

Full Length Research Paper

Photosynthetic response of Egyptian cultivar of broad bean (*Vicia faba* L.) to UV-B and drought, singly and in combination

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Bean plants grown under field conditions were exposed to drought stress (DS) and supplementary ultraviolet-B radiation (sUV-B) singly and in combination (DS + sUV-B). The effects of these two stresses on net photosynthetic rate (P_N), stomatal conductance (g_s), quantum efficiency of photosystem II (Φ_{PSII}), variable to maximum chlorophyll (Chl) fluorescence (Fv/Fm), photochemical (q_p) and non-photochemical (NPQ) Chl fluorescence, biomass and yield were investigated. P_N , g_s , chlorophyll (Chl) content, and NPQ were dramatically reduced due to exposure to DS by 54, 41, 29, and 12% and by 19, 19, 16 and 12% due to exposure to sUV-B, respectively. This reduction resulted in a change in assimilate allocation in favour of shoot growth leading to a decrease in root to shoot ratio and eventually to a decrease in relative growth rate (RGR) of both root and shoot. Seed yield was decreased by 27 and 23% due to DS and sUV-B, respectively. Their interaction was more than additive. q_p showed no significant response to sUV-B. There was antagonistic interaction between DS and sUV-B showing that DS effectively protects against the adverse effects of sUV-B

Keywords: Drought stress (DS), supplementary ultraviolet radiation (sUV-B), quantum efficiency of photosystem II (Φ_{PSII}), net photosynthetic rate (P_N), stomatal conductance (g_s), photochemical (q_p) and non-photochemical (NPQ) Chl fluorescence biomass, yield.

INTRODUCTION

The depletion of stratospheric ozone, caused by the emission of chlorofluorocarbons (CFCs) and other gases, has resulted in increased amounts of ultraviolet-B radiation reaching the Earth's surface (Blumthaler and Ambach, 1990). Global warming and increasing solar UV-B radiation at the Earth's surface are two major concerning factors in climate change (Madronich et al., 1995; Zhao *et al.*, 2005; Hidema and Kumagai, 2006; Agrawal and Rathore, 2007).

Long-term UV-B data are sparse and not very reliable. Moreover, there has been no global network for monitoring surface-level UV-B radiation. Nevertheless, numerous investigators have examined the effects of UV-B radiation on crops in artificial exposures, but large uncertainties in the relevance to climate change of much of the information obtained remain. According to

Runeckles and Krupa (1994), the transfer of results from growth chamber or greenhouse experiments to the ambient environment has been particularly difficult. This appears to be due to the differences in the characteristics of plants grown under these environments and to photorepair under the high photosynthetic photon flux densities encountered in the ambient environment. Studies of the effects of UV-B and drought stress on physiological processes such as photosynthesis and on modes of action are appropriately examined under controlled environment conditions. However, the integration of their effects on the processes affected within the whole organism that ultimately lead to growth can only reliably be investigated using plants growing under true field conditions.

During summer periods, the weather in Egypt is characterized by being anticyclonic with no rainfall and high temperature, so vegetation is often exposed to prolonged periods of drought which is reflected in

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lowering their relative water content and their water potential (Hassan, 2006). During such periods of drought, large depressions in photosynthetic rates are observed in many plants in the Mediterranean (Nogués and Baker, 2000) and maximum rates of CO₂ assimilation occurs either early in the morning or late afternoon (Munakata et al., 1999). This would involve heterogeneity of leaf photosynthesis.

Most plant species develop a biochemical adjustment as a mechanism of protection against environmental stress(s), through induction of reactive oxygen species (ROS), such as Hydrogen peroxide (H₂O₂), superoxide (O₂⁻) and singlet oxygen (¹O₂) (Wu and Tiedemann, 2002) and this is a common response to most stresses (e.g. Hassan, 2006).

UV-B is species specific, as other environmental stresses, (Smith, 2000, Alexieva et al., 2001; Zu et al., 2004). There is paucity on the knowledge concerning the antioxidant response of plants to UV-B (e.g. Costa et al., 2002; Kakani et al., 2003; Agrawal and Rathore, 2007).

Although responses of crop physiology, growth, and yield to one factor of temperature or UV-B radiation have been extensively studied in Northern Europe and the USA (e.g. Kakani et al., 2003; Zhao et al., 2005). However, knowledge of their interactive effects on crops, especially in developing countries, is extremely limited (Agrawal and Rathore, 2007).

The aim of the present study was to investigate the effects of UV-B radiation and / or drought stress on gas exchange characteristics, growth and yield of broad bean (*Vicia faba* L.).

MATERIALS AND METHODS

Seeds of an Egyptian cultivar of bean (*Vicia faba* L.), obtained from a commercial source, were sown 20 cm apart at The Botanical Garden of Faculty of Science, Alexandria University, Egypt on 13/7.2010. Ten days after placing the plants half the plants were subjected to progressive drought by withholding water, while well watered plants were irrigated once a week. Well-watered and water-stressed (DS) plants were divided equally between the two sections in a split-plot design. Consequently, four treatments were distributed in each plot in a randomized Latin square design: (a) control, i.e. without UV-B radiation and well-watered (b) Plots supplied with supplementary UV (sUV-B), (c) Plants subjected to drought stress (DS) without UV-B radiation and (d) plants were subjected to both sUV-B and DS. Twenty plants were used in each treatment.

No fertilisers or other fungicides were applied at either location to avoid interference with the fungicides.

Supplemental UV-B radiation was supplied by filtered Westinghouse FS-40 sunlamps oriented perpendicular to the planted rows and suspended above the plants. Lamps were filtered either with 0.13 mm thick cellulose acetate (transmission down to 290 nm) for supple-

mental UV-B radiation or 0.13 mm Mylar Type S plastic films (absorbs all radiation below 320 nm) as a control. The radiation filtered through the cellulose acetate supplied a weighted daily supplemental irradiance of either 3.0 or 5.1 effective kJ m⁻² UV-BBE using the generalized plant response action spectrum (Caldwell, 1971) normalized to 300 nm. Plants beneath these cellulose acetate filtered lamps received supplemental doses in addition to ambient levels of UV-B radiation. These increased levels of UV-B radiation (supplemental + ambient) (Green et al., 1980). The weighted irradiance of Mylar filtered lamps was 0, so plants beneath these lamps received only ambient levels of UV-B (8.5 effective kJ m⁻² UV-BBE on the summer solstice). Spectral irradiance beneath the lamps was measured with an Optronics Spectroradiometer (Model 742) equipped with a double monochromator with dual holographic grating and interfaced with a Hewlett Packard 85 printing calculator. The Spectroradiometer was calibrated using a National Bureau of Standards traceable 1000 W tungsten halogen lamp and wavelength alignment checked with known mercury emission lines using a Hg Arc lamp.

Non Destructive harvests

Net photosynthetic rate (P_N) and total CO₂ g_s were measured on the youngest fully expanded leaf of the main stem. Gas exchange measurements were carried out seven times at 5 d intervals to cover all growth stages (10 days after sowing) using a LI-6200 portable IRGA (LI-COR, Lincoln, USA) between 10:00 and 14:00 h (Local time). All plants were measured on each day (Hassan, 2006).

Chlorophyll fluorescence analysis

Steady-state modulated chlorophyll fluorescence of attached leaves was measured using a fluorimeter (PAM-2000, H Walz GmbH, Effeltrich, Germany) during the gas exchange measurements. Calculations were made from fluorescence parameters of the maximum quantum efficiency of PSII photochemistry (given by F_v/F_m) and the relative quantum efficiency of PSII electron transport (Φ_{PSII}), the photochemical (q_p) and non photochemical (NPQ) quenching. Measurements of F_v/F_m were made after dark adaptation for 15 min and Φ_{PSII}, and q_p were measured at a PPFD of 500 μmol m⁻² s⁻¹, which was similar to the minimum mean growth PPFD (Nogués et al., 1998).

Destructive harvests

Pigment analysis

Chlorophyll was extracted in acetone from all leaves in

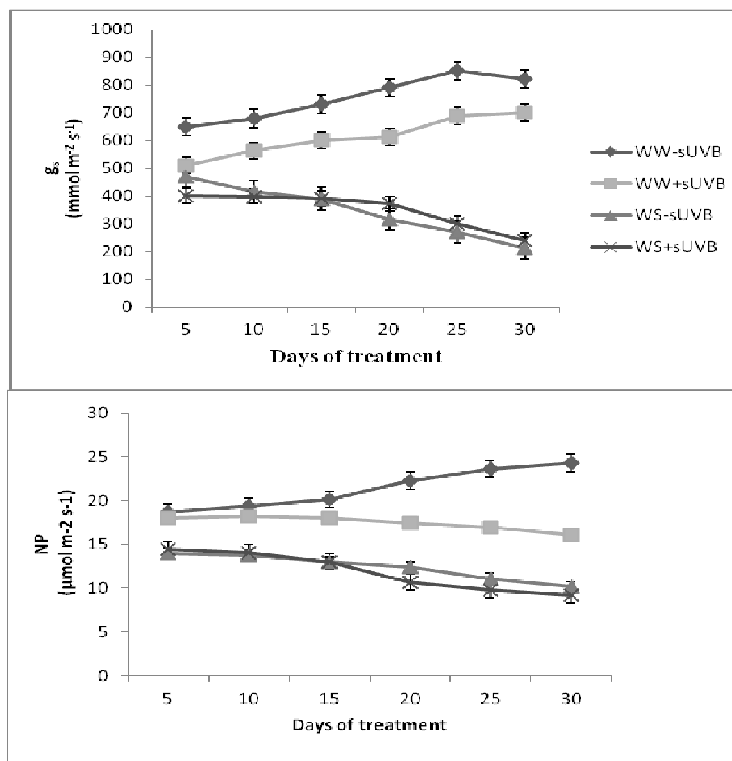


Figure 1. Changes in stomatal conductance (g_s) ($\text{mmol m}^{-2} \text{s}^{-1}$) and Net Photosynthetic rates (P_N) ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Each value is a mean of 8 replicates + 1 SE. WW-sUV-B (well watered plants without sUV-B); WS-sUV-B (plants subjected to water stress only without exposure to sUV-B); WS+ sUV-B (plants subjected to both stresses)

the main stems of three plants per treatment, and determined according to Khan and Khan (1994).

Plant biomass analysis

At the end of the drought and / or sUV-B treatment(s) (45 days after sowing), plants were harvested destructively and oven dried at 80 °C for three days, and analyses of biomass of shoots and roots were carried out. Total plant leaf area was estimated prior to drying using a flat-bed scanner (Hewlett-Packard Scan Jet model Ilcx, San Diego, USA) and analyzed with an image processing program (Nogués et al., 1998).

Statistical analysis

Two way ANOVA was applied to log-transformed (Statgraphics Statistical Package 4, London, UK) data to evaluate effects of DS and/or sUV-B treatments on growth and physiology of the plant. PPFD was used as a covariate in Leaf gas exchange and fluorescence data, there was no covariate used in growth measurements.

RESULTS AND DISCUSSION

Figure 1 showed that drought stress had a higher negative effects on P_N and g_s (-54 and 41%, respectively) than sUV-B treatment (about 19% each), while exposure to both stresses caused reductions by 53 and 44% in these parameters, respectively.

Biomass and yield parameters were represented in Table 1. It was clear that impact of DS and UV when applied singly and in combination had a greater effects on RDW than on SDW which was reflected in significant reductions in RSR (-36 and 33%), number of seeds/pod (-23 and -18%) and fresh weight of seeds/pod (-27 and 23%) due to DS and sUV-B, respectively. Interaction between DS and sUV-B was more than additive and they have synergistic effects on RSR, number of seeds/pod and weight of seeds/pod as they were reduced by 30, 35 and 41% due to this interaction, respectively (Table.1). However, DS had a higher negative impact on leaf number (-40%) than on LA (-10%), which was reflected on a higher reduction on SLA (-23%) (Table.1). In contrast, sUV-B had more negative impact (-45%) on LA than on leaf number (-20%), which was significantly reflected in a comparatively lower SAL (-12%). These effects were

Table 1. Effects of sUV-B and drought stress on growth parameters, yield and chlorophyll content of bean plants.

Parameter	Control	WW + sUV-B	WS – sUV-B	WS + sUV-B
TDW (g)	18.66±1.7 ^c	15.62±1.1 ^b	13.76±0.9 ^a	14.21±1.2 ^a
RDW (g)	1.73±0.08 ^c	0.96±0.05 ^b	0.88±0.05 ^a	0.90±0.04 ^a
SDW(g)	16.93±1.1 ^c	14.66±1.0 ^b	12.88±0.7 ^a	13.31±0.9 ^a
RSR	0.102±0.08 ^c	0.065±0.03 ^a	0.068±0.03 ^a	0.076±0.05 ^b
Leaf no./plant	17.30±1.2 ^c	10.10±0.8 ^a	13.80±1.2 ^b	9.41±0.9 ^a
Leaf area(cm ²)	24.83±1.6 ^c	22.30±1.2 ^b	13.41±0.9 ^a	13.61±1.0 ^a
SLA (m ² kg ⁻¹)	31.60±2.0 ^d	24.30±1.5 ^a	27.91±1.1 ^c	26.09±1.0 ^b
No of seeds/pod	6.31±0.8 ^d	4.83±0.5 ^c	5.19±0.5 ^b	4.11±0.3 ^a
FW of seeds/pod (g)	5.38±0.6 ^d	3.93±0.4 ^b	4.12±0.5 ^c	3.17±0.3 ^a
Chl content (mg g ⁻¹ dwt)	1.78±0.09 ^c	1.43±0.05 ^a	1.58±0.05 ^b	1.45±0.04 ^a

Values are mean of six replicates ± 1 SE. Means not followed by the same letter(s) are significantly different from each other at $P \leq 0.05$.

WW+sUV-B (well watered plants subjected to sUV-B); WS-sUV-B (plants subjected to waters stress only without exposure to sUV-B); WS+ sUV-B (plants subjected to both stresses)

reflected on reducing Chl content with a comparable percentage due to DS (-20%) and sUV-B (-16%) and their interaction (-21%) (Table1).

There was strong correlations between P_N and Chl content ($R^2 = 0.136$), TDW ($R^2 = 0.219$) and RSR ($R^2 = 0.191$) (Data not shown).

UV-B radiation, causes reduction in biomass and yield and photosynthesis in various crop species suggesting that it has an inhibitory effect (e.g. Teramura and Muuralli, 1986; Teramura and Sullivan, 1991; Nogués and Baker, 2000; Agrwal and Rathore, 2007; Moussa and Khodary, 2008). Moreover, drought stress in the present study caused significant reductions in F_v/F_m , Φ_{PSII} , q_p and NPQ, growth and yield parameters and this is in agreement with huge body of literature that stated DS causes limitation in gas exchange and growth parameters (e.g. Nogués et al., 1998; Hassan et al., 1999; Alexieva et al., 2001).

However, the mechanisms involved in the response of plants to both stresses are yet to be identified

RWC, E showed severe reductions due to exposure to DS as they were decreased by 25 and 43%, respectively, while Ψ_w was decreased from -0.4 to -1.38 MPa after 30 days of drought stress (Figure 2). However, RWC and Ψ_w of well watered plants were maintained at about 90% and -0.05, respectively (Figure. 2).

UV-B had similar effects on these parameters and its interaction with DS was synergistic as it reduced RWC and E by 23 and 55%, respectively (Figure. 2).

The exposure to drought stress resulted in slow development of water stress, with the first effect on RWC of bean leaves and there was no significant effect on Φ_{PSII} . This is in agreement with the results of Cornic (1994), who reported insignificant effect of mild drought stress on photosynthetic capacity of wheat leaves.

Furthermore, Nogués et al. (1998) found similar result

on pea leaves.

The photosynthetic assimilates that can be attributed to biomass is ascribed to both leaf area and net photosynthetic rates (e.g. Chisi et al., 2002; Quaggiotti et al., 2004; Hassan, 2006).

The changes in the maximum efficiency of PSII photochemistry after 15 min dark-adaptation (F_v/F_m), quantum yield of PSII electron transport (Φ_{PSII}), photochemical quenching (q_p) and non-photochemical (NPQ) Chl fluorescence are shown in Table.2.

F_v/F_m , q_p and NPQ were decreased by 23, 19 and 12% due to DS and by 25, 17 and 12% due to sUV-B, respectively, while no significant changes ($P \geq 0.05$) in Φ_{PSII} of the dark-adapted leaves in either non-UV-B or UV-B treatment were observed (Table.2). However, there was a significant interaction between DS and sUV-B on F_v/F_m , Φ_{PSII} , q_p and NPQ as they were decreased by 34, 15 and 24%, respectively (Table 2).

In contrast to the results of Nogués et al (1998), who stated that UV-B radiation had no significant effect on leaf number of pea plants, our results showed that both leaf number and leaf area were significantly reduced due to exposure to s UV-B and/or DS which was reflected in reduction in SLA, Chl content, g_s and P_N . The reduction in SLA indicate that UV-B could inhibit either cell expansion or cell division (Ballarè et al., 1995; Hopkins et al., 1997). Nogués et al (1998) did not find a significant effect of UV-B on cell expansion and they ascribed the reduction in leaf area of peas to an inhibitory effect of UV-B on cell division. This was not the case our study, we found a pronounced increase in stomatal frequency of UV-B- treated leaves, and in contrast, stomatal index was reduced, which indicates a significant reduction in cell expansion (data discussed elsewhere). Such observation was confirmed by overall 45% reduction in LA in either well-watered or water-stressed plants. Moreover, previous work of Nogués et al.,

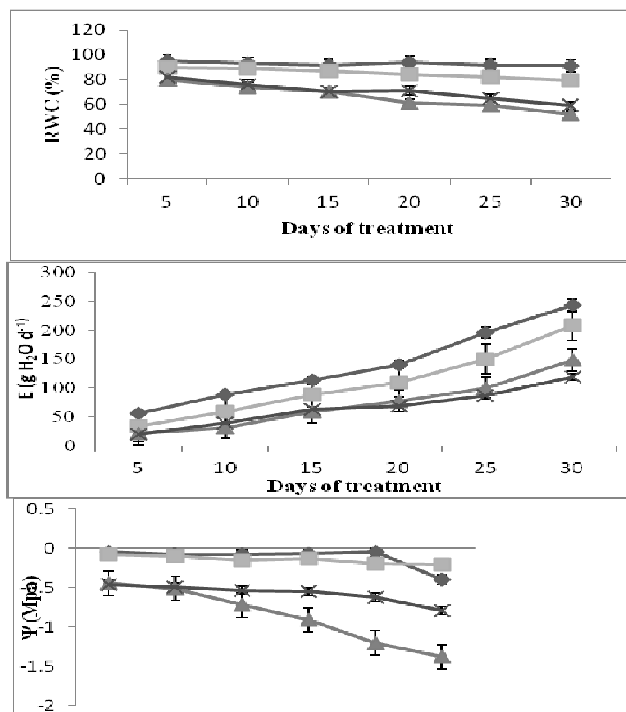


Figure 2. Changes in the leaf relative water content (RWC)(%), leaf water potential (Ψ_w) (MPa) and daily plant evaporation rate (E) ($\text{g H}_2\text{O day}^{-1}$). Legends as Figure1.

Table 2. Effects of sUV-B and drought stress on maximum quantum efficiency of PSII photochemistry (F_v/F_m), the relative quantum efficiency of PSII electron transport (Φ_{PSII}), photochemical quenching (q_p) and non-photochemical (NPQ) Chl fluorescence.

Parameter	Control	WW – sUV-B	WS – sUV-B	WS + sUV-B
F_v/F_m	0.941±0.08 ^c	0.710±0.06 ^b	0.730±0.06 ^b	0.622±0.05 ^a
Φ_{PSII}	0.746±0.07 ^b	0.701±0.06 ^b	0.693±0.06 ^{ab}	0.635±0.04 ^a
q_p	0.871±0.09 ^c	0.723±0.06 ^b	0.704±0.06 ^b	0.658±0.05 ^a
NPQ	0.569±0.08 ^b	0.501±0.04 ^{ab}	0.503±0.05 ^{ab}	0.471±0.05 ^a

(1998) on peas and Logemann et al. (1995) on parsley suggested that it is unlikely that UV-B radiation acts directly on dividing cells and it may affect indirectly by delaying microtubule formation (Staxèn *et al.*, 1993) through transcriptional repression of the genes encoding for a mitotic cyclin and a p34^{cdc2} protein kinase (Logemann et al., 1995).

It was reported that exposure to UV-B causes a rapid loss of photosynthetic competence primarily through effects on Rubisco (Nogués and Baker, 1995; Allen et al., 1997; Moussa and Khodary, 2008). This may be the case in the present study, as we found leaf area growth, biomass and yield were reduced due to exposure to UV-B which suggests reducing photosynthetic supply. However, this contrasts results of Nogués et al. (1998), who found no effects of UV-B on photosynthetic rates and other photosynthetic parameters in pea leaves.

Reduction in P_N could be due to reduction in Chl content, and this is supported with the results of Pal et al. (1999), who found that UV-B irradiated mungbean plants showed reduced chlorophyll content along with lower photosynthetic rates. Recently (Moussa and Khodary, 2008) found similar results in bean and barely leaves. This was in contrast to the finding with peach grown under solar UV-B exclusion where UV-B irradiated plants showed increased P_N but chlorophyll content remained unaffected (Laposi et al., 2002)..

Nevertheless, the reduction in P_N may be due to reduction in g_s (Ziska et al., 1992). The inhibitory effect of UV-B on g_s was clearly through changes in stomatal aperture, since stomatal frequency was increased. The reduction in stomatal aperture must be a direct response to UV-B radiation that was not mediated through P_N (Nogués et al., 1998), this warrants further investigation.

The severe reduction in yield (41% loss in weight of seeds) and biomass (24% loss in TDW) confirmed the synergistic effects of both drought stress and sUV-B.

CONCLUSION

Exposure to DS and sUV-B affect plant growth, photosynthesis and other biochemical processes of bean plants which proved to be sensitive to either DS or sUV-B. The reductions in leaf area and plant biomass were associated with a decline in PN, chlorophyll content and leaf cell numbers and cell division. There was an interaction between sUV-B and DS, where the first delayed and reduced the severity of the latter through a reduction in plant water loss rates and through reductions in leaf area and g_s .

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