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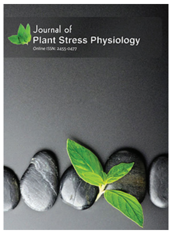
Research Article



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Physiological responses of cowpea simultaneously exposed to water deficit stress and varying light intensities at vegetative and reproductive growth stages

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ABSTRACT

A combination of stresses as it occurs on the field poses more challenges to crop production than individual stress. Crops' response to single stress also differs from that of combined stresses. The morpho-physiological responses of two cowpea varieties (IT89KD-288 and IT99K573-1-1) to a combination of stresses (water deficit stress and high light intensity) were investigated at different growth stages. Three levels of light intensities (L3: 259 Lux- 36%, L2: 394 Lux-55% and L1: 710.2 Lux-100%) were imposed using one, two and zero layer(s) of the net, respectively, while, water deficit stress at four levels (W1: no water stress; 0-5 bars, W2: moderate water stress; 5-15 bars, W3: moderately-severe; 15-40 bars and W4: severe water stress; 40 -70 bars) was imposed differently at vegetative and reproductive growth stages. Data were collected on the cowpea yield, Leaf Temperature (LT), Chlorophyll (C), Photosynthesis (P), Stomatal Conductance (SC) and Canopy Transpiration Rate (CTR). Exposure to W4 under L1 considerably reduced cowpea yield by 80% compared to those grown under L3 and full watering. Reduced light intensity enhanced cowpea grain yield irrespective of water deficit stress and IT89KD-288 was superior to IT99K573-1-1. Reduction in light intensity also increased the SC from 55.18 in L1 to 76.88 in 36 % L3. Full light intensity without water stress (100% light intensity), increased C content, while severe water stress reduced the C content and CTR. Photosynthesis was, however, reduced under low light intensity compared to 100% light intensity. It was also observed that water deficit stress imposed at the reproductive stage did not affect P, CTR and SC unlike that of the vegetative stage. In conclusion, reduced light intensity enhanced cowpea tolerance to water deficit and increased yield. Cowpea response was dependent on growth stage, variety and severity of stress.

KEYWORDS: Light intensity, drought, cowpea, photosynthesis, photo-inhibition

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INTRODUCTION

Climate change poses a great challenge to food security due to the increase in the severity of environmental stresses. Light and water are among the major environmental factors that determine plant physiological performances and growth (Barnabás *et al.*, 2008; Kaushal *et al.*, 2016). They are required for many physiological and biochemical processes in plants (Yang & Zhang, 2006; Du *et al.*, 2010). Water and light are major requirements for plant growth and development. They control the degree of opening and closing of the stomata and water balance (Yu *et al.*, 2004). Water is a major reactant for processes like photosynthesis and serves as a solvent for many hydrolytic reactions. Lack of water and excessive heat arising from high light intensity cause considerable yield loss in agriculture (Farooq *et al.*, 2009; Singh & Reddy, 2011; Kaushal *et al.*, 2016; Balla *et al.*, 2019). It alters various metabolic events like plant-water relations, photosynthetic gas exchange, cell turgor, source-sink relationship, and chloroplast function (Kawamitsu *et al.*, 2000; Khaled, 2010; Anjum *et al.*, 2011).

Light is also important for the formation of chlorophyll, carbon assimilation, transpiration and regulation of growth and development in plants (Dutta, 2003; Lombardini, 2006). The light requirement, however, varies depending on crop species. Exposing green plants to excessive light can cause damage to photosynthetic apparatus (Rollins *et al.*, 2013). The photosynthetic activity of chloroplast is seriously affected when leaves are exposed to excessive light energy, due to oxidative stress induced by the production of reactive oxygen species (Öpik *et al.*, 2005). High light intensity is always accompanied by high temperature and an increase in water loss through evapotranspiration. Depending on the intensity, light has an important role in plants' growth and physiological development.

Combination of stresses such as high light intensity coupled with water deficit stress has been reported to cause photoinhibition, reduction in photosynthesis and yield loss (Pinheiro & Chaves, 2011; Goufo *et al.*, 2017; Qaseem *et al.*, 2019). They disrupt plant metabolism and induce oxidative stress. The detrimental effects of a combination of stress factors like drought and heat stress on crop productivity have been widely reported (Wang & Huang, 2004; Xu & Zhou, 2006; Rollins *et al.*, 2013; Qaseem *et al.*, 2019). Compared to single stress, their combination was reported to stimulate a new pattern of defense mechanisms (Rizhsky *et al.*, 2004). The difference in the metabolite profiling of the plants exposed to single stress and those exposed to combined stresses has been observed. Sugar, for example, was found to replace the common proline that is produced under single stress (Rizhsky *et al.*, 2004). These effects of drought and excessive light intensity on crops are more devastating in developing countries where rain-fed agriculture is being practised (Gagné-Bourque *et al.*, 2016; Goufo *et al.*, 2017).

Cowpea, *Vigna unguiculata* (L.) Walp is a dicotyledonous plant belonging to the family Fabaceae. It is one of the most important food legumes and an annual crop widely cultivated in tropical and subtropical regions. Cowpea leaves, green pods and grain are used for human consumption while the herbage can be used as green manure and animal feed (Shetty *et al.*, 2013). The grain is a good source of human protein, while the haulms are a valuable source of livestock protein (Fatokun, 2015). It is also a source of income for many smallholder farmers in sub-Saharan Africa (Owade *et al.*, 2019). It contributes to the sustainability of cropping systems and soil fertility improvement in marginal lands (Singh *et al.*, 2002; Singh, 2004). Though cowpea is a light loving plant and a relatively drought tolerant plant with an inbuilt ability to survive minimal level of stress through different tolerance mechanisms (Ewansiha & Singh, 2006; Fatokun *et al.*, 2012; Hall, 2012; Goufo *et al.*, 2017), but cowpea yield has been reported to be reduced under stress (Li *et al.*, 2008; Hayatu *et al.*, 2014). Its response to environmental stress also depends on the type of stress, stress duration, genotype, growth stage, the combination of stresses and severity (Zhu *et al.*, 2005; Rampino *et al.*, 2006; Zhou *et al.*, 2007; Singh & Reddy, 2011; Balla *et al.*, 2019). Response to single stress differs from that of multiple stresses (Goufo *et al.*, 2017). As reported by Qaseem *et al.* (2019), drought, high temperature and a combination of both decreased physiological and yield traits in crops irrespective of the genotype and the time of stress application. Significant differences in water stress tolerance have been reported to exist among cowpea genotypes (Singh & Reddy, 2011).

With the increasing level of environmental stress due to climate change, the development of stress tolerant crops is pertinent. Plants generally respond to changes through their physiological processes, such as the rate of photosynthesis, respiration, transpiration and stomatal conductance (Zhao *et al.*, 2006). For instance, photosynthesis has been reported to show a linear relationship with soil water content and SC (Singh & Reddy, 2011). Photosynthetic rate and SC were also found to decline in response to drought. Stomatal conductance influences the supply of CO_2 to the leaf intercellular spaces for photosynthesis and determines the rate of water loss (Yang & Zhang, 2006; Du *et al.*, 2010). Understanding the morpho-physiological responses of different crops to single and multiple stress(es) is, however, important in determining the appropriate traits for genetic improvement. Interactions between cowpea physiology and grain yield in response to single and combined stress(es) need to be investigated at various stages of plant development. However, little information is available on the response of cowpea to a combination of drought stress and variation in light intensities. This study was carried out to (a) determine the morpho-physiological responses of two cowpea varieties to water deficit stress under varying light intensities and, (b) determine the effect of different growth stages on the physiological responses of cowpea to the sole and combined stress(es) of water deficit and varying light intensities.

MATERIALS AND METHODS

Experimental Location, Soil Collection and Pretreatments

The experiment was carried out during the dry season at the crop garden of the Department of Crop Protection and Environmental Biology, University of Ibadan, Ibadan, Oyo state, Nigeria. The soil used for the experiment was collected at the surface layer (0-20 cm) from the departmental crop garden, air-dried, broken up, homogenized and sieved through a 2-mm mesh screen and the composite sample was taken for physico-chemical analysis following standard procedures. The soil was slightly acidic and the textural class was loamy sand. The nitrogen, organic matter and available phosphorus were 0.21 g/kg, 0.77 g/kg and 57.01 g/kg, respectively. Five-kilogram of air-dried soil was weighed into different experimental pots and arranged under different light intensity chambers and open fields (For full light intensity; Control).

Construction of Light Intensity Chambers

To vary light intensity, three wooden chambers were constructed using wooden frames of 1.9 by 1.9 by 3.2 m in dimension. Each chamber was covered on all sides by different layers of 1 mm-size green mesh except 100% light intensity (100%:710 Lux = L1) which was left in an open field without shade to receive full sunlight, 55% light intensity (55%: 394 Lux = L2) was achieved by covering with two layers of mesh net (i.e. 45% light reduction) and to further reduce the amount of light intensities to 36% light intensity (36%: 259 Lux= L3) was by covering with three layers of mesh net (i.e. 64% light reduction) (Akinyele, 2007; Aderounmu, 2010). The available light intensity under each chamber was read daily using a light meter and the average was determined at the end of the experiment. Environmental parameters like relative humidity and soil temperature were also determined under different light intensity chambers using a whirling hygrometer and soil thermometer, respectively. The mean light intensity under 100% light intensity was 710.2 Lux, temperature (39.23°C) and relative humidity was 55.80% while, reduction in light intensity to 36% had 259.0 Lux, temperature, 30.25°C and relative humidity of 64.40%.

Experimental Design, Planting and Treatments Imposition

The experiment was laid out in a 2×2×3×4 factorial experiment, fitted in Randomized Complete Block Design (RCBD) and replicated three times to give a total number of 48 treatment combinations and 144 experimental pots. The treatments were 2 stages of water stress imposition [water deficit stress imposed at the Vegetative Stage (VS) for 3 weeks starting from 2 Weeks After Sowing (WAS) at the seedling stage till the onset of flowering and water deficit stress imposed at the Reproductive Stage (RS) from the onset of flowering at 6 WAS till maturity under different light intensities], two varieties of cowpea seeds (IT89KD-288 and IT99K-573-1-1) which were sourced from the International Institute of Tropical Agriculture (IITA), Ibadan, Oyo state, Nigeria, three levels of light intensities (100% light intensity; L1, 55% light intensity; L2 and 36% light intensity; L3) and four levels of water deficit stress [W1= 100% FC, no water stress (0-5 bars), W2= 75% FC: Moderate water stress (5-15 bars), W3=50% FC: Moderately-severe (15-40 bars), W4= 25% FC: Severe water stress (40 -70 bars)]. Each pot was filled with 5 kg soil and the field capacity of the 5 kg soil was first determined following standard procedure. Each pot was first supplied with 500 ml of water before planting based on the field capacity of the soil. Four seeds of cowpea were sown in each pot and later thinned down to 2 seedlings per pot after seedling emergence. After planting, and before stress imposition, the amount of water for watering was reduced to 250 ml and each pot was receiving 250 ml of water daily. To impose water deficit stress at the vegetative stage and at different levels, two weeks after planting, the water was further reduced to 75% (187 ml) for the pots receiving moderate water stress and the tensiometer reading of 5-15 bars (W2), 50% (125 ml of water everyday) to give moderately-severe water deficit stress of 15-40 bars (W3) and 25% (62.5 ml of water everyday) to impose severe water deficit stress of 40 -70 bars (W4). These bars were achieved using soil probe tensiometers which were carefully inserted in each pot. The control pots with no water stress and maintained at 0-5 bars and those that were to be stressed at the reproductive stage were receiving 250 ml of water every day. Normal watering of 250 ml/day was resumed to the plants after three weeks of stress imposition at the vegetative stage. The plants that were stressed at the vegetative stage started receiving normal watering at five weeks after planting. The same procedure was followed for the plants that were stressed at the reproductive stage (i.e. from the onset of flowering till maturity).

Data Collection

Data were collected on physiological and yield parameters. The physiological parameters were leaf photosynthesis (chlorophyll fluorescence and photosynthetic efficiency of the plant) which was determined automatically using the Portable Fluorometer (leaf photosynthesis system; LI-6400XT, LI-COR Bioscience, USA) and the measurements were taken when the Photosynthetically Active Radiation (PAR) was 1000-1500 nanometer. Stomatal Conductance was determined using Porometer (SC-1 Leaf Porometer, DECAGON, USA). The instrument was used for measuring the area of the stomatal openings of a leaf by the amount of gas passing through it. It is designed to measure vapour flux from the leaf through the stomata. It shows the difference between transpiring leaves and ones that have shut down. This was carried out by calibrating and clipping the sensor head of the porometer onto the leaf and recording SC within 30 seconds during the mid to late morning under saturating light conditions. The time is for the leaf to release enough water vapour that would bring the humidity of the instrument's air chamber to a stable value. The readings were displayed and saved for downloading later. The canopy transpiration rate was determined using an Infrared Camera (Leaf Chamber Fluorometer, LICOR-6400-40, LI-COR, USA) which measures the rate of transpiration under each constructed light chamber. Leaf temperature using an infrared leaf thermometer (Model C-1600, Eco Scientific, China) and the Chlorophyll contents of older and younger leaves using SPAD Meter (SPAD-502, Konica Minolta, Japan). Crop water stress index (CWSI) was also estimated using canopy and air temperature, and this was measured by an infrared camera (InfReC, R300) (Idso *et al.*, 1981) using the formula:

$$CWSI = \frac{(Tc - Ta) - D2}{D1 - D2}$$

Where:
D1 is the maximum canopy and air temperature difference for a stressed crop (the maximum stressed baseline),
D2 is the lower limit canopy and air temperature difference for a well-watered crop (the non-water-stressed baseline), Tc is the measured canopy surface temperature (°C), and Ta is the air temperature (°C).

The yield parameters include the number of pods, pod weight per plant, pod length, total number of grains per pod/per plant and seed dry weight. Plant biomass (Root and shoot dry weights) was determined after oven-drying the harvested plants at 60°C for 72 hours.

Data Analysis

All data collected were analysed using analysis of variance (ANOVA) with the DSAASTAT software package. The treatment means were separated for significant differences using Duncan multiple range test (DMRT) at 5% level of probability. Harvest Index (HI), was computed using the formula:

$$\text{Harvest index(HI)} = \frac{\text{Economic yield}}{\text{Biological yield}}$$

where Economic yield is the total grain weight and Biological yield is the total plant weight (Root and Shoot)

RESULTS

Sole and interactive effects of different light intensities and water deficit stress at vegetative and reproductive stages on physiological parameters of the two cowpea varieties

Leaf Photosynthesis ($\mu molm^{-2}s^{-1}$)

There was a general decrease in the leaf photosynthesis of the two cowpea varieties throughout the growing period in response to water deficit stress and different light intensities. However, there were variations among the treatments and plant growth stages. On the sole effect of light intensity on photosynthesis, reduction in light intensity had a positive effect on leaf photosynthesis as the highest mean value was recorded at 36% light intensity, while the least mean value was recorded at 100% light intensity. The LP was reduced from 11.27 in 36% to 4.50 in 100% light intensity. (Figure 1A). On the overall effect of different water deficit regimes on leaf photosynthesis irrespective of light intensity, the water stress treatments were not different from each other. The difference was, however, observed in the two varieties and IT99K-573-1-1 had a higher mean value compared to IT89KD-288 (Figure 2A). Combined exposure to 100% light intensity and severe water stress at the vegetative stage (L1W4VS), reduced the leaf photosynthesis and the lowest mean value was recorded in this treatment compared to other treatments. At 3 WAS and a week after imposition of water deficit stress at the vegetative stage, though, not significantly different from other treatments, but cowpea plant grown under a reduced light intensity of 36% and treated with moderately-severe water stress at the vegetative stage (L3W3VS) had the highest mean value of leaf photosynthesis at this stage. At 6 WAS, a general reduction in photosynthesis was observed in all the treatments compared to 3 WAS and the reduction was more pronounced in cowpea plants exposed to severe water deficit stress at the vegetative stage. At 9 WAS, the values were still reduced and the reduction was more in 100% light intensity. However, amongst the treatments imposed with water deficit stress at the reproductive stage, the highest mean value of photosynthesis was still recorded under 36% light intensity in cowpea plants exposed to moderate water stress at the reproductive stage (L3W2RS) and was not significantly different from L3W1RS, while the lowest mean value was

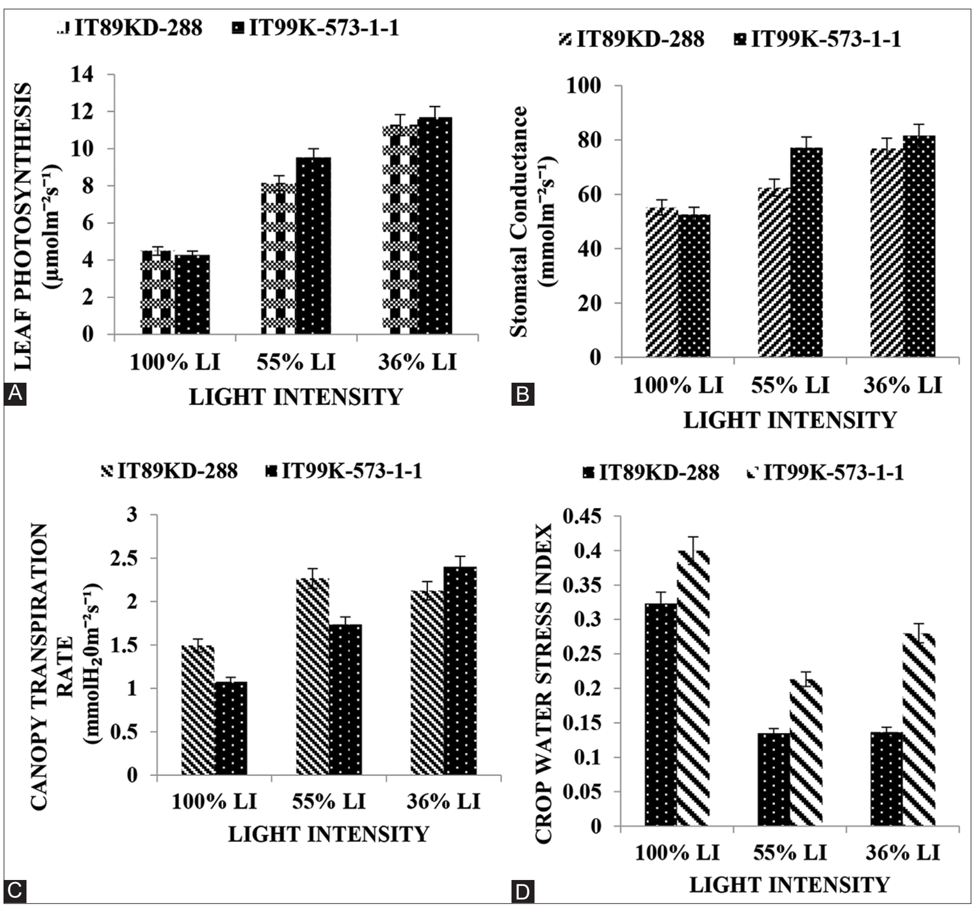

Figure 1: Sole effect of varying light intensities on physiological parameters of IT89KD-288 and IT99K-573-1-1 cowpea varieties (Bars of chart represent standard error)
LI: Light Intensity

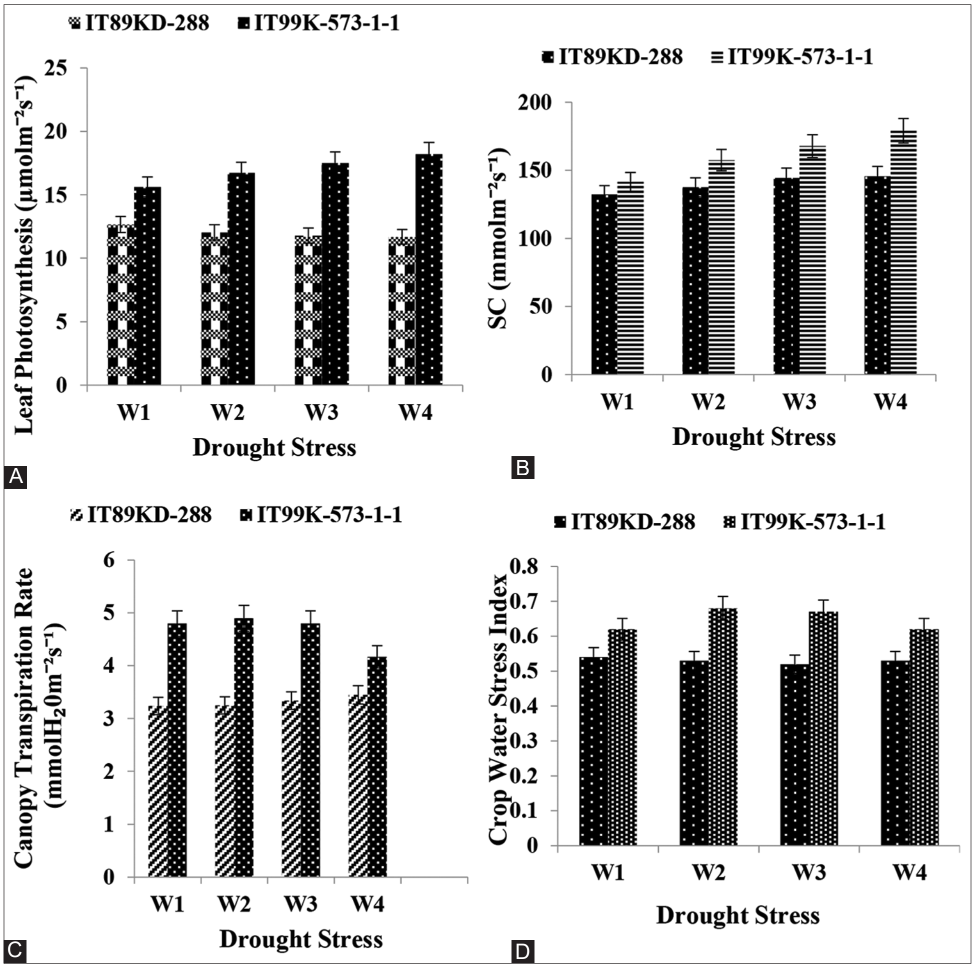

Figure 2: Sole effect of drought stress on physiological parameters of IT89KD-288 and IT99K-573-1-1 cowpea varieties.
NB: W1: Control, no water stress (0-5 bars), W2: Moderate water stress (5-15 bars), W3: Moderately-severe (15-40 bars), W4: Severe water stress (40 -70 bars)

recorded in L1W1RS (100% light intensity and no water stress at reproductive stage). The response was similar for both varieties except that IT99K-573-1-1 had greater leaf photosynthesis at 6 WAS compared to IT89KD-288 (Table 1).

Stomatal Conductance (mmolm^{-2}s^{-1})

Generally, for the two varieties of cowpea, the SC was reduced as the plant aged. It was more at 3 WAS compared to 6 and 9 WAS. Water stress and high light intensity also reduced the SC. Cowpea grown under reduced light intensity had higher SC at 3 WAS (a week after imposition of water deficit stress) than those exposed to high light intensity irrespective of water deficit stress. At 6 WAS, there was a general reduction in the SC of the cowpea leaves under different light intensities. Those stressed at the vegetative stage were more affected than the unstressed plants. At 9 WAS, there was a greater reduction and the water deficit stress imposed at the reproductive stage reduced the SC of the stressed compared to the unstressed (Table 2). Reduction in light intensity increased the SC from 55.18 in 100% LI to 76.88 in 36 % LI. The highest mean value was, therefore, recorded under 36% light intensity which was significantly different from other light intensities while the least mean value was recorded at 100% light intensity (Figure 1B). Meanwhile, as water stress became severe, the SC was decreasing and a similar trend was observed for the two cowpea varieties. The SC was the highest under no water stress (Figure 2B). The trend was the same for the two cowpea varieties but, IT99K-573-1-1 performed better than IT89KD-288 (Figure 1B). For the water stress, this variety also performed better than the other variety.

Canopy Transpiration Rate (CTR)

Generally, the CTR was also influenced by water deficit stress in both varieties. At 3 WAS, the CTR of the stressed and the unstressed was not significantly different from each other but at 6 WAS, water deficit stress drastically reduced the CTR and the reduction was more pronounced under high light intensity. At this period, the lowest CTR value was recorded under 100% light intensity combined with severe water stress at the vegetative stage. At 9 WAS, the highest CTR value was recorded under 36% light intensity in plants exposed to severe water stress at the reproductive stage, while the lowest was recorded under 100% light intensity (Table 3). The water stress generally reduced the CTR and as the stress became severe at the 9 WAS, the CTR was decreasing (Table 3). However, the overall result of

Table 1: Interactive effects of different light intensities and drought stress at vegetative and reproductive stages on leaf photosynthesis ($\mu molm^{-2}s^{-1}$)

Light intensity	Water regimes	Growth stages	IT89KD-288			IT99K-573-1-1		
			3WAS	6WAS	9WAS	3WAS	6WAS	9WAS
L3	W1	RS	21.32	14.00	10.78	20.43	22.63	10.93
	W2		19.43	16.25	11.78	22.53	23.85	11.37
	W3		23.44	16.86	11.18	21.87	24.75	11.92
	W4		23.20	22.14	11.37	24.00	25.80	12.52
	W1	VS	21.43	10.26	0.00	21.43	11.13	0.00
	W2		21.65	8.24	0.00	21.65	12.25	0.00
	W3		24.00	8.07	0.00	24.00	13.35	0.00
	W4		21.48	7.29	0.00	21.48	14.21	0.00
L2	W1	RS	22.67	18.45	7.18	23.00	21.92	8.43
	W2		21.48	18.95	8.05	21.44	22.97	8.66
	W3		19.54	18.00	8.35	22.18	23.07	10.11
	W4		22.65	15.92	9.00	20.43	24.50	10.87
	W1	VS	21.84	8.65	0.00	21.84	9.10	0.00
	W2		21.55	7.57	0.00	21.55	10.29	0.00
	W3		21.44	7.32	0.00	21.44	10.58	0.00
	W4		21.82	6.95	0.00	21.82	12.30	0.00
L1	W1	RS	20.65	18.90	4.25	21.43	21.32	5.43
	W2		20.67	15.22	4.44	20.86	22.67	0.00
	W3		19.70	14.22	4.54	21.09	22.68	5.62
	W4		21.80	12.56	4.75	20.88	21.92	6.01
	W1	VS	20.89	5.70	0.00	18.89	7.67	0.00
	W2		19.85	6.00	0.00	19.85	8.42	0.00
	W3		20.80	6.26	0.00	20.80	10.54	0.00
	W4		20.12	5.26	0.00	20.12	10.57	0.00
	LSD		1.52	2.52	1.6	1.52	2.52	1.6

NB: RS: Imposition of drought stress at reproductive stage, VS: Imposition of drought stress at vegetative stage. L3, L2 and L1=25, 50 and 100% light intensity; W1, W2, W3, W4=no water stress (0-5 bars), moderate water stress (5-15 bars), moderately-severe (15-40 bars), severe water stress (40-70 bars), respectively; WAS: Weeks after Sowing

Table 2: Interactive effects of different light intensities and drought stress at vegetative and reproductive stages on SC ($mmolm^{-2}s^{-1}$)

Light intensity	Water regimes	Growth stages	IT89KD-288			IT99K-573-1-1		
			3WAS	6WAS	9WAS	3WAS	6WAS	9WAS
L3	W1	RS	171.04	198.94	58.08	198.43	201.07	71.39
	W2		260.60	206.66	79.54	281.87	245.20	77.54
	W3		213.47	210.20	81.37	183.30	267.31	79.67
	W4		239.44	218.65	88.54	298.67	290.11	97.98
	W1	VS	236.32	77.63	0.00	241.65	96.81	0.00
	W2		212.32	83.60	0.00	218.98	97.58	0.00
	W3		217.17	86.35	0.00	258.17	97.20	0.00
	W4		214.54	87.45	0.00	251.21	104.57	0.00
L2	W1	RS	241.12	175.43	49.48	245.32	200.35	60.32
	W2		222.83	188.30	55.94	265.43	234.65	80.25
	W3		204.10	192.12	60.44	236.00	260.00	82.07
	W4		208.21	205.67	83.94	179.43	261.66	86.21
	W1	VS	235.48	86.43	0.00	228.81	86.61	0.00
	W2		210.55	86.54	0.00	244.88	87.14	0.00
	W3		213.65	89.17	0.00	232.55	90.18	0.00
	W4		220.10	93.36	0.00	226.77	98.94	0.00
L1	W1	RS	179.20	177.02	56.45	176.33	179.26	54.54
	W2		200.79	178.98	60.20	275.14	190.15	0.00
	W3		208.54	197.49	47.54	206.11	201.82	68.65
	W4		190.45	174.54	56.54	177.77	221.14	87.43
	W1	VS	199.17	77.87	0.00	194.54	84.11	0.00
	W2		199.45	81.09	0.00	225.45	89.75	0.00
	W3		196.07	90.88	0.00	207.00	89.88	0.00
	W4		199.56	93.30	0.00	201.32	97.79	0.00
	LSD		23.06	21.14	10.89	23.06	21.14	10.89

NB: RS: Imposition of drought stress at reproductive stage, VS: Imposition of drought stress at vegetative stage. L3, L2 and L1=25, 50 and 100% light intensity; W1, W2, W3, W4=no water stress (0-5 bars), moderate water stress (5-15 bars), moderately-severe (15-40 bars), severe water stress (40-70 bars), respectively; WAS: Weeks after Sowing

Table 3: Interactive effects of different light intensities and drought stress at vegetative and reproductive stages on canopy transpiration rate (mmol $H_2Om^{-2}s^{-1}$)

Light intensity	Water regimes	Growth stages	IT89KD-288			IT99K-573-1-1		
			3WAS	6WAS	9WAS	3WAS	6WAS	9WAS
L3	W1	RS	6.75	3.54	1.52	9.12	6.04	1.58
	W2		4.98	3.72	0.57	5.25	6.73	1.86
	W3		6.48	4.48	2.76	8.44	6.15	2.79
	W4		4.89	4.74	3.66	5.47	5.65	3.39
	W1	VS	7.02	3.35	0.00	7.02	2.51	0.00
	W2		8.12	2.82	0.00	8.11	3.48	0.00
	W3		4.97	2.72	0.00	4.97	2.28	0.00
	W4		6.13	2.03	0.00	6.13	3.78	0.00
L2	W1	RS	4.43	4.81	1.42	5.32	6.46	1.10
	W2		6.44	5.88	2.57	6.01	6.19	1.44
	W3		8.29	5.97	2.76	9.21	7.01	2.11
	W4		7.43	6.35	2.32	4.95	5.55	2.28
	W1	VS	5.64	1.78	0.00	5.63	3.76	0.00
	W2		6.35	1.59	0.00	6.35	2.27	0.00
	W3		4.98	1.46	0.00	4.98	3.00	0.00
	W4		5.61	1.37	0.00	5.61	2.49	0.00
L1	W1	RS	4.66	4.82	0.62	8.53	6.20	0.96
	W2		7.02	4.60	1.26	5.01	8.00	0.00
	W3		5.01	4.60	1.55	5.45	7.80	1.21
	W4		8.32	5.50	2.54	6.75	5.55	2.13
	W1	VS	7.02	1.14	0.00	7.02	3.87	0.00
	W2		6.24	0.90	0.00	6.24	2.71	0.00
	W3		6.24	0.81	0.00	4.56	2.53	0.00
	W4		4.76	0.70	0.00	4.76	2.02	0.00
	LSD		1.46	1.47	1.22	1.46	1.47	1.22

NB: RS: Imposition of drought stress at reproductive stage, VS: Imposition of drought stress at vegetative stage. L3, L2 and L1=25, 50 and 100% light intensity; W1, W2, W3, W4=no water stress (0-5 bars), moderate water stress (5-15 bars), moderately-severe (15-40 bars), severe water stress (40-70 bars), respectively; WAS: Weeks after Sowing

the effect of varying light intensities showed that a reduction in light intensity increased the CTR compared to 100% light intensity (Figure 1C), but the CTR was reduced as water stress became severe in IT99K-573-1-1, and the reverse was observed in IT89KD-288, though not significant (Figure 2C).

Leaf Temperature

Unlike other physiological parameters determined, the leaf temperature was not seriously affected by the varying light intensities and water deficit as there was no significant difference in all the treatments, especially at 3 WAS. Although in IT89KD-288, at 6 WAS, there was little difference among treatments and L2W4VS (55% light intensity and severe water stress at the vegetative stage) treatment gave the highest mean value which was significantly higher ($P \leq 0.05$) than L1W1VS (No water stress at the vegetative stage under 100% light intensity) that gave the lowest mean value. However, at 9 WAS, amongst the treatments imposed with water deficit stress at the reproductive stage, the highest mean value of 34.67°C was recorded in the control; L1W1RS (full watering at the reproductive stage and exposed to 100% light intensity) and L2W2RS (those that received moderate water stress at reproductive stage under 55% light intensity) and was significantly higher than other treatments (Table 4). The trend was the same for variety 2. Meanwhile, at 6WAS, exposure of IT99K-573-1-1 to 100% light intensity and severe water stress at the vegetative stage (L1W4VS) increased the leaf temperature to 34.23 °C compared to other treatments and the lowest mean value (28.50 °C) was observed in cowpea leaf grown under 55% light intensity and was to be exposed to severe water stress at the reproductive stage (L2W4RS). At 9WAS, amongst the treatments imposed with water deficit stress at the reproductive stage, the highest mean value (34.67 °C) was recorded in cowpea plants exposed to moderately-severe water stress at the reproductive stage under 100% light intensity (L1W3RS). The lowest mean value (30.33 °C) was recorded for cowpea plants grown under 55% light intensity but with no water stress at the reproductive stage (L2W1RS) (Table 4).

Chlorophyll Content

Chlorophyll content was determined for the younger and older leaves and the average was calculated. In the cowpea variety, IT89KD-288, at 3 WAS, 100% light intensity surprisingly increased the chlorophyll content of the cowpea leaf while there was a reduction in the chlorophyll contents under reduced light intensities. At this stage, 100% light intensity gave the highest mean value which was significantly higher than other treatments, while the lowest mean value was observed under 55% light intensity. At 6 WAS, the highest mean value of 63.40 mg/g F.W was also recorded under 100% light intensity while the least mean value was recorded under 36% light intensity and moderate water stress at the vegetative stage. Similarly, at 9 WAS, amongst the treatments imposed with water deficit stress at the reproductive stage, the highest mean value was also recorded in 100% light intensity and in plants treated with moderately-severe water stress at the reproductive

Table 4: Interactive effects of different light intensities and drought stress at vegetative and reproductive stages on leaf temperature (^{o}C)

Light intensity	Water regimes	Growth stages	IT89KD-288			IT99K-573-1-1		
			3WAS	6WAS	9WAS	3WAS	6WAS	9WAS
L3	W1	RS	30	30.17	31.50	28.67	30.27	31.00
	W2		29.83	30.40	32.00	30.33	29.67	31.33
	W3		29.73	30.73	30.33	31.00	29.70	30.83
	W4		30.60	30.87	30.33	30.67	29.23	31.33
	W1	VS	30.43	31.23	0.00	30.33	30.33	0.00
	W2		30.40	31.60	0.00	30.33	32.13	0.00
	W3		30.06	31.80	0.00	30.00	32.10	0.00
	W4		30.37	31.87	0.00	29.67	33.17	0.00
L2	W1	RS	30.50	29.85	31.50	30.33	31.90	30.33
	W2		30.67	30.57	33.00	30.00	31.90	30.67
	W3		29.33	30.93	30.33	30.00	29.43	31.00
	W4		29.67	30.97	30.33	30.00	28.50	31.00
	W1	VS	29.97	31.13	0.00	29.67	31.07	0.00
	W2		30.43	31.40	0.00	30.00	31.00	0.00
	W3		31.23	31.50	0.00	30.33	32.50	0.00
	W4		30.37	32.03	0.00	30.33	33.73	0.00
L1	W1	RS	31.00	30.27	34.67	30.33	30.48	33.00
	W2		29.33	30.67	34.67	30.33	31.08	0.00
	W3		30.00	30.83	34.67	30.33	30.55	34.67
	W4		30.33	30.93	33.00	31.00	30.38	32.33
	W1	VS	29.77	22.97	0.00	32.00	33.33	0.00
	W2		30.36	25.47	0.00	33.33	33.90	0.00
	W3		30.06	25.00	0.00	33.33	33.83	0.00
	W4		30.67	26.27	0.00	35.33	34.23	0.00
	LSD		40.63	2.10	1.73	1.53	2.09	1.73

NB: RS: Imposition of drought stress at reproductive stage, VS: Imposition of drought stress at vegetative stage. L3, L2 and L1=25, 50 and 100% light intensity; W1, W2, W3, W4=no water stress (0-5 bars), moderate water stress (5-15 bars), moderately-severe (15-40 bars), severe water stress (40-70 bars), respectively; WAS: Weeks after Sowing

stage. Though, this was not significantly different (P≤0.05) from other treatments but significantly different (P≤0.05) from treatments imposed with water deficit stress at the reproductive stage under a reduced light intensity of 36%. This trend was the same in both cowpea varieties (Table 5). The difference was, however, more pronounced in IT99K-573-1-1 at 9 WAS and L1W4RS (100% light intensity and severe water stress at the reproductive stage) had significantly higher chlorophyll content (66.83 mg/g F.W) compared to other treatments imposed with water deficit stress at the reproductive stage, and the least mean value of chlorophyll content in the leaf was recorded for L3W2RS (36% light intensities and moderate water stress at reproductive stage) treatment.

Crop Water Stress Index (CWSI) and Drought Factor Index of cowpea

There was a decrease in the crop water stress index from 6 WAS to 9 WAS. Water-stressed plants had lower values when compared to unstressed plants. High light intensity also reduced the CWSI compared to the reduced light intensities. At 6 WAS, IT89KD-288 in L3W3RS (36% light intensity and moderately-severe water stress at the reproductive stage), had the highest mean value (0.85) which was significantly different from other treatments and at 9 WAS the trend was the same. The crop water stress index greatly decreased for cowpea plants exposed to water deficit stress at the reproductive stage compared to the values obtained at 6 WAS when these plants were not yet stressed. Reduction in light intensity also increased the CWSI. The reduced light intensity treatments; L3W4RS (36% light intensity and severe water stress at reproductive stage) and L2W4RS (55% light intensity and severe water stress at reproductive stage) had the highest mean values (0.41) at 9 WAS which was significantly different (P≤0.05) from other treatments and higher than 100% light intensity (Table 6). This trend was also observed for the cowpea variety IT99K-573-1-1. Generally, there was a decrease in crop water stress index from 6 WAS to 9 WAS as observed for the IT89KD-288. At 6 WAS, plants stressed at the vegetative stage with water deficit had lower values compared with unstressed plants at the vegetative stage under different light intensities. Reduced light intensities also increased the CWSI and L3W2RS (36 % light intensity with moderate water stress at the reproductive stage) had the highest mean value (0.94) which was significantly different (P≤0.05) from other treatments, while L2W4VS (55% light intensity and severe water stress at vegetative stage) and L1W4VS (100% light intensity and severe water stress at vegetative stage) treatments had the lowest mean value (0.39). Similarly, at 9WAS, the crop water stress index greatly decreased for treatment imposed with water deficit stress at the reproductive stage. L3W3RS (36 % light intensity and moderately-severe water stress at the reproductive stage) had the highest mean value (0.43) at 9 WAS which was significantly different (P≤0.05) from other treatments (Table 6). However, on the crop water stress index, the highest mean value was recorded at 100% light intensity and severe water stress while the least mean value was recorded at 36% light intensity (Figures 1D and 2D). DFI values; 0 ≤ DFI ≤ 0.54 are highly drought tolerant HT, 0.55 ≤ DFI ≤ 0.65 are

Table 5: Interactive effects of different light intensities and drought stress at vegetative and reproductive stages on chlorophyll content (mg/g F.W)

Light intensity	Water regimes	Growth stages	IT89KD-288			IT99K-573-1-1		
			3WAS	6WAS	9WAS	3WAS	6WAS	9WAS
L3	W1	RS	47.27	48.47	36.70	46.53	52.47	45.63
	W2		47.17	50.60	38.70	46.00	42.80	38.27
	W3		48.27	52.33	39.87	47.03	43.73	49.43
	W4		48.07	51.77	37.73	45.77	46.33	49.07
	W1	VS	47.10	52.70	0.00	47.10	58.67	0.00
	W2		46.30	45.83	0.00	46.30	47.43	0.00
	W3		46.70	47.63	0.00	46.70	44.47	0.00
	W4		47.73	54.80	0.00	47.73	53.60	0.00
L2	W1	RS	46.25	46.05	36.70	56.53	50.43	45.23
	W2		44.83	47.13	38.70	52.00	44.37	42.20
	W3		45.00	47.53	39.87	51.40	45.87	40.20
	W4		41.07	51.30	37.73	51.67	42.67	54.77
	W1	VS	43.37	55.37	0.00	43.37	46.67	0.00
	W2		45.80	50.97	0.00	45.80	46.07	0.00
	W3		44.40	50.80	0.00	44.40	44.67	0.00
	W4		47.53	55.50	0.00	47.53	45.73	0.00
L1	W1	RS	44.17	54.73	57.07	49.03	53.10	55.77
	W2		44.93	52.27	57.47	45.93	52.27	0.00
	W3		45.10	61.23	59.50	43.97	55.23	58.83
	W4		47.00	63.40	53.60	45.50	59.63	66.83
	W1	VS	56.97	61.90	0.00	56.97	59.07	0.00
	W2		50.57	55.80	0.00	50.57	51.60	0.00
	W3		48.53	52.07	0.00	54.53	57.00	0.00
	W4		51.70	58.83	0.00	53.70	47.30	0.00
	LSD		4.88	9.66	5.36	4.88	9.66	5.36

NB: RS: Imposition of drought stress at reproductive stage, VS: Imposition of drought stress at vegetative stage. L3, L2 and L1=25, 50 and 100% light intensity; W1, W2, W3, W4=no water stress (0-5 bars), moderate water stress (5-15 bars), moderately-severe (15-40 bars), severe water stress (40-70 bars), respectively; WAS: Weeks after Sowing

Table 6: Interactive effects of different light intensities and drought stress at vegetative and reproductive stages on crop water stress index

Light intensity	Water regimes	Growth stages	IT89KD-288		IT99K-573-1-1	
			6WAS	9WAS	6WAS	9WAS
L3	W1	RS	0.73	0.14	0.81	0.28
	W2		0.72	0.21	0.94	0.30
	W3		0.85	0.26	0.84	0.43
	W4		0.77	0.41	0.87	0.34
	W1	VS	0.44	0.00	0.47	0.00
	W2		0.46	0.00	0.56	0.00
	W3		0.38	0.00	0.42	0.00
	W4		0.45	0.00	0.50	0.00
L2	W1	RS	0.68	0.14	0.79	0.21
	W2		0.73	0.21	0.91	0.40
	W3		0.65	0.26	0.89	0.34
	W4		0.71	0.41	0.78	0.32
	W1	VS	0.32	0.00	0.44	0.00
	W2		0.30	0.00	0.51	0.00
	W3		0.37	0.00	0.52	0.00
	W4		0.23	0.00	0.39	0.00
L1	W1	RS	0.65	0.32	0.79	0.40
	W2		0.70	0.34	0.69	0.00
	W3		0.56	0.35	0.93	0.19
	W4		0.64	0.29	0.77	0.40
	W1	VS	0.43	0.00	0.43	0.00
	W2		0.28	0.00	0.44	0.00
	W3		0.33	0.00	0.43	0.00
	W4		0.38	0.00	0.39	0.00
	LSD		0.15	0.08	0.15	0.08

NB: RS: Imposition of drought stress at reproductive stage, VS: Imposition of drought stress at vegetative stage. L3, L2 and L1=25, 50 and 100% light intensity; W1, W2, W3, W4=no water stress (0-5 bars), moderate water stress (5-15 bars), moderately-severe (15-40 bars), severe water stress (40-70 bars), respectively; WAS: Weeks after Sowing moderately tolerant, MT, 0.64 ≤ DFI ≤ 0.69 are moderately susceptible while 0.70 ≤ DFI ≤ 1.0 are highly susceptible, the effects of different light intensities and drought stress at vegetative and reproductive stages on Drought Factor Index (DFI) of IT89KD-288 and IT99K-573-1-1 cowpea varieties showed that IT89KD-288 with value -0.78 is highly drought tolerant while IT99K-573-1-1 with value -0.59 is moderately drought tolerant.

Sole and Combined Effects of Different Light Intensities and Water Deficit Stress on Yield Parameters

Reduction in light intensity to 55% and 36% had a positive effect on the number of pods for both cowpea varieties. The lowest light intensity of 36% with no water stress gave the highest number of pods, while 100% light intensity and at all levels of water deficit stress had the least number of pods (Figure 3). This reduction in light intensity also had a positive effect on pod weight/pot and pod length with 36% light intensity without water stress treatment recording the highest mean value, while 100% light intensity at all levels of water deficit stress had the lowest mean value. Reduction to 36% light intensity with no water stress had the highest mean pod length while 100% light intensity gave the lowest mean value (Data not shown). On the number of grains/pod and seed weight, exposure to 36% light intensity without water deficit stress also gave the highest mean value of grains per pod while cowpea plants grown under 100% light intensity had little or no grain. Cowpea grown under 36% light intensity with no water stress also had the highest seed weight value, while 100% light intensity had the lowest value (Figure 4). On the harvest index, cowpea exposed to 36% light intensity with no water stress had the highest mean value (56%) harvest index and 100% light intensity with no water stress and at all levels of water deficit stress had the least (Figure 5). The total dry weight was also enhanced by light reduction to 36% light intensity though, not significantly different ($P \leq 0.05$) from 55% light but greatly differ from all other treatments, while the lowest mean value was recorded at 100% light intensity with severe water stress at the reproductive stage (Figure 6). For the sole effect of different light intensities on the yield parameters of the two cowpea varieties, exposure to full light intensity (100%) had a negative effect on the two cowpea varieties. The highest pod number and length were recorded at 36% light intensity which was not significantly higher than 55% light intensity while the lowest mean value was recorded under 100% light intensity. The same trend was observed for grain weight, the number of grains per pod and total dry matter. (Figure 7). Control treatment (no water stress) was significantly higher than other water deficit treatments followed by treatments that received moderate water stress. For each variety, severe water stress had the least values of the number of pods, grain

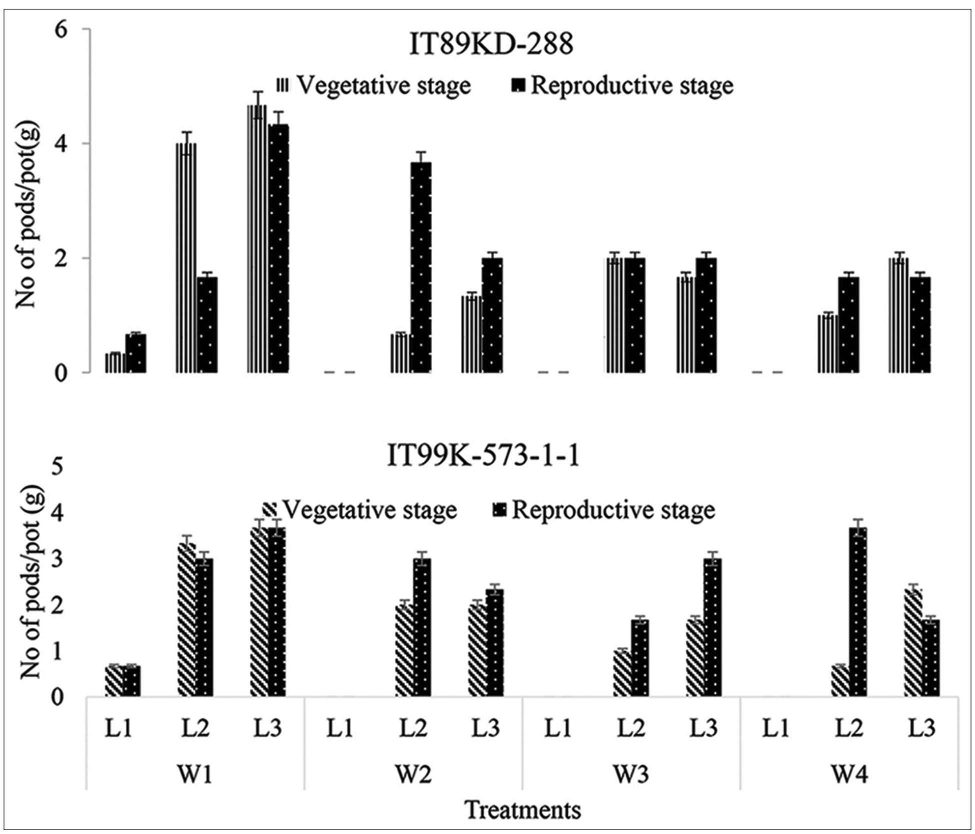

Figure 3: Interactive effects of different light intensities and water deficit stress at vegetative and reproductive growth stages on number of pods of the two cowpea varieties (Bars of chart represent standard error).

NB: Reproductive Stage: Imposition of drought stress at reproductive stage, Vegetative Stage: Imposition of drought stress at vegetative stage. W1= no water stress (0-5 bars), W2=moderate water stress (5-15 bars), W3=moderately-severe (15-40 bars), W4=severe water stress (40-70 bars), L1=100%:710.2 Lux, L2=55%:394 Lux, L3=36%:259 Lux

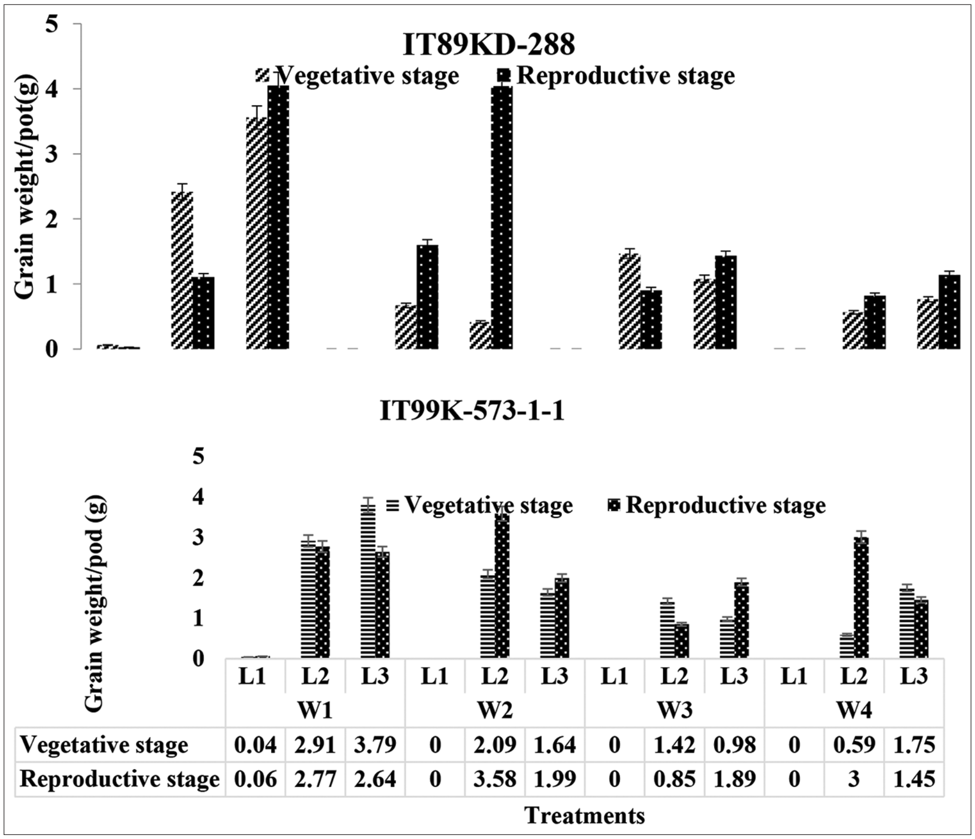

Figure 4: Interactive effects of different light intensities and water deficit stress at vegetative and reproductive growth stages on grain/seed weight (Bars of chart represent standard error)

NB: Reproductive Stage: Imposition of drought stress at reproductive stage, Vegetative Stage: Imposition of drought stress at vegetative stage. W1= no water stress (0-5 bars), W2=moderate water stress (5-15 bars), W3=moderately-severe (15-40 bars), W4=severe water stress (40-70 bars), L1=100%:710.2 Lux, L2=55%:394 Lux, L3=36%:259 Lux

weight, number of grains per pod and total dry matter, also it was observed that IT99K-573-1-1 had significantly higher mean yield values compared to IT89KD-288 across the parameters considered (Figure 8).

DISCUSSION

Crop yield is highly dependent on its genetic compositions and the prevailing environmental conditions. Interaction between plants and the environment is what results in physical growth and development. Favourable environmental conditions lead to optimum yield while the yield is adversely affected under environmental stress. The effect on crop physiological processes, however, depends on the type of stress, duration and intensity (Surendar *et al.*, 2013). Combined stresses have been reported to have positive or negative effects on crop productivity with one stress antagonizing or cushioning the effect of the other (Rizhsky *et al.*, 2002, 2004; Wang & Huang, 2004; Xu & Zhou, 2006). As was observed in this study, the combination of drought and high temperature arising from high light intensity is more deleterious to crop growth and yield compared to individual stress. The stage of exposure is also very important and water-stressed plants at the vegetative stage had reduced growth parameters compared to those that were stressed at the reproductive stage (Data not shown). This, according to Barnabas *et al.* (2008), was attributed to the importance of water at the initial phase of plant growth and establishment. Efficient photosynthesis and stem reserve accumulation during the vegetative phase have a decisive role in the formation of generative organs and eventual crop yield (Adelusi & Aileme, 2006; Manivannan *et al.*, 2007). This could have been responsible for the reduction in the yield of the cowpea stressed at the vegetative stage compared to those stressed at the reproductive stage.

However, it was observed that reduced light intensities with or without water deficit stress enhanced the growth and yield of cowpea better than full light intensity. The yield was reduced under full exposure to sunlight. The yield reduction with regard to water deficit stress was also more pronounced under full light intensity. This was because low light intensity reduced the rate of leaf transpiration and helps in conserving water for photosynthesis. Plants grown in low light intensity also respond to low light stress by devoting more of their available carbon to shoot growth and biomass accumulation. A combination of the two stresses could have therefore increased the internal leaf temperature compared to the shaded and unstressed cowpea plants (Wang & Huang, 2004; Xu & Zhou, 2006).

Physiological traits are mostly affected by environmental stresses (Surendar *et al.*, 2013; Rudack *et al.*, 2017; Jacques *et al.*, 2020).

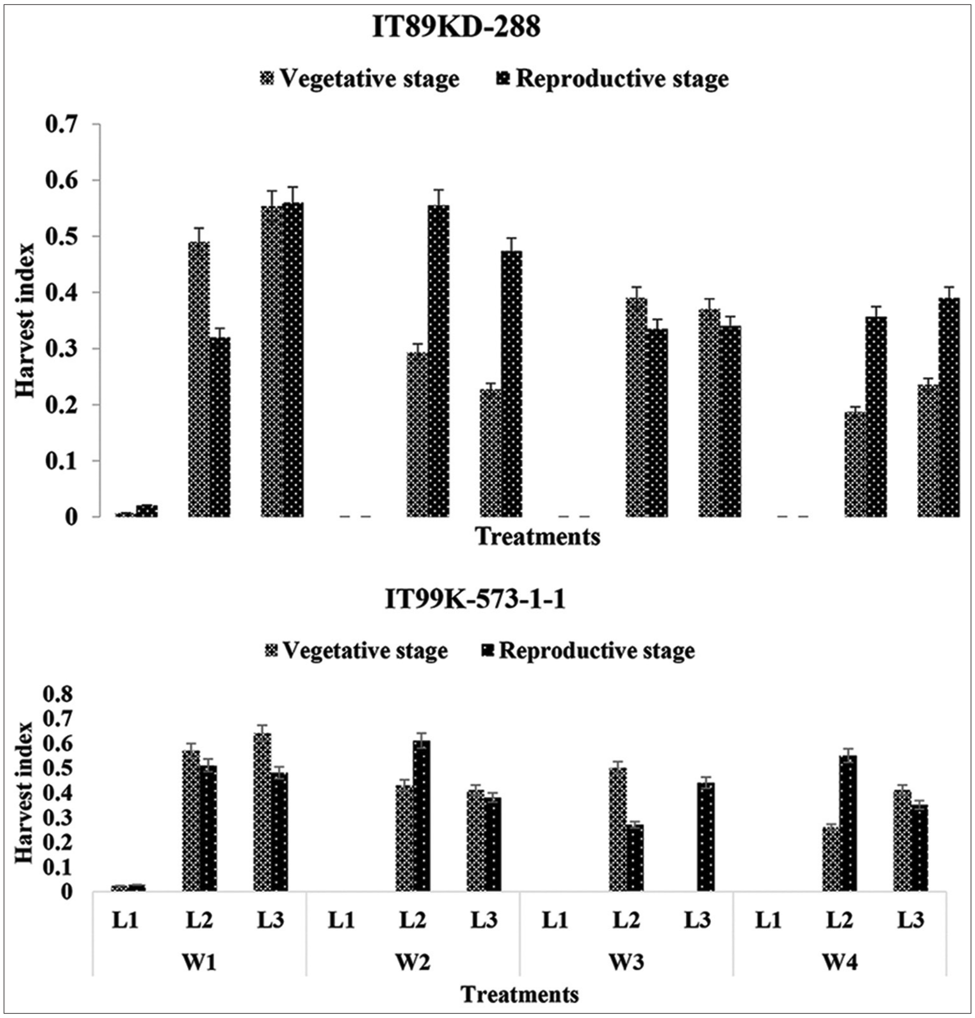

Figure 5: Interactive effects of different light intensities and water deficit stress at vegetative and reproductive growth stages on harvest index (Bars of chart represent standard error)
NB: Reproductive Stage: Imposition of drought stress at reproductive stage, Vegetative Stage: Imposition of drought stress at vegetative stage. W1= no water stress (0-5 bars), W2=moderate water stress (5-15 bars), W3=moderately-severe (15-40 bars), W4=severe water stress (40-70 bars), L1=100%:710.2 Lux, L2=55%:394 Lux, L3=36%:259 Lux

The plant physiological processes (LP, SC, LT, CTR) are also affected by the combination of water deficit stress and high light intensity. The higher leaf canopy temperature recorded under combined 100% light intensity and severe water stress could be due to the effect of stomatal closure/resistance to reduce water loss in response to water deficit stress in plants, hence increase in leaf temperature (Surendar *et al.*, 2013; Jacques *et al.*, 2020). The plant normally opens its stomata during the day to release water vapour which will in turn bring a cooling effect on the plant. The stomata, however, close up under drought stress for water conservation. During water stress, it has been reported that plant secrets Abscisic acid (ABA) in the root and is transported in the xylem to the shoot, where it causes stomatal closure and reduces leaf expansion, thereby preventing the dehydration of leaf tissues (Jia & Zhang, 2008). This closure of the stomata, according to Vurayai *et al.* (2011), is the initial defence mechanism displayed by the plants under water deficit stress. The increase in the transpiration rate of the control plants (No water stress under 100% light intensity) could have resulted in the cooling effect on the plant leaf and consequent reduction in the leaf temperature.

Similarly, the SC decreased under high light intensity as the severity of water stress increased. Cowpea plants under 100% light intensity had the least mean values for SC. This was consistent with the reports of Surender *et al.* (2013) and Jacques *et al.* (2020). The reduction in SC was to reduce leaf transpiration under water stress (Lawlor, 2002; Singh & Reddy, 2011; Ocheltree *et al.*, 2014). This was in line with the findings of Brito *et al.* (2013) that plants under stressful conditions tend to close their stomata to minimize water loss and maintain turgor. The stomatal closure during water stress has however been described as one of the strategies for survival to maintain the high internal water potential of the leaf (Boguszewska-Mańkowska *et al.*, 2018). This in turn might have reduced the internal concentration of CO_2 which consequently reduced the photosynthetic rate. The photosynthetic rate has been reported to decline as the internal concentration of carbon

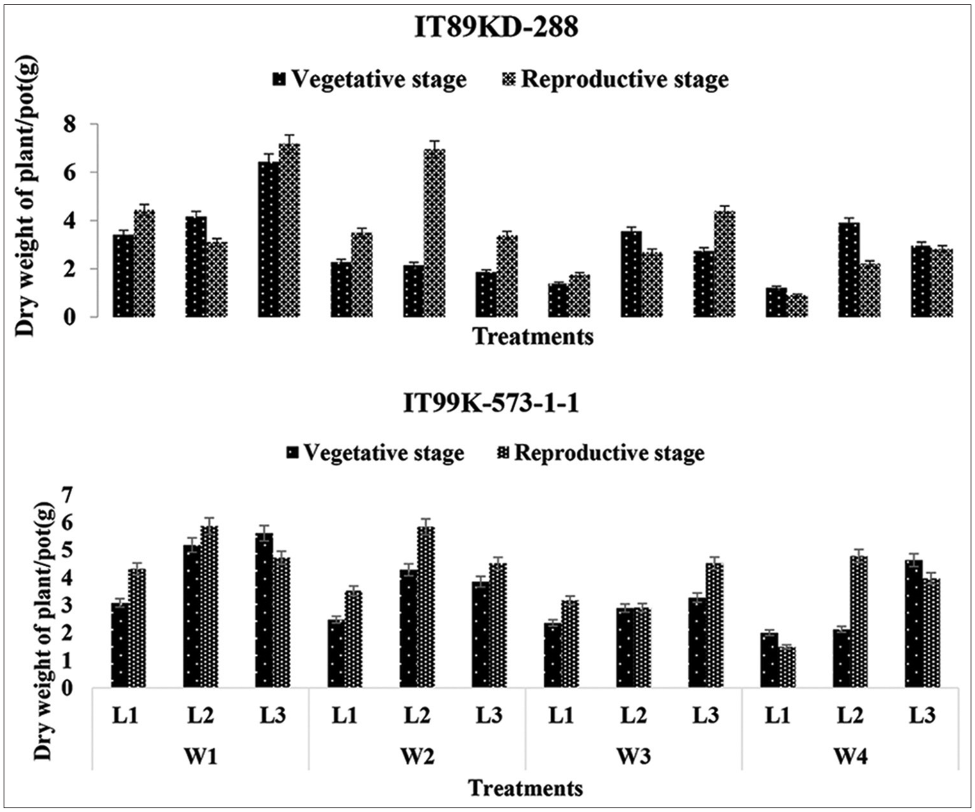

Figure 6: Interactive effects of different light intensities and water deficit stress at vegetative and reproductive growth stages on total plant biomass (Bars of chart represent standard error)
NB: Reproductive Stage: Imposition of drought stress at reproductive stage, Vegetative Stage: Imposition of drought stress at vegetative stage. W1= no water stress (0-5 bars), W2=moderate water stress (5-15 bars), W3=moderately-severe (15-40 bars), W4=severe water stress (40-70 bars), L1=100%:710.2 Lux, L2=55%:394 Lux, L3=36%:259 Lux

dioxide decreased due to stomatal closure, especially under excessive heat (Brestic *et al.*, 2016; Jacques *et al.*, 2020). This in turn caused a reduction in biomass accumulation and overall crop yield under water deficit stress (Anjum *et al.*, 2003; Bhatt & Rao, 2005; Kusaka *et al.*, 2005; Shao *et al.*, 2008).

Though, with varietal differences, due to variation in genetic composition (Bertolini *et al.*, 2019), the leaf photosynthesis, SC, transpiration rate, and crop water index were generally reduced under water stress, especially with 100% light intensity. Photosynthesis is one of the major physiological processes targeted under environmental stress. The closure of the stomata by the plants exposed to water stress under full light intensity as reflected by the reduction in SC could have also reduced the leaf photosynthesis due to the stomatal resistance to the influx of carbon dioxide (Flexas & Medrano, 2002). The SC of water-stressed plants has been found to determine the supply of CO_2 to the leaf intercellular spaces. The reduction in the rate of photosynthesis of the plant exposed to high light intensity was similar to what was reported by Flexas *et al.* (2004). This could also be linked to the damage of leaf photosynthetic apparatus under high light intensity due to photoinhibition. Excessive light intensity increases leaf transpiration and destroys chloroplasts (Flexas & Medrano, 2002; Stancato *et al.*, 2002; Sarvikas *et al.*, 2006). Besides, the high temperature under high light intensity, in combination with drought stress has been reported to cause protein catabolism, disruption in nitrogen metabolism and lipid peroxidation (Xu & Zhou, 2006). The cowpea plants grown under 100% light intensity had reduced leaf photosynthesis and the highest mean values of leaf temperature which might have damaged photosynthetic pigments as well as the reduction in enzymatic activities (Barnabas *et al.*, 2008). Another consequence of water stress is turgor loss which reduces the size of cells leading to reductions in leaf expansion and shoots extension. Plants required more water for photosynthetic apparatus and dry matter yield. These coupled with the leaf area reduction will definitely decrease the light absorption capacity of the leaf and photosynthesis (Lombardina, 2006; Anjum *et al.*, 2011). The reduction in photosynthesis consequently results in slower growth and reduced plant biomass. However, Water stress at the vegetative stage had a pronounced effect on photosynthesis. Leaf photosynthesis was observed to be significantly higher in cowpea plants subjected to water deficit stress at the reproductive stage than in the vegetative stage. This could be attributed to the ability of the plant to develop adequate photosynthetic apparatus due to water availability during the vegetative stage. It has also been established that water deficit stress is a very important limiting factor in the initial phase of plant growth and establishment; it affects both elongation and expansion (Anjum *et al.*, 2003; Bhatt & Rao, 2005; Kusaka *et al.*, 2005; Shao *et al.*, 2008).

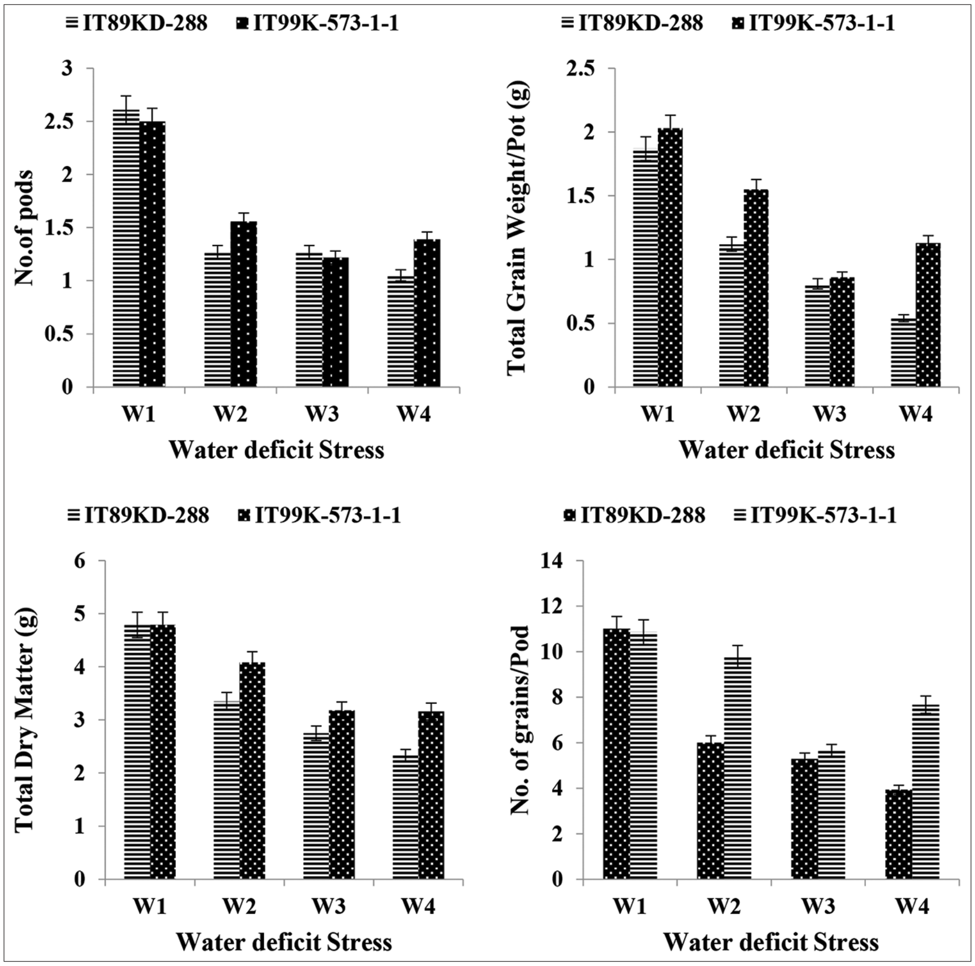

Figure 7: Sole effect of water deficit stress at vegetative and reproductive growth stages on yield parameters of IT89KD-288 and IT99K-573-1-1 cowpea varieties (Bars of chart represent standard error)
W1: Control, no water stress (0-5 bars), W2: Moderate water stress (5-15 bars), W3: Moderately-severe (15-40 bars), W4: Severe water stress (40 -70 bars)

The closure of the stomata in response to water deficit stress and high light intensity also affected the CTR. As stress duration increased and at 6 WAS, it was observed that CTR was drastically reduced in response to severe water stress especially under high light intensity compared to control treatment (No water stress). This observation has earlier been reported by different researchers (Jia & Zhang, 2008; Singh *et al.*, 2011; Surendar *et al.*, 2013; Balla *et al.*, 2019). Leaf temperature and drought have been reported to be negatively correlated with transpiration rate (Surendar *et al.*, 2013). It means that the higher the leaf temperature, the lower the rate of transpiration and vice versa. The reasons have been attributed earlier to the closure of the stomata in water deficit stressed plants for water conservation in response to water stress as a result of the increase in ABA production and rapid movement from root to shoot (Jia & Zhang, 2008; Jacques *et al.*, 2020). Water stress has also been reported to reduce the leaf area of the plant so as to reduce transpiration. In addition, the reduction of leaf water potential and closure stomata are the instantaneous reaction to water insufficiency, which in turn point towards a decline in CO_2 uptake and photosynthesis (Li *et al.*, 2008; Du *et al.*, 2010).

Meanwhile, the highest value of chlorophyll content was recorded under high light intensity. It was observed that plants grown in low light had light green leaves while plants grown in full light had dark green leaves. The response was also growth-stage dependent and the concentration was more at 6 compared to 3 WAS. This result was consistent with the finding of Tran (2018), where 100% light exposure treatment gave the highest chlorophyll content. In another report, light-enhanced chlorophyll formation was found to occur under illumination compared to darkness and the longer the duration of illumination, the greater the enhancement of chlorophyll formation (Zhang *et al.*, 2016). The reason for this finding was explained in two ways; it shows the importance of light in chlorophyll formation (Zhang *et al.*, 2016) or chlorophyll formation as a stress tolerance strategy. Light has been reported to be an important factor in the formation of chlorophyll (Dutta, 2003). The pent-ultimate precursor (Protochlorophyllide) of chlorophyll is said to reduce by NADPH to Chlorophyllide in the presence of light. In another school of thought, the increase in chlorophyll production might be due to light and water stresses. Hossain *et al.* (2012) reported that an increase in chlorophyll is one of the non-enzymatic strategies for ameliorating the

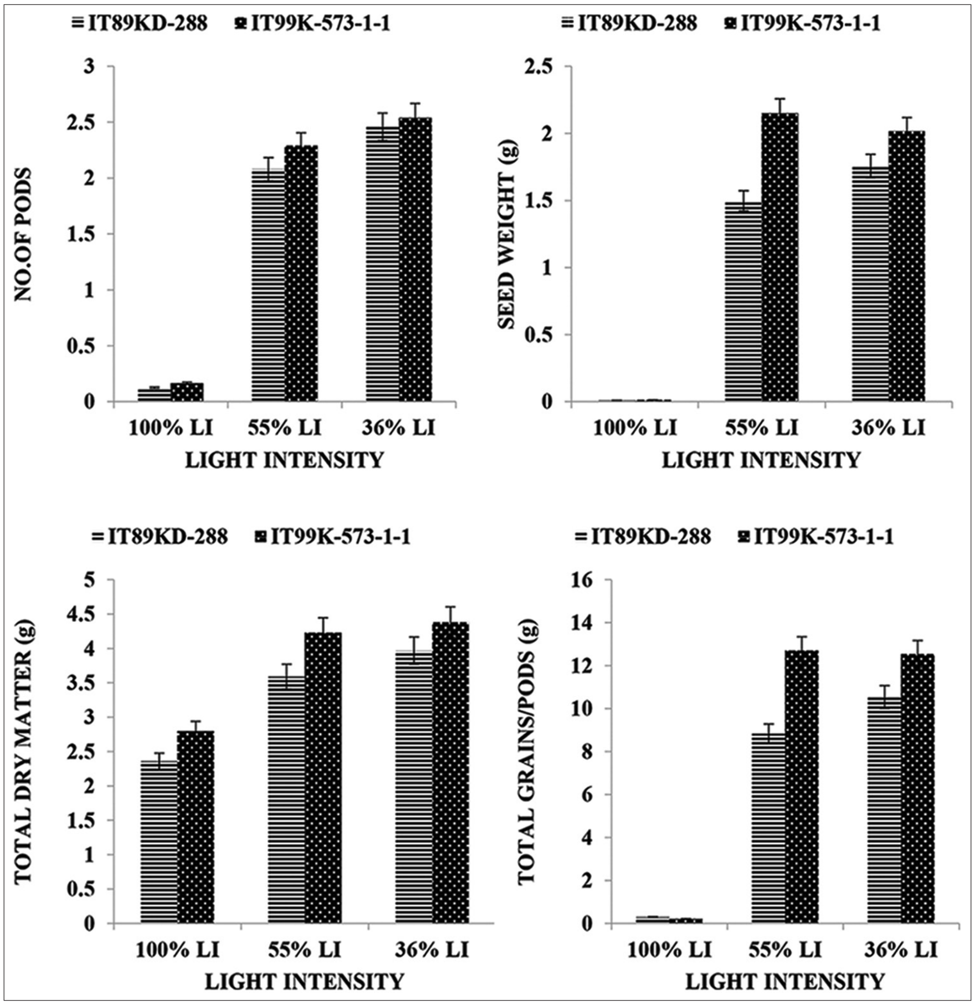

Figure 8: Sole effect of varying light intensities on yield parameters of IT89KD-288 and IT99K-573-1-1 cowpea varieties (Bars of chart represent standard error)
LI: Light Intensity

oxidative stress resulting from environmental stresses. This was confirmed in this study, where water deficit stress at the vegetative stage coupled with 100% light intensity was found to increase the chlorophyll content of the stressed cowpea leaf compared to the unstressed, while there was a reduction in the chlorophyll contents under reduced light intensities. However, considering the sole effect of water stress on chlorophyll, there was a general reduction in chlorophyll concentration, and this could be attributed to the importance of water in metabolic processes like chlorophyll formation. According to Goufo *et al.* (2017), the reduction is again assumed to be a drought response mechanism and was meant to minimize the light absorption by chloroplasts so as to prevent desiccation. In another opinion, drought-induced reduction in leaf pigment production is considered to be an indicator for oxidative stress and this might be attributed to pigment photo-oxidation, chlorophyll degradation and/or chlorophyll synthesis deficiency (Keenan *et al.*, 2010).

The cowpea yield and yield components were found to generally reduce under 100% light intensity compared to low light intensity irrespective of drought stress. No yield was recorded for cowpea plants that were exposed to full sunlight intensity and severe water deficit stress. These results showed that, as important as light is to the plant, excessive light limits crop growth and yield. There is a tolerance level for every plant, but if these thresholds are exceeded especially under combined stresses, this could result in serious damage and disruption of normal physiological processes and overall yield. The combination of light and water stress under full light intensity might have in turn caused a deviation from the optimal conditions for growth and development (Stone, 2001). Shortening of developmental phases and disruption of all the processes associated with carbon assimilation (transpiration, photosynthesis and respiration) have been linked to excessive heat. These have been attributed to the detrimental effects of high temperature (that usually accompany high light intensity) on enzymatic activities and physiological processes (Hurkman *et al.*, 2003; Jiang *et al.*, 2003; Yamakawa *et al.*, 2007). Enzymes work best under an optimum temperature. Temperatures higher than 35°C have been reported to decrease the activity of ribulose 1, 5-bisphosphate carboxylase/oxygenase (Rubisco), thereby limiting carbon fixation during photosynthesis. An increase in temperature above the tolerable level has been reported to cause serious damage to the reproductive development of the crop, especially in combination with drought (Liu *et al.*, 2005; Yang & Zhang, 2006). Temperatures above 30 °C during floret formation have also been reported to cause complete sterility in crops (Saini & Westgate, 2000). Water stress during flower induction and inflorescence development has also been reported to cause a delay in flowering (anthesis) or cause complete inhibition of flowering and pod formation (Sinclair & Jamieson, 2006; Qasem & Biftu, 2010; Suleiman & Ahmed, 2010). Reduced photosynthesis as a result of water deficit and excessive heat under 100% light intensity could have also resulted in reduced biomass accumulation and total yield loss (Surendar *et al.*, 2013).

CONCLUSION

The current study showed the importance of the combination of drought and high temperature as key stress factors with a high potential impact on cowpea yield. Water and light could be classified as the main factors affecting the growth and yield of cowpea, especially during seedling establishment. Though cowpea can tolerate moderate water stress, the combination of water stress with excessive light intensity is deleterious to cowpea yield. The reduction in stomatal conductance and canopy transpiration rate showed that cowpea closes their stomata for water conservation under drought stress and high light intensity. The reduced SC as a result of stomatal closure also affected cowpea photosynthesis and eventual yield. Stomatal resistance could therefore be the major physiological process affecting cowpea photosynthesis and limiting yield under stress. In this study, it was also observed that an increase in chlorophyll concentration under high light intensity, could be one of the biochemical strategies for cowpea stress tolerance. The response of cowpea plants to light intensity and water deficit stress was also dependent on cultivar, growth stage and the severity of water stress. Variety IT99K-573-1-1 showed better adaptation to stress compared to IT89KD-288 and also gave better grain yield production under reduced light intensity and water deficit stress. This study on morpho-physiological responses of cowpea to stress has helped in determining how one or a combination of physiological processes interact with each other to manage environmental stress. Leaf temperature was high under combined drought and high light intensity with low Canopy Transpiration Rate (CTR) and Stomatal Conductance. This in turn reduced the CO_2 intake, overall photosynthesis and yield. Drought and high light intensity, therefore, decrease stomatal conductance, leaf water potential, CTR, carbon uptake and yield of cowpea. Since stomatal conductance affects leaf temperature through leaf transpiration and photosynthesis through CO_2 resistance, plants must balance between reducing stomatal conductance to conserve water and at the same time preventing extreme leaf temperatures that will in turn affect metabolic rates and physiological processes. To enhance cowpea productivity under environmental stress, the provision of shade could therefore be employed. Reduced light intensity used in this study, served as a water conservation mechanism and reduced the effect of high light intensity and water deficit stress on cowpea. Cowpea, therefore, requires low light intensity under water deficit stress for optimum yield.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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