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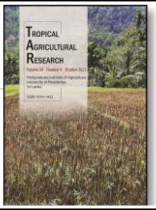

RESEARCH

Impact of Mild Water Stress During the Flowering Stage on Leaf Functional Traits and Yield of Selected Cowpea Varieties Grown in The Low Country Dry Zone of Sri Lanka

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ABSTRACT

Cowpea [*Vigna unguiculata* (L.) Walp.] is an important legume growing in tropical regions. Cowpea is grown in the Dry Zone of Sri Lanka as an inter-season crop. Rising temperatures and unpredictable precipitation patterns are major factors contributing to soil moisture stress in tropical agriculture. Despite the short life cycle, it is highly likely that cowpea experiences mild soil moisture stress (around 70% of field capacity) conditions at flowering stage due to enhanced evapotranspiration in response to increasing air temperature. In this study, five cowpea varieties were subjected to two soil moisture conditions; field capacity and mild water stress, at the onset of flowering under a split-plot design for two consecutive inter-seasons with the objectives to determine the leaf gas exchange and hydraulic traits of cowpea exposed to soil moisture stress and the underlying relationships between yield reduction and leaf gas exchange, hydraulic, and agronomic traits. The yield reduction ($p<0.05$) in the five varieties tested was associated with a reduction in leaf net assimilation rate, number of pods/plant, and number of seeds/pod. Variety-dependent reductions in leaf functional traits in many varieties leading to a reduction in yield parameters ($p<0.05$) were obvious under mild water stress conditions. Despite the water stress variety, Waruni performed well in both moisture conditions. As conclusion, cowpea varieties for inter-season cultivation should be selected based on ability to maintain yield under mild water stress conditions. A special emphasis should be placed on commencing cultivation as soon as the main crop is harvested to better utilize the residual moisture.

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INTRODUCTION

Cowpea [*Vigna unguiculata* (L.) Walp.] holds significant importance as one of the vital legumes cultivated in tropical and subtropical regions worldwide (Tan *et al*., 2012; Carvalho *et al.,* 2017; Singh *et al*., 2007). This crop thrives in tropical areas owing to its remarkable nitrogen-fixing ability (Carvalho *et al.,* 2017), high yield, and nutrient-rich composition, including high-quality protein. Additionally, cowpea exhibits remarkable adaptability to abiotic stresses like drought and high temperatures (Ehlers *et al.,* 1997). These invaluable features collectively position cowpea as a key crop in tackling climate change and addressing food insecurity (Carvalho *et al*., 2019). However, cowpea's reliance on rain-fed conditions in many cultivation areas exposes them to the uncertainties of changing precipitation patterns (Anyia *et al.,* 2013). Consequently, cowpea-based cropping systems under rain-fed conditions are more prone to mild water stress, which ultimately affects the overall crop performance.

Rising global temperatures and unpredictable precipitation patterns are major factors contributing to soil moisture stress in numerous tropical agricultural systems worldwide (Golldack *et al.,* 2014). Legume crops are extensively cultivated in rain-fed regions, where the increasing frequency and intensity of droughts pose significant challenges to maintaining high crop productivity (Nadeem *et al.,* 2019; Varaprasad, 2005). Soil moisture stress, particularly during crucial growth stages like flowering and grain filling, profoundly affects crop yields (Siddique *et al.,* 2001). The occurrence of drought events, with varying frequency and severity, leads to reduced grain yield, plant biomass, and overall yield components in legumes (Delmer *et al*., 2005; Pushpavalli *et al.,* 2015).

In cowpea cultivation, the most critical stages susceptible to water stress conditions are just prior to and during bloom (Pejic *et al*., 2013), the flowering and fruiting stages (Carvalho *et al.,* 2000), and the seed-filling stage (Cordeiro *et al*., 1998). Since cowpea has a relatively short growth cycle of around 60 days, there is a potential risk of mild water stress occurring under rain-fed conditions during the flowering stage, which typically takes place approximately 30 days after planting. Such water stress can lead to a decrease in the overall yield, which is closely linked to changes in leaf gas exchange rates. In particular, water stress in cowpea results in reduced transpiration, stomatal conductance, and photosynthesis (Anyia *et al.,* 2003; Han, 2016). Several cowpea varieties are especially vulnerable to water stress during floral development (Dadson *et al.,* 2005; Uarrota, 2010). The reduced leaf gas exchange and photosynthesis under water stress further diminish the availability of carbohydrates for pod filling (Uarrota, 2010). Given that the final seed yield in cowpea is determined by the number of pods per plant, the number of seeds per pod, and the hundred-seed weight, any water stress conditions can dramatically reduce all these yield components (Ahmed *et al.,* 2010).

In line with other tropical and sub-tropical regions in Sri Lanka, the average temperature is steadily increasing at a rate of 0.01–0.03°C per year (Fernando and Chandrapala, 1995; Nissanka *et al*., 2011; Premalal and Punyawardena, 2013). Future rainfall estimates for Sri Lanka predict that dry areas will become even drier, while wet and intermediate zones may become wetter than their current state due to altered monsoonal patterns, including shifts in onset dates and higher variability in distribution (Mambe *et al*., 2012 and Premalal and Punyawardena., 2013). Cowpea is typically cultivated in the dry zone of Sri Lanka as an inter-season crop between the two major rice growing seasons: *Yala* and *Maha*, relying on rain-fed conditions. To better understand the impact of mild water stress on cowpea yield and physiological performance, it is essential to determine the relationship between these factors. In this study, we investigated this relationship by examining the yield reduction and leaf gas exchange traits of five commonly grown cowpea varieties over two consecutive inter-seasons with the objectives; (1) to determine the leaf gas exchange and hydraulic traits of cowpea exposed to soil moisture stress in the dry zone of Sri Lanka, and (2) to investigate underlying relationships between yield reduction and leaf gas exchange traits, with hydraulic, and other agronomic traits under soil moisture stress. For that, we hypothesized that mild water stress would (i) reduce yield parameters by limiting gas exchange rates, (ii) increase carbon loss per unit carbon gain due to decreased rates of net assimilation and increased leaf respiration rates, and (iii) lead to reductions in yield components, ultimately resulting in overall yield reductions associated with increased carbon loss per unit carbon gain.

METHODOLOGY

Study site

The experiment was carried out under a rain shelter with transparent roofing at the Field Crop Research and Development Institute (FCRDI) in Mahailuppallama, Sri Lanka (8.1117, 80.4669). The institute is situated in the low country dry zone within the agroecological region DL1b, where the average annual rainfall is 1,094 mm, and the mean annual temperature ranges from 23.3 to 32.1°C. This region experiences a distinct rainless period lasting for 8 to 9 months. The soils in this area consist of Reddish Brown Earth (RBE) on the upper slopes of the catena and Low Humic Gley (LHG) in the valleys. Meteorological data during the experiment were obtained from the Meteorological Station at FCRDI, Mahailuppallama.

Experimental design

A field experiment was conducted to assess the performance of five commonly grown cowpea varieties (Waruni, Dhawala, MI-35, Bombay, and ANKCP 1) in Sri Lanka, under two watering conditions. The experiment followed a split-plot design with three replicates per treatment. The main plot factor involved two watering conditions: well-watered (WW) up to field capacity (FC) and mild water-stressed (WS) down to 70% of FC. Meanwhile, the cowpea varieties were used as the subplot factor.

Initially, all plots were managed at FC until the onset of flowering. Subsequently, half of the plots were subjected to mild water stress, maintaining the moisture level at 70% of FC, while the other half continued to be kept at FC (refer to Fig 1 for illustration). To monitor the moisture levels accurately, moisture sensors and a data logger (ZL6, Meter Environment, USA) were utilized. Whenever necessary, water was supplied through an irrigation system to maintain the required moisture levels in the plots.

This study was repeated twice during two consecutive inter-seasons with a fallow period in between. The first season spanned from August 2020 to October 2020, while the second season took place from February 2021 to April 2021, and both seasons followed the same treatment structure.

Crop establishment and management

In the first season, the land underwent ploughing to a depth of 25-30 cm using a tine tiller, followed by harrowing with a rotavator to achieve a loose and friable bed. To prevent water seepage between plots, drains were dug to a depth of 1.5 m around all the plots, and double-layer polyethylene sheets were buried along both sides of the drain wall. A drip irrigation system was established to provide water coverage for the root zone of all cowpea plants. Additionally, the soil was sterilized using a water-dissolved fungicide (Captan).

The selected cowpea varieties' seeds were sourced from certified seed lots of FCRDI, Mahaillupallama. Seeding was carried out with two seeds per hole, spaced at 30 cm × 15 cm. Before sowing, the seeds were treated with a fungicide (4 g Captan per 1 kg of seeds). Fertilizers were applied based on the recommendations of the Department of Agriculture, consisting of a basal dose of 35:100:75 kg/ha of urea, triple superphosphate, and muriate of potash. At the onset of flowering, a top dressing of 30 kg/ha of urea was applied. Manual weeding was performed during the 3rd, 5th, and 6th weeks after planting.

To protect the crop from fungi, Folicur Tebuconazole fungicide 250g/L EW was sprayed 7 days after sowing. Additionally, after 32 days of sowing, Imidacloprid was applied to control Aulacophora. For the treatment of *Sclerotium rolfsii* fungi, Homai (Thiophanate-methyl 50% (w/w) + Thiram 30% (w/w) WP) was used. Folicur Tebuconazole 250g/L EW was sprayed on the crop for protection from fungi 7 days after sowing. After 32 days of sowing. Imidacloprid was applied to control Aulacophora.

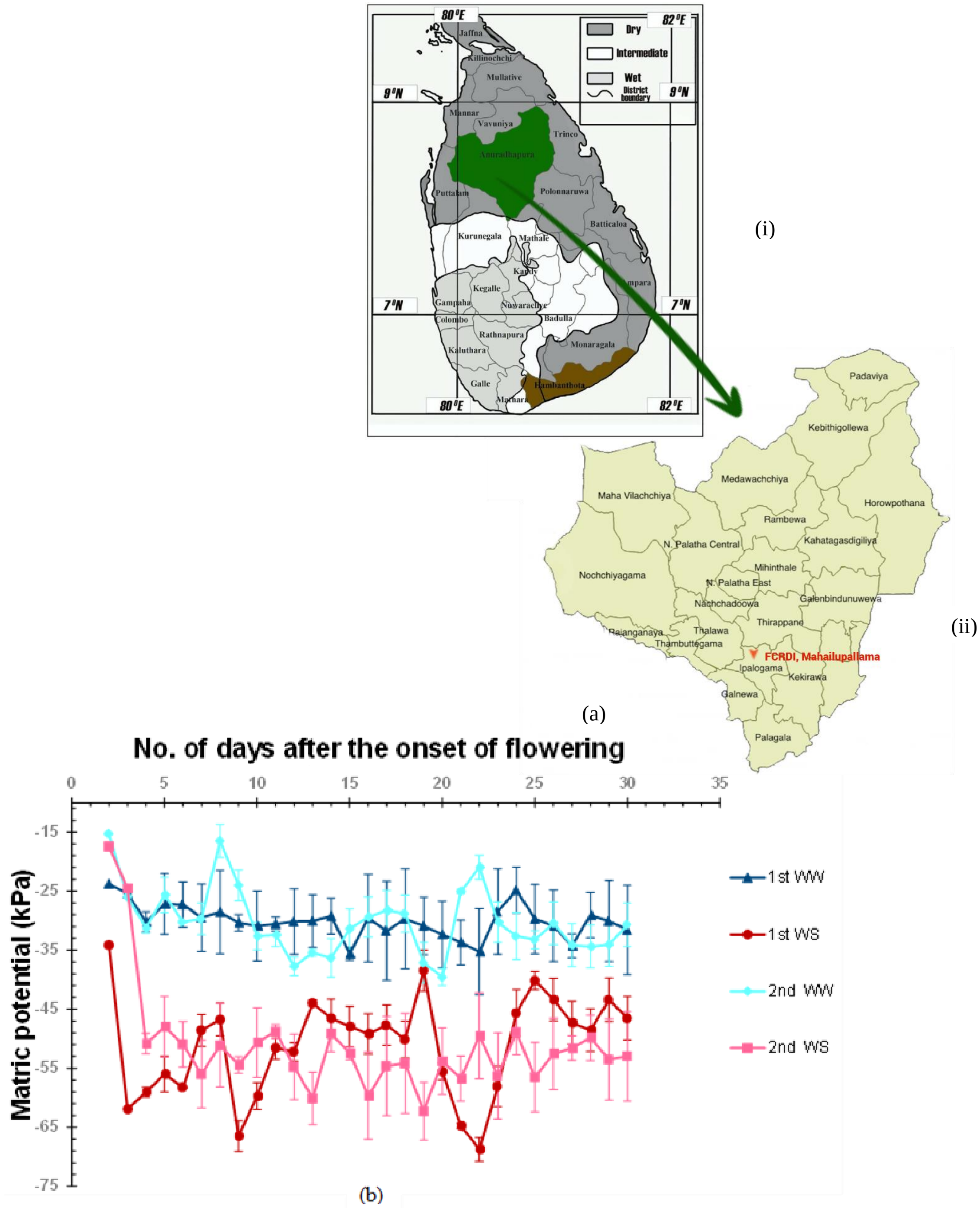

Figure 1: a (i) - Three climate zones and the districts of Sri Lanka. Source: Warnasekara *et al.*, 2002 and a (ii) - Study location, FCRDI, Mahaillupallama. b - Variation in matric potential over time after treatments were imposed on the experimental site: well-watered (WW) and mild water-stressed (WS). 1st and 2nd indicated in the figure denote the first and second seasons respectively. The average matric water potential values of -30 kPa (field capacity) and -50 kPa (70% of field capacity) were maintained in well-watered and mild water-stressed conditions, respectively

Measurements

Physiological data: Net photosynthetic rate (A_{sat}) under an average ambient photosynthetic photon flux density of 1000 µmol m^{-2} s^{-1} was measured at ambient CO_2 concentration and the average growth temperature of 32°C. Leaf dark respiration rate (R_D) was measured by turning off the light source after dark and adapting the leaves for 30 minutes. The R_D/gross photosynthetic rate –(A_g) was calculated as the ratio between R_D and the gross photosynthetic rate (A_g = A_{sat} + R_D). All physiological measurements were made at the 50% flowering stage in 12 cowpea plants (representing three replicate plots) of a variety using the LICOR-6400 XT infrared gas analyser (Li 6400 XT, LiCOR Bioscience, USA). All these measurements were taken from recently matured fully expanded healthy leaves between 9.00 a.m. and 1.00 p.m. Water use efficiency (WUE) and stomatal conductance (g_s) were also obtained from the infrared gas analyser.

Agronomic data: Seed yield and yield components (number of pods per plant, number of seeds per pod, hundred seed weight at harvesting and at storing moisture level of 12%, and total grain yield) were recorded at the harvesting stage. Using a randomly placed quadrate, the number of plants per square meter was counted. Then those plants were used to estimate the number of pods per plant and the number of seeds per plant. Using these yield components, the total grain yield was calculated in kilograms per hectare. The moisture level of the seeds was measured using a seed moisture meter (GMK – 303RS, G-won Hitech Co., Ltd, South Korea). The fresh weight and dry weight of leaves were measured after oven drying leaves for 48 hours at 60°C to a constant weight. Then the leaf dry matter content (LDMC) was calculated as the ratio of leaf dry mass to hydrated leaf fresh mass, while leaf mass per area (LMA) was calculated as the ratio between leaf dry weight (g) and leaf area (m^{-2}).

Data analysis

All statistical analyses were conducted in R software version 1.1.453 (RStudio Team, 2016). Linear mixed effect models (lmer function) were fitted using the lme4 package to determine whether water treatments affected the tested parameters. The mean separation was done using the glht function of the Multcomp package for Tukey's range test. The Mann-Whitey U test was used to analyse count data.

RESULTS AND DISCUSSION

Impact of mild water stress on leaf functional traits of cowpea varieties

A mild water deficit, occurring below 70% of field capacity (FC), resulted in a significant ($P<0.05$) decline in the net photosynthesis rates of all five cowpea varieties in both inter-seasons (Figs. 2a and b). The leaf dark respiration rate also significantly ($P<0.05$) decreased in the MI35 variety during both seasons under mild water stress, whereas the other varieties did not show a significant change ($P=0.05$) (Figs. 2c and d). This lack of significant change in the rest of the varieties may be attributed to variations in their tolerance to water stress.

The ratio of carbon loss per unit carbon gain (R_D/A_g) demonstrated a significant increment ($P<0.05$) in MI-35 and ANKCP 1 during both seasons under mild water stress (Figs. 2e and f). In contrast, the Waruni and Bombay varieties exhibited significantly ($P<0.05$) lower carbon loss per unit carbon gain in both seasons under mild water stress conditions. Dhawala, on the other hand, showed marked variation in its response to moisture stress between the two seasons, with only a significant reduction observed in the second season. Furthermore, the water use efficiency (WUE) decreased when the soil water potential was maintained around -51 kPa. The moisture stress treatment led to a 28% decrease in mean water use efficiency, resulting in a 24% decrease in yield across all varieties (Figs. 4g and h).

Photosynthesis is closely related to plant responses and adaptations to biotic and abiotic stresses, with stress conditions leading to changes in photosynthesis rates (Anyia *et al.,* 2003). In this study, the decrease in the rate of photosynthesis was accompanied by stomatal closure (r= 0.6, p< 0.05) (Figs 2a and b). The mean decline in net photosynthesis (38%) was similar to the mean reduction in the conductance of the stomata to CO_2 (38%). Further, drought stress induces partial stomatal closure in leaves, regulating photosynthesis and transpiration rates and, consequently, water use efficiency (Farquhar *et al*., 1989, Yoo *et al*., 2009, Tankari *et al*., 2019). Similarly, cowpea experiences reduced photosynthesis and stomatal conductance (gs) under drought stress conditions (Han *et al.,* 2016, Anyia *et al.,* 2003). The mild water stress in this study led to a reduction in the physiological activities responsible for carbon gain, resulting in decreased leaf biomass, plant growth, and productivity (Table 1).

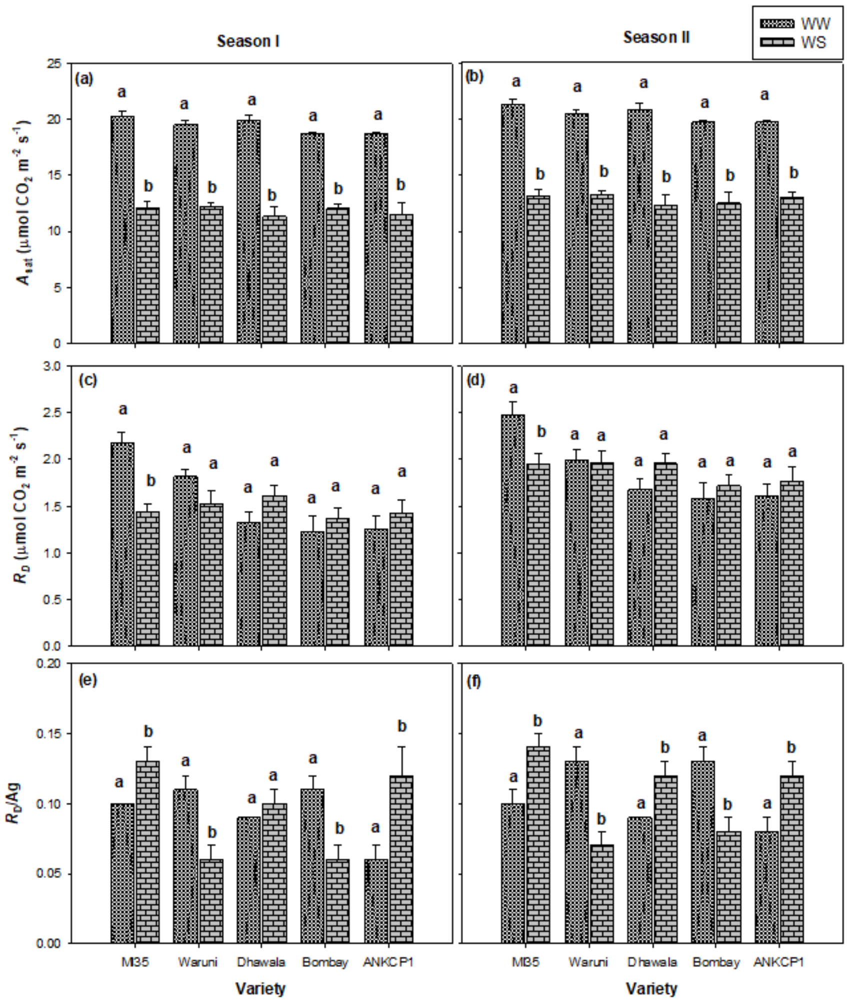

Figure 2: Leaf physiological traits of five cowpea varieties grown under well-watered conditions or Field Capacity (WW) and mild water stress (70% of Field Capacity (WS) in Mahailuppallama, Sri Lanka. The panels are (a) and (b): light-saturated net photosynthetic rate (A_{sat}) at the ambient level of CO_2 (400 ppm) and photosynthetic photon flux density at 1000 μmol m^{-2} s^{-1} measured at 32°C leaf temperature in two growing seasons, (c) and (d): rate of dark respiration (R_D) measured at the ambient level of CO_2 (400 ppm) and at 32°C leaf temperature in two growing seasons, (e) and (f): ratio between RD and gross photosynthetic rate ($A_g = A_{sat} + R_D$) at 32°C leaf temperature in two growing seasons respectively. The whiskers in the bars are the standard errors of the means. Different lower-case letters indicate significant differences in the experimental factor at P<0.05 according to the Tukey's range test.

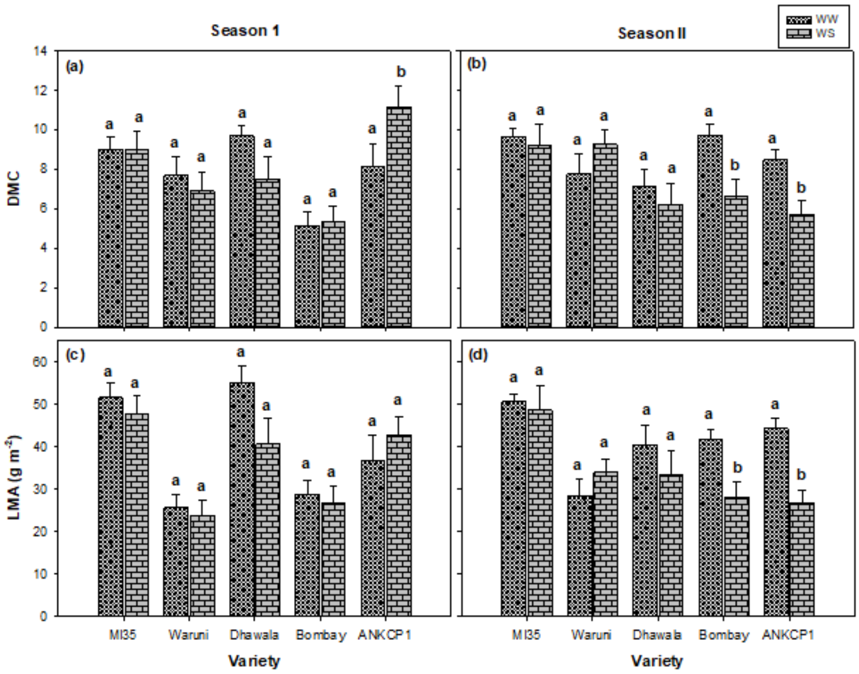

Figure 3: Leaf physiological traits of five cowpea varieties grown under well-watered conditions or field capacity (WW) and mild water stress or 70% of field capacity) in Mahailuppallama, Sri Lanka. The panels are (a) and (b): the ratio between leaf dry weight (g) and leaf area (m^{-2}) (LMA)in two growing seasons; and (c) and (d): the ratio of leaf dry mass to fresh mass (DMC) in two growing seasons. The whiskers in the bars are the standard errors of the means. Different lower-case letters indicate significant differences in the experimental factor at $p < 0.05$ confidence interval according to the Tukey's range test.

Table 1: Total yield of five cowpea varieties under two water treatments in two seasons and yield reduction under the water stress conditions in Mahailuppallama, Sri Lanka

Season	Varietal yield (kg ha^{-1})				Total yield (kg ha^{-1})		
	Variety	Well-watered	Mild water stress	% decline	Well-watered	Mild water stress	% decline
	ANKCP 1	1399±32	1022±44	22			
	Bombay	1202±50	929±26	30			
1	Dhawala	1404±20	1252±37	11	1382±36	1072±37	22
	MI-35	1428±22	1121±41	23			
	Waruni	1476±51	1033±5	27			
	ANKCP 1	1444±20	1302±63	26			
	Bombay	984±107	612±49	20			
2	Dhawala	1438±16	823±26	43	1321±45	968±54	26
	MI-35	1318±52	970±79	10			
	Waruni	1420±17	1131±50	38			

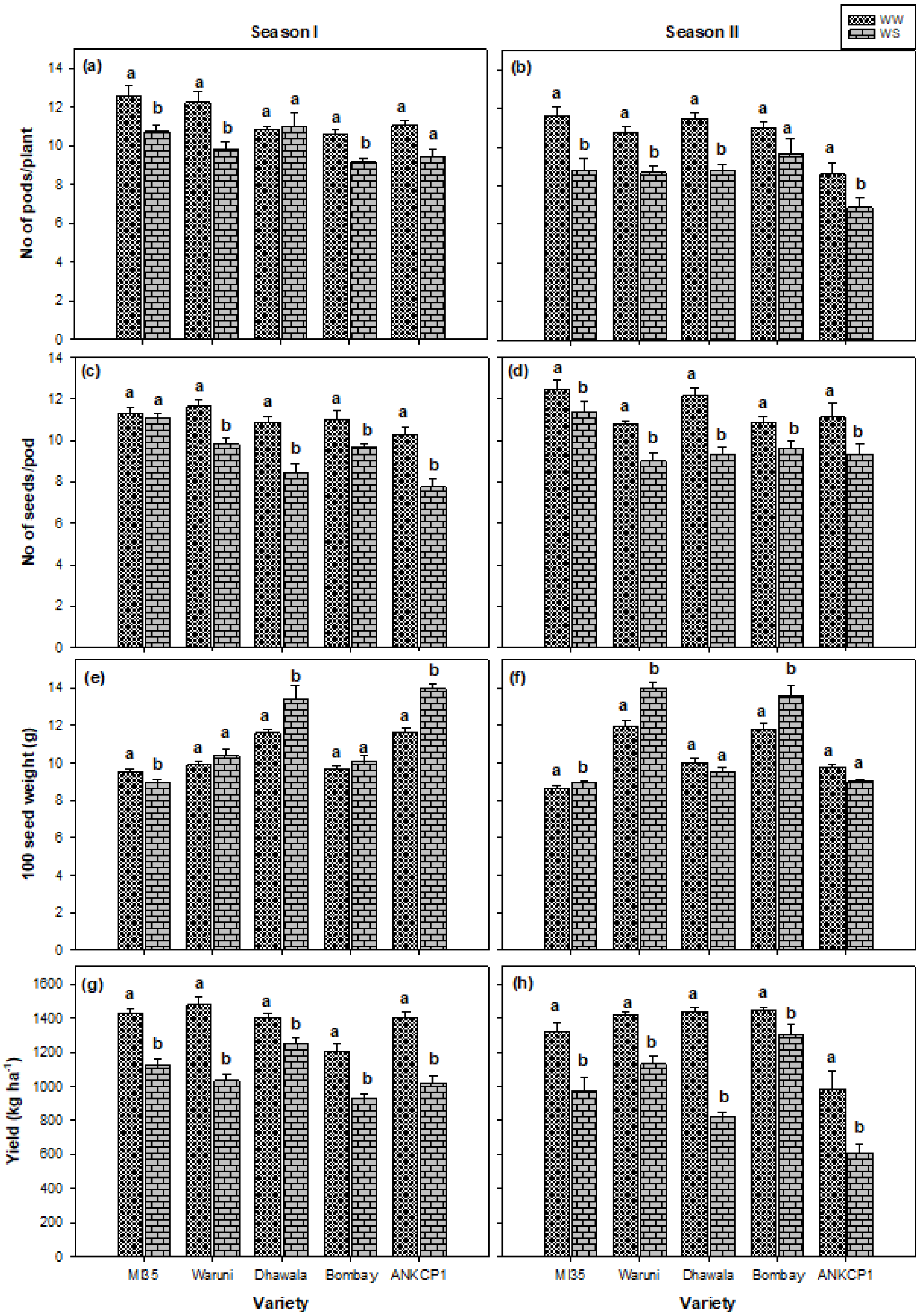

Figure 4: Yield and yield parameters of five cowpea varieties grown under well-watered conditions or field capacity (WW) and mild water stress (70% of field capacity) in Mahailuppallama, Sri Lanka. The panels are (a) and (b): the number of pods per plant in two growing seasons, (c) and (d): the number of seeds per pod in two growing seasons, (e) and (f): the hundred seed weight in two growing seasons, and (g) and (h): total yield (kg ha^{-1}) in two growing seasons. The whiskers in the bars are the standard error of the means. Different letters indicate significant differences in the experimental factor at $p < 0.05$ according to the Tukey's range test and Mann-Whitey U test for the count data.

Under mild water stress conditions, the dry matter content (DMC) of ANKCP 1 significantly (P< 0.05) increased in the first season (Fig. 3a), while DMC and leaf mass per area (LMA) significantly (P< 0.05) decreased in the second season (Figs. 3b and d). Among the other varieties, only Bombay showed a substantial change in leaf DMC in the second season. Furthermore, except for ANKCP 1 and Bombay, there were no substantial changes in LMA in the second season, indicating minimal structural changes in leaf architecture under mild water stress conditions (Andrea *et al*., 2005).

Impact of mild water stress on yield parameters of selected cowpea varieties

Mild water stress had a significant (P<0.05) impact on the number of pods per plant in three varieties, namely MI-35, Waruni, and Bombay, during the first season. Additionally, during the second season, mild water stress significantly reduced the number of pods per plant in MI-35, Waruni, Dhawala, and ANKCP 1 (Figs 4a and b, respectively). The number of seeds per pod was significantly reduced (P<0.05) in all varieties except for MI-35 during the first season, and in all varieties during the second season (Figs 4c and d, respectively). Meanwhile, the weight of hundred seeds remained unchanged in MI-35 during both seasons, but it increased in Dhawala and ANKCP 1 during the first season, as well as in Waruni and Bombay during the second season under mild water stress. However, no clear pattern related to changes in hundred seed weight was evident among varieties and between seasons (Figs 4e and f). Moreover, the total yield showed a significant reduction (P<0.05) in all five cowpea varieties during both seasons under mild water stress. When averaged across varieties, the total yield decreased from 1,382±36 kg/ha to 1,072±37 kg/ha (22%) during the first season (Figure 4g) and from 1,321±45 kg/ha to 968±54 kg/ha (26%) during the second season (Figure 4h) under mild water stress conditions. Overall, when averaged across seasons, a 24% reduction in total yield was observed in response to mild water stress (Table 1).

Under the conditions of mild water stress, there was an increase in dry matter allocation to the seeds in Dhawala and ANKCP 1 during the first season, and in Waruni and Bombay during the second season, as evidenced by the increase in hundred seed weight (Figs. 4e and f). Despite this, an overall reduction in yield was observed in all the tested varieties due to a significant (P<0.05) reduction in the number of seeds per pod under mild water stress conditions. Among the tested varieties, the highest yield reduction (42%) was evident in Dhawala during the second season (Fig 4h).

Cowpea is particularly susceptible to moisture stress, especially during the flowering and pod-filling stages (Aboamera, 2010; Dasila *et al*., 2016). Thus, the reduction in total yield can be attributed to the combined effect of the reduced rate of leaf net photosynthesis and yield parameters, including a reduced number of pods per plant and a reduced number of seeds per pod under mild water stress.

CONCLUSIONS

The yield reduction observed in all five tested varieties was associated with a decrease in leaf net assimilation rate, as well as a reduction in the number of pods per plant and the number of seeds per pod. Despite an increase in leaf mass per area (LMA) and dry matter content (DMC) in Waruni and ANKCP 1, the reduction in yield parameters due to mild water stress was evident and varied among the different varieties under the dry zone conditions in Sri Lanka. Therefore, when selecting cowpea varieties for inter-season cultivation, their yield potential under water stress conditions should be considered.
Among the five cowpea varieties studied, the variety Waruni demonstrated a better performance in terms of yield under both moisture conditions. Additionally, to maximize the efficient use of residual moisture in cowpea fields, cultivation should commence promptly after the main crop is harvested. This approach can help make the most of available water resources and optimize cowpea productivity in regions prone to water stress.

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