DESERT

The effects of different timings and severity of drought stress on gas exchange parameters of mungbean

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Abstract

Mungbean (*Vigna radiata* (L.) Wilczek) or green gram as a dryland grain legume is exposed to varied timings and severity of drought stress, resulting in variability in photoassimilate production. In order to evaluate some physiological responses in one mungbean cultivar to timing and severity of drought stress, a 3-replicate RCBD (randomized complete block design) field experiment was carried out during year 2004 year at the experimental farm of University College of Agriculture and Natural Resources, University of Tehran. Plants were exposed to either moderate or severe water deficit at either vegetative (VS) or reproductive growth stages (RS). Parameters were recorded at the middle stages of vegetative growth. In general, water stress reduced net photosynthesis rate (Pn), stomatal conductance (g_s), transpiration rate (Tr) and leaf relative water content (RWC) while increasing leaf temperature (T). The greatest effects of drought on these parameters occurred at reproductive stage. Photosynthetic water use efficiency increased and decreased during VS and RS respectively. The results showed a clearly close correlation between RWC and g_s in VS ($r=0.912^{**}$) and RS ($r=0.976^{**}$) treatments. Although water stress at vegetative growth stage significantly decreased Pn, g_s, Tr, and RWC, these parameters were recovered upon rewatering at reproductive stage. It is concluded that to maximize mungbean Pn in dry zones, irrigation should be extended across all growth stages, especially during the reproductive stage.

Keywords: Mungbean; Drought stress; Net photosynthesis rate; Stomatal conductance

1. Introduction

Mungbean (*Vigna radiata* (L.) Wilczek), grown mainly in the central and southern regions of Asia, is one of the least researched and the most underexploited of the major grain legumes crops (De Costa et al., 1999). Mungbean crops are grown in the short rainy season in southern Asia (Thomas et al., 2003). A common feature of the climate in this region is the uncertainty of rainfall, therefore probable significant soil water deficit leading to plant water deficit at various stages of growth. Most prominant aspect of growth and development mungbean is that the plant is sensitive to drought stresses, as a consequence of which

growth and development go significantly below potential (El Hafid et al., 1998).

The decrease in crop biomass production is frequently observed in response to water deficit. This could either arise from a decrease in the extent of solar radiation intercepted by the canopy or a decrease in the efficiency with which the intercepted radiation is used to accumulate dry matter, or a combination of both. The loss in accumulation efficiency is be associated with a decline in photosynthesis capacity (Muchow et al., 1986; Lopez et al., 1996 and Siddique et al., 1999). During many years past, many workers have been interested in understanding how drought limits photosynthesis. While much of the reported drought-induced decrease in CO_2 assimilation could be attributed to stomatal closure, part of it has also been attributed to direct effects of dehydration on biochemical reactions of

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photosynthesis namely non-stomatal factors (Siddique et al., 1999). However, the relative magnitude of stomatal and non stomatal factors limiting photosynthesis, in the drought stress condition depends upon the degree of water on deficit, rate, duration of exposure and the stage of crop growth (El Hafid et al., 1998; Siddique et al., 1999 and Xue et al., 2004).

Photosynthetic water use efficiency (PWUE), defined as the ratio of amount of carbon gain to amount of water loss, is thought to play an important role acclimatation, in acclimation, productivity and the capability of survival under drought stress (Inman-Bamber and Smith., 2005) . Plants can achieve a high PWUE through either a high rate of net carbon assimilation or a low rate of transpiration, or both. Typically plants with a favorable water status have a low ratio of internal to external CO_2 concentration (C_i/C_a) (depleted in CO_2), whereas droughted plants have a high C_i/C_a and are enriched in CO_2, reflecting the trade between net photosynthesis and transpiration (Cabuslay et al., 2002; Da Matta et al., 2003).

Knowledge of water relation is fundamental to improved crop management in arid and semi-arid areas. Among several methods used to characterize internal plant water status under drought condition, relative water content (RWC) is an integrative indicator, used successfully to identify drought resistant crops (Rosales-Serna et al., 2004). RWC has been used to determine the effect of soil moisture deficit in studies on mungbean (Pandey et al., 1984), common bean (Rosales-Serna et al., 2004), dry bean (Zanella et al., 2004), and sugarcane (Inman-Bamber and Smith, 2005).

Under natural conditions, drought usually occurs in association with high temperature and this resulting in photo-inhibition of photosynthesis system (French and Turner, 1991). Pandey, et al., (1984) reported that the temperature of leaves increased as leaf RWC decreased. Also, Lawn, (1982), observed that reduced water vapor conductance was accompanied by higher leaf temperature.

Relatively little work has been done to compare the effects of different irrigation regimes on gas exchange parameters in mungbean (Lawn., 1982; Pandey et al., 1984 and Uprety and Bhatia., 1989). The effects of drought stress on mungbean photosynthesis are not yet fully elucidated, and less is known about these effects at the different growth stages. Therefore, a fundamental understanding of the intrinsic factors which could increase the ability of breeders to improve mungbean to withstand water deficit is indispensable (Faver et al.,

1996). An identification of these traits, related to higher assimilation capacity and greater photosynthesis under prolonged water stress, followed by an incorporation of these traits into current breeding programs could improve mungbean production in drought prone areas. The objective of this research was to investigate, under field conditions, the effects of different water stress regimes on the gas exchange parameters of an indeterminate mungbean cultivar at vegetative and reproductive growth stages.

2. Materials and methods

2.1. Site and climates

Experiments were commenced on May 5 and harvests done on August 10, 2004 at the Experimental Farm of University College Agriculture and Natural Resources, University of Tehran, Karaj (35° 55' N, 54° 50' W and on elevation of 1320 m above sea level), Iran. The soil at the site was a flat, deep, clay-loam with gravimetric water content of 21% at field capacity and 8.3% at permanent wilting point. Rainfall, pan evaporation (class A), maximum and minimum temperatures were continuously recorded in the meteorological station next to the experimental site. Some climatic conditions from sowing to maturity were as fallows: weekly average maximum temperature ranged from 25 to 34°C with increased trend towards maturity. The weekly minimum temperature was ranged from 15.5 to 20 °C. Mean day-time evaporation from vapor pan ranged from 1.9 to 15.3 mm. Average rainfall from sowing to maturity was 17.9 mm, with 4.4 mm of rain from weeks 3 to 5 and then 11.8 mm from weeks 9 to 11. From week 12 there was only 1.7 mm of rain until maturity.

2.2. Experimental design and crop management

The experiment was laid out in a Randomized Complete Block Design (RCBD) with three replications. Three weeks after germination (at the four-leaf stage) plants were exposed to the following treatments:
(i) Well-watered (control), (W1).
(ii) Moderate stress in the vegetative stage, (W2)
(iii) Severe stress in the vegetative stage, (W3).
(iv) Moderate stress, imposed both at vegetative and reproductive stages, (W4).
(v) Moderate stress in the reproductive stage, (W5).

(vi) Severe stress in the reproductive stage, (W6).

Adequately watered (control) plots were irrigated weekly. Moderate and severe stressed plots were watered when 70 and 100% of soil available water depleted. For the vegetative growth stage, stress treatments were imposed from appearance of the fourth leaf to flowering, stressed plants being reirrigated along with control plants until maturity. In the case of reproductive growth stage, stress was imposed from flowering to maturity. Plants were deemed to have reached the reproductive phase when 50% of plants in a plot had at least one open flower (Thomas et al., 2003).

To determine times of sampling as well as rewatering, soil water content was measured using a moisture meter (Delta-T device, Cambridge, UK). The depths of measuring water content were 30 and 50 cm. The soil water content in 0-30 cm layer was determined by gravity meter. A 1 m plastic access tube of with 2 cm diameter was installed in the middle of each plot in all the treatments at sowing. The device had a cylindrical sensor equipped with light-sensitive eyes. To determine soil water content, the moisture sensor was inserted into the access tube, and then soil water content measured. Using the data of soil moisture assessed by moisture meter and gravimetric measurements, the percentage of available soil water in the root zone was estimated by the equation (Martin et al., 1990),

$$D(\%) = \frac{1}{n} \sum_{1}^{n} \frac{FCi - \theta i}{FCi - Wp} \times 100 \qquad (1)$$

Where n is the number of depths used in the soil moisture sampling, FCi the soil moisture at field capacity for ith layer, θi the soil moisture in ith layer and WP the representing soil moisture at permanent wilting point. Finally, the percentage depletion of available soil water in the root zone was calculated as:

Available soil water depletion$(\%)$=100-D   (2)

Seeds used in this experiment were of Partov indigenous variety, selected from pulse Collection of University College of Agriculture and Natural Resource, University of Tehran. The planting date was May 5, 2004. Seeds were sown by hand, at a planting distance of 50 cm × 5 cm. Excess seeds were sown and then seedlings were thinned to obtain a desired population of 40 plants m^{-2}. A plot consisting of 5 rows was 2.5m wide and 5m long. 30 days after sowing, weeds within and between the plots were controlled both by hand and by field application of Glyphosate herbicide. Fertilizer was applied along rows at rates of 120-100-100

($N-P_2O_5-K_2O$) according to Thomas et al (2003). Nitrogen fertilizer was split into two applications, namely at planting and 30 day after planting.

2.3. Gas exchange parameters

Gas exchange parameters were assessed at midway of either vegetative or reproductive growth stages. Net photosynthesis rate (Pn, in $\mu mol. \, m^{-2}. \, s^{-1} \, CO_2$), transpiration rate (Tr, in $mmol . \, m^{-2}. \, s^{-1} \, H_2O$), leaf temperature (T, in $^{\circ}C$), internal CO_2 ratio (C_i, in $\mu l \, l^{-1}$), and stomatal conductance to water vapor (g_s, in $mol \, m^{-2} s^{-1} \, H_2O.$) were recorded using an LCA-4 portable, open-system infrared gas analyzer (Analytical Development Company, Hoddeson, UK) under natural saturating photosynthetic photon flux ($>600 \, \mu mol \, m^{-2} \, s^{-1}$) . Leaves were inserted into leaf chamber of 1 cm^2 cross section. For each selected plant measurements were made, on the abaxial surface of the second fully-expanded leaf in the upper canopy, three times during the morning between 07:30 and 11:30 h, so that each set of recordings on each plant was taken as average values for gas exchange parameters. The Photosynthetic water use efficiency (PWUE in $\mu mol \, CO_2. \, mol^{-1} \, H_2O$) was found out as the ratio of Pn and Tr, as described by Maroco et al. (2000).

2.4. Relative water content (RWC)

Three individual leaves of the plants were collected and immediately weighed (fresh weight, FW). Intact leaves were transferred to sealed amber flask, rehydrated in 1 L of distilled water for 5 h until fully turgid at $4^{\circ}C$. They were surface dried and reweighed (turgid weight, TW). Leaf samples were then oven dried at $72^{\circ}C$ for 48 h and reweighed (dry weight, DW). The RWC was calculated by the following formula (Lazcano-Ferrat and Lovatt, 1992):

$RWC(\%) = (FW - DW)/(TW - DW) \times 100$ (3)

2.5. Statistical analysis

Data normality was tested and confirmed by using Minitab software. Statistical analyses were performed using Mstatc and SPSS softwares. The significance of the difference between the treatments was analyzed by means of a standard two-way analysis of variance. Means were compared using Duncan test with a significance level of $P \le 0.05$. Correlations between parameters were analyzed by standard methods of Pearson-correlation analysis. Graphs

and tables were drawn by help of Excel software.

3. Results and discussion

Gas exchange parameters were evaluated at the vegetative and reproductive growth stages. To precisely assess these parameters under drought stress as well as plant response after rewatering, data were collected and interpreted on the basis of growth stages.

3.1. Vegetative stage

3.1.1. Stomatal conductance (g_s), transpiration rate (Tr) and leaf relative water content (RWC)

A common response to water stress is stomatal closure, which reduces both flux of CO_2 and water vapor (Ogbonnaya et al., 1998). Results showed that, water deficit during vegetative growth stage significantly ($\alpha = 0.01$) affects stomatal conductance (g_s) as well as transpiration rate (Tr) (Figures 1A & 1B). During imposition of drought, g_s and Tr were reduced either of the water deficit treatments, but the g_s and Tr values under moderate stress were significantly ($P \leq 0.05$) higher than those under severe stress. The observed decline in g_s and Tr indicated that drought caused stomatal conductance inhibition with a negative reflex on the photosynthetic uptake and transpiration rate (Zanella et al., 2004). Many experiments have shown that stomata close in response to hydraulic signals (i.e. RWC and leaf water potential) when soil moisture decreases (Maroco et al., 2000; Ismail et al., 2002 and Xue et al., 2002). A positive relationship was observed between leaf water status and stomatal closure ($r=0.912^{**}$) at vegetative growth stage. RWC values showed variation across treatments (Fig. 1C). Water stress treatments were brought about with significant reduction in the relative water content of leaves. However the depression of RWC was relatively less in moderate stress (10% relative to control) treatment. On the contrary, severe stress treatment exhibited maximum reduction in RWC (20% relative to control) at this stage. These results are consistent with findings of Clavel et al. (2005).

3.1.2. Net photosynthesis rate (Pn) and photosynthetic water use efficiency (PWUE)

Both moderate and severe drought stress significantly decreased Pn. Moderate and severe drought stress induced reductions in Pn were 25 and 50%, respectively, as compared with the control treatment (Fig. 1D). These results are in

general agreement with Liu et al, (2004). Under moderate drought stress condition, the reduction in Pn was accompanied by a parallel decrease in stomatal conductance. This suggests that the stomatal closure is the first response to water stress. It is assumed to be the main cause of impaired photosynthesis due to drought, and since the stomatal closure limits CO_2 availability to the mesophyll (Siddique et al., 1999; Xue et al., 2002). In our experiment, it was observed that the reduction in Pn due to severe stress treatment (50%) was higher than that of stomatal conductance (37%), and therefore indicating the dominance of non-stomatal factors in reducing net photosynthesis rate in this treatment. The increase in the C_i (internal CO_2 concentration) ratio (data not shown) under severe drought is consistent with this interpretation, since increase in this ratio demonstrates decreased uptake of CO_2 due to non-stomatal inhibition of photosynthesis. Inman-Bamber and Smith, (2005) observed that under moderate stress ($\psi_{leaf} < -0.9$MPa), reduction in photosynthesis was mostly due to lower stomatal conductance and not initiated from reduced enzyme activities and low metabolic levels.

Contrary to Pn, exposure of mungbean plants to water deficit significantly increased the rate of photosynthetic water use efficiency (PWUE). However, severe stress and control treatments exhibited higher and lower PWUE, respectively (Fig. 1E). The high PWUE in stressed plants was presumably due to additional CO_2 flux into leaves. Because of the partial closure of stomata, the resistance to water movement relatively increases more than the resistance to CO_2 movement, and therefore should reduce Tr more than it reduces Pn (Da Matta et al., 2003).

3.1.3. Leaf temperature

The leaf temperature measurements, taken in stressed and non-stressed plants at the halfway of vegetative growth stage indicated a significant ($P \leq 0.05$) overall difference (Fig. 1F). In general leaf temperature was higher in the stressed treatments. Moderate and severe stressed plants showed 1.3 to 2.2°C higher leaf temperature than control plants (Fig.1F). Similar results have been reported by Hashem et al., (1998) who observed leaf temperature in stressed plants of two varieties of *Brassica napus* was generally 1 to 2°C higher than that in watered plants. In view of reported decline in photosynthesis, less photochemical energy would be spent on CO_2 assimilation. Consequently the photochemical energy would

need to be consumed by alternative pathways. One possibility is the loss of energy as heat that leads to leaf temperature increase (Da Matta et al., 2003).

3.1.4. Reproductive stage

Water deficit treatments at reproductive growth stage were applied from emergence of the first flower to 95% pod maturity according to Thomas et al. (2003). Gas exchange parameters were assessed at the middle way of this stage for all stress treatments. In this stage, stress treatments at vegetative stage were irrigated simultaneously with control plants.

3.1.5. Stomatal conductance (g_s), transpiration rate (Tr) and leaf relative water content (RWC)

The stomatal behavior and transpiration rate under different water stress regimes at reproductive stage are presented in Figures, 2A and 2B. Similar to vegetative stage, different drought stress treatments at reproductive growth stage significantly reduced g_s and Tr values. Moderate and severe stressed plants showed 86 to 88% lower stomatal conductance than did control plants, respectively. Stomatal conductance decreased with age of plants regardless of stress treatments (Figures. 1A, 2A), therefore control treatment at reproductive stage showed 75% lower stomatal conductance than control treatment at vegetative stage. These results are in general agreement with those of Uprety and Bhatia, (1989) and Siddique *et al,* (1999) who reported that stomatal resistance in the leaves of wheat (*Triticum aestivum* L.) and mungbean increased with aging of the plants.
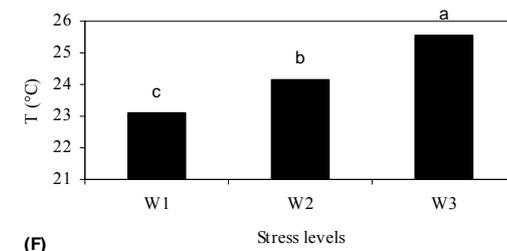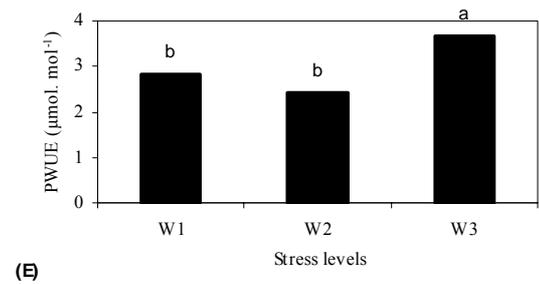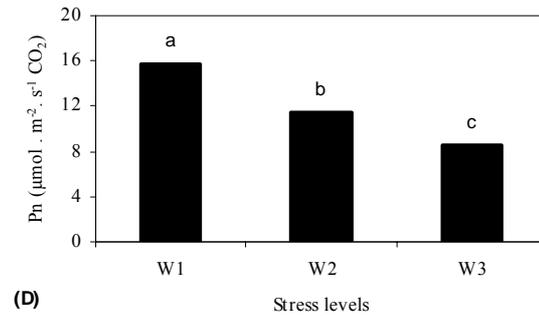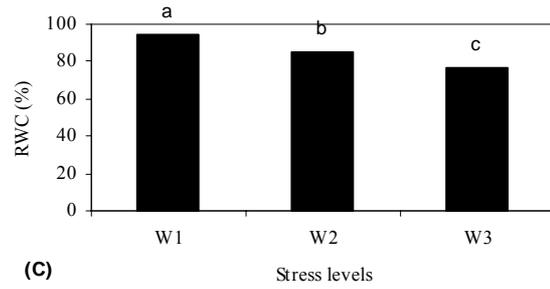
(A)

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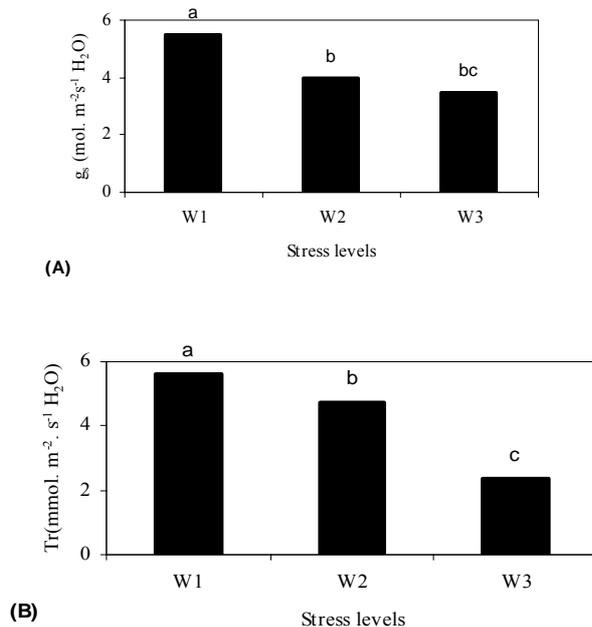
Fig. 1. Stomatal conductance- g_s (A), transpiration rate- Tr (B), leaf relative water content- RWC (C), Net photosynthesis rate- Pn (D), photosynthetic water use efficiency- PWUE (E), and leaf temperature - T (F) in mungbean plants under different stress levels at vegetative growth stage. Control =W1: plots were irrigated weekly; moderate stress at vegetative stage = W2; severe stress at vegetative stage= W3. Moderate stressed plots were watered when 70% of soil available water depleted and severe stressed plots when 100% of soil available water depleted. Different small letters represent statistical significant (p≤0.05, Duncan test). Each bar represents mean of three replicates

Results also showed that RWC decreased with age of plants (Fig. 2C). In stressed plants at

reproductive stage, RWC decreased by 12 and 23%, relative to control, in the moderate and severe stress treatments, respectively. RWC in stressed plants at reproductive stage was positively correlated with g_s (r=0.976[**]), suggesting that the higher reduction in g_s due to ageing is probably related to lower RWC in this stage than that in vegetative stage. Ogbonnaya et al., (1998) observed that stomatal conductance was decreased significantly (P <0.01) throughout the growing season, accompanying the general decline in RWC.

Although the g_s and Tr parameters decreased under both stress treatments in the vegetative stage, they were recovered after rehydration at the onset of flowering. Similar results have been obtained by Zanella et al., (2004).
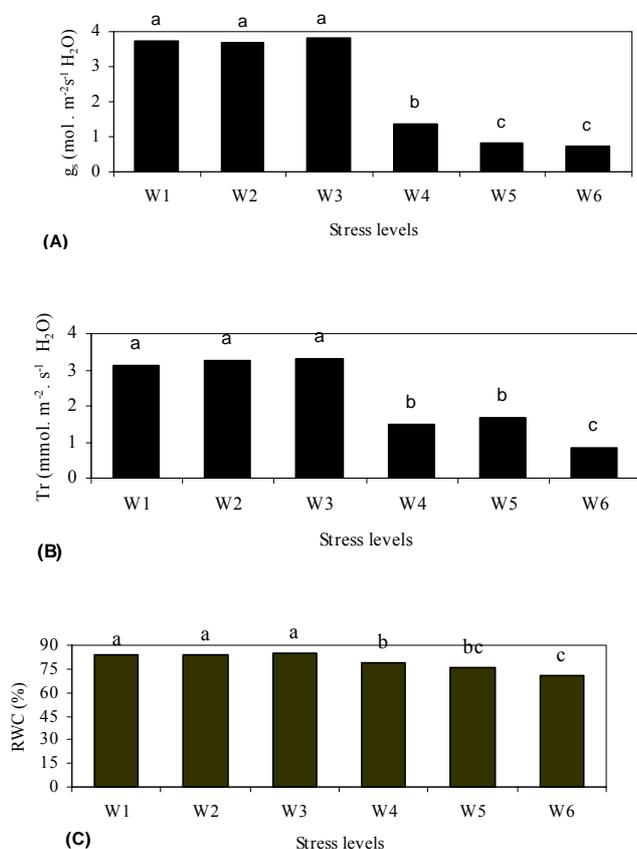

(A)

(B)

(C)

Fig. 2. Stomatal conductance- g_s (A) and transpiration rate- Tr (B), and leaf relative water content - RWC (C) in mungbean plants under different stress levels at reproductive growth stage. Control=W1: plots were irrigated weekly; moderate stress at vegetative stage=W2; severe stress at vegetative stage= W3; moderate stress at vegetative and reproductive growth stages=W4; moderate stress at reproductive growth stage=W5; severe stress at reproductive growth stage=W6. Moderate stressed plots were watered when 70% of soil available water depleted and severe stressed plots watered when 100% of soil available water depleted. On similar small letters represent statistical significant (p ≤ 0.05, Duncan test). Each bar represents mean of three replicates

3.1.6. Net photosynthesis rate (Pn) and photosynthetic water use efficiency (PWUE)

Similar to g_s, data showed that during exposure to water deficit, the reduction of Pn was greater at reproductive than that at the vegetative stage (Figs. 3A and 3B). On the other hand, photosynthetic capacity decreased significantly (P≤0.05) throughout the growing season, therefore severe stress at reproductive stage indicated 37% lower Pn than severe stress treatment at vegetative stage. These results are in general agreement with those of Maroco et al. (2000) and Ogbonnaya et al. (1998). Enhanced rates of respiration concomitant with declining photosynthetic rates have been reported in several species during leaf senescence (Maroco et al., 2000).

The importance of non-stomatal limitation of photosynthesis under water stress in the reproductive stage is indicated by some increase in internal CO_2 concentration (C_i) (data not shown), which is accompanied by 87% decline in Pn as compared to control in reproductive stage and at severe stress treatment. Mitra and Ghldiyal (1988) suggested that due to the higher protein content of grain legume seeds, the nitrogen requirement of the seed during seed development was very high and that places high nitrogen translocation demand on vegetative tissues. This translocation may result faster decline of photosynthesis rate in stressed plants as compared to non-stressed ones. Although the reduction in g_s for moderate and severe stress were similar, Pn decline in severe stress was significantly more than in moderate treatment. The data indicate that non-stomatal factors were largely responsible for the high reduction in photosynthesis when plants were severely stressed in the reproductive growth stage (Figs. 2A and 3A).

Similar to g_s, the lower level of Pn for plants stressed at vegetative stage (i.e, W1 and W2 treatments) were similar to that of control plants after stress elimination at flowering (Fig. 3A). Miashita et al. (2004) reported that photosynthesis rate in kidney-bean following drought stress was rapidly recovered after re-watering. It was thought that remarkably complete recovery was probable due to the restoration of photosynthesis rate by stomatal closure and accumulation of ABA, except in leaf CO_2 which suffered cell destruction or metabolic damage (Ismail et al., 2002).

Even though repeated moderate stress at both vegetative and reproductive stages, relative to control treatment, significantly decreased Pn, reduction was smaller than that in the cases of

moderate and severe stress imposed at reproductive stage.

In contrast to vegetative stage, water deficit during the reproductive stage significantly decreased ($p \leq 0.05$) photosynthetic water use efficiency. Control and severe stressed plants showed 1.47 and 0.45 (μmol CO_2. mol^{-1} H_2O) PWUE values, respectively (Fig. 3B). Observed decline in PWUE in reproductive stage was mainly due to the higher reduction in Pn and Tr in the reproductive growth stage.
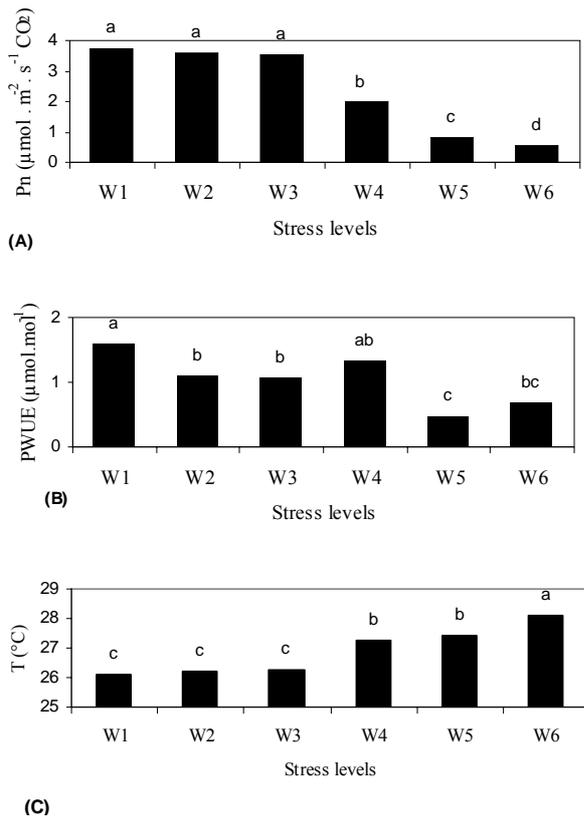

Fig. 3. Net photosynthesis rate-Pn (A), photosynthetic water use efficiency-PWUE (B), and leaf temperature-T (C) in mungbean plants under different stress levels at reproductive growth stage. For more details refer to Fig 2

3.1.7. Leaf temperature

Contrary to g_s and Pn, plant leaf temperature increased with age of plant (Fig. 3C). Similar results were obtained with plants under stress. Similarly, Pandey et al., (1984) observed that leaf temperature was low in vegetative stage while high in reproductive stage. Similar to vegetative stage, as stress level increased, leaf temperature rase. Leaf temperature of moderate and severely stressed plants, as compared with control, significantly increased (by 1.25 and 2°C), respectively.

Leaf temperature relationships are employed to estimate water stress in plants, because leaf temperature is a function of transpiration rates (Lawn, 1982). Therefore, an inverse relationship might be expected between changes in leaf temperature, and those of leaf conductance, given the cooling due to evaporation associated with water loss in transpiration. A comparison of means (Figures. 1F, 2A, 3C) suggested that this was the case, at least for stressed plants. Leaf temperature was the highest for the leaves with the lowest stomatal conductance (i.e, in the stressed treatments). Conversely, in the irrigated plots, leaf temperatures were the lowest, while conductance the highest. The stressed plants, therefore, began to face heat stress, and that is why breeders rarely attempt to separate heat from drought tolerance. Heat accompanied by drought causes release of ammonia from decomposition of protein from injured plant tissues (Ogbonnaya et al., 1998).

4. Conclusion

It is concluded that drought treatments in vegetative and reproductive growth stages negatively affect photosynthesis as well as all gas exchange parameters. This experiment demonstrated that both stomatal and non-stomatal factors limit leaf gas exchange and assimilation capacity in mungbean. Stomatal factors were responsible for declines in assimilation capacity when plants experienced mild water deficit (i.e, depletion of 70% soil available water). Under severe stress (i.e, depletion of 100% soil available water), non-stomatal factors played the dominant roles in limiting leaf gas exchange and assimilation capacity. On the other hand, the inhibitory effect of drought stress at vegetative stage on leaf photosynthesis could be mostly attributed to stomatal limitation, while drought stress at reproductive stage mainly decreased photosynthesis by means of non-stomatal factors. This cultivar exhibited, to some degree, avoidance of dehydration by reducing plant water loss through controlling stomatal water loss in response to declining RWC. Reduced water vapor conductance was accompanied by higher leaf temperature and lower Pn. This work enabled us to further understand the physiological response to water stress in this legume and to demonstrate that gas exchange parameters, measured during and after water stress treatments seem reliable physiological parameters to evaluate drought tolerant mungbean cultivars.

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