



## Gas Exchange and Chlorophyll Fluorescence's Characteristics of *Hyoscyamus muticus* L. at Different Phenological Stages under Extreme Arid Environmental Conditions, South-Western Desert, Egypt



Usama A.A. Radwan<sup>(1)#</sup>, Mohammad M. Saleh<sup>(2)</sup>

<sup>(1)</sup>Department of Botany, Faculty of Science, Aswan University, 81528, Aswan, Egypt;

<sup>(2)</sup>Department of Physics, Faculty of Science, Aswan University, Sahari, 81528, Aswan, Egypt.

**H**YOSCYAMUS *muticus* L. is an adaptable plant of hyper arid environment. Changes in photosynthesis rate, transpiration, stomatal conductance, instantaneous water use efficiency, chlorophyll fluorescence and photosynthetic pigments characteristics were analyzed in the course of phenological stages including seedling, vegetative, flowering and fruiting to reveal the adaptive mechanisms of this species to withstand high irradiance during its life cycle. All measurements were taken under wide range of photosynthetically active radiation (PAR). *H. muticus* showed significant differences of physiological processes at different phenological stages, the highest rates of photosynthesis (5 and 5.23  $\mu\text{molm}^{-2}\text{s}^{-1}$ ) was recorded at vegetative stage and the highest transpiration rate was recorded at relatively high PAR at seedling stage. Otherwise, lowest transpiration rates (0.18  $\text{mmolm}^{-2}\text{s}^{-1}$ , 0.19  $\text{mmolm}^{-2}\text{s}^{-1}$  and 0.197  $\text{mmolm}^{-2}\text{s}^{-1}$  were noticed at vegetative, flowering and fruiting stages, respectively) at highest PAR (2500  $\mu\text{molm}^{-2}\text{s}^{-1}$ ). Stomatal conductance limitations in seedling, flowering and fruiting stages of *H. muticus* exhibited reductions of photosynthesis rate ( $P_n$ ), transpiration rate ( $E$ ) and instantaneous water use efficiency ( $WUE$ ) in response to PAR increments. The plant fluoresces behaviour recorded significant increments and decrements in minimal fluorescence from dark-adapted leaf ( $F_0$ ) and maximal fluorescence from dark-adapted leaf ( $F_m$ ) respectively, and significant declines in the ratio of PSII photochemistry maximum quantum efficiency to quantum yield ( $F_v/F_m$ ) (0.75200, 0.75167, 0.68833 and 0.4800) along with progressing phenological stages. In parallel with the later ratio decline, there was a significant decrement in chlorophyll *a*, chlorophyll *b*, chlorophyll (*a+b*) and carotene *H. muticus* has adapted different adaptive mechanisms to thrive the combination of water scarcity and high irradiance along its life cycle in hyper arid environment.

**Keywords:** Chlorophyll fluorescence, Instantaneous water use efficiency, Phenological stages, Photosynthesis, Photosynthetic active radiation, Pigments, Stomatal conductance, Transpiration.

### Introduction

Observations related to the phenology of the desert plants have a pivotal role for monitoring of the different stages involved through its life-cycle. Various physiological mechanisms that occur in plant cells were found to be controlling the plant at different phenological stages (Yuan et al., 2009; Fabio et al., 2010). Desert plants

facing a great challenge of high irradiance, where maximum diurnal seasonal irradiance averages ranged from 2000 to 2400  $\mu\text{molm}^{-2}\text{s}^{-1}$  (Radwan et al., 2005; Radwan, 2007).

Environmental factors are abiotic in desert habitats which are mainly controlled by high irradiance and drought. Positive correlation between  $P_n$  and PAR leads to alogarithmic and

#Corresponding author email: radusa2009@yahoo.com

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quadratic function light response curve (Guo et al., 2005; Li et al., 2006; Zhou et al., 2007; Li et al., 2009).

The tolerance of plants to drought stress depends on both intensity and duration of stress as well as the plant species' phenological stages (Parameshwarappa & Salimath, 2008). The effects of drought stress on CO<sub>2</sub> assimilation rate, transpiration rate, and water use efficiency has been investigated in many plant species (Pireivatlou et al., 2008; Ranjbarfordoei et al., 2013). Differences in photosynthetic pigments contents play important roles in light harvesting during water depletion (Farooq et al., 2009; Jaleel et al., 2009).

The evident fluorescence emissions of dark-adapted leaves are qualitatively correlated with their photosynthetic rates. This is based on the observation by Kautsky and his colleagues, the changes in fluorescence emissions are qualitatively correlated with changes in CO<sub>2</sub> assimilation (Kautsky et al., 1960). Butler's model, which predicts the use of PSII fluorescence emission to monitor changes in photochemistry, requires the stability of fluorescence and heat loss rates (Butler, 1978). Photochemistry of photosystem II (PSII) competes with the processes of fluorescence and heat loss through excitation energy in the pigment antenna of PSII. The electron transfer resulting from the reaction centers chlorophyll of PSII (P680) to the plastoquinone acceptor of PSII. This quenches fluorescence producing the process which is known as photochemical quenching process (Duysens & Sweers, 1963).

However, it is now well established that large changes can occur in the heat loss rate from the PSII antenna, a process termed as non-photochemical quenching (Kramer et al., 2004; Krause & Jahns, 2004). Light-addition technique is used to quantitatively determine the fraction of fluorescence quenching that is attributable to photochemical and non-photochemical quenching processes, as the maximum plastoquinone reduction of light in leaves can be achieved by rapidly exposing leaves to a very large increase in light (Bradbury & Baker, 1981; Bradbury & Baker, 1984). The applied light is a saturated flash for less than one second with sufficient intensity as to maximising the plastoquinone reduction (Schreiber et al., 1986; Dietz et al., 1985).

Chlorophyll fluorescence measurements technique has become a widely used as a routine Non-destructive quantitative determination of these processes by fluorimeters that use weak modulated measuring beam with the value of providing a continuous measure of the relative quantum yield of fluorescence (Schreiber, 2004), alongside the study of the functioning photosynthetic apparatus are considered as indicator of the plant's response to environmental stress (Stirbet & Govindjee, 2011). Using fluorometer leaf chamber controls the photorespiration, makes it possible to measure the PSII photochemistry quantum yield which is directly related to the CO<sub>2</sub> assimilation quantum yield by the leaf (Genty et al., 1989).

Stomatal function and chlorophyll fluorescence parameters depend on the course of leaf development and phenological stages, phenological interactions to the environment might lead to a better understanding of plant functioning in short-term as well as in long-term point of view (Romá & Josep, 2004; Nesterenko et al., 2006; Čaňová et al., 2008; Urban et al., 2013).

*Hyoscyamus muticus* L. considered as a highly economical plant, with growing interests for cultivation in extreme arid regions, exposed to drought stress. It is one of the most important influences on photosynthesis and plant productivity (Abd El-Gawad et al., 2017; Souza et al., 2004).

Desert plants affected by water deficit may subjected to an imbalance between photochemical activity at photosystem II (PSII) and electron requirement for photosynthesis, leading to a certain degree of damages in PSII reaction center (Calatayud et al., 2006).

*H. muticus* proved to be with efficient energy budget in hyper arid environmental conditions (Radwan, 2008). Further investigations have hitherto been performed to follow the adaptation mechanisms of the plant for the mitigation of such conditions. The photosynthetic characteristics carried out by desert plant under harsh abiotic stresses are considered as a major field in plant eco-physiological studies (HaiLong et al., 2008). Desert plants pursued several mechanisms to overcome effectively the disadvantage of unfavorable conditions and limited resources

to complete their life cycle. Increment of photosynthesis and reduction of transpiration can enhance water use efficiency (Otieno et al., 2005; Bloch et al., 2006). The current research was to reveal the mechanisms of *H. muticus* to withstand the harsh environmental conditions during its different phenological stages.

### Materials and Methods

#### Plant materials and growth conditions:

Seedlings of *H. muticus* emerges at Aswan university campus (23°59'56"N 32°51'41"E) at the South Western Desert of Egypt in November 2019 in sandy soil. Vegetative stage extended to late December 2019. Flowering stage started at late January 2020 and fruiting stage at February to the end of March. Seedling emerges accidental growth (germination) accompanied with presence of available water in soil. The mean temperature at the coldest month is between 10°C and 20°C and that of the hottest month is more than 30°C. The mean minimum and maximum temperature for Aswan were 9.5°C and 42°C, respectively.

Six homogenous individuals were selected and marked for gas exchange measurements along different phenological stages. The soil moisture contents (0-50cm depth) around the roots was monitored along the different phenological stages, and were ranged from 12% (3% above field capacity) at seedling stage to 6% (2% above wilting point) at fruiting stage by using soil moisture meter module 5910A (Radwan, 2008).

#### Gas exchange measurements:

Light response curves of  $P_n$ ,  $E$  and  $C$  measurements carried out by using IRGA system (Module CI-340) and  $PAR$  range (0-2500  $\mu\text{mols}^{-1}\text{m}^{-2}$ ) was adjusted by using light module (CI-301LA), based on Research Unit for Study Plants of Arid Lands (RUSPAL)'s meteorological station readings (Ali et al., 2018). Non-destructive six measurements were taken on mature and fully expanded 5<sup>th</sup> and 6<sup>th</sup> leaves at different phenological stages. The  $WUE$  was calculated from the ratio:  $WUE = P_n/E$  (Dos Santos et al., 2017).

#### Chlorophyll fluorescence measurements:

The chlorophyll fluorescence parameters were determined by using CI-340 Handheld Photosynthesis System connected to CI-510CF Chlorophyll Fluorescence Module (Modulated

light intensity of 0.25  $\mu\text{E}$  at 12mm, 3000  $\mu\text{E}$  at 12mm for flash light intensity, Modulation frequency of 8~80Hz, Bifurcated light guide fiber optic probe, of 64×100×160mm dimensions and LC-1 Square 25mm×25mm (6.25  $\text{cm}^2$ ) Leaf chamber), CID, Bio-Science, Camas, WA, USA. Measurements were made on the uppermost fully expanded leaves at different phenological stages. The Chlorophyll Fluorescence Module measures fluorescence simultaneously as following: Low Fluorescence value:  $F_0$ -dark,  $F_s$ -ambient, High Fluorescence value:  $F_m$ -dark,  $F_{ms}$ -ambient and the ratio of PSII photochemistry maximum quantum efficiency ( $F_v/F_m$ ) to quantum yield ( $Y$ ). In general the fluorescence emission from a leaf,  $F$  is defined by  $[I \times A_{leaf} \times fraction_{PSII} \times \phi_F]$  where,  $I$  is the incident Photosynthetic Photon Flux Density ( $PPFD$ ) on the leaf,  $A_{leaf}$  is the proportion of incident  $PPFD$  that is absorbed by the leaf,  $fraction_{PSII}$  is the fraction of absorbed  $PPFD$  that is received by PSII and,  $\phi_F$  is the quantum yield of fluorescence. It is defined by  $k_F/(k_F + k_H + k_P P)$ , where  $k_F$ ,  $k_H$  and  $k_P$  are the rate constants for the decay of excitation energy in PSII by fluorescence, heat loss, and photochemistry, respectively, and  $P$  is the fraction of PSII reaction center that is open. At  $F_0$ , PSII reaction center are maximally open,  $P = 1$ , and the fluorescence quantum yield,  $\phi_{F_0}$  is given by  $k_F/(k_F + k_H + k_P)$ . At  $F_m$ , the PSII reaction center are maximally closed,  $P = 0$ , and photochemistry cannot occur, thus  $k_P P = 0$  and the fluorescence quantum yield,  $\phi_{F_m}$  is given by  $k_F/(k_F + k_H)$ . Thus,  $\phi_{F_v}/\phi_{F_m}$  is given by  $(\phi_{F_m} - \phi_{F_0})/\phi_{F_m} = k_P/(k_F + k_H + k_P P)$ . This shows that this ratio estimates the maximum quantum yield of PSII photochemistry. Assuming that  $I$ ,  $A_{leaf}$  and  $fraction_{PSII}$  are constant for measurements of  $F_0$  and  $F_m$ , then  $F_v/F_m$  can be used to estimate the maximum quantum yield of PSII photochemistry. This simple model requires a number of other assumptions that are not necessarily correct for all situations (Blankenship, 2002; Liu et al., 2012).

#### Pigments contents:

The measurements of pigment content in leaves of *H. muticus* plants at different phenological stages were performed during the experimental period, from seedling until fruiting stages. Chlorophyll concentrations were determined by using a spectrophotometer (Spectronic 501/601) (Arnon, 1949; Kirk & Allen, 1965).

The above mentioned parameters were analyzed by using MINITAB12 statistical program

“One way Analysis of Variance” (Minitab Inc., 1998; Bower, 2000; Rusciano et al., 2020).

## Results

*Pn* of *H. muticus*'s seedlings Fig. 1 (a-d) exhibited a low record of  $0.025\mu\text{molm}^{-2}\text{s}^{-1}$  at zero  $\mu\text{molm}^{-2}\text{s}^{-1}$ . *PAR* gradually increased reaching its maximum ( $5.4\mu\text{molm}^{-2}\text{s}^{-1}$ ) at  $1000\mu\text{molm}^{-2}\text{s}^{-1}$  (*PAR*) and declined gradually ranged from  $4.99\mu\text{molm}^{-2}\text{s}^{-1}$  at  $1125\mu\text{molm}^{-2}\text{s}^{-1}$  (*PAR*) reaching  $0.48\mu\text{molm}^{-2}\text{s}^{-1}$  at highest *PAR* ( $2500\mu\text{molm}^{-2}\text{s}^{-1}$ ). The highest *Pn* values (5 and  $5.23\mu\text{molm}^{-2}\text{s}^{-1}$ ) were recorded in vegetative

stage prior to flowering stage under high *PAR* of 1750 and  $2000\mu\text{molm}^{-2}\text{s}^{-1}$ , respectively. The study plant at flowering stage showed negative values of *Pn* ranged from  $-3.36$  to  $-0.42\mu\text{molm}^{-2}\text{s}^{-1}$  at low *PAR* range ( $0-375\mu\text{molm}^{-2}\text{s}^{-1}$ ) and increased gradually reaching its maximum of  $3.38\mu\text{molm}^{-2}\text{s}^{-1}$  at highest *PAR* ( $2500\mu\text{molm}^{-2}\text{s}^{-1}$ ). Negative *Pn* values at fruiting stage ( $-2.3$  and  $-0.3\mu\text{molm}^{-2}\text{s}^{-1}$ ) were recorded at lower *PAR* range ( $0-500\mu\text{molm}^{-2}\text{s}^{-1}$ ). Thereafter increased gradually reaching its maximum of  $4.117\mu\text{molm}^{-2}\text{s}^{-1}$  at highest *PAR* ( $2500\mu\text{molm}^{-2}\text{s}^{-1}$ ). From One-way analysis of variance *Pn* significant changes were attributed to different phenological stages were:  $F=4.77$  and  $P<0.005$ .

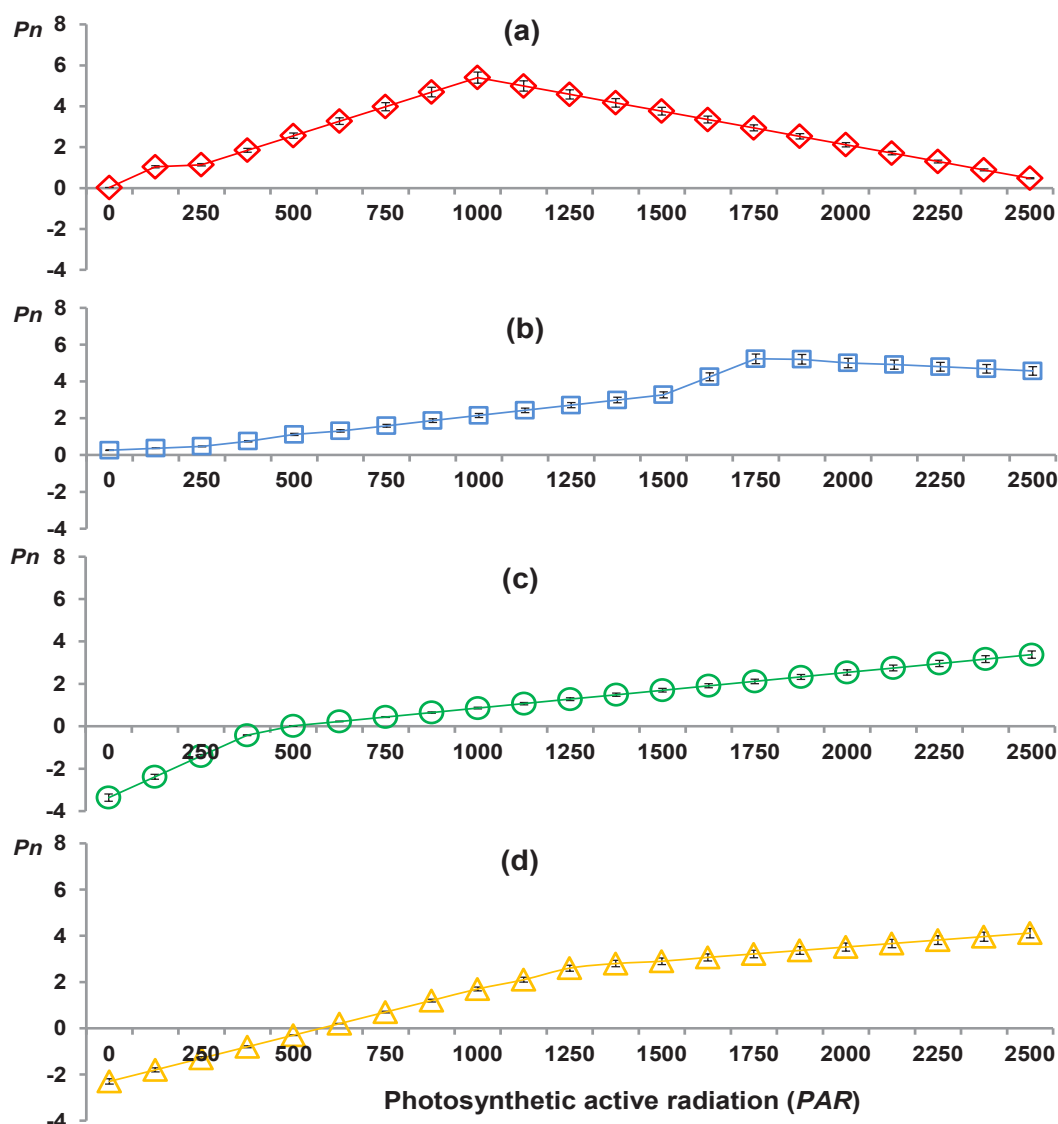


Fig. 1 (a-d). Light response curves of *Pn* (photosynthesis rate) of *H. muticus* at different phenological stages (a) seedling, (b) vegetative, (c) flowering and (d) fruiting [(*Pn* vs. Phenological stages:  $F=4.77$ ;  $P<0.005$ )]

$E$  for seedlings of *H. muticus* at different phenological stages (Fig. 2 (a-d)) was recorded as follows: Seedling stage  $E$  increased gradually ranged from  $0.02\text{mmolm}^{-2}\text{s}^{-1}$  at zero  $\mu\text{molm}^{-2}\text{s}^{-1}$  reaching its high value ( $0.38\text{mmolm}^{-2}\text{s}^{-1}$ ) at relatively high  $PAR$  ( $2250\mu\text{molm}^{-2}\text{s}^{-1}$ ). At vegetative stage highest  $E$   $0.57\text{mmolm}^{-2}\text{s}^{-1}$  was achieved at  $1000\mu\text{molm}^{-2}\text{s}^{-1}$ , and decreased rapidly reaching  $0.18\text{mmolm}^{-2}\text{s}^{-1}$  at  $2500\mu\text{molm}^{-2}\text{s}^{-1}$  ( $PAR$ ). Flowering stage  $E$  records showed stability ranged from  $0.32\text{mmolm}^{-2}\text{s}^{-1}$  to  $0.30\text{mmolm}^{-2}\text{s}^{-1}$  under  $PAR$  range from zero to  $2125\mu\text{molm}^{-2}\text{s}^{-1}$  reaching its minimum ( $0.19\text{mmolm}^{-2}\text{s}^{-1}$ ) at high  $PAR$  ( $2500\mu\text{molm}^{-2}\text{s}^{-1}$ ). At Fruiting stage  $E$  showed stability along  $PAR$  range ( $0-2375\mu\text{molm}^{-2}\text{s}^{-1}$ ) and declined to  $0.197\text{mmolm}^{-2}\text{s}^{-1}$  at high  $PAR$  ( $2500\mu\text{molm}^{-2}\text{s}^{-1}$ ). From One-way analysis of variance,  $E$  of *H.*

*muticus* showed significant changes attributed to differences in phenological stages where:  $F=4.75$  and  $P<0.005$ .

$C$  exhibited stability at seedling stage along the full range of  $PAR$  (Fig. 3 (a-d)). At vegetative stage; stomatal conductance tends to increase rapidly ranged from  $10.250\text{mmolm}^{-2}\text{s}^{-1}$  at zero  $\mu\text{molm}^{-2}\text{s}^{-1}$  to a maximum of  $21.48\mu\text{molm}^{-2}\text{s}^{-1}$  at  $2500\mu\text{molm}^{-2}\text{s}^{-1}$ . Flowering and fruiting stages showed highest values  $15.98\text{mmolm}^{-2}\text{s}^{-1}$  at lower  $PAR$  ranged from  $375$  to  $750\mu\text{molm}^{-2}\text{s}^{-1}$ , then declined to minimum values  $11.22$  and  $8.08\text{mmolm}^{-2}\text{s}^{-1}$  at highest  $PAR$  ( $2500\mu\text{molm}^{-2}\text{s}^{-1}$ ). From One-way analysis of variance,  $C$  of *H. muticus* showed significance variations attributed to differences in phenological stages where:  $F=14.24$  and  $P<0.0001$ .

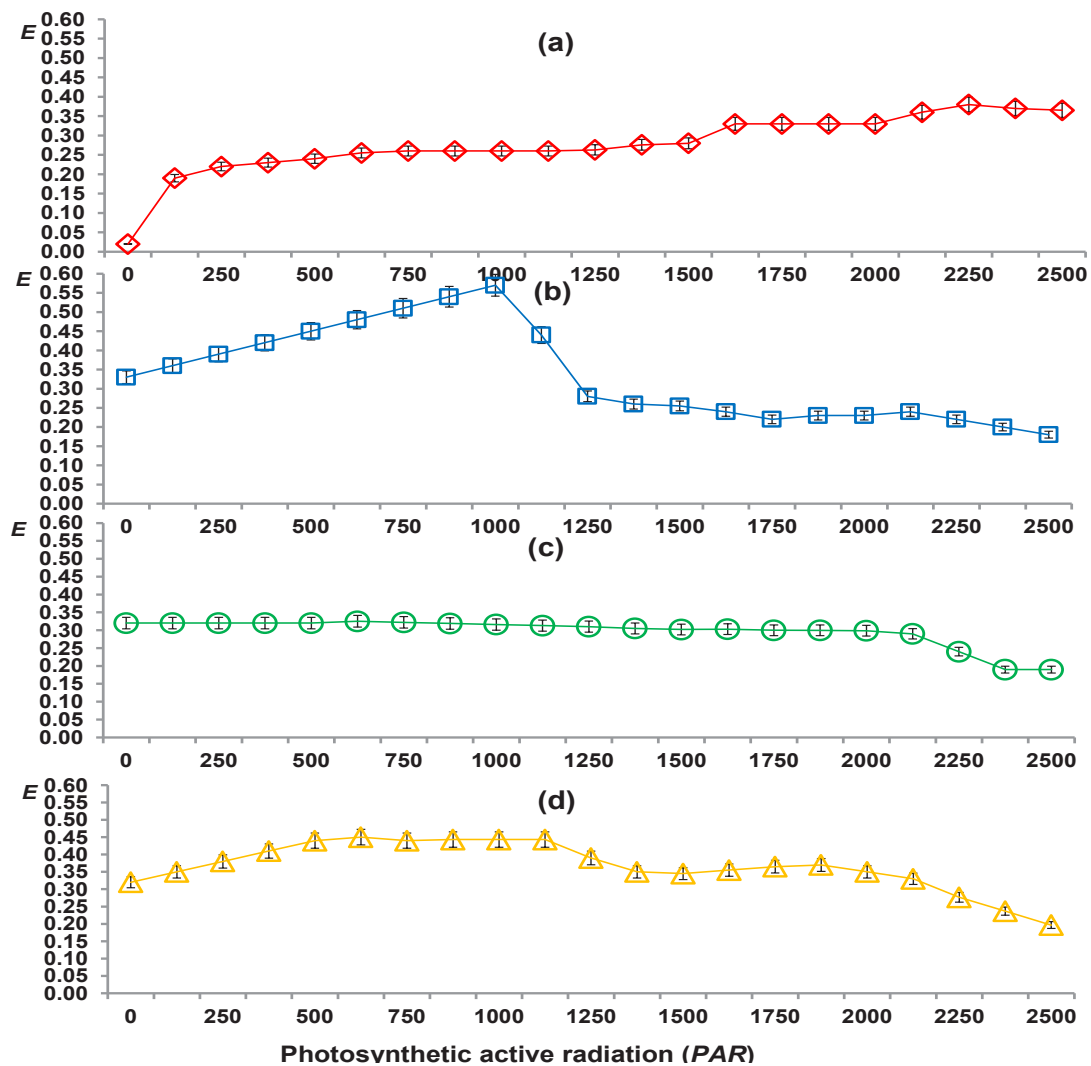


Fig. 2 (a-d). Light response curves of  $E$  (transpiration) of *H. muticus* at different phenological stages (a) seedling, (b) vegetative, (c) flowering and (d) fruiting [ $E$  vs. phenological stages:  $F=4.75$ ;  $P<0.005$ ]

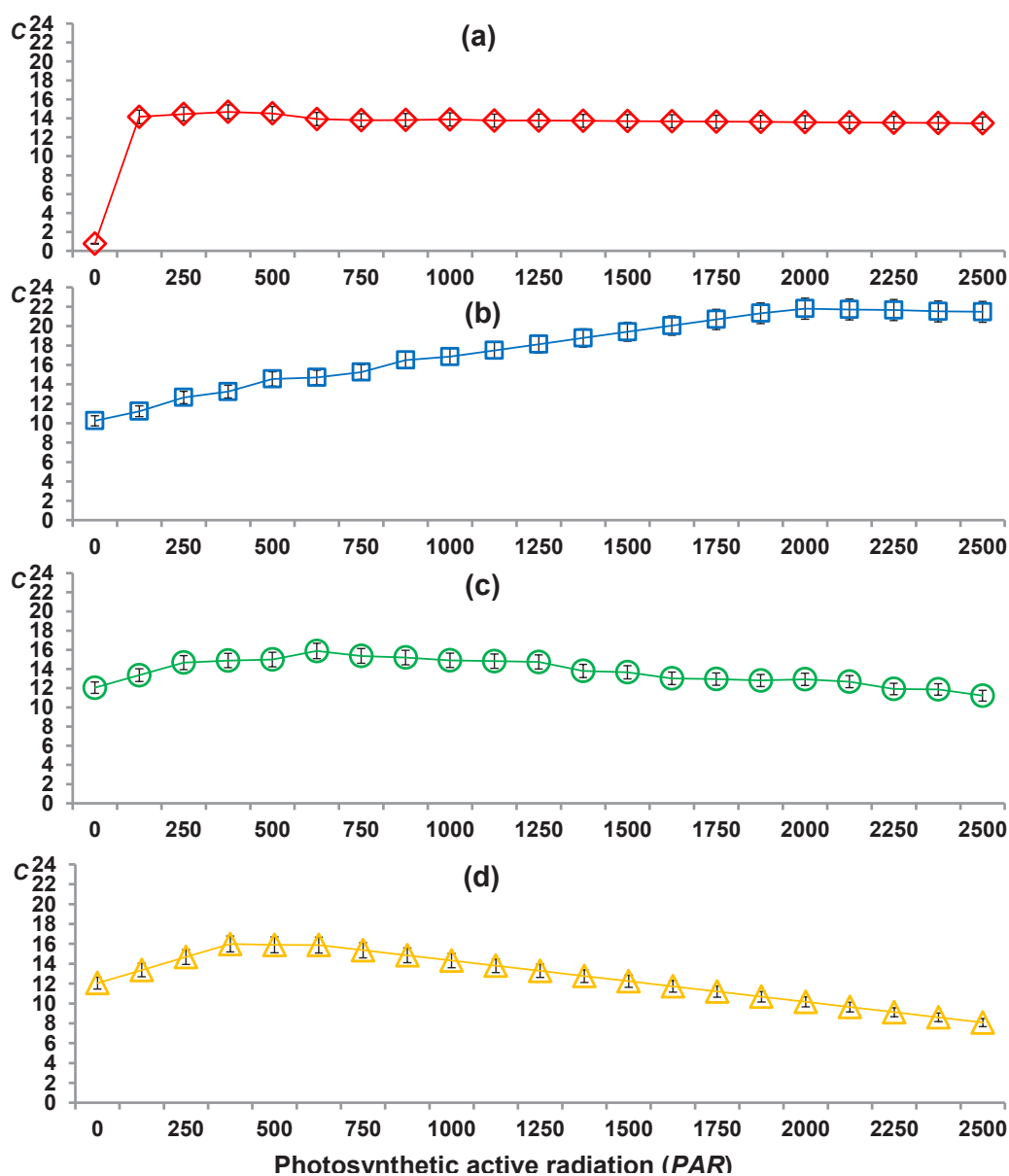


Fig. 3 (a-d). Light response curves of C (stomatal conductance) of *H. muticus* at different phenological stages (a) seedling, (b) vegetative, (c) flowering and (d) fruiting [C vs. phenological stages:  $F=14.24$ ;  $P<0.0001$ ]

Calculated  $WUE$  at different phenological stages (Fig. 4 (a-d)) was of high values ( $23.78$  and  $25.38 \mu\text{molm}^{-2}\text{s}^{-1}/\text{mmolm}^{-2}\text{s}^{-1}$ ) at high  $PAR$  range ( $1750-2500 \mu\text{molm}^{-2}\text{s}^{-1}$ ), which were recorded in vegetative stage plants. On the other hand, maximum  $WUE$  ( $20.76 \mu\text{molm}^{-2}\text{s}^{-1}/\text{mmolm}^{-2}\text{s}^{-1}$ ) was recorded in seedlings at  $1000 \mu\text{molm}^{-2}\text{s}^{-1}$ . Otherwise, at maximum  $WUE$  values;  $17.79$ , and  $20.93 \mu\text{molm}^{-2}\text{s}^{-1}/\text{mmolm}^{-2}\text{s}^{-1}$  were recorded in *H. muticus* plants during flowering and fruiting stages, at  $2500 \mu\text{molm}^{-2}\text{s}^{-1}$  ( $PAR$ ), respectively. From One-way analysis of

variance,  $WUE$  significant changes attributed to differences in phenological stages where:  $F=4.3$  and  $P<0.01$ .

Table 1 showed increments in  $F_0$  along with progressing phenological stages. Where, means of  $F_0$  were;  $11.67$ ,  $32.00$ ,  $44.00$  and  $100.67$  were recorded in seedling, vegetative, flowering and fruiting stages of *H. muticus*, respectively. From One-way analysis, significant changes in  $F_0$  were attributed to different phenological stages where;  $F= 3739.31$ ,  $P<0.0001$ .



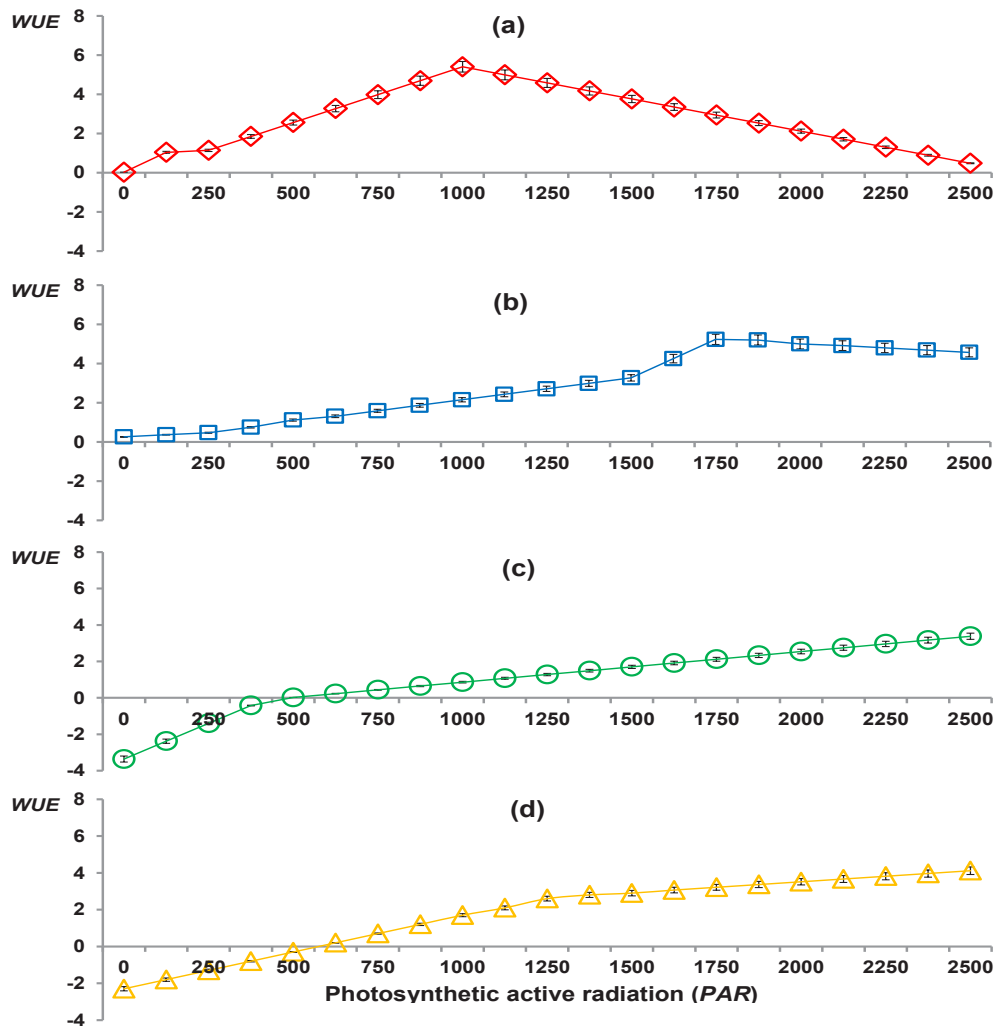


Fig. 4 (a-d). Light response curves of WUE (instantaneous water use efficiency) of *H. muticus* at different phenological stages (a) seedling, (b) vegetative, (c) flowering and (d) fruiting [WUE vs. Phenological stages:  $F=4.30$ ;  $P<0.01$ ]

TABLE 1. Parameters of chlorophyll fluorescence measured in *H. muticus* at different phenological stages (seedling, vegetative, flowering and fruiting)

Chlorophyll fluorescence parameters	Low Fluorescence value $F_0-s$ ( $F_0 - \text{dark} \& F_s - \text{ambient}$ )	High Fluorescence value $F_m-ms$ ( $F_m \text{ dark} \& F_{ms} - \text{ambient}$ )	Ratio of PSII photochemistry maximum quantum efficiency to quantum yield ( $F_v/F_m - \text{dark}, Y - \text{ambient}$ )
Phenological stage			
Seedling	11.67±0.58	422.00±2.65	0.75200±0.00458
Vegetative	32.00±1.00	177.00±1.00	0.75167±0.00929
Flowering	44.00±1.00	129.00±3.00	0.68833±0.00551
Fruiting	100.67±1.53	29.00±1.00	0.4800±0.00819
Pooled standard deviation	1.08	2.12	0.00715
F	3739.31	$1.9 \times 10^4$	973.55
P	$P<0.0001$		

$F_0$ , minimal fluorescence from dark-adapted leaf;  $F_m$ , maximal fluorescence from dark-adapted leaf;  $F_v/F_m$ , maximum quantum efficiency of PSII photochemistry; Y, PSII quantum yield of fluorescence.

Decrements were recorded in  $F_m$  along with progressing phenological stages. Where, means of  $F_m$  were; 422.00, 177.00, 129.00 and 29.00 at seedling, vegetative, flowering and fruiting stages of *H. muticus*, respectively. From One-way analysis, significant changes in  $F_m$  were attributed to different phenological stages where;  $F=1.9 \times 10^4$ ,  $P<0.0001$ .

The ratio of PSII photochemistry maximum quantum efficiency to quantum yield showed significant declines along with progressing phenological stages where, means of ratio were; 0.75200, 0.75167, 0.68833 and 0.4800 at seedling, vegetative, flowering and fruiting stages, respectively. From One-way analysis, significant changes in ratio were attributed to different phenological stages where;  $F=973.55$ ,  $P<0.0001$ .

Table 2 showed that gradual decrements in soil water contents exhibited alteration in pigments concentrations. Chlorophyll *a*, chlorophyll *b* and Carotene showed highly significant changes attributed to processing of phenological stages. From One-way analysis,  $F$  were 719.61, 183.24 and 30.00, respectively;  $P<0.0001$  for all above mentioned pigments concentrations. Otherwise, Chlorophyll ratio (*a/b*) showed insignificant changes. Chlorophyll (*a+b*) showed significant decrements ( $P<0.0001$ ) in parallel to the decrements of the ratio of PSII photochemistry maximum quantum efficiency to quantum yield.

## Discussion

*H. muticus*' physiological characteristics could be attributed to its different phenological stages that allow them to take advantage of the high light intensities through water loss regulation and carbon gain, and in turn water use efficiency, this is

considered as important mechanisms for endemic desert plant to maintain the plant photosynthetic capacity during vegetative stage.

Abiotic stresses such as high irradiance and water stress have a great influence on phenological phases of desert plants (Ocheltree et al., 2014; Baya & Moghadam, 2019), and enhancing reduction of stomatal conductance for water loss minimisation and variable dynamic photosynthesis (Pinheiro & Chaves, 2011).  $P_n$  of *H. muticus* at seedlings (plant establishment) lowest record, gradually increased reaching its maximum with the increment of  $PAR$ , and then declined gradually to minimum levels at highest  $PAR$ .

In desert plant the photosystem damage prevented by competing with the energy absorbed during photochemical process (Roach & Krieger-Liszky, 2014). The highest  $P_n$  of *H. muticus* achieved at vegetative, flowering and fruiting stages under high  $PAR$ , which could be related to enhancement of photosynthetic efficiency under abiotic stress of high irradiance (Larcher, 2003). Otherwise,  $P_n$  at flowering and fruiting stages showed negative values under lower  $PAR$  ranges, negative  $P_n$  values associated with dark respiration, which produce energy during plant growth (Jones, 2014). Stomatal conductance ( $C$ ) exhibited stability at seedling stage along the high range of  $PAR$ . Improved water use efficiency related to the reduction of stomatal conductance in plants under stress by photosynthesis maintenance and decrement of transpiration at high range of  $PAR$  (Broeckx et al., 2014). Desert plants grow under short-term water stress conditions reduce stomatal aperture which in turn leads to transpiration decrement (Doheny-Adams et al., 2012).

TABLE 2. Concentration of photosynthetic pigments in the leaves of *H. muticus* measured at different phenological stages (seedling, vegetative, flowering and fruiting)

Photosynthetic pigments	Chlorophyll a (mg.g <sup>-1</sup> )	Chlorophyll b (mg.g <sup>-1</sup> )	Carotene (mg.g <sup>-1</sup> )	Chlorophyll a+b (mg.g <sup>-1</sup> )	Chlorophyll a/b (mg.g <sup>-1</sup> )
Phenological stage					
Seedling	1.8040± 0.0241	0.88400 ±0.00894	0.16600 ±0.00548	2.6880 ± 0.0217	2.0460 ±0.0391
Vegetative	1.6700± 0.0158	0.81000± 0.03082	0.16400 ±0.01140	2.4800± 0.0235	2.0660 ±0.0924
Flowering	1.4180 ±0.0130	0.68600 ±0.00548	0.14000± 0.00707	2.1040± 0.0182	2.0660± 0.0055
Fruiting	1.4100 ±0.0071	0.67200± 0.00837	0.12800 ±0.00447	2.0820 ±0.0045	2.0960± 0.0351
Pooled standard deviation	0.0162	0.01681	0.00758	0.0185	0.0532
F	719.61	183.24	30.00	1279.59	0.75
P			P<0.0001		P>0.05



Prolonged drought enhances production of leaves with low stomatal conductance (Franks et al., 2015; Silva et al., 2020). Flowering and fruiting stages,  $C$  declined to minimum values at highest  $PAR$  ( $2500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Stomatal closure is an adaptive strategy for limitation of water loss under the stress of water deficiency (Centritto et al., 2009). At seedling stage  $E$  increased gradually reaching its highest value at high  $PAR$ . Vegetative, flowering and fruiting stages  $E$  records showed its lowest values at high  $PAR$ . Plants adjusting the relationships between  $Pn$  and  $E$  through stomatal changes in order to maximize  $\text{CO}_2$  assimilation, as an adaptation to drought stress, and reduce levels of tissue damage (Yuping et al., 2017; Duursma et al., 2019). Transpiration rates of plants grow in sandy soil are lowered at the expense of photosynthesis rate to survive in dry habitats (Hatfield et al., 2001; Niu et al., 2003; Allison & Jones, 2005). The results of this study suggest that *H. muticus* at vegetative, flowering, fruiting stages maximized  $Pn$  and minimized  $E$  leading to higher instantaneous  $WUE$  with increasing of irradiance stress. Monitoring of phenological stages explain desert plant survival under abiotic stress (Cleland et al., 2007). In arid regions abiotic stresses involving high light intensities, drought stress, and high evaporation rates, which affect photosynthesis (Zhang et al., 2011). Plant phenology directly regulates growth, evapotranspiration, and nutrients uptake (Lianhong et al., 2003). The knowledge of different phenological interactions to the environmental prevailing conditions might lead to better understanding of plant functioning in short-term and long-term stresses (Urban et al., 2013). In early successional conditions with resources available, plants promote their photosynthetic production by having higher photosynthetic ability leaves, which can utilize high irradiance (Kikuzaw, 1995) and other extreme environmental conditions (Coops & Waring, 2011).

The desert winter annual endemic species revealed the maintenance of optimal conditions for high rate of photosynthetic assimilation during the short growing season as adaptations to desert environment (Mulroy & Rundel, 1977). The high leaf boundary layer conductance of *H. muticus*' leaves exhibited a great ability to withstand the high  $PAR$  and drought stress, by the main adaptive mechanisms of efficient energy budget by balancing energy absorbed to loss, through the

ability to lower leaf temperature, which in turn decrease leaf absorption percentage, decrease leaf conductance and transpiration (Radwan, 2008). In irradiated leaves, the two photosystems, PSII and PS1, in series perform the photosynthetic light reactions and associated electron transport in highly coordinated cooperation to a transient in Chlorophyll fluorescence yield (Kautsky & Hirsch, 1931; Lichtenthaler, 1992).

When plants are exposed to abiotic and biotic stresses (such as drought, heat, salinity, cold, or pathogen infection) in the light, decreases in  $F_v/F_m$  are frequently observed. Such a widespread phenomenon  $F_v/F_m$  measurements provide a simple and rapid way of monitoring stress. Unfortunately, the reasons for stress-induced decreases in  $F_v/F_m$  are often complex. Stressing photosynthetic tissues in the light can result in increases in non-photochemical quenching processes, which decrease  $F_m$ . Such quenching may not recover during a short period of dark adaptation, or even overnight, and results in decreases in  $F_v/F_m$  (Adams & Demmig-Adams, 2006; 2004).

In many stress situations increases in non-photochemical quenching can often be accompanied by photo inactivation of PSII reaction center, which then dissipate excitation energy as heat rather than as photochemistry (Melis, 1999). Photoin activation can lead to oxidative damage and loss of PSII reaction center (Aro et al., 1994), both of which are associated with an increase in  $F_0$  (Bradbury & Baker, 1986; Osmond, 1994).

However, identification of the intrinsic causes of such decreases can often be difficult. As water depletion accompanied with high irradiance in all stages which mainly reflected in the parameters of chlorophyll fluorescence. Chlorophyll fluorescence parameters values exhibited a statistically highly significant negative attributed to water deficiency stress in the assimilatory organs of *H. muticus* (Mihaljevi et al., 2021).

It showed significant increments in  $F_0$  records along with progressing phenological stages. The increase in  $F_0$  was initiated in seedling stage and reached to the highest value (101) in fruiting stage. The  $F_0$  value increased due to impaired transferred excitation energy from the antenna to the reaction center (Schreiber et al., 1998). Thus,

the increase in  $F_0$  observed in *Smirnova iranica* plants studied may be associated with damage to the photosynthetic apparatus, such as inactivation reaction center of PSII (Ranjbarfordoei et al., 2013).

The  $F_m$  decrements were recorded in *H. muticus* along with progressing phenological stages. However, caution must be exercised when attempting to interpret the significance of decreases in  $F_m$  or increases in  $F_0$  that occur as a result of a stress treatments (Ranjbar, 2015). These chlorophyll fluorescence levels were determined by the physicochemical properties of PSII and the optical properties of the leaf. Unfortunately, during many stress treatments, especially when changes in leaf water status occur, the optical properties of the leaf can change markedly and modify  $A_{leaf}$  (Baker Neil, 2008). Significant decrease in  $F_m$  was initiated in seedling stage and reached to the lowest value (29) in fruiting stage. The reduction of  $F_m$  can be associated with increased non-photochemical dissipation as heat or may be related to the decrease in the activity of the water-splitting enzyme complex (Cicero et al., 2012). Our results on  $F_0$  and  $F_m$  agree with the findings of on *Medicago sativa* when exposed to drought (Li et al., 2015).

Changes in  $fraction_{PSII}$  can occur owing to changes in thylakoid membrane structure and organization. Such modifications will result in changes in  $F_0$  and  $F_m$  that are independent of changes in  $\phi_{F_0}$  and  $\phi_{F_m}$  (Baker Neil, 2008). The ratio of PSII photochemistry maximum quantum efficiency to quantum yield showed significant declines along with progressing phenological stages. The increase of water deficit accompanied with progressing of phenological stages provided the decline in  $F_v/F_m$ . Extending phenological stages along with increasing water deficiency stress resulted in significant reduction in  $F_v/F_m$ . Our results regarding  $F_v/F_m$  records revealed that decrements in  $F_v/F_m$  indicate that, PSII and the key reactions of photosynthesis are inhibited (Zhao et al., 2014).

Gradual decrements in soil water contents exhibited alteration in pigments concentrations, of a significant decline through the phenological stages. A typical symptom of abiotic stresses are the reduction of total pigments content, as a result of either slow synthesis or fast breakdown, has been considered as (Mafakheri et al., 2010).

The decreases of Chl. ( $a+b$ ) and *Carotene* were paralleled with decrease of  $F_v/F_m$ , which indicated that pigments breakdown was accompanied by the decreasing of the maximum photochemical efficiency (Ranjbar, 2015). Chlorophyll ratio ( $a/b$ ) showed insignificant changes. Chlorophyll ( $a+b$ ) showed significant decrements in parallel to the decrements of the ratio of PSII photochemistry maximum quantum efficiency to quantum yield. Reduction of light absorbance due to photosynthetic pigments content decrements recognized as a photo protection mechanism' phenomenon (Galmes et al., 2007; Elsheery & Cao, 2008). The ratio Chl. ( $a/b$ ) tended to increase with progressing of phenological stages, although significant differences did not occur. Lack of significant effects of water deficiency on the Chl. ( $a/b$ ) indicates that the size of photosystems has not changed (Fahl et al., 1994). The results of this research focused on some physiological potential mechanisms, and to explain the existence withstanding of *H. muticus* in harsh environmental conditions.

### Conclusion

The results of the current research revealed that *H. muticus* during vegetative, flowering, fruiting stages maximized  $Pn$ , minimized  $E$  to optimize instantaneous  $WUE$  and the absorbed light energy can be lost from PSII resulting in slight minimization in chlorophyll fluorescence' quantum yields to overcome the irradiance stress.

### Abbreviations:

$Pn$	Photosynthesis rate	$E$	Transpiration rate
$PSII$	Photosystem II	$C$	Stomatal conductance
$WUE$	Water use efficiency	$F_m$	Maximal fluorescence from dark-adapted leaf
$PAR$	Photosynthetically active radiation	$F_0$	Minimal fluorescence from dark-adapted leaf
$F_v/F_m$	maximum quantum efficiency of PSII photochemistry	$Y$	PSII quantum yield of fluorescence

*Conflicts of interest:* No conflicts of interest have been declared.

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تبادل الغازات والخصائص الضوئية للكلوروفيل في نبات السكران (*Hyoscyamus muticus* L.) في مراحل فينولوجية مختلفة تحت ظل ظروف بيئية قاحلة شديدة الجفاف، بالصحراء الجنوبية الغربية، مصر

أسامه أحمد عبد الوهاب رضوان<sup>(1)</sup>، محمد صالح<sup>(2)</sup>

<sup>(1)</sup> قسم النبات - كلية العلوم - جامعة أسوان - 81528 - أسوان- مصر، <sup>(2)</sup> قسم الفيزياء - كلية العلوم - جامعة أسوان - 81528 - أسوان- مصر.

تم متابعة التغييرات في معدل البناء الضوئي، النتج، توصيلية الثغور، كفاءة الاستخدام اللحظي للمياه والخصائص الضوئية للكلوروفيل وخصائص أصباغ التمثيل الضوئي في نبات *Hyoscyamus muticus* L. القابل للتكيف في بيئة شديدة الجفاف في سياق المراحل الفينولوجية (بأدره، نمو خضري، تزهير وإثمار) للتعرف على الآليات التي يستطيع النبات بها التكيف مع ماقد يتعرض له من الإشعاع العالي خلال دورة حياته.

حيث أظهر نبات *H. muticus* اختلافات كبيرة في العمليات الفسيولوجية في مختلف المراحل الفينولوجية. تم تسجيل أعلى معدلات التمثيل الضوئي (5 و 5.23 ميكرومول/م<sup>2</sup> ثانية<sup>-1</sup>) في مرحلة النمو الخضري كما تم تسجيل أعلى معدل نتج في مرحلة البادرات أثناء الزيادة النسبية للإشعاع الضوئي النشط (PAR)

كما لوحظت أدنى معدلات النتج (0.18 ملليمول/م<sup>2</sup> ثانية<sup>-1</sup>، 0.19 ملليمول/م<sup>2</sup> ثانية<sup>-1</sup> و 0.197 ملليمول/م<sup>2</sup> ثانية<sup>-1</sup>)، في مراحل النمو الخضري والإزهار والإثمار، على التوالي وعند أعلى قيمة للإشعاع الضوئي النشط (PAR) (2500 ميكرومول/م<sup>2</sup> ثانية<sup>-1</sup>).

كما أدى النقص في توصيلية الثغور خلال مراحل البادرات، والإزهار والإثمار إلى انخفاض معدلات كل من التمثيل الضوئي ( $Pn$ )، والنتج ( $E$ ) وكفاءة استخدام المياه اللحظية ( $WUE$ ) كاستجابة للتزايد في الإشعاع الضوئي النشط (PAR).

وقد تم تسجيل زيادات معنوية في الحد الأدنى من الوميض ( $F0$ ) وكذلك نقص معنوي في قيم الحد الأقصى من الوميض ( $Fm$ ) في الأوراق التي لها القدرة على التكيف مع الظلام.

وأظهرت النتائج انخفاض نسبة الكفاءة الضوئية ( $PSII$ ) بالمقارنة مع العائد الكمي خلال المراحل الفينولوجية المختلفة للنبات.

كما تم تسجيل انخفاض ملحوظ في محتوى الأوراق من الأصباغ التمثيلية. كما أظهرت النتائج قدرة النبات على التكيف مع ندرة المياه وارتفاع نسبة الإشعاع الضوئي خلال المراحل المختلفة من دورة حياته تحت الظروف البيئية شديدة الجفاف.