



## Impact of fluctuating actinic high light stress on biomass and yield of cassava

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### Abstract

Cassava (*Manihot esculenta* Crantz) is a staple crop grown in the tropics for food as a major calorie source as well as in industrial use. In natural environment, crops undergo rapidly changing light conditions which affects the photosynthetic efficiency. When exposed to excess photon flux densities, plants undergo non-photochemical quenching (NPQ) by which the excess energy is harmlessly dissipated as heat in order to protect the plants from photo-damage. Upon the transition to low or optimal light for photosynthesis, the slow rate of recovery of NPQ can limit effective photosynthetic efficiency which consequently results in low crop productivity. In the present study, the physiological and fluorescence responses of six field grown cassava genotypes to intermittent high red actinic light (IHL) were examined and compared against control plants grown under ambient light conditions. From the results, it was seen that overall average values of plant height and fresh above ground biomass (ABM) were higher under IHL conditions ( $206.6 \pm 26.5$  cm and  $2.34 \pm 0.67$  Kg respectively), while high crop biomass (CBM) was observed in control condition ( $3.11 \pm 0.86$  Kg). It was found that Sree Suvarna had the maximum CBM under both the control and IHL conditions ( $4.31 \pm 0.32$  Kg and  $4.11 \pm 0.44$  Kg respectively). Higher average values of  $P_n$  measured was  $34.04 \pm 1.6 \mu\text{mol m}^{-2}\text{s}^{-1}$  (Control - Sree Suvarna), NPQ was  $2.12 \pm 0.36$  (IHL - Sree Athulya) and  $q_N$  was  $0.85 \pm 0.03$  (Control - Sree Pavithra). Significant difference in fluorescence parameters and crop yield were observed between the light conditions and also between the cassava varieties. It was inferred that IHL has obviously affected the NPQ induction/relaxation process which resulted in reduced CBM compared to that under control condition.

**Keywords:** Cassava, intermittent high light condition, NPQ induction and relaxation, crop biomass

### Introduction

Cassava (*Manihot esculenta* Crantz.) popularly known as tapioca is an important staple food and industrial crop to a large population in Asia, Africa and Latin America. Cassava which is one of the main food source for carbohydrate is a drought resistant crop and is grown mainly by resource limited small scale farmers, which demands for the significance of maximum yield under diverse environmental conditions. Photosynthesis is the

basis of existence of life on earth. Light is one of the most prime requirements for photosynthesis and is also one of the most changing environmental factors. Plants need protection from the excess light greater than  $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$  which is usually encountered during sunny days. Several methods are adopted by plants to avoid absorption of excessive light by movement of leaves, adjustments in light harvesting antenna sizes etc (Hirth et al., 2013). Alternative electron transport pathways and

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thermal dissipation methods are also followed by plants which help to remove the excessively absorbed light energy thereby protecting the photosynthetic apparatus (Long et al., 1994; Niyogi, 1999; Zhao et al., 2017). Not all the light falling on leaves is used for photosynthesis and a portion of the incident light is emitted back as fluorescence or wasted as heat. Leaves in the field under natural conditions is exposed to fluctuating sunlight – full sunlight to shade and vice versa as the light intensity received by the plants is controlled by the position and angle of the leaves, time of the day, presence of clouds, presence of wind, its speed and direction and presence of upper leaves of same crop or other crops. Under full sunlight, when the light falling on the leaves is more than that can be used for photosynthesis, non photochemical quenching (NPQ) occurs as a mechanism to protect the photosynthetic apparatus from damaging (Muller et al., 2001). NPQ process involves quenching of singlet excited state Chl and happens via enhanced internal conversion to the ground state which is non radiative decay, in which the excess energy is harmlessly dissipated as heat. On exposure to high and low lights, xanthophylls cycle occurs which reduces the CO<sub>2</sub> fixation with minimal heat dissipation (Holt et al., 2004; Kromdijk et al., 2016; Ruban, 2016). In the xanthophyll cycle, under saturating high light intensity ( $>1000 \mu \text{ mol m}^{-2} \text{ s}^{-1}$ ), violaxanthin is converted rapidly via the intermediate antheraxanthin to zeaxanthin, which eventually leads to an increase in CO<sub>2</sub> fixation and this reaction is reversed under non saturating low light levels (Demmig Adams and Adams, 1992, 1996) where the zeaxanthin is converted to violaxanthin in the presence of zeaxanthin epoxidase (ZE). In higher plants, NPQ is the central process by which the excess energy is harmlessly dissipated as heat in order to protect the plants from photodamage (Muller et al., 2001).

The importance of NPQ for the protection of the photosynthetic apparatus is supported by its ubiquity in the plant kingdom (Niyogi and Truong, 2013). However, it has been reported that NPQ exerts an effect on the rate of PSII photochemistry by increasing the dissipation of excitation energy by non-radiative processes in the pigment matrices of PSII, which consequently results in a decrease in the efficiency of delivery of excitation energy for PSII photochemistry in low light intensities (Genty et al., 1989). In fact, it has been estimated that the slow reversibility of NPQ can limit the daily canopy carbon uptake of crops grown in the field by up to 30% (Zhu et al., 2004). By mutation in tobacco plants, faster NPQ switching rate was obtained which increased the biomass production by ~15% (Kromdijk et al., 2016).

Rapidly changing light conditions in the field affect carbon gain and plant productivity because photosynthetic responses to these light fluctuations are not instantaneous. So it has become necessary to understand how the plants in changing environmental light conditions acclimate to

light in the field (Lawson et al., 2012). As in the lower light condition, than that required for Pn saturation, the lack of light may limit photosynthesis and the extra time delay taken for the recovery of PSII antenna from the quenched to the unquenched state may affect the productive photosynthesis adversely (Kromdijk et al., 2016). Upon the transition from low to light conditions higher than that required for Pn saturation, the process of carbon fixation is not immediately started and a delay period up to several minutes may occur in the photosynthetic induction process, before attaining full rate of photosynthesis (Rabinowitch, 1956). Hence there exists a trade off between the metabolic cost of photodamage and the reduction in quantum yield due to NPQ and any unbalance in this trade off causes reduction in plant productivity up to 32% (Zhu et al., 2004).

The asymmetry between the rate of change of NPQ induction and NPQ relaxation could be worsened by repeated or prolonged exposure to fast changing light conditions. Consequently, the photosynthetic quantum yield of CO<sub>2</sub> fixation is also transiently depressed as the recovery rate of PS II antennae from the quenched to unquenched state also slows down on transition of incident light from high to low intensity (Kromdijk et al., 2016). It is seen that in several C3 and C4 crop species, a 10% to 15% limitation in photosynthesis occurred upon a slow rate of transition from low to high light as the leaves took time to reach steady state conditions (McAusland et al., 2016). Similarly, on transition from low to high light intensity, there is a delay in time taken for photosynthetic induction to achieve maximum photosynthetic efficiency (Chazdon and Pearcy, 1986; Taylor and Long, 2017). To find the cassava genotypes that are yield efficient under fluctuating light conditions, relation between tuber yield and fluorescence parameters, NPQ and Pn parameters of six different cassava genotypes under IHL and control light conditions was evaluated in this experiment. It was found that plant height and Above ground Biomass (ABM) was higher in IHL plants than in control plants, whereas, Crop Biomass (CBM) was higher in control plants. Also, it was seen that plants subjected to IHL showed higher NPQ and qN values and lower Pn values.

## Materials and Methods

### Plant growth conditions

Six popular cassava genotypes were selected for the study. All the plants were field grown, fertilized and kept well watered under natural conditions. Stem cuttings were planted with a plant spacing of 1m×1m. After four months, one set of the plants was maintained as control plants and another set of the plants was given additional intermittent high red actinic light (IHL) which provided an additional PAR of  $900 \mu \text{ mol m}^{-2} \text{ s}^{-1}$  (Fluorotronix, 200W, full spectrum Led plant grow light). The lights were mounted using a pole at a height of 1ft above the

top of the plants and the height of the light arrangements was adjusted periodically according to the plant height. In IHL, plants were exposed to high light for a period of 15 minutes followed by ambient light for 15 minutes during the day for the crop growth period. All the gas exchange and fluorescence measurements were taken on fifth fully grown leaf from the top.

### Physiological measurements

Licor-6400 portable photosynthesis system (Li-COR Inc, NE, USA) with leaf chamber fluorometer was used for Chlorophyll fluorescence and NPQ measurements. For dark measurements, the leaves were dark adapted by covering using black paper with clip for 20 minutes. This was conducted on plants grown under control (ambient light) condition and IHL condition. The maximum fluorescence ( $F_m$ ), variable fluorescence ( $F_v$ ) and the minimal fluorescence ( $F_o$ ) were measured on the dark adapted leaves. In both control and IHL plants, steady state fluorescence ( $F_s$ ), maximum fluorescence ( $F_m'$ ) and Variable Fluorescence ( $F_v'$ ) were measured under a fixed external PAR of  $3000 \mu\text{mol m}^{-2}\text{s}^{-1}$ . All the measurements were done each day between 11.00 and 13.30 hours at ambient day tropical temperature ( $30 \pm 2^\circ\text{C}$ ) at a  $\text{CO}_2$  concentration of  $350 \text{ mmol mol}^{-1}$  inside the leaf chamber.

### Leaf Chlorophyll estimation

Leaf chlorophyll estimation was done using DMSO method. The cut leaves were dissolved in 10 ml of DMSO and kept in oven at  $60^\circ\text{C}$  for 1 hour. After 1 hour, the solution was made to cool to room temperature and leaf chlorophyll content was estimated using Thermo Scientific Evolution 201 UV-Visible Spectrophotometer. For the determination of Chl a and Chl b, the following equation was used.

$$\text{Chl a (mg/g FW)} = (14.85 A_{665} - 5.14 A_{648})$$

$$\text{Chl b (mg/g FW)} = (25.48 A_{648} - 7.36 A_{665})$$

### Plant height and Biomass

All the plants under control and IHL conditions were harvested and plant height and above ground biomass and crop yield was determined.

### Data analysis

Box plots were used to compare the values at control and IHL conditions. The results were subjected to Two way Analysis of Variance (ANOVA) and TUKEY test (Assaad et al., 2015).

### Results and Discussion

To investigate the difference on plant growth under control and IHL conditions and also on genotype wise variations, plant height, fresh Above ground Biomass (ABM) and fresh Crop Biomass (CBM) were estimated.

Plant height and ABM were higher in IHL plants than in control plants, whereas, CBM was higher in control plants. Higher overall average values of plant height and ABM observed under IHL conditions were  $206.6 \pm 26.5 \text{ cm}$  and  $2.34 \pm 0.67 \text{ Kg}$  respectively (Table 2). And highest overall average of CBM was in control plants ( $3.12 \pm 0.86 \text{ Kg}$ ). Variety wise, maximum plant height was measured in M4 (IHL) of  $256.7 \pm 15.3 \text{ cm}$ , maximum ABM in the variety Sree Swarna (IHL) of  $3.06 \pm 1.36 \text{ Kg}$  and maximum CBM in the variety Sree Suvarna (control) of  $4.31 \pm 0.32 \text{ Kg}$ . (Fig. 1).

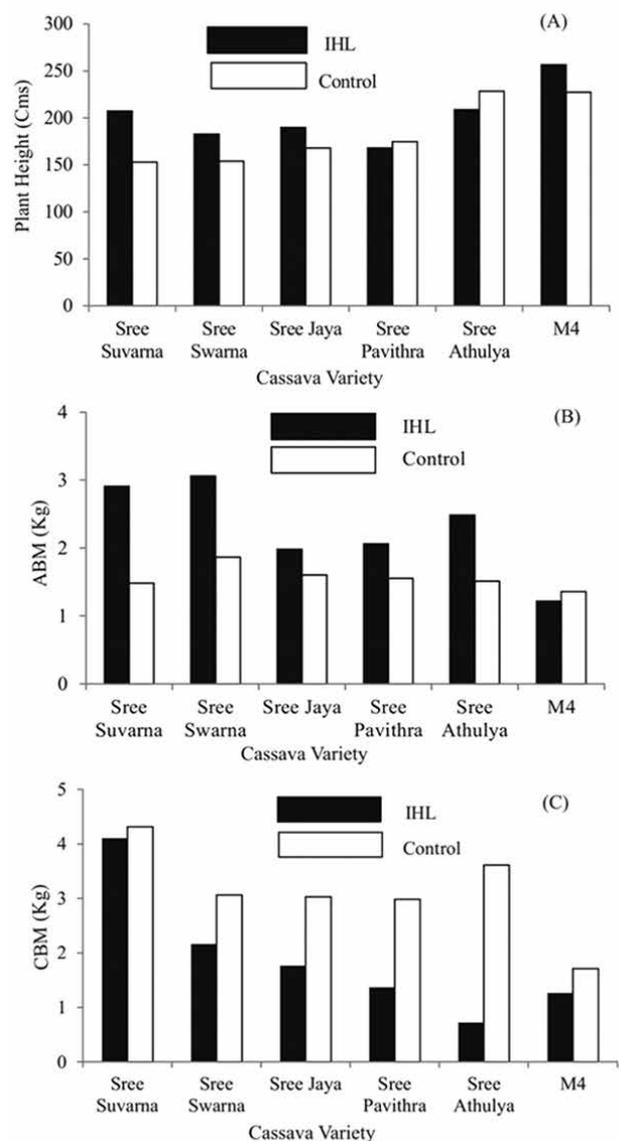


Fig. 1. (A) Plant height, (B) Above ground biomass (ABM), and (C) Crop Biomass (CBM) of cassava varieties under IHL and control conditions. The  $p$ -values obtained from 2 Way ANOVA and TUKEY tests were  $<0.05$  both between treatments and between varieties and the interaction of treatment and variety were 0.04, 0.097, 0.57, 0.116 and 0.006.

Table 1. Maximum net photosynthetic rate (Pn), NPQ and qN of cassava leaves grown under control and intermittent high light (IHL) conditions. Values were measured by giving a uniform external PAR of 3000  $\mu\text{mol m}^{-2}\text{s}^{-1}$ 

Treatment	Variable	Pn ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ )	NPQ	qN
IHL	Sree Suvarna	31±2.62 <sup>ab</sup>	1.49±0.02 <sup>ac</sup>	0.78±0.015 <sup>ab</sup>
	Sree Swarna	28.2±1.57 <sup>ab</sup>	1.67±0.03 <sup>ab</sup>	0.84±0.034 <sup>a</sup>
	Sree Jaya	25.3±1.18 <sup>ab</sup>	1.75±0.11 <sup>ab</sup>	0.81±0.021 <sup>ab</sup>
	Sree Pavithra	26.5±3.34 <sup>ab</sup>	1.95±0.15 <sup>ab</sup>	0.85±0.027 <sup>a</sup>
	Sree Athulya	28.8±0.86 <sup>ab</sup>	2.13±0.22 <sup>a</sup>	0.82±0.01 <sup>ab</sup>
	M4	22.8±2.95 <sup>b</sup>	1.64±0.1 <sup>ac</sup>	0.83±0.014 <sup>ab</sup>
Control	Sree Suvarna	34±0.95 <sup>a</sup>	0.99±0.24 <sup>c</sup>	0.71±0.049 <sup>bc</sup>
	Sree Swarna	32.4±1.31 <sup>a</sup>	1.57±0.02 <sup>ac</sup>	0.63±0.034 <sup>c</sup>
	Sree Jaya	31.2±0.97 <sup>ab</sup>	1.76±0.18 <sup>ab</sup>	0.79±0.009 <sup>ab</sup>
	Sree Pavithra	28.2±1.11 <sup>ab</sup>	1.43±0.08 <sup>bc</sup>	0.8±0.021 <sup>ab</sup>
	Sree Athulya	32.7±1.8 <sup>a</sup>	2.06±0.02 <sup>ab</sup>	0.8±0 <sup>ab</sup>
	M4	31.1±1.31 <sup>ab</sup>	1.67±0.10 <sup>ab</sup>	0.80±0.013 <sup>ab</sup>
P value	Treatment	<0.001	0.017	<0.001
	Var	0.043	<0.001	0.002
	T×V <sup>1</sup>	0.57	0.116	0.006

Table 2. Plant height, ABM, Crop BM, Leaf Chl a and Leaf Chl b of cassava leaves grown under control and intermittent high light (IHL) conditions.

Treatment	Variable	Plant height	ABM	Crop BM	Chl a	Chl b
IHL	Sree Suvarna	207±6.36 <sup>ab</sup>	2.91±0.082	4.11±0.25 <sup>ab</sup>	0.93±0.04 <sup>de</sup>	0.2±0 <sup>ac</sup>
	Sree Swarna	183±6.36 <sup>ab</sup>	3.06±0.784	2.16±0.64 <sup>ac</sup>	0.48±0.04 <sup>fg</sup>	0.07±0.01 <sup>d</sup>
	Sree Jaya	190±31.2 <sup>ab</sup>	1.98±0.681	1.77±0.63 <sup>ac</sup>	0.83±0.12 <sup>def</sup>	0.11±0.02 <sup>cd</sup>
	Sree Pavithra	194±30.4 <sup>ab</sup>	2.39±0.921	1.88±0.62 <sup>ac</sup>	0.87±0.06 <sup>def</sup>	0.13±0.01 <sup>cd</sup>
	Sree Athulya	209±17.3 <sup>ab</sup>	2.48±0.228	0.72±0.27 <sup>c</sup>	0.43±0.02 <sup>g</sup>	0.06±0.0 <sup>d</sup>
	M4	257±8.82 <sup>a</sup>	1.22±0.149	1.27±0.33 <sup>bc</sup>	0.76±0.01 <sup>eg</sup>	0.12±0.00 <sup>cd</sup>
Control	Sree Suvarna	153±19.1 <sup>b</sup>	1.48±0.084	4.31±0.18 <sup>a</sup>	1.61±0.05 <sup>a</sup>	0.29±0.03 <sup>a</sup>
	Sree Swarna	154±5.51 <sup>ab</sup>	1.87±0.384	3.06±0.19 <sup>ac</sup>	1.43±0.04 <sup>ab</sup>	0.18±0.01 <sup>bc</sup>
	Sree Jaya	168±15.2 <sup>ab</sup>	1.6±0.197	3.03±0.65 <sup>ac</sup>	1.4±0.10 <sup>ac</sup>	0.18±0.08 <sup>bc</sup>
	Sree Pavithra	175±9.6 <sup>ab</sup>	1.55±0.055	2.98±0.23 <sup>ac</sup>	1.36±0.18 <sup>ac</sup>	0.24±0.03 <sup>ab</sup>
	Sree Athulya	228±21.6 <sup>ab</sup>	1.51±0.066	3.61±1.27 <sup>ab</sup>	1.03±0.01 <sup>ce</sup>	0.18±0.01 <sup>bc</sup>
	M4	227±37 <sup>ab</sup>	1.36±0.366	1.71±0.45 <sup>ac</sup>	1.19±0.06 <sup>bcd</sup>	0.14±0.02 <sup>cd</sup>
P value	Treatment	0.068	0.006	0.002	<0.001	<0.001
	Var	0.009	0.193	0.002	<0.001	<0.001
	T×V <sup>1</sup>	0.625	0.535	0.252	0.04	0.097

Values are means ± SEM, n = 3 per treatment group. <sup>a-g</sup>Means in a row without a common superscript letter differ ( $P < 0.05$ ) as analyzed by two-way ANOVA and the TUKEY test. Different superscript letters indicate significant differences ( $P \leq 0.05$ ) between Control and IHL treatments  $T \times V^1 = \text{Treatment} \times \text{Variety}$  interaction effect.

Higher growth (plant height and above ground biomass) observed in IHL plants are mainly because of the higher daily dose of irradiant light in IHL plants compared with the control plants (Wagner et al., 2006). Lower crop productivity obtained under IHL is attributed to the

close correlation between the rate of recovery from the photoprotected state and the biomass production when the plants are subjected to periodical light fluctuation (Wang et al., 2002). A lagging response of photosynthesis occurs on occurrence of light fluctuation, which may

consequently result in limitation of crop productivity (Slattery et al., 2018). Any change in light intensity, even if it is for a few seconds may cause change in plant photosynthesis (Yamori et al., 2016).

Plants subjected to IHL showed an increase in NPQ and qN and significantly lower Pn compared to the corresponding values of control plants, when measured at a uniform PAR of  $3000 \mu \text{ mol m}^{-2} \text{ s}^{-1}$ . Highest Net photosynthetic rate (Pn) was observed in the variety Sree Suvarna under both control ( $34.05 \pm 1.64 \mu \text{ mol m}^{-2} \text{ s}^{-1}$ ) and IHL conditions ( $30.96 \pm 4.54 \mu \text{ mol m}^{-2} \text{ s}^{-1}$ ), with the same variety measuring highest CBM (Control-  $4.31 \pm 0.32 \text{ Kg}$ ). From the results, it can be seen that higher measured Pn explains for the obtained high productivity. Higher NPQ was observed in leaves exposed to IHL indicating that more energy was dissipated as heat, indicating that these leaves suffered photoinhibition (Table 1). Similar to NPQ, qN also showed higher values in IHL plants with the overall average values of NPQ as ( $1.58 \pm 0.36$  and  $1.76 \pm 0.23$  in control and IHL respectively) and qN as ( $0.76 \pm 0.07$  and  $0.82 \pm 0.03$  in control and IHL respectively). Highest crop biomass obtained, correlated with the highest leaf Chl a and Chl b values measured in the variety Sree Suvarna with values Chl a of  $1.61 \pm 0.09$  (control) and  $0.93 \pm 0.06$  (IHL). Correspondingly, maximum Chl b was measured in the same variety with values  $0.29 \pm 0.06$  and  $0.20 \pm 0.01$  under control and IHL respectively. Between control and IHL conditions, Chl a, Chl b, Pn, NPQ, qN, ABM and CBM showed significant difference, whereas, between the varieties except ABM all the parameters showed significant difference. Interactive effect of Treatment over cassava varieties was significant only for Chl a and qN.

Lower values observed in leaf Chl a and Chl b of IHL plants is also attributed to the increased irradiant light. With increase of average light intensity, decrease in the number of light harvesting units occur which results in the decrease of leaf chlorophyll content (Janssen et al., 2001; Friedman and Alberte, 1986). Under IHL condition, the plants were repeatedly switching between high and ambient light at an interval of 15 minutes each, which caused switching of NPQ induction and relaxation process. Even though plants under control light condition experienced light fluctuations upon cloud covering or upper leaf movement, compared to the IHL plants, the variation was much less. In a longer term, the time delay between NPQ induction and relaxation was intensified by repeated exposure to high and ambient light in IHL plants and consequently the time taken for PSII reversibility on high to low light transition resulted in low crop yield (Long et al., 1994; Zhu et al., 2004).

The enhancement in NPQ under IHL condition is apparently associated with dissipation of photon energy by NPQ, thus preventing damage to the photochemical pathway before the energy is accumulated as reactive

intermediate substances in the photosynthetic chain (Li et al., 2014; Ralph et al., 2002). Increase in NPQ is also attributed to the xanthophylls cycle activity (Ruban, 2016). At a PAR of  $3000 \mu \text{ mol m}^{-2} \text{ s}^{-1}$ , the plants under IHL were exposed to additional light intensity which further increased the NPQ response and hence higher NPQ values were obtained when compared to those under control light condition.

## Conclusion

Non uniformity of environmental conditions and fluctuation in light is inherent in nature. It is seen that the plants have natural mechanisms to improve protection process, when light increases. Even though, higher plant growth and above ground biomass was found higher in IHL plants, higher crop biomass was obtained in plants under ambient light conditions. In IHL plants, variation in light intensity caused either NPQ induction or relaxation which consequently reduced the photosynthetic efficiency. Regardless of application of IHL, the plants were not able to properly utilize the extra light energy in terms of crop yield which consequently reduced the tuber biomass. It can be concluded from this study that plants grown under IHL condition had greater plant growth and above ground biomass, but had low crop productivity. This signifies the relation between NPQ variation with fluctuating light and crop productivity. This study was done on six popular varieties of cassava and the result showed that the variety Sree Suvarna which has higher crop yield at control condition ( $4.31 \pm 0.32 \text{ Kg}$ ), also has higher crop yield under IHL condition ( $4.11 \pm 0.44 \text{ Kg}$ ) and found to be tolerant to light fluctuations. Significant difference in fluorescence parameters and crop yield were observed between the light conditions and also between the cassava varieties. Further detailed research could be done to evaluate more cassava varieties that shows good tolerance to light fluctuation and has better performance in terms of crop yield under varying light condition.

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## References

- Assaad, H. I., Hou, Y., Zhou, L., Carroll, R.J. and Wu, G. 2015. Rapid publication-ready MS-Word tables for two-way ANOVA. *Springer Plus*, **4**:33.
- Chazdon, R. L. and Pearcy, R.W. 1986. Photosynthetic responses to light variation in rainforest species. *Oecologia*, **69**:524-531.
- Demmig-Adams, B., and Adams, W.W. 1992. Photoprotection and other responses of plants to high light stress. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, **43**:599-626.

- Demmig-Adams, B., Adams III, W. W., Barker, D. H., Logan, B. A., Bowling, D. R. and Verhoeven, A. S. 1996. Using chlorophyll fluorescence to assess the fraction of absorbed light allocated to thermal dissipation of excess excitation. *Physiol. Plant.*, **98**:253-264.
- Friedman, A. L. and Alberte, R. S. 1986. Biogenesis and light regulation of the major light harvesting chlorophyll-protein of diatoms. *Plant Physiol.*, **80**:43-51.
- Genty, B., Briantais J-M., and Baker, N. R. 1989. The relationship between the quantum yield of photosynthetic electron-transport and quenching of chlorophyll fluorescence. *Biochim. Biophys. Acta*, **990**:87-92.
- Hirth, M., Dietzel, L., Steiner, S. et al. 2013. Photosynthetic acclimation responses of maize seedlings grown under artificial laboratory light gradients mimicking natural canopy conditions. *Front. Plant Sci.*, **4**:1-12.
- Holt, N. E., Fleming, G. R., and Niyogi, K. K. 2004. Toward an understanding of the mechanism of nonphotochemical quenching in green plants. *Biochemistry*, **43**:8281-8289.
- Janssen, M., Slenders, P., Tramper, J., Mur, L.R., Wijffels, R.H. 2001. Photosynthetic efficiency of *Dunaliella tertiolecta* under short light/dark cycles. *Enzyme Microb Tech.*, **29**:298-305.
- Kromdijk, J., Glowacka, K., Leonelli, L., Gabilly, S. T., Iwai, M., Niyogi, K. K. and Long, S. P. 2016. Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science*, **354**:857-861.
- Lawson, T., Kramer, D. M. and Raines, C. A. 2012. Improving yield by exploiting mechanisms underlying natural variation of photosynthesis. *Current Opinion in Biotech.*, **23**:215-220.
- Li, T., Heuvelink, E., Dueck, T.A., Janse, J., Gort, G. and Marcelis, L.F.M. 2014. Enhancement of crop photosynthesis by diffuse light: quantifying the contributing factors. *Annu Bot*, **114**:145-156.
- Long, S. P., Humphries, S. W. and Falkowski, P. G. 1994. Photoinhibition of photosynthesis in nature. *Annu Rev of Plant Physio and Plant Mol Biol.*, **45**:633-662.
- McAusland, L., Vialet-Chabrand, S., Davey, P., Baker, N. R., Brendel, O. and Lawson, T. 2016. Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency. *New Phytol.*, **211**:1209-1220.
- Muller, P., Li, X.P. and Niyogi, K.K. 2001. Non-photochemical quenching. A response to excess light energy. *Plant Physiol.*, **125**:1558-1566.
- Niyogi, K.K. 1999. Photoprotection revisited: genetic and molecular approaches. *Annu Rev Plant Physiol Plant Mol Biol*, **50**:333-359.
- Niyogi, K.K. and Truong, T.B. 2013. Evolution of flexible non-photochemical quenching mechanisms that regulate light harvesting in oxygenic photosynthesis. *Current opinion in plant Biol.*, **163**:307-314.
- Rabinowitch, E. I. 1956. Photosynthesis and related processes. *Interscience Publishers, Inc., New York & London*. **2**(2):1211-2088.
- Ralph, P.J., Polk, S., Moore, K.A., Orth, R.J. and Smith, W.A. 2002. Operation of the xanthophyll cycle in the seagrass *Zostera marina* in response to variable light. *J. Exp. Mar. Biol. Ecol.*, **271**:189-207.
- Ruban, A.V. 2016. Non-photochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protection against photodamage. *Plant Physiol.* **170**:1903-1916.
- Slattery, R., Walker, B., Weber, A. and Ort, D. 2017. The Impacts of Fluctuating Light on Crop Performance. *Plant Physiol.*, **176**(2):990-1003.
- Taylor, S. H. and Long, S. P. 2017. Slow induction of photosynthesis on shade to sun transitions in wheat may cost at least 21% of productivity. *Philos. Trans. R. Soc. Lon. B. Biol. Sci.*, **372**(1730):2016.0543.
- Wagner, H., Jakob, T. and Wilhelm, C. 2006. Balancing the energy flow from captured light to biomass under fluctuating light conditions. *New Phytol.* **169**:95-108.
- Wang, Q., Zhang, Q.D., Zhu, X.G., Lu, C.M., Kuang, T.Y. and Li, C.Q. 2002. PSII photochemistry and xanthophyll cycle in two super high yield rice hybrids, Liangyoupeijiu and Hua-an 3, during photoinhibition and subsequent restoration. *Acta Botanica Sinica*, **44** (11):1297-1302.
- Yamori, W., Makino, A. and Shikanai, T. 2016. A physiological role of cyclic electron transport around photosystem I in sustaining photosynthesis under fluctuating light in rice. *Nat. Sci. Rep.*, **6**:20147.
- Zhao, X., Chen, T., Feng, B., Zhang, C., Peng, S., Zhang, X., Fu, G. and Tao, L. 2017. Non-photochemical Quenching Plays a Key Role in Light Acclimation of Rice Plants Differing in Leaf Color. *Front in Plant Sci.*, **7**:1968.
- Zhu, X.G., Ort, D.R., Whitmarsh, J. and Long, S.P. 2004. The slow reversibility of photosystem II thermal energy dissipation on transfer from high to low light may cause large losses in carbon gain by crop canopies: a theoretical analysis. *J. Exp. Bot.*, **55**:1167-1175.