MI), and low (LI) irradiance and full (FW), medium (MW), and low (LW) soil water supply. Values are mean ± SE (n = 5).

M. micrantha meant that photoinhibiton was attributed to a photoprotective process rather than photodamage induced by irreversible degradation of D_1 protein (Chow 1994). On the other hand, all the values of F_v/F_m under LI were below 0.80, suggesting that prolonged extreme shading caused stress in *M. micrantha*. *C. odorata*, however, showed a greater stability with F_v/F_m ratio in the range 0.80 - 0.83 for all measuring times and among all treatments (Fig. 1*G*,*H*,*I*), indicating that the PS 2 photochemistry of *C. odorata* was less responsive to the varying irradiance and soil moisture.

The association of increased NPQ with increasing Z content or increasing xanthophyll pool size was frequently observed (Demmig-Adams and Adams 1992, Gilmore 1997). In the present study, NPQ of *M. micrantha* increased with enhanced drought under FI and LI, and the high NPQ occurred under FI-LW implying that *M. micrantha* at drought dissipate excess excitation energy as heat under high irradiance. However, high NPQ of *C. odorata* was observed only in MW and LW of FI treatment. Meanwhile, Z content and the total xanthophyll pool increased from LI to FI in both species (Table 1). These results demonstrated that the xanthophyll cycle was involved in the photoprotection in both species when they are exposed to the combined high irradiance and drought stress.

In conclusion, our results indicated that both species developed effective mechanisms for their acclimations to high irradiance. *M. micrantha* possessed higher Chl *a*/*b* ratio and mainly achieved photoprotection by a thermal dissipation mechanism, while *C. odorata* was less sensitive to changing irradiance and soil moisture, though xanthophyll cycle is involved in its photoprotection under combined high irradiance and drought stress.

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Zvelebil, M., Baum, J.O.: **Understanding Bioinformatics. -** Garland Science, Taylor & Francis Group, New York - London 2008. 772 pp. ISBN 0-8153-4024-9.

Marketa Zvelebil is the team leader of cancer informatics at The Breakthrough Toby Robins Breast Cancer Research Centre in UK and Jeremy O. Baum is an Honorary Teaching Fellow in the School of Crystallography in Birkbeck College, UK. This comprehensive (more than 700 pp.) book originated as an authors' textbook for teaching bioinformatics at both undergraduate and postgraduate levels, because of the need to bridge the gap between the simplistic introduction and the very detailed monographs.

The book begins with the introduction to the structure of nucleic acids and their roles in living systems, including a brief description of translation of DNA to mRNA and subsequently into proteins. The structure and organization of proteins is also discussed. This information is very basic, but for the people without any biological knowledge as mathematicians or statisticians it can be useful. The further text is divided into seven parts devoted to individual topics. These parts contain both, "Application chapters", which provides a fast and straightforward route to understanding the main concept and "Theory chapters", which gives more details and presents the underlying mathematics. In the second part the readers are introduced into the principles of sequence alignments, variety of analyses of sequences, searching with nucleic acid or protein sequences and the most widely used appropriate databases (*FASTA*, *BLAST*, *BLOCKS*, *PROSITE*, *PHI-BLAST*, *PRATT*, *etc.*). The part 3 deals with evolutionary processes, it presents the method to obtain phylogenetic trees from sequence dataset. The part 4 leads us through the utilization of the special programs for gene prediction, prediction of promoter region and other steps in genome analysis. The following part 5 provides the methods of predicting the secondary structure on sequence. The specialized prediction methods for transmembrane proteins are mentioned. The next part 6 deals with protein tertiary structure, and focuses on principles of homology modelling. The structure-function relationships are also discussed. The last part helps us to analyzed large-scale experiments with large numbers of data (microarrays, 2D electrophoreses, SAGE). The text is accompanied with three appendices: a) probability, information and Bayesian analysis; b) molecular energy functions and c) function optimization.

Book has very good graphic arrangement. Within each chapter every section is introduced with a flow diagram to help the student to visualize and remember the topics covered in that section. The text is supplemented with many illustrative colour figures and schemes, colouring boxes with samples of applications or additional information. It was not possible to summarize all current knowledge in this book and therefore at the end of each chapter there are references to original papers and specialized monographs to help reader to widen their knowledge and skills.

"Understanding bioinformatics" is written for advanced undergraduate and graduate students, but in my opinion this book is very useful for many scientist utilizing new progressive methods based on analyzing of large datasets, because all research workers in the areas of biomolecular science are now expected to be competent in several areas of sequence analysis and often, additionally, in protein structure analysis and other more advanced bioinformatics techniques. I could recommend this book to all laboratory bookcases.

R. PODLIPNÁ (*Praha*)