

Original Article

Diurnal Variations of Gas Exchange Characteristics in Leaves of Anise Hyssop (*Agastache foeniculum*) under Normal, Drought Stress and Recovery Conditions

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Abstract

Net photosynthesis rate (Pn), stomatal conductance (gs) and transpiration rate (E) of anise hyssop were measured during the four cloudless days, in reference to diurnal fluctuations of leaf temperature (Tleaf), leaf vapor pressure deficit (VPD leaf) and photosynthetic photon flux density (PPFD) in well watered (WW), stressed (S) and recovered (R) plants. An analysis of measured data showed that there was an evident midday depression of photosynthesis at stress and recovered plants. The highest of net photosynthesis was observed at 11:00, 8:00 and 7:00 a.m for well watered, stressed and recovered plants, respectively. Net photosynthesis rate, stomatal conductance and transpiration rate were higher in well watered than stressed plants while leaf vapor pressure deficit and leaf temperature was lower in well watered plants. Stomatal conductance and transpiration were also positively correlated with leaf vapor pressure deficit and net photosynthesis rate in well watered plants while correlation between these parameters was not significant in stressed plants. In total, the midday depression of net photosynthesis might be due to stomatal and non-stomatal limitations.

Key words: Anise hyssop, Net photosynthesis, Stomatal conductance, Transpiration, Leaf temperature

Introduction

Medicinal and aromatic plants are of prime economic importance because of the continuous and increasing demand for their products by local and foreign market [1]. Anise hyssop is one of the most important plants in this regard. Anise hyssop (*Agastache foeniculum* Kuntze syn: *Hyssopus anethiodorus* Nutt., *H. anisatus* Nutt. And *H. foeniculum* Sevensel) of the family Lamiaceae (Labiatae) is a perennial medicinal and spice plant native to the North America [2]. The plant has gained importance in America, Asia, and Europe as a component of tea mixtures and as a flavoring in confections. This plant produces aromatic oils that are used in foods, drugs, perfumes and cosmetic industries. Anise hyssop has also been reported to be a valuable source of nectar for honey bee forage. The herb is used for seasoning food and in flavoring liqueurs. The essential oil has

been found to possess antimicrobial and antifungal properties. It is also used for stomach and bloat [3]. According to global circulation models [4] rainfall scarcity might become worse in the near future over the Mediterranean area. Intense drought periods might reduce crop yield and quality of production. Drought stress reduces yield of medicinal and aromatic plants by three main mechanisms: First, whole canopy absorption of incident photosynthetically active radiation may be reduced, either by drought induced limitation of leaf area expansion, by temporary leaf wilting or rolling during periods of severe stress, or by early leaf senescence. Second, drought stress decreased the efficiency with which absorbed photosynthetically active radiation is used by the crop to produce new dry matter (the radiation use efficiency). This can be detected as a decrease in the amount of crop dry matter accumulated per unit of photosynthetically active radiation absorbed over a given period of time,

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or as a reduction in the instantaneous whole canopy net CO₂ exchange rate per unit absorbed photosynthetically active radiation. Third, drought stress may limit grain yield of medicinal and aromatic plants by reducing the harvest index [5]. It is therefore important to understand to what extent water stress impairs physiological processes such as photosynthesis in crops.

Photosynthesis is an important process that is carried out in all living land plants. It involves the conversion of light energy into chemical energy. It is a primary process in plant productivity. The site of photosynthesis in plants is predominantly in the green leaf and the productivity of plants directly depends upon the chlorophyll bearing surface area, irradiance, and their potential to utilize CO₂. Plant biomass production depends upon the amount of water use for growth as well as on water use efficiency (WUE). Productivity in crop plants may be increased by WUE, and one of the major factors for enhanced WUE is net CO₂ assimilation rate. Thus, final biological or economical yield can be increased by increasing the net CO₂ assimilation rate [6].

Water deficit reduces the growth of plants by reducing leaf area, the most important factor affecting crop productivity. Drought stress lowers the water potential of the growing plants, leading to dehydration, decreased stomatal conductance, altered chlorophyll fluorescence, photoinhibition of photosystem II (PSII), conformational changes in membrane-bound ATPase enzyme complex, as well as decrease in both activity and concentration of rubisco enzyme [6].

Drought tolerant plant shows some active mechanisms which allow it some degree of control over water loss under water stress [7]. One of these mechanisms is the control of water loss by stomatal closure, which has been identified as a common and early event in plant response to water deficit under field conditions [8]. This decrease in gas exchange restricts water losses, but simultaneously also reduces daily carbon assimilation at the leaf level, decreasing in the long-term net carbon gain by the whole plant.

It is well-established that the stomatal response is complex, because it is dependent on a number of environmental factors, including light, CO₂, humidity, wind velocity and temperature, and on internal factors such as tissue water status (leaf turgor and/or water potential) and chemical signals (e.g. cytokinins or abscisic acid, (ABA)) [9,10].

Plants are exposed to variable photosynthetic photon flux density (PPFD), temperature and humidity in the field. At low PPFD, more than 80% of the absorbed light energy may be utilized for CO₂ assimilation.

However, excess light during midday can inhibit photosynthesis [11]. The midday depression of photosynthesis likely results primarily from long periods of high PPFD [12]. Other possible causes of midday depression include an increase in leaf to air vapour pressure deficit (VPD_{leaf-air}) [13], high temperature [14] and feedback inhibition of photosynthesis by sugar accumulation [15]. The soil moisture could also cause midday depression, because it decreases the moisture content of leaves and increases stomatal resistance, thereby restricting the effective use of CO₂ [7]. In general, the depression might be due to stomatal and non-stomatal limitations.

Drought limitation to photosynthesis has been reported in many studies [16], of which a few documents covered the photosynthetic responses to cycled water deficit. As reported, full recovery of net photosynthetic rate has been observed as drought stress is eliminated following rewatering [17,18]. Plants of *Lonicera japonica* Thumb. With tetraploid chromosome have a higher drought resistance during water deficit and more rapid recovery after rewatering in terms of gas exchange and chlorophyll fluorescence compared to those with diploid chromosome [19]. The literature on response of medicinal plant as gas exchange factors under water stress conditions is low. Variations in Photosynthesis of two clonal thymol-type thyme selections were studied by Letchamo et. al [20]. and they concluded water stress significantly decrease net photosynthesis of two clonal, The lowest Pn, 5.88 μmol CO₂ m⁻²s⁻¹, was obtained from clone Laval-2, after 40 days of growth under 50% soil water amount. The same result was recorded in two cultivar of *Salvia miltiorrhiza* [21]. Water stress significantly decreased net photosynthetic rate, stomatal conductance, and maximum photochemical efficiency (F_v/F_m) of two jasmine genotypes [22]. Niu and Rodriguez [23] showed that leaf net photosynthesis rate, stomatal conductance and transpiration of *Agastache urticifolia* decreased with progressive in water stress. The same results was observed in oleander [24]. An experiment conducted by Zhang et al., [25], showed that the diurnal net photosynthetic rate of *Angelica sinensis* exhibited a double peak pattern, and the peaks occurred at 9:45 a.m and 4:45 p.m respectively. At present, investigations of *Agastache foeniculum* were mainly focused on the chemical components and conventional planting techniques [26-29]. Diurnal response of photosynthesis of anise hyssop to drought stress has not been described yet. The aim of this study was investigation of diurnal changes of net photosynthetic rate and relative

parameters in plant subjected to water stress, well watered and recovered plants, in addition to identify the relationship between diurnal changes in the net photosynthetic rates and environmental factors.

Materials and Methods

Place and Conditions of the Experiment

The experiments were carried out at Tarbiat Modares University, at Paykan Shahr, situated 16 km away from Tehran, Iran. The station is located at 1215 m above sea level, latitude 35°, 43' North, altitude 51°, 8' East. The ecological situation of the station was characterized by semi-dry climate with 229.2 mm annual precipitation. Soil composition was: sand 77%, clay 8%, silt 15%, pH 7.7, available K 770 ppm, available P 140 ppm, total N 0.15%, organic C 1.73%, Ca 5045 ppm, Mg 381 ppm, Fe 9.08 ppm, Zn 3.37 ppm, Cu 0.87, Mn 10.63 ppm, B 0.6 ppm and EC 1.04 DS/cm.

Plant Materials and Water Deficit Treatment

The seeds of *A. foeniculum* were provided from Department of Medicinal and Aromatic Plant Corvinus University in Budapest. The seeds were sown on sandy loam soil into grows at optimum depth of 0.5 cm in rows. Each plots size was of 2 m × 2 m (4 m²). Spacing in the rows was 30 cm. The plants were thinned to 20 cm within rows and allowed to establish. All agronomic management practices were performed as needed. The plants were allowed to grow under same condition till the height of plant reached to 15 cm. Then half of plant was subjected to water stress. The treatments were well watered plants (100% of field capacity), water stressed plants (55% of FC) and recovery plant. In the well watered plants, moisture of soil medium was kept close to field capacity. Water stress was imposed by withholding water until severe drought stress was reached. Severe water stress was considered when the soil moisture content was 55% FC [27]. Thereafter, plants were maintained at this intensity of drought stress for a few days by adding the amount of water they lost during the day. After this period of stress-acclimation plants were consecutively re-watered to field capacity and the recovery of photosynthetic traits was followed. The level of water stress was monitored by TDR portable meter (TRASE System 1 6050X1, Soil Moisture Equipment Crop., USA).

Gas Exchange Measurements

Gas exchange parameters were investigated from May 30-31 for well watered and stressed plants and June 1-2 for recovered plants, in 2009 under natural environmental conditions. The parameters of gas exchange were measured on the 5th and 6th nearly full expanded leaves with three replicates between the hours of 06:00 and 20:00 during bright sunlight on clear, cloudless days. Determination of leaf net CO₂ assimilation rate (Pn), stomatal conductance (gs) and transpiration (E) were made with Infra-red gas analyzer (LCA₄, ADC Co. Ltd., Hoddesdon, UK). Instantaneous water use efficiency (WUE_{inst}) was calculated as A/E ratio. Apparent quantum yield (AQY) was calculated as A/PPFD ratio.

Statistical Analysis

The data were analyzed by one-way ANOVA using SAS software. Treatment means were separated with Duncan's multiple range test (P<0.05).

Results

Diurnal Changes of Environmental Parameters

Diurnal changes in environmental variables on a typical sunny day are presented in fig. 1 and 2. Air temperature was lowest (19.2 °C and 15.4 °C) at 6:00 a.m and then gradually increased, reaching a maximum of 36.2 °C and 33.8 °C at 3:00 p.m in stress and recovery days, respectively (Fig. 1). During the day, PPFD first increased and then decreased in both days (Fig. 2). It increased gradually from 6:00 a.m, reached its maximum value (2267 and 2190.3 μmol photon m⁻² s⁻¹) at 1:00 p.m and 12:00 p.m, and then decreased to a minimum (51 and 49 μmol photon m⁻² s⁻¹) at 8:00 p.m for stress and recovery days, respectively.

The changes of T_{leaf} of well watered (WW) plants closely followed the course of T_{leaf} of stressed (S) plants during the day, with an equal or a slightly lower value than that of T_{leaf} of S plants at each hour. The maximum T_{leaf} measured at 3:00 p.m was 38.7 and 40.3 °C for WW and S plants, respectively. The maximum T_{leaf} for recovered (R) plants was about 37.4 °C at 3:00 p.m (Fig. 3). VPD_{leaf} followed a diurnal pattern, being lowest at sunrise and increasing to a maximum at around 3:00 p.m (Fig. 4). VPD_{leaf} of S plants was higher than WW and R plants.

Diurnal Changes of Gas Exchange Parameters

The anise hyssop plants presented different trends in Pn under various conditions. As indicated in fig. 5, Pn of WW plants showed a single peak diurnal curve;

Pn was low in the early morning ($0.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), increasing quickly with time and reaching a maximum value ($16.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at 11:00 a.m. Thereafter, Pn decreased gradually independent of increase in PPFD. Diurnal changes in S and R plants showed similar circadian rhythms. Pn of R plants increased very quickly early in the morning ($9.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 7:00 a.m) and then decreased slowly, reached a minimum value ($6.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 12:00 p.m), followed by slow recovery at 2:00 p.m. Although Pn of plants grown under stress had two peaks, the second peak was not clear; another difference was that Pn showed a slight increase to $5.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 10:00 a.m.

During the day, the photosynthetic rate was clearly influenced by changes in light intensity and soil moisture content. In fact, the maximum Pn value was about $16.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 11:00 a.m for WW plants, which was 1.5 and 2.5 fold higher than the maximum values observed for S and R plants occurred at 8:00 a.m and 7:00 a.m, respectively.

The WW plants showed an increase in g_s early morning until 9:00 a.m, then maintained a high level ($40\text{-}56 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) during the period from 9:00 a.m to 5:00 p.m, after that, dropped drastically to minimum at 8:00 p.m. The g_s for S plants increased to $23 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ at 8:00 a.m, then declined at 9:00 a.m to 10:00 a.m, it showed an increase during 11:00 a.m to 12:00 p.m and did not change dramatically between 12:00 p.m and 7:00 p.m except for a slight decrease at 5:00 p.m. Interesting, highest level of g_s in R plants was observed at 6:00 a.m could be attributed to irrigation at previous day, it showed a decline trend from 7:00 a.m to 12:00 p.m and after that a peak was observed at 3:00 p.m and then decreased gradually (Fig. 6). The average of g_s in WW plants was 2.9 and 1.4 fold higher than S and R plants, respectively.

The similar diurnal changes of Pn and g_s observed in WW plants suggest that both processes are dependent. This idea was supported by correlation analysis (Table 1). Similarly, a positive relationship between g_s and Pn was earlier observed in neem [30] fig. and peach trees [31]. In contrary, correlation between Pn and g_s of anise hyssop was not significant in plants which grown under stress and recovery conditions (Table 2 and 3). So it may concluded to non-stomatal limitation is dominant in these condition. Anyway, stomatal performance is determined by PPFD, VPD_{leaf} , T_{leaf} and the conditions in the root system which affected photosynthesis rate. Regarding light availability, our result showed that there was no PPFD limitation to photosynthesis;

rather, high PPFD could lead to photoinhibition and photooxidation of leaf tissues. Such a situation of extensive PPFD would be found during 10:00 a.m to 5:00 p.m especially in plant encountered with water stress. Therefore, the decline in Pn and g_s of anise hyssop was grown under stress might be associated with high PPFD and a substantial increase in VPD

leaf .

The higher Pn rate in plants grown on normal condition could be attributed to better root system efficiency that can effect on stomatal aperture as compared to plants subjected to water stress.

As expected, E was strongly affected by PPFD, g_s , VPD and T_{leaf} , exhibited the daily E pattern resembled those of g_s in plant under three conditions. The lowest E was observed in the early morning (6:00 a.m), while highest rate for E was recorded between 3:00 p.m to 4:00 p.m that could be attributed to high VPD, T_{leaf} and PPFD (Fig. 7). The lower transpiration rate observed in plants under stress condition was due to a lower stomatal conductance (r_E , $g_s = 0.75$).

Discussion

Normally, plants show two types of curves for diurnal changes in Pn; single- peak and double peak curves [32]. In our study, S and R plants showed double curves; the first peak appeared at 8:00 a.m and 7:00 a.m, respectively and the second peaks were occurred at 2:00 p.m for both plants. The decrease in Pn of S plants from 8:00 a.m to 1:00 p.m reached $2.63 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, while it only increased by $3.21 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ from 1:00 p.m to 2:00 p.m, indicating that the Pn of S plants decreased quickly but recovered slowly. In spite, for R plants, Pn showed low decline from 7:00 a.m to 12:00 p.m (9.7 to $6.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and even there was no midday depression in Pn of WW plants. This result was in agreement with Zhou et al. [33], who found that diurnal changes in Pn of *Pueraria lobata* showed a single peak curve and no midday depression occurred. The same result was obtained with *Saposhnikovia divaricata* in response to water supply[34]. In contrast, Zhang et al. [25] found that diurnal change in Pn of *Angelica sinensis* was a double-peak pattern, and the peaks occurred at 9:45 and 16:45 h, respectively. The leaves of *Panax ginseng* and *P. quinquefolium* showed different pattern for Pn under different environmental conditions [35].

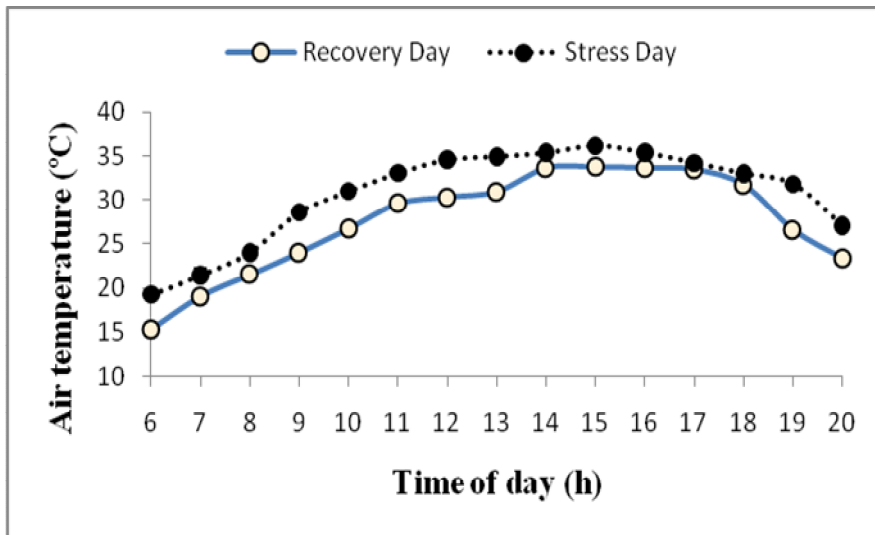


Fig. 1 Diurnal fluctuation of air temperature during stress and recovery days.

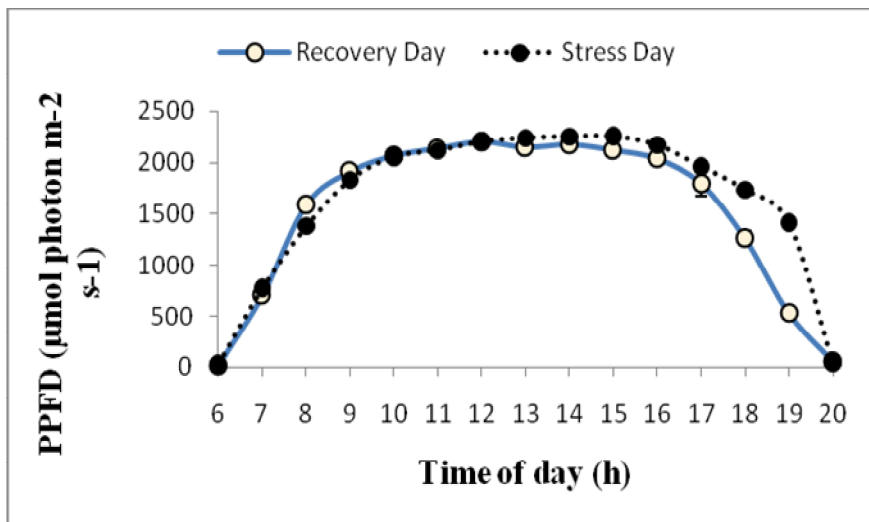


Fig. 2 Diurnal fluctuation of PPFD during stress and recovery days.

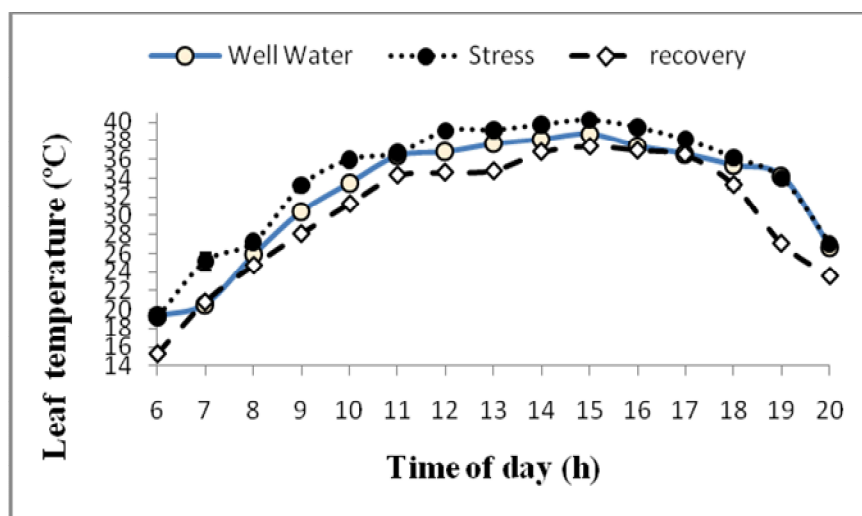


Fig. 3 Diurnal fluctuation of T_{leaf} of well watered, stressed and recovered plants.

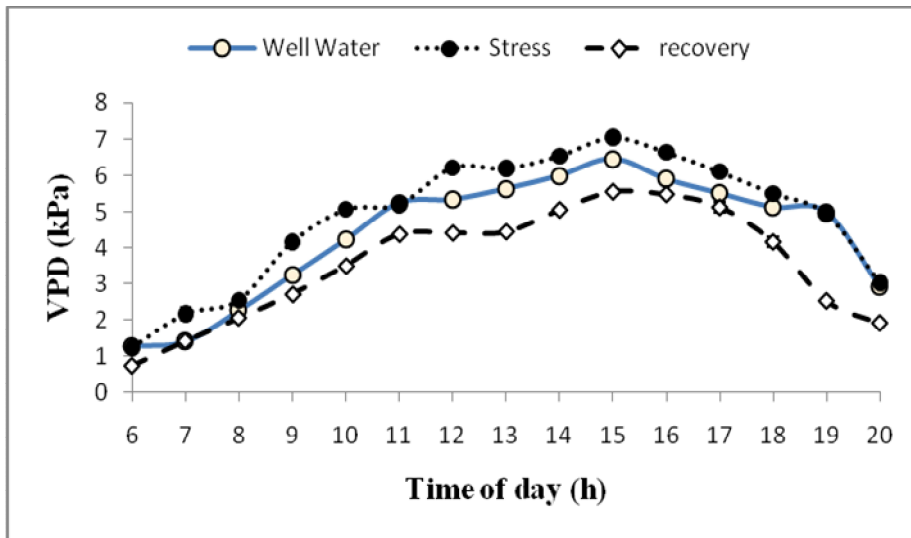


Fig. 4 Diurnal fluctuation of VPD_{leaf} of well watered, stressed and recovered plants.

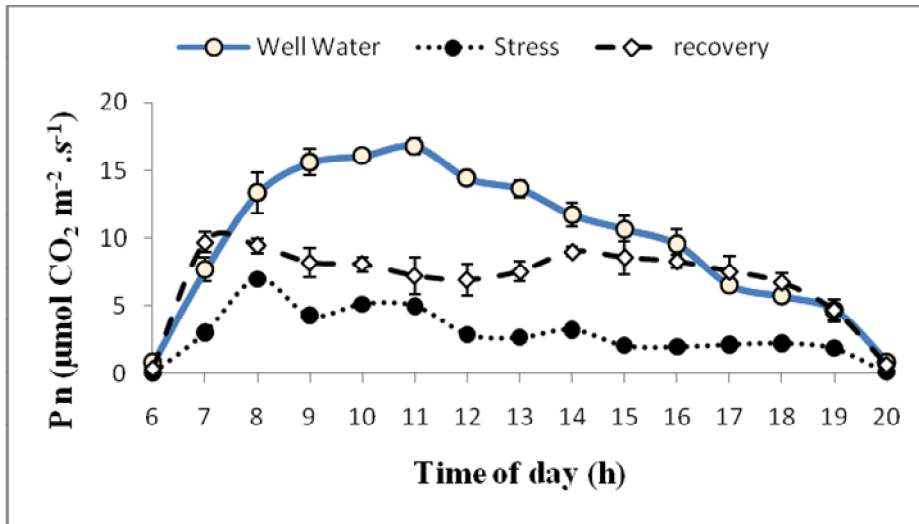


Fig. 5 Diurnal fluctuation of Pn of well watered, stressed and recovered plants.

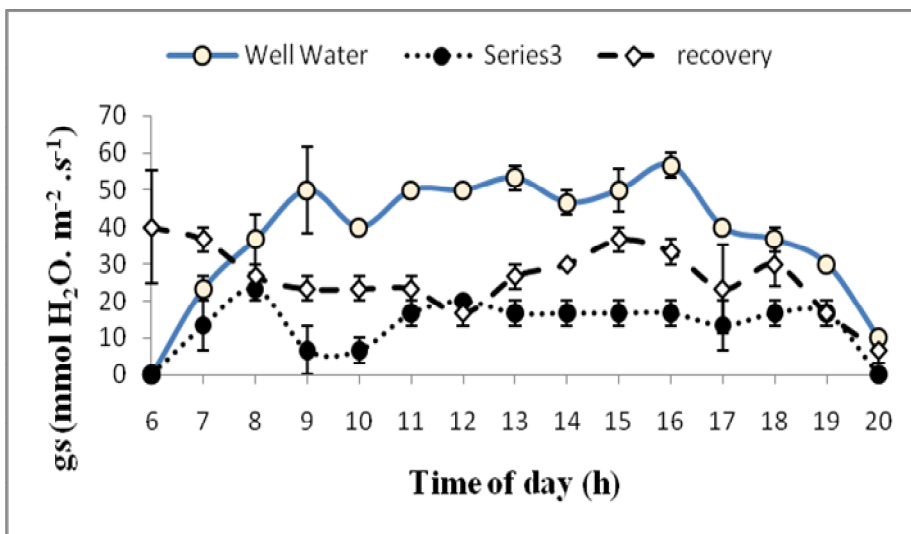


Fig. 6 Diurnal fluctuation of gs of well watered, stressed and recovered plants.

Table 1 Correlation analysis between traits in WW plants

	PPFD	VPD _{leaf}	E	T _{leaf}	gs	Pn	WUE
PPFD ¹							
VPD _{leaf}	0.841**						
E	0.912**	0.925**					
T _{leaf}	0.894**	0.985**	0.928**				
gs	0.951**	0.753**	0.901**	0.817**			
Pn	0.735**	0.329	0.526*	0.446	0.789**		
WUE	-0.204	-0.663**	-0.455	-0.595*	-0.104	0.373	
AQY	-0.843**	-0.780**	-0.749**	-0.817**	-0.803**	-0.456	0.234

**Correlation is significant at the 0.01 level.

*Correlation is significant at the 0.05 level.

1) PPFD = photosynthetic photon flux density; VPD_{leaf} = leaf vapor pressure deficit; E = transpiration rate; T_{leaf} = leaf temperature; gs = stomatal conductance; Pn = net photosynthesis rate; WUE = water use efficiency; AQY = Apparent quantum yield.

Table 2 Correlation analysis between traits in S plants

	PPFD	VPD _{leaf}	E	T _{leaf}	gs	Pn	WUE
PPFD ¹							
VPD _{leaf}	0.867**						
E	0.829**	0.920**					
T _{leaf}	0.917**	0.986**	0.900**				
gs	0.650**	0.506	0.747**	0.546*			
Pn	0.461	0.020	0.073	0.160	0.490		
WUE	0.025	-0.421	-0.383	-0.292	0.113	0.783**	
AQY	-0.386	-0.715**	-0.583*	-0.618*	0.019	0.616*	0.798**

**Correlation is significant at the 0.01 level.

*Correlation is significant at the 0.05 level.

1) PPFD = photosynthetic photon flux density; VPD_{leaf} = leaf vapor pressure deficit; E = transpiration rate; T_{leaf} = leaf temperature; gs = stomatal conductance; Pn = net photosynthesis rate; WUE = water use efficiency; AQY = Apparent quantum yield.

Table 3 Correlation analysis between traits in R plants

	PPFD	VPD _{leaf}	E	T _{leaf}	gs	Pn	WUE
PPFD ¹							
VPD _{leaf}	0.802**						
E	0.658**	0.863**					
T _{leaf}	0.837**	0.984**	0.790**				
gs	0.088	0.055	0.408	0.063			
Pn	0.752**	0.495	0.569*	0.544*	0.309		
WUE	0.295	-0.157	-0.196	-0.037	-0.101	0.680**	
AQY	-0.944**	-0.824**	-0.612*	-0.868**	0.034	-0.606*	0.192

**Correlation is significant at the 0.01 level.

*Correlation is significant at the 0.05 level.

1) PPFD = photosynthetic photon flux density; VPD_{leaf} = leaf vapor pressure deficit; E = transpiration rate; T_{leaf} = leaf temperature; gs = stomatal conductance; Pn = net photosynthesis rate; WUE = water use efficiency; AQY = Apparent quantum yield.

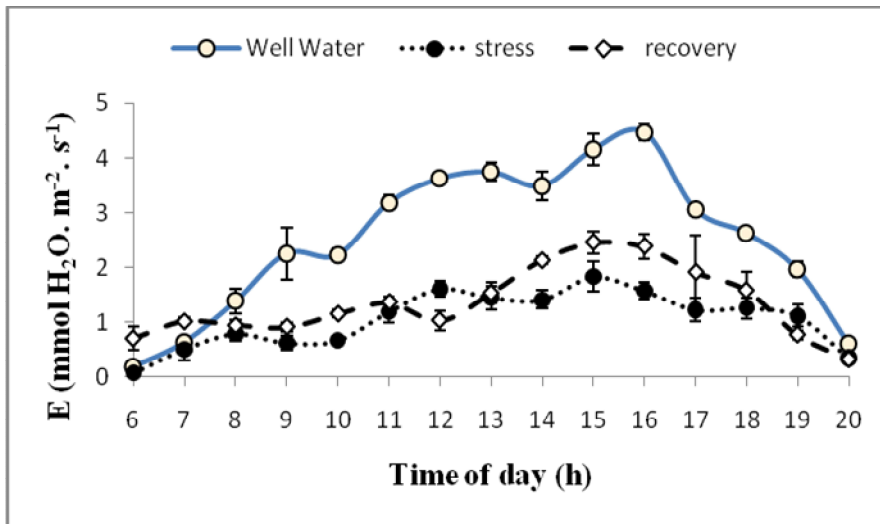


Fig. 7 Diurnal fluctuation of E of well watered, stressed and recovered plants.

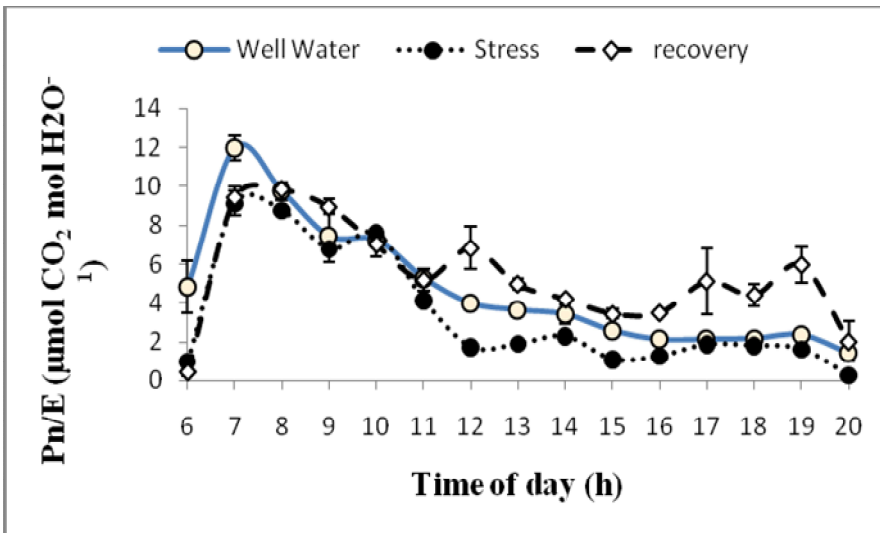


Fig. 8 Diurnal fluctuation of WUE of well watered, stressed and recovered plants.

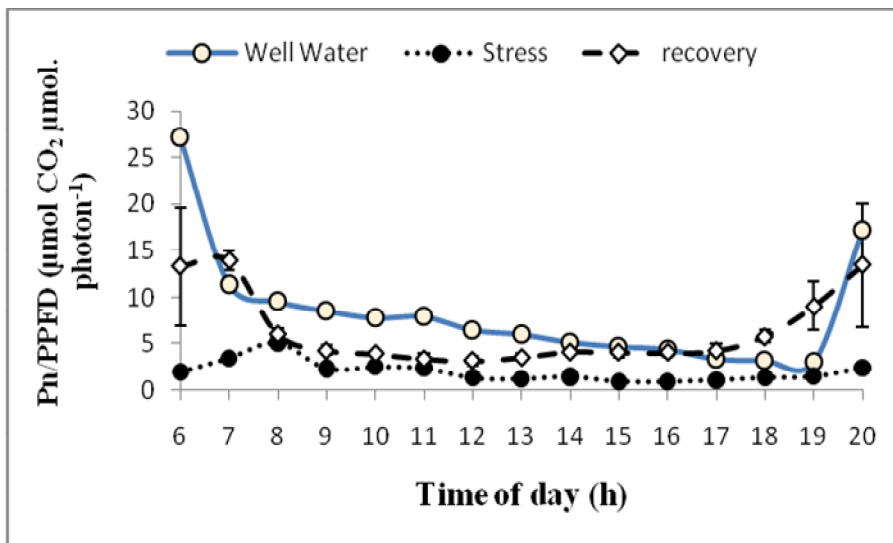


Fig. 9 Diurnal fluctuation of AQY of well watered, stressed and recovered plants.

As for leaves grown under low light intensity (10% light transmission rate, LTR shade), diurnal changes of net photosynthetic rate were showed in single peak, the maximum value of Pn was at 12:00 am - 1:00 pm. As the increase of light intensity (grown under 20%, 30% and 40% LTR shade), Pn was increased, higher Pn was measured from 9:00-11:00 am to 12:00 am-1:00 pm, and then Pn was declined at 2:00-4:00 p.m. Anyway Midday depression in Pn is critical for plants growing in adverse conditions and with adjustment through this midday depression, photosynthesis can effectively continue, even when plants are faced with excessive water loss, that may destroy organelles related to photosynthesis. Some previous studies stated that the Pn decrease is due to photoinhibition caused by strong light at noon [23]. Our result showed that Pn of anise hyssop is more depend to water status of plant and diurnally trend of plant can be changed with level of water in soil, as plant encountered with water stress, midday depression occurred. It seems that Pn of plants is depended to species, growth stage of plant and environmental conditions [36].

The decrease in Pn at noon may be caused by either stomatal or non-stomatal limitation. Partial closure of stomata at noon is a response to the decrease of photosynthesis activity via decrease in CO₂ concentration in mesophyll cells. In the other hand, rubisco activity, the most critical enzyme in photosynthesis directly affects the photosynthesis rate of plants. The optimum temperature of rubisco enzyme ranges from 25 to 30 °C. Water stress in plants can lead to increase in temperature in leaf that could cause the decrease of rubisco activity [37]. However, midday depression in Pn is accompanying with strong light, high temperature and low humidity conditions. In our study, we cannot exclude the effect of high temperature and high PPFD on photosynthesis of anise hyssop plant was grown in field condition.

The monoterpenes are secondary metabolites formed in chloroplasts from fleshy fixed carbon and their levels may depend on CO₂ acquisition and formation of photosynthesis intermediates. However, water stress increased monoterpenes concentration while photosynthesis was significantly inhibited in mint, rosemary [38] and anise hyssop [27], these contrasting trends indicating that a large fraction of carbon is allocated to monoterpenes formation under stress condition in anise hyssop. Accumulation of monoterpenes in water stressed plants may have ecological functions, such as defense or storage. In the other hand, the buildup of secondary compounds in medicinal plant could also mitigate oxidative

damages in chloroplasts caused by free radicals accumulation under water stress, as it was speculated that terpenes could replace photorespiration in protection from photodamage under stress conditions [38].

Anise hyssop showed 69.2% recovery in Pn after rewatering. Galmes et al [39] found that the recovery of photosynthesis 24 h after rewatering ranged from 10% to 70% of control plants. Ignace et al [40] reported that the photosynthesis recovery may depend on the temporal variation of antecedent soil moisture. The lower root development and severely impaired vascular capacity for water transport due to previous drought may be responsible for the incomplete recovery of photosynthesis and gs in stressed plants after rewatering. The gs response to water stress and rewatering largely depends on the species, growth forms and leaf habits [41]. However, a slower recovery of Pn in water stressed plants upon rehydration suggest that basic mechanism of photosynthetic biochemistry and photochemistry might be impaired in this plant due to water stress. This might lead to the conclusion that decreases in Pn result not only from the reduced gs, but also due to impairment of metabolic activities associated with drought stress [42]. The chloroplast and mitochondrial structure can also be affected by a water deficit. The chloroplast structure such as thylakoids usually is not alter under moderate water deficit and is damage only under severe stress conditions. It is well known that the drop of soil moisture will cause the cell destruction and change the growth hormone content in a leaf. It is considered that recoveries became incomplete by the effects of these complex factors under drought stress [43]. Anyway, further experiment should be taken in the wide range from short time responses to long term acclimation after rewatering.

In conclusion, leaf net CO₂ assimilation rate in anise hyssop showed different diurnal pattern in well watered plant with stressed and recovered plants. The midday depression was due to stomatal and non-stomatal limitations in stressed plant and did not observed in well watered plant. However, these results do not clearly explain the mechanisms causing the difference in decline in Pn of anise hyssop under different conditions. Thus, various approaches, including the evaluation of radiation less energy dissipation levels and the antioxidative system against active oxygen species induced at high PPFD and water stress, are needed.

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