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Combined Effect of High Day and Nighttime Temperatures and Water Deficit Stress on Phenology, Growth, Photosynthesis, Yield and Seed Quality in Soybean

Kanchan Jumrani* and Virender Singh Bhatia

ABSTRACT: *India ranks fourth in terms of area and fifth in production of soybean in the world. Both drought and heat stress influence an array of processes including physiological, growth, developmental, yield and quality of crop. Therefore, the main objective of the current study is to provide an overview of the influences of these two stresses independently and in combination. Soybean genotype JS 97-52 was planted in four green houses maintained at an average temperature of 26, 29, 32 and 35°C. At each temperature, pots were divided into three sets, one set was unstressed (well irrigated) while second and third set were subjected to water stress at vegetative and reproductive stage, respectively. Data on phenology, dry matter accumulation, photosynthesis, seed yield and its attributes were recorded. There was a significant interaction of temperature and water stress. Increasing temperatures and imposition of water stress significantly reduced the root growth, nodule weight, rate of photosynthesis, seed yield and attributes. The highest yield (14.3 g/pl) was observed at 26°C, which was significantly reduced by 21, 44 and 72% at 29, 32 and 35°C, respectively. Similarly, compared to unstressed plants (15.1 g/pl) there was a mild reduction in yield in plants stressed at vegetative stage (27%) and a severe reduction in plants stressed at reproductive stage (87%). Photosynthesis was also reduced as the temperatures increased and when water stress was imposed at two stages. Quality of soybean seeds in terms of germination and vigour declined with the increasing temperatures and water stress. Thus, there is an urgent need to develop plants, which are tolerant to temperature and water deficit stress.*

Key Words: *Photosynthesis, Seed yield, Soybean, Temperature, Water stress*

INTRODUCTION

Soybean [*Glycine max* (L.) Merrill] is the most important grain legume of the world, which contributes significantly to edible oil, protein concentrate for animal feed, food uses and various industrial products including biodiesel. Since 1970, the yearly percentage increase in soybean production area has been the highest among major crops and the global demand for soybean still continues to grow. India has been one of the major contributors to global soybean expansion during the past 40 years. Starting from an area and production of just 30,000 ha and 14000 tons in 1970, the crop has expanded to 10.5 million ha with 12.4 million tons of production in 2012 [1] making soybean as number one oil seed crop in India. The crop is predominantly grown on vertisols and associated soils with an average crop season rainfall of about 900 mm which varies greatly across locations and years [2]. Over the years, the crop has been instrumental in providing sustainable livelihood and improving the socioeconomic conditions of large number of small and marginal farmers of rainfed agro-ecosystem of India.

Despite spectacular growth in area and production, the productivity of soybean has more or less remained stagnated to about 1.1 t/ha which is the major cause of concern. Occurrence of drought and high temperature conditions at one or the other stage of crop growth are considered to be the major factors limiting productivity of crop in India [2]. Also there is now a scientific consensus for an observed increase in average temperatures, and a change in rainfall rates in the 20th century across the world [3]. Also, depending on the future climate scenarios, the IPCC has projected a temperature rise of 0.5-1.2°C by 2020, 0.88-3.16°C by 2050 and 1.56-5.44°C by 2080 for the Indian region. Increased frequencies of extreme events such as drought have also been projected for

* Directorate of Soybean Research, Khandwa Road, Indore 452 001, India
Corresponding Author E mail: kanchan.jumrani@gmail.com

the future climate. Thus, the projected climate change would further accentuate the problem of drought and high temperature which in turn will affect the productivity of soybean crop.

The majority of studies thus far have focused on the response to a single environmental stress, such as drought or high temperature [4] and very little is known about the combined effects of high temperature and occurrence of drought on crop growth and yield. However, under field conditions, both of these stresses often occur in combination. Simultaneous occurrence of multiple stresses increases the deleterious effect, such that the effect considerably exceeds the simple additive effects of the action alone (cross-synergism). Similarly, a plant subjected to a single stress can be capable of increasing its resistance to subsequent or other stress (cross-adaptation). Few studies that examined the impact of the combined effects of drought and heat stress suggested that the combination of drought and heat stress had a significantly higher detrimental effect on growth and productivity of crops than when each stress was applied individually [5-6]. In addition, the combination of drought and heat stress was found to alter physiological processes such as photosynthesis, accumulation of lipids, and transcript expression [7-8]. To reduce the adverse impact of these two factors, it is necessary to understand their impacts individually as well as their interaction on growth and yield of the soybean. Therefore, the objectives of the present study were to analyze the impact of increased temperatures and water stress imposed at different growth stages and their interaction on soybean growth and yield.

MATERIALS AND METHODS

The experiment was conducted under green house conditions at ICAR-Directorate of Soybean Research, Indore.

Green houses/temperature treatments

Four green houses of 20 x 10 ft size were used in the experiment. These green houses were maintained at day/night temperatures of 30/22, 34/24, 38/26 and 42/28˚C with an average temperature of 26, 29, 32 and 35˚C, respectively

Planting of soybean

In each green house soybean variety JS 97-52 was grown in cement pots filled with soil and farm yard manure mixed in the ratio of 2:1. The pots were soaked with tap water 24 hr before planting. Ten seeds of uniform size treated with recommended fungicides and Bradyrhizobium culture were sown in each pot. A week after germination, thinning was done to three plants per pot.

Imposition of soil moisture stress

At each temperature, pots were divided into three sets, one set was control (Unstressed) while second and third sets were subjected to water stress at vegetative (25 DAS) and beginning seed fill (R5 stage) [9], respectively. In both the stress treatments, the plants were subjected to moisture stress to about -3.0 MPa after which the water stress was released.

Observations recorded

The data on phenology, dry matter and leaf area were recorded periodically. Leaf water potential was measured using Psychrometers (Wescor, USA), leaf area using automatic leaf area meter (Licor, model LI- 3100 USA), photosynthetic rate by portable Infra Red Gas Analyzer (Licor, USA, model 6400XT), protein content in seeds by Kjeldahl method, seedling vigour and vigour test by the methods [10-11]. At harvest, data on seed yield and yield attributes were recorded.

RESULTS AND DISCUSSION

Impact of temperature and water stress on phenology

Understanding crop phenology or the growth stages of a crop is fundamental to crop management. While temperature is usually the critical environmental factor driving phenology, other factors such as water stress can also modify it significantly [12]. In the present study, increasing temperatures significantly reduced the time taken to flowering. The average days to flowering was 47 days at 26˚C which was reduced to 32 days at 35˚C (Table 1). Stress imposed at vegetative phase led to a slight delay in flowering as compared to control plants (Table 1). The total duration of the crop decreased with increasing temperatures. The average days to maturity, was 117 days at 26 ˚C and declined to 112, 101 and 99 days at 29, 32 and 35˚C, respectively (Table 1). The interaction of temperature and water stress was significant and stress imposed at vegetative phase led to delay in maturity whereas stress at reproductive stage led to decline in maturity as compared to unstressed plants. Hence, increase in temperature would significantly modify the soybean phenology and reduce the time taken to complete life cycle.

Impact of temperature and water stress on growth parameters

Leaf area, dry matter (Root + shoot), nodule number, nodule weight and leaf photosynthesis, were recorded periodically and the data for the sampling after the release of water stress are presented in (Table 1). Increasing temperatures and stress imposed at vegetative and reproductive stages significantly reduced all the growth parameters studied. In plants grown at 26 ˚C, the average leaf area/plant was 174.8 cm^2, which was significantly reduced to 168.6, 156.6 and 125.3 cm^2 in plants grown at 29, 32 and 35˚C, respectively. In unstressed plants, the average leaf area/plant was 190.6 cm^2, which was significantly reduced to 162.7 and 100.7 cm^2 in plants subjected to water stress at vegetative and reproductive stages, respectively (Table 1). Leaf expansion is among the most sensitive growth processes to drought and also temperature [13]. Heat and drought stress can also influence total leaf area through its effect on initiation of new leaves, which is decreased under these stresses. Continued heat and drought stresses can accelerate leaf senescence [14] and lead to death of leaf tissue, resulting in leaf drop, particularly old and mature leaves.

Table 1
Effect of temperature and water stress imposed at vegetative and reproductive stages on soybean phenology, leaf area, total biomass (root + shoot) and nodule dry weight

Treatments		*Days to flower*	*Days to maturity*	*Leaf Area (cm^2)*	*TBM (g/pl)*	*Nodule weight (g/pl)*
Temp	26 ˚C	47	117	174.8	35.4	1.28
	29 ˚C	44	112	168.6	30.2	1.18
	32 ˚C	34	101	156.6	25.9	0.96
	35 ˚C	32	99	125.3	23.3	0.87
Water stress	Unstressed	39	110	190.6	35.7	1.46
	Vegetative Stress	41	116	162.7	28.5	1.11
	Reproductive Stress	39	97	100.7	23.9	0.65
	Mean	39	107	151.3	28.7	1.07
LSD (P≤0.05)						
A. Temperatures		1.1	1.3	8.09	2.61	0.48
B. Water stress		1.0	1.1	6.9	2.26	0.42
Interaction A x B		2.0	2.3	13.9	4.52	NS

The average dry matter and nodule dry weight/plant was 35.4 and 1.28 g/pl in plants grown at 26 ˚C which was reduced to 23.3 and 0.87 g/pl when the plants were grown at 35˚C. Imposition of water stress at vegetative (28.5 and 1.11 g/pl) and reproductive (23.9 and 0.65 g/pl) stages resulted in significant reduction in average dry matter and nodule weight as compared to average values of unstressed plants (35.7 and 1.46 g/pl). A significant decline in growth due to drought and heat stress has also been reported by [15]. Except for nodule dry weight, the interaction of temperature and water stress treatments was significant indicating that the impact of temperature was significantly different in plants which were well irrigated (control) and plants which were subjected to water stress at vegetative and reproductive stages (Table 1). In general, the impact of temperature on growth parameters was of lesser magnitude in unstressed plants and very high in the plants subjected to water stress at reproductive stage.

Impact of temperature and water stress on photosynthesis

Similar to above parameters, the leaf photosynthetic rate was also reduced as the temperatures increased and when water stress was imposed at reproductive stage. The light response curves of leaf photosynthetic rate in unstressed plants and plants subjected to water stress at reproductive stage (Ψ_L= -2.0 MPa) are presented in Fig. 1. The maximum rate of photosynthesis in unstressed plants at all the PAR values was observed at 26 ˚C, which reduced marginally at 29˚C and more severely at 32 and 35˚C, respectively (Fig. 1a). Similarly, compared to unstressed plants, the rate of photosynthesis decreased significantly at all the temperatures. However, under water stress conditions, the differences were very marginal in plants grown at 26, 29 and 32˚C while reduction was of greater extent at 35˚C (Fig. 1b). The high temperature conditions require increased transpiration to maintain the canopy temperature and hence may induce stomatal opening but reduce the net photosynthesis even under irrigated conditions [16]. On the other hand, the reduced photosynthesis under water stress conditions could be attributed to closer of stomata. However, the severe adverse effect on the leaf photosynthesis of plants subjected to combination of temperature and water stress could be attributed to both stomatal and

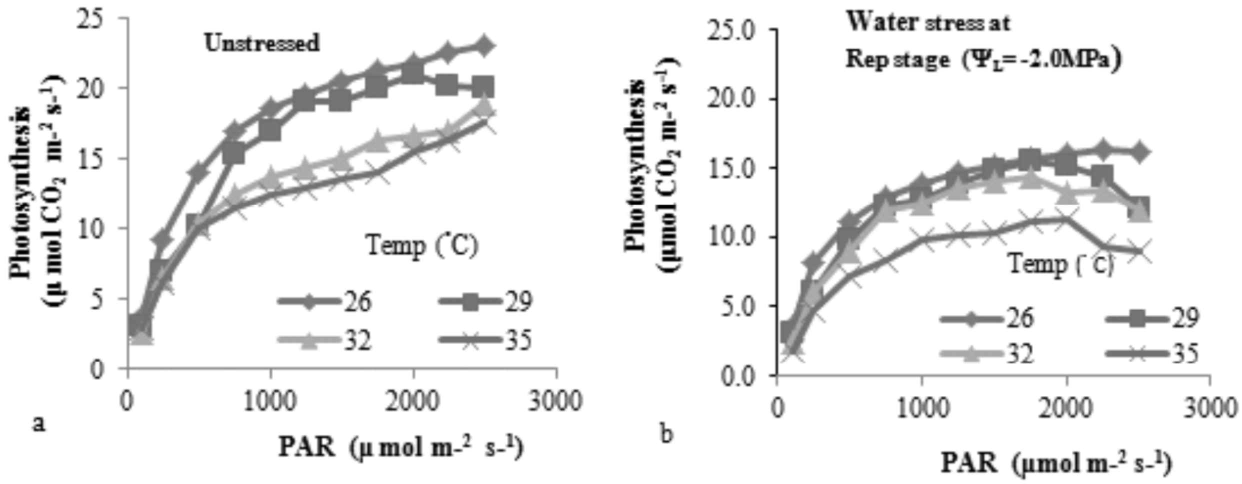

Figure 1: Interactive effects of temperature and water stress at reproductive stage on light response curve for photosynthesis in soybean

non-stomatal limitations such as weakened PS II function and nitrogen levels as well as enhanced lipid peroxidation [17].

Impact of temperature and water stress on seed yield and yield attributes

High temperature [18] and water stress [19] significantly reduced the seed yield in soybean. However, interactive effects of drought and heat stress on reproductive processes of crop plants including soybean have not been well defined and quantified and therefore needs investigation [20]. In the present study, the imposition of water stress at vegetative and reproductive stages resulted in significant reduction in yield as compared to unstressed plants. Averaged over all the water stress treatments, the highest yield (14.3 g/pl) was observed at 26˚C, which was significantly reduced by 21, 44 and 72% at 29, 32 and 35˚C, respectively (Table 2). When averaged over all the temperatures highest yield was observed in unstressed plants (15.1 g/pl) and showed a mild reduction in plants stressed at vegetative stage (27%) and a severe reduction in plants stressed at reproductive stage (87%).

Similar effect of temperature and water stress was observed for most the yield attributes that including total biomass at harvest, harvest index, pods/plant, seeds/pod and 100 seed weight explaining the drastic reduction in yield (Table 2). However, among the yield attributes, maximum effect was observed for seed size as when averaged over water stress treatments the 100 seed weight was reduced from 8.2 g at 26˚C to 3.9 g at 35˚C. Similarly, when averaged over temperature treatments, compared to unstressed plants (7.8 g) the 100 seed weight showed a marginal decline in plants subjected to water stress at vegetative phase (7.1 g/pl) while reduction in plants stressed at reproductive stage was very severe (3.6 g). The

Table 2
Main effects of temperature and water stress imposed at vegetative and reproductive phase on soybean yield and yield attributes of soybean

	Treatments	*Yield (g/pl)*	*TBM (g/pl)*	*HI (%)*	*Pods/pl*	*Seeds/pl*	*100 seed wt (g)*
Temp	26 ˚C	14.3	37.9	34	78	2.2	8.2
	29 ˚C	11.3	31.9	32	72	2.1	6.9
	32 ˚C	8.1	24.0	30	62	1.7	5.7
	35 ˚C	4.0	17.3	21	52	1.5	3.9
Water stress	Unstressed	15.1	37.1	39	76	2.3	7.8
	Vegetative Stress	11.1	28.9	37	74	2.3	7.1
	Reproductive Stress	2.1	17.3	11	48	1.10	3.6
	Mean	9.4	27.8	29	66	1.9	6.2
	LSD ($P \leq 0.05$)						
	A. Temperatures	0.97	2.16	3.6	4.8	0.18	0.49
	B. Water stress	0.84	1.87	3.2	4.1	0.16	0.43
	Interaction A x B	1.68	3.74	NS	8.3	0.32	0.85

decrease in seed size due to decline in seed-filling in response to drought and heat stress has also been reported earlier by several workers [21-22].

Significant temperature x water stress interaction was observed for seed yield and other attributes indicating that prevailing ambient temperatures differentially affected the growth and yield in unstressed plants and plants subjected to water stress at vegetative and reproductive stages. In general, the magnitude of reduction in seed yield and its attributes was very high when plants were subjected to water stress at higher temperatures (32 and 35˚C). Also the magnitude of reduction was very high in plants subjected to water stress at reproductive as compared to vegetative stage (Fig. 2).

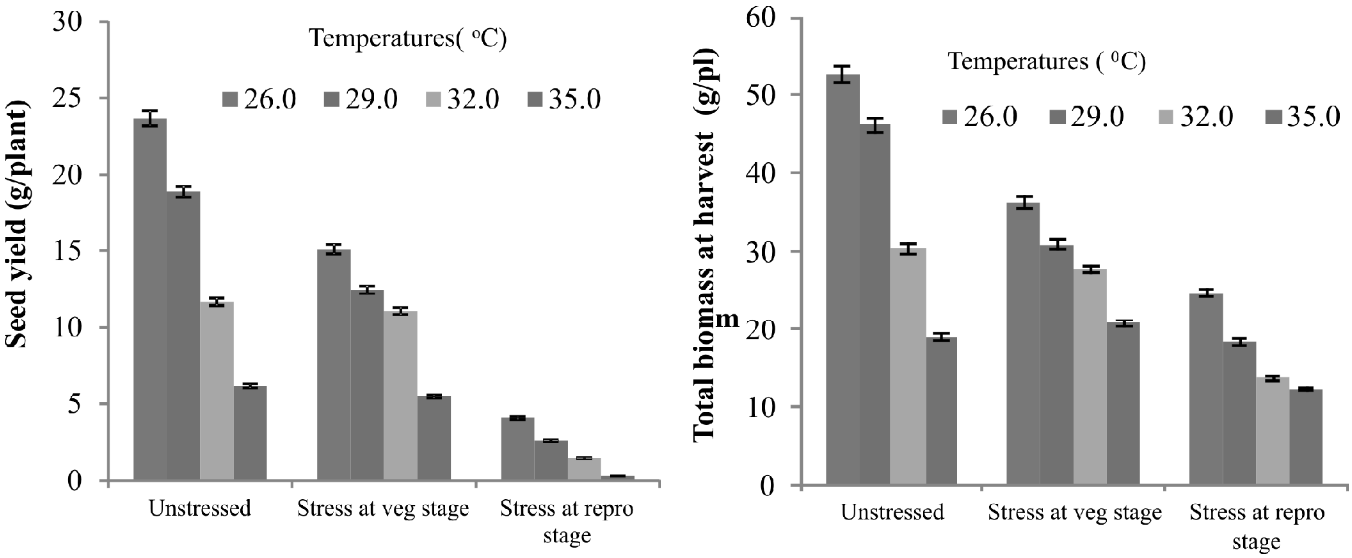

Figure 2: Interactive effects of temperature and water stress imposed at vegetative and reproductive stages on seed yield and total biomass at harvest in soybean

Impact of temperature and water stress on seed quality

The protein content in seeds at harvest also showed a decreasing trend which was declined from 40 to 34% as the temperatures increased from 26 to 35°C and also protein content was declined when the plants were subjected to water stress at vegetative and reproductive stages as compared to control plants (Fig. 3). This clearly indicated that increasing temperatures and occurrence of drought at high temperatures would have a negative effect on the nutritive quality of soybean seeds. The reduction in seed could be attributed to reduction in nitrogen availability due to adverse impact of both temperature and water stress on biological nitrogen fixation.

Soybean seed is very sensitive to climatic conditions at seed formation and maturity stages and looses viability under high temperature and high humidity conditions [23]. In the present study, also the quality of soybean seeds in terms of germination and vigour declined with the increasing temperatures and water stress imposed at vegetative and reproductive stages as compared to unstressed plants (Fig. 4 a). The maximum vigour index was observed in soybean seeds harvested from the unstressed plants grown at 26 ˚C (1238) which declined marginally by 9% and a severe decline of 25 and 63% in seeds harvested from plants grown at 29, 32 and 35 ˚C. When water stress was imposed both at vegetative and reproductive stages led to further decline in seed vigour at all the temperatures as compared to unstressed plants and the magnitude of loss was of higher degree in seeds collected from plants subjected to water stress at reproductive phase. Using tetrazolium salt the seed vigor was evaluated according to their topographical staining. The stained seeds were grouped and seeds were classified in six different vigour classes i.e. high vigour (HV), vigour (V), medium vigour (MV), low vigour (LV), very low vigour (VLV) and Dead (D). It was found that with increase in temperature there was decline in there was decline in percentage of high vigour and vigorous seeds and water stress imposed at two stages further declined the seed quality and more of low, very low vigour and dead seeds were formed (Fig. 4b). Hence, the increasing temperatures will result in poor quality of seeds harvested by the farmers and the problem of seed quality will be further compounded by occurrence of drought in soybean. This would indirectly have implications on availability of quality soybean seeds for planting and on the productivity of soybean due to poor plant stand if the farmers plant the poor quality seeds.

CONCLUSION

The results of the present study clearly indicated that the increase in mean air temperature above 26˚C adversely affected the growth, yield and quality of soybean seeds. However, the magnitude of reduction in these parameters was of higher degree at mean air temperature of 32 and 35˚C. Occurrence of water stress at reproductive stages was found to be more detrimental to soybean growth, yield and quality characteristics as compared to water stress at vegetative stage at all the temperatures. Significant temperature x water stress interaction for seed yield and other attributes indicated that temperatures differentially affected the growth and yield in unstressed plants and plants subjected to water stress at vegetative and reproductive stages.The magnitude of reduction in seed yield and attributes was very high when plants were subjected to water stress at higher temperatures (32 and 35˚C). Also the magnitude of reduction was very high in plants subjected to water stress at reproductive as compared to vegetative stage. Thus, the projected future climate in terms of increased temperature and drought could severely reduce the productivity of soybean in India and there is an urgent need to develop plants which could sustain such situations. To achieve this, there is an urgent need to evaluate germplasm lines which are tolerant to combined effects of temperature and water stress particularly at reproductive stage.

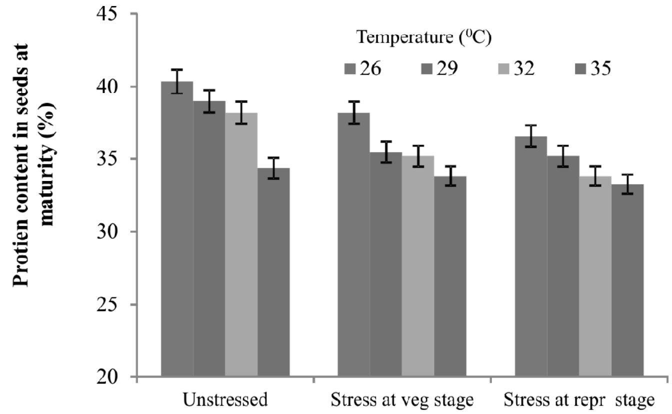

Figure 3: Interactive effects of temperatures and water stress imposed at vegetative and reproductive stage on protein content (%) of soybean

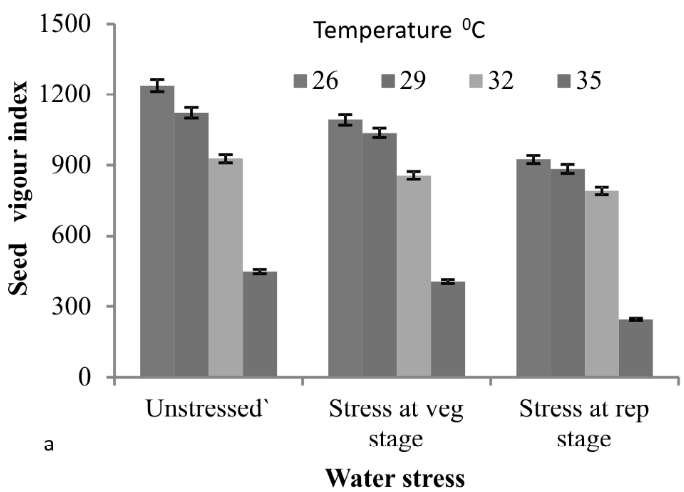

Figure 4: (a) Interactive effects of temperatures and water stress imposed at vegetative and reproductive stages on seed vigour of soybean, (b) different categories of vigour in soybean seeds

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