Growth, Yield and Photosynthetic Activity of *Vigna radiata* L. Grown at Different Temperature and Light Levels

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(Received 29 September 1999. Accepted 26 September 2002. Corresponding author: Abdul Karim (akarim@citech.co.net). *Present address: Department of Agronomy, Bangabandhu Sheikh Mujibur Rahman Agricultural University, Salna, Gazipur-1703, Bangladesh. Abbreviations: Fv/Fm, maximum photochemical efficiency of PSII; FΔ/Fm, quantum yield of PSII electron transport; Pn, photosynthetic CO₂ assimilation rate; PSI, photosystem I; PSI!, photosystem II.)

Abstract: Two varieties of mungbean (*Vigna radiata* L.), BARImug 2 (M2) and BARImug 3 (M3) were grown under 1) 12-h light at 700 μmol m⁻² s⁻¹ (HL) at 30°C/12-h darkness at 25°C (HL+LT), 2) 12-h HL at 40°C (HT)/12-h darkness at 25°C (HL+HT) and 3) 12-h light at 200 μmol m⁻² s⁻¹ (LL) at HT/12-h darkness at 25°C (LL+HT), and their growth, yield and photosynthetic activities were analyzed. The plants grown under LL+HT were the tallest followed by those grown under HL+HT and HL+LT, in this order. The leaf area was the largest under HL+LT followed by LL+HT and HL+HT. In general, the plants grown under HT had lower biomass compared with those grown at LT. Grain yield was zero (no pod setting) under HL+HT in both varieties, but that under LL+HT was 30-40% of that under HL+LT. M3 produced higher grain yield as well as higher biomass than M2 under both HL+HT and LL+HT. The yield reduction under LL+HT was primarily due to the substantial reduction in the number of pods per plant as well as number of seeds per pod. HT decreased the photosynthetic CO₂ assimilation rate (Pn), and the plant under HL+HT had lower Pn than those under HL+LT. The heat acclimation of photosynthetic apparatus was considered to proceed more easily under HL than under LL, because the photochemical efficiency of PSII (Fv/Fm) and quantum yield of PSI! electron transport (FΔ/Fm) after heat shock at 50°C were greatly higher in the plants grown under HL+HT than those under HL+LT. It was concluded that HL at HT inhibited pod setting but accelerated the heat acclimation of photosynthetic apparatus of mungbean.

Key words: Chlorophyll fluorescence, Drymatter allocation, Photosynthesis, Pod setting, *Vigna radiata* L.

Mungbean (*Vigna radiata* L.) cultivation is increasing in the tropics and subtropics for its short growth duration, synchronous fruiting pattern and good fit into the existing cropping patterns in these regions. The optimum average temperature for mungbean cultivation has been reported to be 28-30°C (Pochhman, 1991). However, this crop is grown in summer when the temperature and irradiance fluctuate frequently. Because of tropical monsoon the irradiance fluctuation is so high that within a short span of time it may drop from full sunshine (> 2000 μmol m⁻² s⁻¹) to less than 100 μmol m⁻² s⁻¹ PFD. The temperature is normally high throughout the long summer but shows regular fluctuation.

The deleterious effect of high temperature stress on plant photosynthetic processes is well known and has been studied comprehensively (Berry and Björkman, 1980; Weis and Berry, 1988; Karim et al., 1999). Photosystem II (PSII), in particular, is the heat sensitive component of photosynthetic system, whereas photosystem I (PSI), stromal enzymes, and chloroplast envelope are comparably thermostable (Berry and Björkman, 1980; Mamedov et al., 1993). Plant productivity has also been reported to be damaged by high temperature (Hall, 1992; Ismail and Hall, 1998; Talwar et al., 1999). Usually the vegetative growth is affected less by high temperatures though the reproductive process is damaged even by a slightly higher temperature than the optimal growth temperature.

The thermostability of PSII has been reported to vary substantially with the environmental factors (Havaux, 1992). However, the role of light in thermotolerance is less clear. In some reports light has been shown to reduce damage to PSII during heat stress (Weis and Berry, 1988; Havaux et al., 1991) while some reports pointed out the injurious effects of light on photosynthetic machinery during heat stress (Ageeva, 1977; Al-Khatib and Paulsen, 1989). High-temperature stress under a long photoperiod is considered to be more injurious to pod formation than that under short day conditions (Hall, 1992).

The role of different irradiance levels in the heat tolerance of photosynthetic apparatus as well as in the crop productivity has not been sufficiently studied, especially in tropical grain legumes. Under tropical field conditions the light intensity and temperature change dramatically and the plants have to adapt to the changing environment. This study was initiated to analyze i) the growth, yield and participation of each plant organ to biomass production, ii) the dynamics of CO₂ assimilation rate in response to changing light intensity, and iii) the heat acclimation of photosynthetic apparatus in *Vigna radiata* L. under different temperature and light conditions.
Materials and Methods

1. Plant materials and growth conditions

Two mungbean varieties, BARImug 2 (M2) and BARImug 3 (M3), collected from Bangladesh Agricultural Research Institute were used in this study. Both the varieties have a synchronous fruiting pattern and are commonly cultivated in the farmers’ field. In a preliminary trial at 40/25°C (day/night) M3 produced higher biomass than M2. Seeds were germinated in Petri-dishes in the dark at room temperature. After the emergence of the radical, germinated seeds were transferred to 15-L plastic pots containing 4 kg powered kaolinitic ultisol. The soil was prepared by mixing with NPK fertilizers (14 : 14 : 14) at 0.5g kg⁻¹ soil.

The plants were divided into three groups and all plants were initially grown in three growth chambers (TGE-91-1-S, TABAI ESPC CORP, Osaka, Japan) equipped with halogen lamps (MT 1500 BD/BH, GS, Kyoto, Japan) till emergence at a common temperature of 30/25°C (day/night). The photon flux density (PFD) was 700 μmol m⁻² s⁻¹ (high-intensity light, HL) in two growth chambers, and was reduced to 200 μmol m⁻² s⁻¹ (low-intensity light, LL) by means of cheesecloth in the remaining one. After emergence the temperature in one of the HL- and LL-growth chambers were adjusted to 40/25°C (high temperature, HT), while the remaining one at 30/25°C (low temperature, LT). In a preliminary trial, the leaf temperature of the uppermost fully developed penultimate mungbean leaves at reproductive stage was monitored during light phase under such conditions with a copper–constantan thermocouple attached to the abaxial side of the leaves. The leaf temperature was 29±0.5 and 39±1.6°C at LT and HT, respectively. The LT is supposed to be optimum temperature for the growth of mungbean (Poehlman, 1991) and HT to represent the day temperature in hot summer of tropical countries growing mungbean. Since the night temperature during summer fluctuate less unlike day temperature, it was maintained at 25°C in all the growth chambers. The 12-h photoperiod and a vapor pressure deficit (VPD) of 1.5 kPa were common in all the growth chambers. Therefore, all together three growth conditions were 1) 12-h HL at LT/12-h darkness at 25°C (HL+LT), 2) 12-h HL at HT/12-h darkness at 25°C (HL+HT) and 3) 12-h LL at HT/12-h darkness at 25°C (LL+HT). The plants were grown under these conditions till maturity. Photosynthetic parameters were measured at flowering.

2. Growth and yield parameters

Plant height, leaf area, specific leaf area, yield and yield contributing characters were recorded at maturity for 10 plants.

3. Measurement of photosynthetic CO₂ assimilation rate

The photosynthetic CO₂ assimilation rate (Pn) in intact fully developed penultimate leaves was measured with an infra red gas analyzer (LCA-4, ADC Herts, UK). A portable light unit (Type PLU2-002, ADC; 12V 20W Dichroic white light 60 VWFL lamp) was mounted on the radiation shield of the leaf chamber to control light intensity by using different neutral density filters. The temperature of the leaf chamber was controlled at 30 or 40°C with a temperature control unit (PLC temperature controller, Shimadzu, Japan). The measurements were made at PFDs of 200, 400, 700, and 2000μmol m⁻² s⁻¹, only when the leaf temperature and CO₂ assimilation rate were fully stabilized.

4. Heat-shock treatment and chlorophyll a fluorescence

The penultimate detached whole leaves of the plants developed under the three experimental conditions were placed in a beaker (500 mL). Moist tissue paper was kept inside the beaker to prevent desiccation of the leaves. The beaker was then dipped up to the neck for 15 min into temperature-controlled circulated hot water at 40, 45, 50 or 55°C. The maximum photochemical efficiency of PSII (Fv/Fm) was determined after dark adaptation of the heat-treated leaves for 15 min using a portable pulse amplitude modulated fluorometer (MINI-PAM, H. Walz, Effeltrich, Germany) connected to an optical leaf clip holder (2030-B). The actinic light (150 μmol m⁻² s⁻¹) from an external halogen lamp (2050-H) fixed with the leaf clip holder (2030-B) was then turned on for 12 min, which was sufficient for attaining steady state, to record quantum yield of PS II electron transport (ΔF/Fm).

5. Determination of chlorophyll

Leaf chlorophyll was extracted with 80% acetone.

Results and Discussion

1. Growth and yield parameters

High temperature delayed flowering as well as maturity. Mungbean plants flowered 28, 33 and 35 days after emergence under HL+LT, HL+HT and LL+HT, respectively. The plants under HL+LT matured 58 days after emergence but those under LL+HT matured 75 days after emergence. Plant height was increased by exposure to HT and the plants under LL+HT were the tallest (Table 1). Under HL+LT M2 and M3 had a similar plant height, though M3 was taller than M2 under HL+HT and LL+HT. HT seriously reduced the leaf area and the plants under HL+HT had the minimum leaf area. Specific leaf area (SLA) was highly influenced by both light intensity and temperature. The plants under HL+HT had a very large SLA and those under LL+HT had a very small SLA. HT seriously decreased biomass. The synergetic effect of temperature and light intensity largely depended on crop variety
Table 1. Effect of temperature and irradiance on plant characters in mungbean.

| Treatments | Plant height (cm) | Leaf area (cm²) | Specific leaf area (mg cm⁻²) | Total biomass (g plant⁻¹) |
|------------|------------------|-----------------|-----------------------------|--------------------------|
| HL+LT**    | 47.50            | 48.83           | 653.50                      | 574.50                   |
|            | ±1.88            | ±2.33           | ±55.64                      | ±65.38                   |
| HL+HT**    | 58.33            | 75.83           | 296.75                      | 362.25                   |
|            | ±3.51            | ±2.65           | ±33.13                      | ±21.69                   |
| LL+HT**    | 76.50            | 82.50           | 372.75                      | 412.00                   |
|            | ±3.33            | ±3.24           | ±14.40                      | ±25.61                   |

Table 2. Effect of temperature and irradiance on yield and yield-contributing characters in mungbean.

| Treatments | Pods plant⁻¹ | Seeds pod⁻¹ | Seed size (mg) | Grain wt. Plant⁻¹ (g) |
|------------|--------------|-------------|----------------|-----------------------|
| HL+LT**    | 12.83        | 11.00       | 10.60          | 10.90                 |
|            | ±1.35        | ±0.68       | ±0.36          | ±0.27                 |
| HL+HT      | -            | -           | -              | -                     |
| HL+LT**    | 5.50         | 5.83        | 7.27           | 8.11                  |
|            | ±0.43        | ±0.54       | ±0.58          | ±0.29                 |

(Hall, 1992). Light intensity had little effect on the production of biomass at HT in M3 though biomass under HL+HT was slightly higher than under LL+HT in M2.

The pod setting was completely inhibited under HL+HT. However, pod setting under LL+HT was 43 and 53% of that under HL+LT in M2 and M3, respectively (Table 2). Similarly, the number of seeds per pod under LL+HT was 69 and 74% of that under HL+LT in M2 and M3, respectively. By contrast, the seed size under LL+HT was similar to that under HL+LT. Although the plants under HL+HT did not produce any grains, the grain yield under LL+HT was 30 and 43% of that under HL+LT in M2 and M3, respectively.

The percentage participation in each plant organ in biomass production is shown in Fig. 1. Under HL+LT stem and leaf occupied a similar proportion of biomass while the grain showed the highest and pod-shell the lowest proportion. Under HL+HT the biomass consisted only leaf and stem. The large participation of stem in biomass production under HL+HT was due to the large plant height (Table 1). The participation of grain and pod-shell in biomass production was markedly low under LL+HT. Under HL+LT the two cultivars showed a similar percentage participation of each organ in biomass production, though under LL+HT the grain occupied a slightly higher percentage in M2 than M3 (Fig. 1).

Plant growth is often reduced at high temperatures and the mechanism has been well studied (Blum, 1988; Ismail and Hall, 1998; Karim et al., 2000). Moreover, Hall (1992) and Suzuki et al. (1999) have reported on the deleterious effect of high temperatures on pollen fertility and pod setting in legumes. However, the role of light intensity on pollen fertility has not been sufficiently studied. We have checked the pollen viability following the method described by Suzuki et al. (1999). We observed that pollen grains of the plants under HL+HT were totally damaged while more than 90% pollen grains were viable in the plants grown under LL+HT (data not shown).

As shown in Fig. 1, the stem reserve was much larger under LL+HT compared with that under HL+LT. This is probably due to the smaller number of pods/plant (reduced sink size) under HL+HT as indicated in Table 2. However, the unaffected grain size indicates...
Fig. 1. Percentage participation of each plant organ in biomass production in two mungbean (Vigna radiata L.) varieties, BARImug 2 (M2) and BARImug 3 (M3), grown under HL + LT (12-h 700 μmol m⁻² s⁻¹ PFD at 30°C/12-h darkness at 25°C), HL + HT (12-h 700 μmol m⁻² s⁻¹ PFD at 40°C/12-h darkness at 25°C), and LL + HT (12-h 200 μmol m⁻² s⁻¹ PFD at 40°C/12-h darkness at 25°C). Values are means of 10 replications.

that the photoassimilate transportations to individual grain was not disturbed by HT. Although we used only two mungbean varieties, they showed a significant difference in high-temperature tolerance in terms of grain yield and biomass production. These differences suggested the existence of genetic variation in high temperature tolerance in mungbean, as was reported earlier for other legumes (Hall, 1992; Talwar et al., 1999).

2. Physiological parameters

Neither temperature nor light intensity affected chlorophyll content significantly. However, the plants under LL + HT contained a slightly larger amount of chlorophyll than the plants under HL (Fig. 2). By contrast, Pn measured at either 30 or 40°C was higher in the plants grown under HL + LT than in the plants under HT, irrespective of their growth light intensities. The difference in Pn between the treatments became wider as the measuring light intensity increased (Fig. 3). Plants grown under HL + HT had the higher Pn compared with those grown under LL + HT. In general M3 had slightly higher Pn than M2. The findings confirm the earlier reports that high temperature decreases the Pn (Stamp et al., 1983; Karim et al., 2000; Talwar et al., 1999) and shade-adapted plants have low capacity for photosynthetic heat tolerance (Demmig-Adams and Adams, 1992; Skillman and Osmond, 1998) irrespective of their growth temperature.

The CO₂ assimilation at high temperatures may be limited by an imbalance in the regulation of carbon metabolism related to down-regulation of ribulose-1,5-biphosphate carboxylase/oxygenase (Weis and Berry, 1968). On the other hand, shade-acclimated leaves have low capacities not only for photosynthetic electron transport but also for photoprotective responses such as thermal energy dissipation (Demmig-Adams and Adams, 1992; Skillman and Osmond, 1998). They therefore experience sustained inactivation of the photosynthetic process at a much lower level of PFD than do sun-acclimated leaves.

The plants grown under HT showed higher PSII efficiency than those grown under LT (Fig. 4). Moreover, there was a clear indication that HL accelerated the heat acclimation of photosynthetic apparatus. The heat shock at 50°C did not impair the PSII activity of the leaves developed under HL + HT, that is, Fv/Fm measured after dark adaptation of the leaves and ΔF'/F'm measured at steady state were not affected by the heat shock (Fig. 4). However, the PSII activity of the leaves developed under LL + HT was impaired seriously at 50°C. The plants developed under LT showed a faster decrease in photochemical efficiency than the plants under HT. The better performance of the photosynthetic apparatus in the leaves developed under HL + HT than that in the leaves under HL + LT confirms the importance of heat acclimation for the thermoresistance of plants. There have been several reports that thermostability of membrane energization in chloroplasts increases with the heat acclimation (Yordanov et al., 1987; Chauhan and Senboku, 1996), although the cause of this phenomenon is still not clear.

Light-induced modification of heat stability of the photosynthetic apparatus observed in this study is considered to be a complex phenomenon. There have been controversial reports on the effect of light on photosynthetic heat tolerance. In some reports, light has been shown to reduce damage to PSII during heat stress (Weis and Berry, 1988; Havaux et al., 1991) while some reports pointed out the injurious effect of light on photosynthetic machinery during heat stress (Ageeva, 1977; Al-Khatib and Paulsen, 1989). Havaux et al.
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Fig. 2. Chlorophyll contents in leaves of two mungbean (Vigna radiata L.) varieties, BARImug 2 (M2) and BARImug 3 (M3), grown under HL + LT (12-h 700 µmol m⁻² s⁻¹ PFD at 30°C/12-h darkness at 25°C), HL + HT (12-h 700 µmol m⁻² s⁻¹ PFD at 40°C/12-h darkness at 25°C) and LL + HT (12-h 200 µmol m⁻² s⁻¹ PFD at 40°C)/12-h darkness at 25°C). Values are means of five replications. Bars indicate SE.

Fig. 3. Photosynthetic CO₂ assimilation rate (Pn) at various photon flux densities (PFD) of two mungbean (Vigna radiata L.) varieties, BARImug 2 (M2) and BARImug 3 (M3), grown under HL + LT (12-h 700 µmol m⁻² s⁻¹ PFD at 30°C/12-h darkness at 25°C), HL + HT (12-h 700 µmol m⁻² s⁻¹ PFD at 40°C/12-h darkness at 25°C) and LL + HT (12-h 200 µmol m⁻² s⁻¹ PFD at 40°C)/12-h darkness at 25°C). Values are means of five replications. Bars indicate SE.

(1991) proved that light at high temperature prevents the loss of oxygen evolution and variable fluorescence, and reduces the stimulation of PSI cyclic transport. Weis (1982) also noticed that the heat sensitive functions of chloroplasts in spinach such as stromal carboxylation reaction, the light-induced electrical field gradient across the thylakoid membrane and overall CO₂ assimilation were less affected by heat if the chloroplasts were heated.
in the light. However, the HL-induced adaptation of photosynthetic apparatus to heat stress did not contribute for higher total biomass production (Fig. 4 and Table 1). These findings indicate a complex nature of plant response to light in mungbean under heat stress conditions.

In this paper we demonstrated the role of light intensity in photosynthetic activity and crop productivity of mungbean under heat stress conditions. HL inhibited pod setting under heat stress, but accelerated the heat acclimation of photosynthetic apparatus in mungbean. Opposite to this findings 50% pod setting was possible under LL+HT, though the photosynthetic apparatus was relatively thermolabile. There was no relationship between the adaptation of photosynthetic apparatus to heat stress and biomass production. Therefore, more detailed study is necessary to understand the role of light intensity in the complex nature of plant response to heat stress.

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