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Research Article

EVALUATION OF CRITICAL LIMIT OF LOW LIGHT INTENSITY THROUGH PHOTOSYNTHETIC AND PHOTOSYSTEM-II MECHANISMS IN BLACKGRAM (*Vigna mungo* L.)

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Abstract: Experiments were carried out to evaluate the impact of low solar irradiance as commonly observed in agroforestry practices on physiological functions of blackgram (*Vigna mungo* L.). Low solar irradiance brought down regulation of CO_2 assimilatory functions, photochemical efficiency and related photosynthetic traits in blackgram. Down regulation of CO_2 assimilatory functions was associated with the less photosynthetic electron supply for net CO_2 assimilation rate (PN). From the analysis of the photosynthetic photon flux density (PPFD) versus PN response curve and PPFD versus intercellular CO_2 (Ci) response curve, it has been clearly demonstrated that compensation irradiance (CI), thylakoid electron transport (ETR), photosynthetic water use efficiency (WUE) and *in-vivo* carboxylation efficiency (CE) were the major determinants for low solar irradiance induced reduction in physiological functions leading to carbon assimilation. Rate of the PPFD saturated PN (sat) decreased by 2.25% in 67% solar irradiance, whereas, the reduction was as high as 49.52% in 25% solar irradiance. The reduction in ETR was directly corroborated with the reduction in PN and many other photosynthetic traits depending upon the level of solar irradiance captured by understorey crops of agroforestry systems. Our results revealed that blackgram has acclimated CO_2 assimilatory function through photosynthetic traits and more importantly by decreasing the compensation irradiance (from 56.42 to 10.10μmol $m^{-2}s^{-1}$) under low irradiance. It is observed that 67% solar irradiance would be a critical limit for the crop as reduction of yield (%) was relatively low in it than in 50% sun light and 25% sun light when compare to open grown crops.

Keywords: *Inter cellular CO_2, In-vivo carboxylation efficiency, Net rate of CO_2 assimilation, Photosynthetic photon flux density, Thylakoid electron transport rate*

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Introduction

Blackgram (*Vigna mungo* L.) is one of the important pulse crops commonly grown in agroforestry systems in India. In agroforestry practices the canopy coverage created by the trees changes the light microenvironment conditions for the understory crops or low light grown plants. Currently, there are a limited number of comparable references in the optimal low light conditions for growth and development of low light grown crops in agroforestry systems. In addition to climate, nutrients and water which have been understood to be primary factors influencing the growth and development of plants, light intensity or solar irradiance is also one of the most essential driving forces for plant's survival, economic yield of crops and sustainability [1-4]. Compared to an open pasture environment, the modified microclimate under trees have reduced solar radiation, a lowered red : far-red light ratio, a more moderate temperature regime, higher humidity, lower rates of evapotranspiration and higher soil moisture levels.

Low light intensity directly affected photosynthetic apparatus by disrupting all major components of photosynthesis, including the thylakoid electron transport, the carbon reduction cycle and the stomatal control of the CO_2 supply [5,6]. Through the process of photosynthesis, light energy is used to produce ATP and NADPH in the light reaction and subsequently it leads to the CO_2 assimilation and carbon gain. Under field conditions, photosynthesis and CO_2 assimilation of leaves grown in low solar irradiance is very important for the total carbon budget of the plants [7]. Major functional processes of the plants are dependent mainly on photo synthesis and CO_2 metabolism differing in various climatic factors including quantity and quality of light [8,9]. The magnitude of the ability of crops to cope with low solar irradiance will determine its adaptability to the environmental conditions.

Therefore, it is obvious that capacity of CO_2 assimilation and related chloroplast functioning in crops growing under low solar irradiance are most important factors to decide their adaptation [10,11]. As net rate of CO_2 assimilation (PN) is linked with the functioning of gas exchange through stomata, leaf intercellular CO_2 (Ci), environment around chloroplast, *in-vivo* carboxylation efficiency (CE) of the enzyme RUBISCO (ribulose bisphosphate carboxyoxygenase) and CO_2 assimilatory function holds much importance for better understanding the low solar irradiance induced changes on it [12]. Similarly thylakoid electron transport is an important phenomenon connected with the performance of photosystem II (PSII) of the chloroplast apparatus which supply the electrons required to reduce CO_2 and regeneration of RuBP [13]. Supply of electrons for CO_2 assimilation by the chloroplast requires light and thus importance of evaluation of ETR requires much emphasis for physiological acclimation of plants under low solar irradiances.

Unstable light intensities or variable solar irradiances affects the plants in all types of environments and any kind of constraints to the availability of solar irradiance to the crops will impair the growth and ultimately its productivity [14]. To cope with the constraint of fluctuating solar irradiance, it is crucial to understand the important physiological processes which are directly linked with the acclimation strategies of the crops [15,16]. Photosynthesis is the prime process which is first affected in plants by any change in the environment or microclimate. Thus, differential responses in the rate of CO_2 assimilation and the associated processes in the chloroplast would certainly determine the efficiency of low irradiance adaptability of crops grown under fluctuating light intensities or low solar irradiance which requires much more studies for getting mechanistic insights [17].

Blackgram is an important pulse crop generally grown in agroforestry practices in India. With the microclimatic moderation of agroforestry systems, growing season is also characterized with cloudy environment during monsoon and thus it experiences low light availability. The photosynthetic process of this crop thus faces constraint which somehow to be adjusted accordingly for acclimation to low solar irradiance. Therefore, in the present study we have investigated the photosynthetic and photosystem-II limitations of blackgram (*Vigna mungo* L.) under varying solar irradiances as commonly seen in agroforestry practices through comprehensive experiments on photosynthetic traits and photosystem-II activities.

Materials and methods

Plants and location

Blackgram (*Vigna mungo* L. variety- Pant U-35) plants were grown in field under three different level of solar irradiances (67%, 50% and 25%) in separate net houses and in open (100% solar irradiance) at Central Agroforestry Research Institute, Jhansi, India (25° 27/ N latitude and 78°35/ E longitude, 271 m above MSL), during *kharif* (*rainy*) season in 2011-2012. Different intensity of solar irradiances was achieved in various net houses (25m×8m×3m) having diverse porosity of high density polyethylene was used to cover the respective net house. A randomized-block design of six replications was used. Blackgram was also grown in the open field in full sunlight adjacent to the net house area and this was considered as with 100% solar irradiance or control. The experimental site having black soil with a mean pH 7.02. The average annual rainfall of the area was 960-975 mm with a usual of 50-54 *rainy* days per year. The average maximum temperature ranges from 47.4 °C (June) to 23.5 °C (January) and mean minimum temperature from 27.2 °C (June) to 4.1 °C (December). May and June were the hottest months. All the standard agronomic practices were followed during the cropping period.

Real-time measurement of photosynthetic and chlorophyll fluorescence traits

A portable photosynthesis system (LI-6400XT, Licor, U.S.A.) attached with a leaf chamber fluorometer (LCF-6400-40) was used for simultaneous measurements of chlorophyll fluorescence and gas exchange rates in 100%, 67%, 50%and 25% solar irradiances grown plants. Estimation of photosynthetic traits and chlorophyll fluorescence parameters were conducted on intact mature leaves (top most) attached to the plants during 40-50 days after sowing. The measurements were conducted in the morning between 9:30 to 10:30 (local time) to achieve similar microclimatic conditions. Each leaf was dark adapted for about 25 min. in the sample chamber and at this point CO_2 efflux from the leaf was taken as rate of dark respiration. CO2 concentration of leaf chamber flurometer was fixed at 385 µmol mol-1 and light response curves were made at different levels of photosynthetic photon flux densities (PPFD) after dark measurements using a LED source attached with the leaf chamber. The compensation irradiance (CI) was estimated from the PN versus PPFD response curve. To obtain various levels of CO2for generating PN versus Ci response curve, the system's external CO2injector was used and PPFD was set at 1500 µmol $m^{-2}s^{-1}$. *In-vivo* Carboxylation efficiency (CE) and CO_2 compensation concentration (Γ) were determined from the PN versus Ci response curve taking PN versus Ci slope. Leaf temperature was maintained at the ambient atmospheric temperature (29°C) with ±0.5°C and leaf-air VPD was 1.2 to 1.5kPa throughout the measurement. CO_2 assimilation, stomatal conductance and fluorescence (Fs) were regularly monitored to ensure that they reached a steady-state before readings were taken.

Different chlorophyll fluorescence parameters such as maximal fluorescence under dark (Fm) and under light exposure (Fm'), steady state fluorescence at any given time (Fs) and minimal fluorescence under dark (Fo) and just after light exposure (Fo') which were required for estimation of different components of photochemical events and electron transport rate across PSII (ETR) of the leaf were recorded following the standard techniques [18,19].

Effective PS II quantum yield ($\Phi_{PS\,II}$) was measured as

$\Phi_{PSII} = (Fm'-Fs)/Fm'$

The rate of non-cyclic electron flow across PS II (ETR) was determined from the chlorophyll fluorescence data as

$ETR = \Phi_{PS\,II} \times PPFD \times 0.84 \times 0.5$

Where, 0.84 is the leaf fractional absorptance of incident PPFD and 0.5 is the fraction of absorbed PPFD which is absorbed by the light harvesting complex of PS II as widely accepted for C_3 species [20]. All the measurements were conducted in six plants from each category of treatment (*i.e*., three categories of low solar irradiances and open grown 100% solar irradiance plants) and thus each data point is the average of six replications.

Estimation of total chlorophyll

Chlorophyll of leaves was extracted with the help of acetone and DMSO (dimethyl sulphoxide) mixtures (1:1) and estimated following Arnon (1949) [33] method.

Estimation of crop yield

For grain yield estimation, eighteen plants from each category of low solar irradianceor100% solar irradiance (full sunlight) were tagged and harvested to determine the grain yield. Mean of eighteen plants were calculated to get per plant yield.

Data analysis

The data collected from the experimental site were subjected for ANOVA (analysis of variance) to compare the significance of means of all the treatments (*i.e*., three regimes of low solar irradiances and open grown 100% solar irradiance plants). A statistical software (SYSTAT-11) was used for the final analysis followed by calculation of LSD (least significant difference). Data points were plotted for equations using MS-Excel-2007 software.

Results

Through the PPFD versus PN curves, we have observed that the pattern of light energy use efficiency was different amongthe plants grown under different solar irradiances [Fig-1]. PN at low PPFD of 100 µmol $m^{-2}s^{-1}$ [PN(100)] in 100% solar irradiance and moderate irradiance (67% solar irradiance) grown blackgram was comparable without much difference. But PN(100) in very low solar irradiance (50% and 25% solar irradiance) was significantly less [Table-1]. PN(sat) of 100% solar irradiance and moderate irradiance (67%solar irradiance) grown blackgram was almost twice the PN (sat) in 25%solarirradiance grown plants. The PN(sat) in 100% solar irradiance grown plants was 28.26µmol $m^{-2}s^{-1}$ and it decreased with decrease in irradiance intensity as observed in 67%solarirradiance(26.16µmol $m^{-2}s^{-1}$), 50%solarirradiance(19.46 µmol $m^{-2}s^{-1}$) and 25% solar irradiance(13.42 µmol $m^{-2}s^{-1}$) respectively [Table-1]. In open or 100% solar irradiance grown plants the ETR was 212 µmol$m^{-2}s^{-1}$ whereas in 67% solar irradiance grown plants the ETR was 190 µmol $m^{-2}s^{-1}$ and gradually decreased in 50% solar irradiance (133 µmol $m^{-2}s^{-1}$) and 25% solar irradiance (120 µmol $m^{-2}s^{-1}$) consistently [Table-1]. The quantum of light required to saturate PN was much higher in case of the plants grown under 100% solar irradiance and moderate irradiance *i.e*., under67% solar irradiance [Fig-2]. Photosynthetic water uses efficiency (WUE) decreased with decrease in solar irradiance [Table-1]. Transpiration rate (E) also decreased as the solar irradiance decreased. Effective quantum yield of PSII (ΦPSII) also decreased under low solar irradiances which resulted in limited ETR. Compensation irradiance (CI) was studied through the analysis of linear equation of PN versus PPFD slope, which gradually decreased as the solar irradiance decreased [Fig-2]. In open (100% solar irradiance) grown blackgram the values of CI were 56.42 µmol $m^{-2}s^{-1}$ and in 67% solar irradiance it was 30.49 µmol $m^{-2}s^{-1}$ whereas, in 50% and 25% solar irradiances the CI were 19.77 µmol $m^{-2}s^{-1}$ and 10.10 µmol $m^{-2}s^{-1}$ respectively. Maximum reduction in the photosynthetic traits was noted in the 25% solar irradiance, followed by 50% solar irradiance, while a moderate reduction was recorded in 67% solar irradiance in comparison to open (100% solar irradiance) grown plants [Table-1].

In the present study with blackgram, the *in-vivo* carboxylation efficiency (CE) and PNmax(Ci) progressively decreased with decrease in solar irradiance level [Table-2]. However, CO_2 compensation concentration (Γ) progressively increased with decrease in irradiance level [Fig-3].

Table-1 *Comparative photosynthetic traits of blackgram indicating low solar irradiance induced limitations to CO_2 assimilatory functions*

Treatment	$P_{N\,(100)}$	$P_{N\,(sat)}$	WUE	E	CI	ETR	Φ_{PSII}
100% Irradiance	5.15±0.31	26.59±0.09	5.20±0.43	5.29±0.51	56.42±0.57	212.70±0.36	0.31±0.0005
67% Irradiance	4.82±0.09	25.99±0.41	4.91±0.20	5.23±0.25	30.49±0.57	190.50±0.65	0.28±0.0009
50% Irradiance	3.40±0.01	19.46±0.17	4.70±0.21	4.05±0.29	19.77±0.58	133.18±2.63	0.26±0.0052
25% Irradiance	3.31±0.10	13.42±0.38	3.52±0.29	3.89±0.26	10.10±0.44	103.55±0.41	0.24±0.0009
LSD(p = 0.05)	0.46	0.8	0.81	0.94	1.47	3.73	0.01

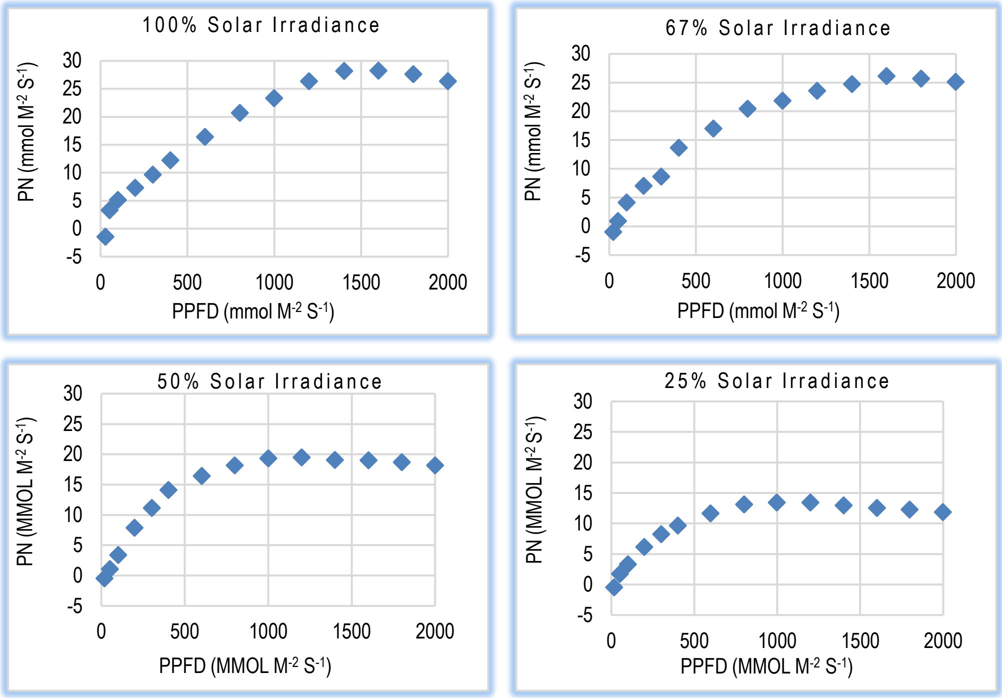

Fig-1 Net CO_2 assimilation rate (PN) versus Photosynthetic photon flux density (PPFD) response curve of blackgram under different level of solar irradiance

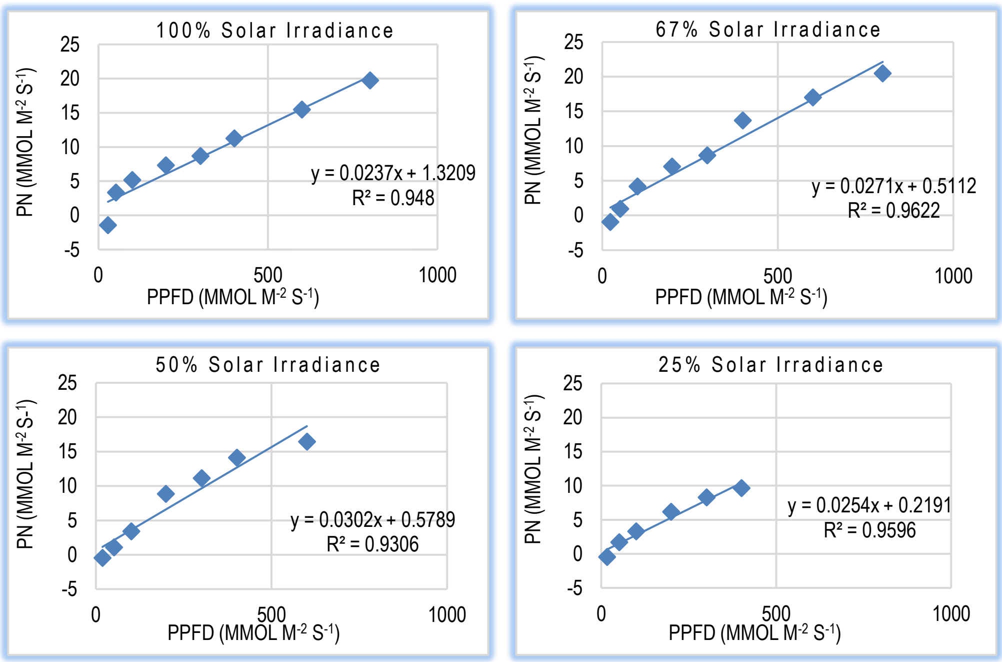

Fig-2 Linear equation for PN (CO_2 assimilation) versus PPFD (photosynthetic photon flux density) to compare the CO_2 compensation irradiance (CI) of blackgram as influenced by different level of solar irradiance

Linear regression analysis among the photosynthetic traits like PNmax(ci), Γ and CE indicated the impact of low solar irradiances on their interrelationship and functional association in the important pulse crop [Fig-4]. In present investigation, grain yield per plant was maximum in open (100% solar irradiance) grown plants and gradually decreased as the irradiance level decreases [Fig-5]. As expected low solar irradiance grown plants showed more chlorophyll content than 100% solar irradiance grown plants [Fig-6].

Discussion

From our results, it has been clearly evident that different level of solar irradiance as commonly experienced in agroforestry systems or under cloudy weather of monsoon season has far reaching impact on functional aspects of crops which manifested in its grain yield production. The major determinants for such impact were the CO_2 assimilatory functions and associated photosynthetic traits. These were mainly expressed at the level of leaf gas exchange and chloroplast photochemical activities as well.

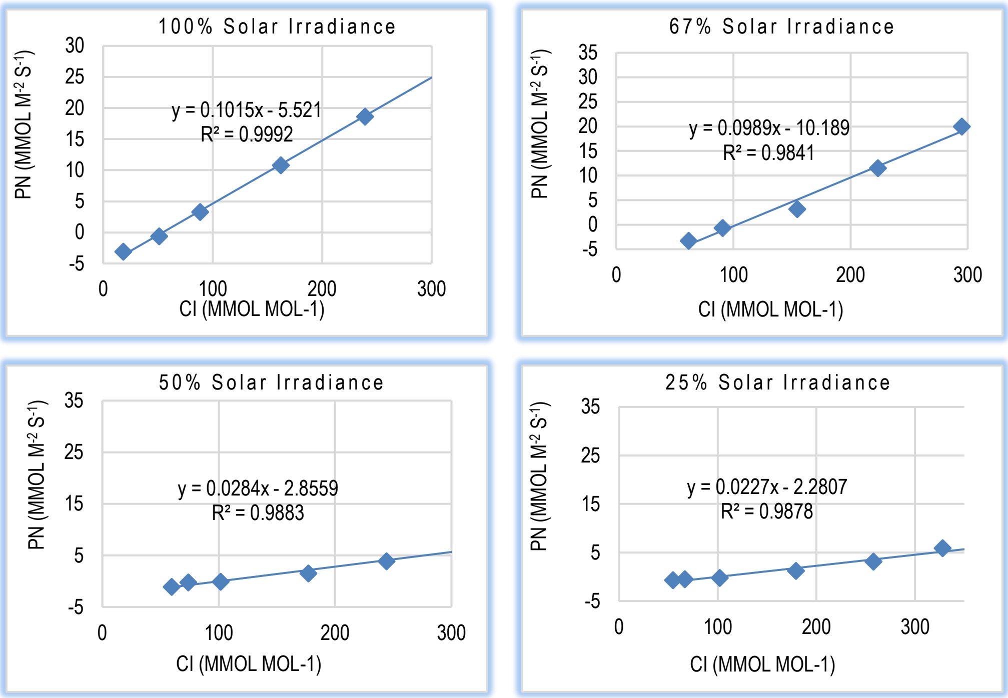

Fig-3 Linear equation for PN (CO_2 assimilation) versusCi (intercellular CO_2) to compare slope and the CO_2 compensation concentration (Γ) of blackgram as influenced by different level of solar irradiance

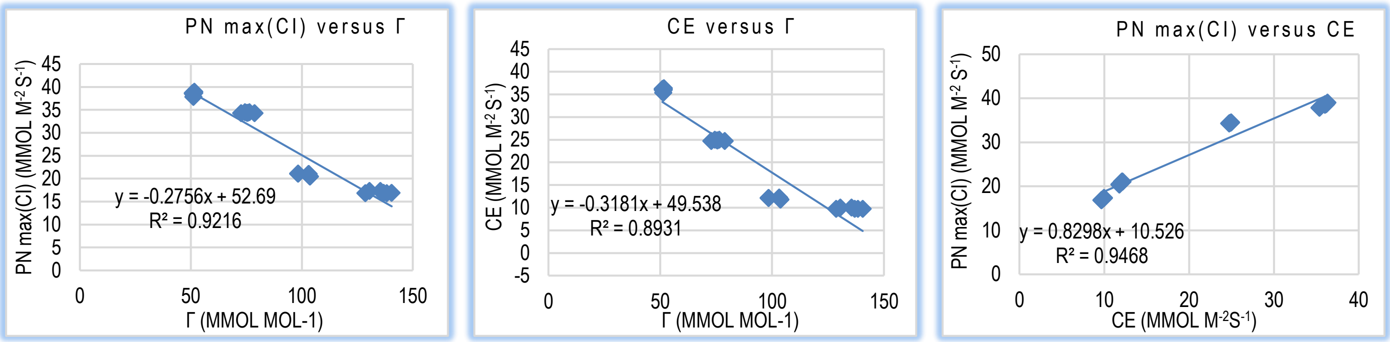

Fig-4 Interrelationship between some photosynthetic traits indicating their functional association in blackgram as influenced by solar irradiance. [Pooled data from all the four level of solar irradiance used]

The different CO_2 assimilatory functions as observed in PN versus PPFD curve of different level of solar irradiance clearly indicated the level of photosynthetic efficiency of blackgram. It has been noticed through PN versus PPFD curve that the reduction in PN (100) and PN (sat) under low solar irradiance was principally due to downregulation in ETR under these conditions. ETR is very much important for continuing CO_2 reduction and RuBP regeneration during photosynthetic reactions [21]. Due to downregulation in PSII activity, ΦPSII (effective quantum yield of PSII) reduced under low solar irradiance which resulted in limited ETR [Table-1]. This ultimately indicated towards reduced supply of RuBP due to shortage of sufficient photosynthetic electrons in the low solar irradiance. The limited ETR will clearly diminish the CO_2 assimilation as it has been noted. Simultaneously, the quantum of light required to saturate the PN was much higher in case of the plants grown under open (100% solar irradiance) or moderate irradiance (67% solar irradiance) in comparison to very low irradiances like50% or 25% solar irradiances. This clearly stated the limitation of photosynthetic apparatus of the plants grown under low solar irradiance which is a major influential cause for differential photosynthetic functions. This holds general importance for the crops conventionally grown in *rainy* season (June to September) which experience low solar irradiance due to cloudy weather.

Even after the supply of light increased, the plants grown under 50% solar irradiance could not use the light energy for CO_2 assimilation as efficiently as the plants did in case of 100% solar irradiance and moderate irradiance grown plants [Fig-1]. This indicated that the low sunlight or low solar irradiance has conspicuously affected the photosynthetic processes at cellular and functional level and finally affected yield and productivity of crop [Fig-5]. Thus, physiological constraints due to fluctuating or low solar irradiance in economically important plant are crucial challenge which needs to be addressed aptly [22, 23].

Low solar irradiance-induced adaptation in such environment is a sign of functioning of photosynthetic apparatus through changing their light requirement to saturate PN. The role of CE in conjunction with PN remains to be elucidated for various types of stresses [24]. Photochemical reactions are well associated with the efficiency of net CO_2 assimilation and quantum yield of CO_2 fixation. Reduction in CE with decreased in solar irradiance evidently supports the low irradiance-induced effects on the entire photosynthetic apparatus of the plants [Table-2]. From these typical curves, it was clear that low solar irradiance poses too much limitation to ETR for the pulse crop [Table-1]. As expected, we have also observed that the essential intercellular CO_2 to saturate PN were different in different light intensities [Fig-2].

Table-2 *Comparative photosynthetic traits related to in-vivo carboxylation efficiency in blackgram as affected by low solar irradiance*

Treatment	$P_{N\,max(Ci)}$	Γ	CE
100% Irradiance	38.40±0.21	51.25±0.14	35.88±0.18
67% Irradiance	34.37±0.04	75.48±0.90	24.82±0.04
50% Irradiance	20.82±0.14	101.71±1.15	12.01±0.08
25% Irradiance	16.98±0.10	135.03±2.06	9.79±0.06
LSD (P = 0.05)	0.37	3.41	0.29

Under low light intensity or low solar irradiance, insufficient ATP is produced to allow for carbon fixation and carbohydrate biosynthesis that might leadto reduced plant efficiency [25,26]. Our experimental results clearly indicated that low solar irradiance has conspicuously affected the CO_2 assimilation at functional level and it clarified at greater details on the low solar irradiance-induced physiological limitation [27].

We have noted the acclimation of blackgram to varying solar irradiances through increasing leaf chlorophyll content and at functional level as well. Increased chlorophyll content indicated a noteworthy trend for maximizing light harvesting [28-32]. In blackgram the *in-vivo* carboxylation efficiency (CE) and WUE progressively decreased with decreased irradiance level [Table-2]. Reduction in CE with decrease in irradiance level has been reflected with decrease in PN. Compensation irradiance (CI) and CO_2 compensation concentration (Γ) indicated considerable role to the photosynthetic capacity at varying light intensity depending upon the irradiance level. Dependence of PN on the light driven impact on CI and Γ in varying solar irradiance has been supported by our results with the linear correlation analysis [Fig-4]. We determined the inter-relationship of such photosynthetic traits which clarified the understanding of the physiological acclimation of plants under low irradiance constraints.

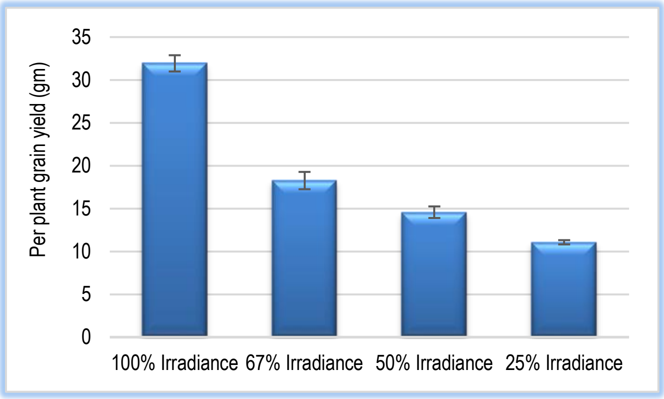

Fig-5 Grain yield (per plant) of blackgram as affected by different level of solar irradiance

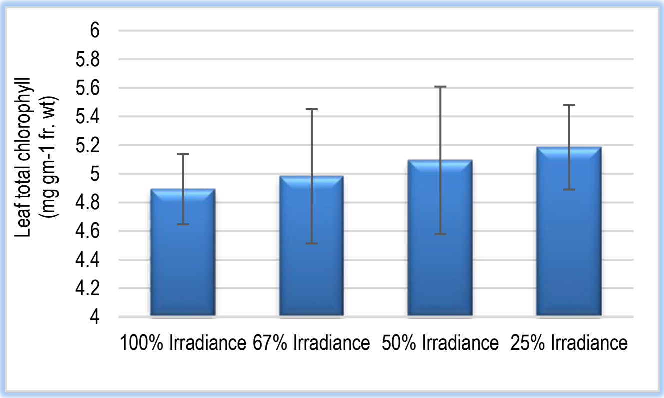

Fig-6 Leaf total chlorophyll content of blackgram indicating photosynthetic moderation through different level of solar irradiance

Conclusion

Towards better understanding the low light acclimation, we concluded that CO_2 assimilatory functions and the photosynthetic traits like ETR, CI, Γ and CE determined the differential responses of blackgram under the influence of solar irradiance. Our results also resolved that low solar irradiance-induced down regulation in photosynthetic and photosystem-II activity are associated with the physiological limitation of an important pulse crop like blackgram. It is observed that 67% solar irradiance (33% shade) would be a critical limit for the crop as percentage loss of yield was relatively low in it than in very less sun light (50% and 25%) when compared to open grown crops. Interrelationship among the photosynthetic traits as we demonstrated through the analysis of linear correlation indicated its usefulness as traits for improving and resolving the constraints due to low solar irradiance (low incident light)in agroforestry practices under changing climatic situations.

Application of research: Our results also resolved that low solar irradiance-induced down regulation in photosynthetic and photosystem-II activity are associated with the physiological limitation of an important pulse crop like blackgram. The results and findings of this paper are useful to improve and resolve the constraints due to low solar irradiance (low incident light)in agroforestry practices under changing climatic situations.

Research Category: Solar irradiance

Abbreviations: CE- *In-vivo* carboxylation efficiency; CI- Compensation irradiance; Ci- Leaf intercellular CO_2; ETR- Thylakoid electron transport rate; ΦPSII- Effective quantum yield of photochemical energy conversion; PN(sat)- PPFD saturation rate of net CO_2 assimilation; Γ- CO_2 compensation concentration; WUE- Photosynthetic water use efficiency.

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Author Contributions: All authors equally contributed

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Study area / Sample Collection: ICAR-Central Agroforestry Research Institute, Jhansi, 284003, Uttar Pradesh, India

Cultivar / Variety / Breed name: Blackgram (*Vigna mungo* L.) Pant U-35

Conflict of Interest: None declared

Ethical approval: This article does not contain any studies with human participants or animals performed by any of the authors.
Ethical Committee Approval Number: Nil

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