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*Research Article*

# Acclimation of Ecophysiological and Agronomic Traits to Increasing Growth Temperature in Three Cowpea Genotypes Grown in Anuradhapura, Sri Lanka

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The future of food crop production is uncertain due to the negative effects of global warming. Cowpea is grown in warm environments including in Sri Lanka, where less is known about the potential acclimation of ecophysiological and agronomic traits to increasing temperatures. We evaluated the acclimation potential of yield components and ecophysiological traits of three recommended cowpea genotypes to the seasonal variation in growth temperature in Anuradhapura, Sri Lanka. This study was conducted at the Faculty of Agriculture, Rajarata University of Sri Lanka, in two consecutive seasons with average daytime temperatures of 30.4°C and 33.2°C. Three genotypes, Dhawala, Waruni, and MI-35, were tested in this study, and their rates of leaf photosynthesis and respiration at the 50% flowering stage and final yield parameters were measured at their respective average growth temperatures in both seasons. The total yield per hectare showed an average decrease of 16%, 17%, and 22% in the Dhawala, Waruni, and MI-35 genotypes at high average growth temperature, respectively. These reductions were associated with the reduction in the number of seeds per pod, hundred seed weight, and number of pods per plant, suggesting that there could be an among-genotype variation in flower abscission, fertilization, and biomass partitioning during the season in which the average growth temperature was high. In the season with high average growth temperature, genotype Dhawala showed an increased carbon gain per unit carbon loss and increased water use efficiency compared to MI-35 and Waruni genotypes. Therefore, genotype Dhawala is a better candidate than MI-35 and Waruni genotypes in the face of global warming, which may be considered in further breeding programs and market preferences. More work is proposed to examine the patterns of biomass partitioning and radiation use efficiency in three cowpea genotypes at elevated temperatures.

## 1. Introduction

The recent acceleration of global climate change poses detrimental impacts on multiple sectors, including global food production. Global warming, the tendency of the average Earth's surface temperature to increase with time [1], is the most commonly used parameter of climate change [2]. Anthropogenic activities may have caused approximately 1.0°C of global warming with a further increase of 0.8°C to 1.2°C by 2052 [3]. According to the IPCC Special Report on the impacts of increment in global warming of 1.5°C, global temperatures are likely to reach an increment of 1.5°C between 2030 and 2052 causing yield reductions in major agricultural crops.

Global warming is closely associated with high-temperature events that are projected to increase in magnitude, duration, and frequency [4]. The growth, development, and yield formation of crops may respond differently to these characteristics. If it continues to increase at the current rate, it is more likely to experience substantial yield losses in crops, particularly if the magnitude of warming reaches 2°C or beyond [5, 6]. If episodes of high temperatures are overlapped with the critical growth periods of crops, reductions in yield would be observed if respiratory losses are increased relative to the gross carbon gain [7, 8]. If spikes of high temperature are observed during the flowering stage, reductions in seed yields may be observed [9]. Therefore, the adaptation of the agricultural sector to global warming includes the evaluation of the yield components of existing crop cultivars to episodes of increasing average growth temperature. Furthermore, the vulnerability of tropical cropping systems to unpredictable weather patterns in recent decades [8, 9] has made the evaluation of the productivity and resilience of individual crops to the impacts of global warming imperative for decision-making in the face of climate change [10].

Cowpea (*Vigna unguiculata* (L.) Walp.) is a widely grown grain legume in drier regions and marginal areas of the tropics and subtropics [11]. It is a multipurpose legume that provides a high-quality protein for human consumption and livestock, which also plays an important role in soil nutrient cycling through biological nitrogen fixation [12–14]. All parts of the plant are used as food rich in protein and vitamins. The immature pods and leaves are used as vegetables, while snacks and main dishes are prepared from the grains [15]. Cowpea grows well in hot-to-moderate temperatures and is therefore considered an integral element in both hot-dry and hot-humid agroecosystems. Cowpea shows optimum growth in regions with an average temperature of around 25°C in summer [13, 16]. Consumer preference for cowpeas is determined by their variations in seed size, colour of the skin, texture, eye colour, seed weight, carbohydrate, nutrient content, etc. [17, 18]. Farmers grow varieties that consumers are more likely to buy.

While cowpeas are believed to be suitable for warm environments, evidence suggests that both vegetative and reproductive growth and development are affected by high growth temperatures. The growth and yield characteristics of this crop are affected by temperature, making the growth temperature a critical environmental determinant of the final yield [19]. Temperature stress causes alteration in physiological processes such as photosynthesis, respiration, and lipid accumulation. The solubility of oxygen is decreased more than $CO_2$ in high temperatures and causes an increase in photorespiration and lowers the photosynthetic rate [20, 21]. Furthermore, an increased frequency of temperature stress can disrupt the physiological processes of plants resulting in photosynthetic inhibition, reduced nitrogen anabolism, higher protein catabolism, and accumulation of the end products of lipid peroxidation [16]. Further, leaf area expansion and development are drastically reduced due to high temperatures [22]. The high-temperature limit to yield is related to a reduced period of pod development and is associated with the early senescence of plants [16, 23]. Although the literature strongly supports the yield limitation of cowpea with high temperature, it is unclear whether structural and physiological adjustments are made in individual plants in response to high growth temperature (i.e., acclimation) [8, 24].

Among the cultivated legumes, cowpea is an essential component in rain-fed tropical cropping systems, including the dry zone farming systems of Sri Lanka [25, 26]. Although this crop is traditionally grown in both *Yala* (April to June) and *Maha* (November to January), the two main cultivation seasons of Sri Lanka the Department of Agriculture of Sri Lanka (DOASL) recommend cowpea as the main inter-season (March to May and July to September) crop [27]. Many farmers cultivate cowpea as their major cash crop given that cowpea can be grown in marginal temperature and soil moisture conditions with considerable yield in the dry zone of Sri Lanka [26].

The seasonal temperature variation in the dry zone of Sri Lanka offers an opportunity to evaluate the crop performance at different growth temperatures and estimate the potential acclimation response of yield components and ecophysiological traits. In this experiment, we evaluated the acclimation potential of yield components and ecophysiological traits of three recommended cowpea genotypes to the seasonal variation in the growth temperature in Anuradhapura, Sri Lanka. We hypothesized that the three cowpea genotypes exhibit a similar or high net carbon gain and show a similar or low carbon loss in response to high growth temperatures. In terms of acclimation, we further hypothesized that the yield components are increased at high growth temperatures compared to those grown at low growth temperatures.

## 2. Materials and Methods

*2.1. Experimental Location.* This experiment was conducted at the Research Unit of the Faculty of Agriculture, the Rajarata University of Sri Lanka, Anuradhapura (8°37′N, 80°42′E), located in the north-central province of Sri Lanka, during two consecutive seasons in 2019 and 2020. Meteorological data were collected by the Meteorological Station of the Faculty of Agriculture, Rajarata University of Sri Lanka, and verified by a second station located 5 kilometers away at the Meteorological Department in Anuradhapura. During the first and second seasons, the average daytime temperature was $30.4°C \pm 0.2$ and $33.2°C \pm 0.3$, respectively (Figure 1).

*2.2. Experimental Design.* Three treatments (three genotypes of cowpea: Dhawala, Waruni, and MI-35) were planted under field conditions in a randomized complete block design (RCBD) with four replicates per treatment as blocks. The plot size was $5 \times 3.5$ m (17.5 $m^2$). The inter-row spacing and intra-row spacing were maintained at 30 cm and 15 cm, respectively, as recommended by DOASL. Cultivating in two consecutive seasons under the same agronomic conditions and at the same location enabled us to provide two growth temperatures to the crop plants.

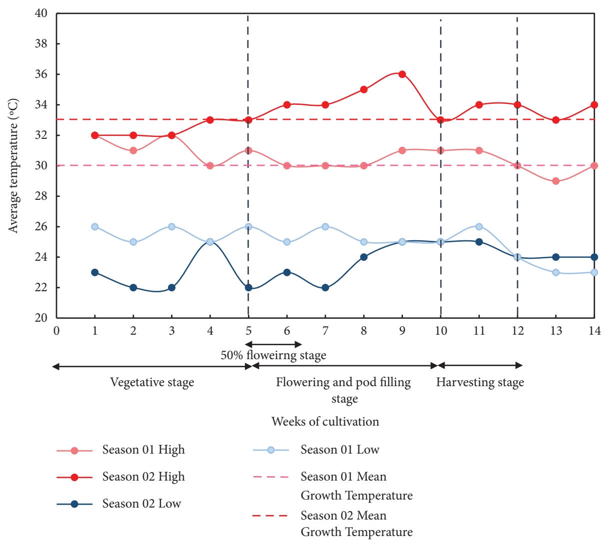


Figure 1: Weekly minimum and maximum temperature during two seasons that three cowpea varieties were cultivated in Anuradhapura, Sri Lanka.

*2.3. Crop Establishment and Management.* For both seasons, the land was plowed to a depth of 25–30 cm using a tine tiller. It was subsequently harrowed with a rotavator to obtain a loose and friable bed. The seeds of the selected cowpea genotypes were obtained from certified seed lots of the DOASL seed farm in Pelwehera, Sri Lanka. Two seeds were planted per hill at a depth of 4 cm. One week after sowing, thinning and gap-filling were done. Excess seedlings were removed to maintain spacing and replanted to maintain the desired plant population. Fertilizer was added as per the recommendation of DOASL. A base dose of 35 : 100 : 75 kg/ha of N: $P_2O_5$: $K_2O$ was applied using urea (46%), triple superphosphate (46%), and potash muriate (60%). As the top dressing, 30 kg/ha of urea was applied at the onset of flowering. The plots were irrigated depending on the soil moisture to maintain the field capacity in both seasons. Manual weeding was practiced 3$^{rd}$ and 6$^{th}$ week after planting.

*2.4. Measurement Protocols*

*2.4.1. Physiological data.* All physiological data were measured with a LI-6400 XT infrared gas analyzer (Li 6400XT, LiCOR Bioscience, U.S.A.) during the 50% flowering stage. Three replicates from each genotype were used to measure physiological data. Light saturated net photosynthetic rate ($A_{sat}$) was measured at 400 ppm $CO_2$, 2200 $\mu$mol·m$^{-2}$·s$^{-1}$ of photosynthetic photon flux density. Dark respiration ($R_D$) was measured at 400 ppm $CO_2$ after turning off the light and covering the leaves selected with aluminum foil and a black cloth for 30 min. For comparison purposes, both $A_{sat}$ and $R_D$ were measured at a leaf temperature of 32°C, which is the mean annual temperature of the experimental location. All these measurements were taken from recently matured, fully expanded, healthy leaves between 9.00 a.m. and 11.00 a.m.

*2.4.2. Agronomic data.* Seed yield and yield components such as number of pods per plant, number of seeds per pod, 100 seed weight at harvesting and at storing in 12% moisture level, and total grain yield were recorded. 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, total grain yield was calculated in kilograms per hectare. The mean leaf area at the 50% flowering stage was measured using twenty leaves from each genotype and using ImageJ software for area calculation. The fresh weight and dry weight of leaves were measured after oven drying the leaves for 48 hours at 60°C. The leaf dry matter content and the leaf mass per area were calculated following the standard methods.

*2.5. Data analysis.* The slope of each measured trait was compared between growth seasons using the standardized major axis regression (SMR) test. Varietal differences in all parameters were tested using one-way ANOVA and the LSD mean separation method, and seasonal changes in all parameters were compared using the SMR test in all three genotypes. Finally, the effect of changes in environmental temperatures over two seasons on the total yield of each cowpea genotype was estimated using the SMR test. All statistical analyses were conducted in R software (RStudio Team, 2016).

## 3. Results

*3.1. Changes in Agronomical and Anatomical Traits in Response to Growth Temperature.* We anticipated that the yield components of warm-grown cowpea genotypes should be higher than those of the respective genotypes exposed to low growth temperature (Table S1). Contrary to our expectations, the total yield per hectare decreased by 213.83 kg·ha$^{-1}$ ($p < 0.05$), 222.50 kg·ha$^{-1}$ ($p < 0.05$), and 297.66 kg·ha$^{-1}$ ($p < 0.05$) in the Dhawala, Waruni, and MI-35 genotypes, respectively (Figure 2(a)). The significant yield reduction of MI-35 was associated with the significant reduction of number of seeds per pod ($p < 0.05$). Likewise, the yield decline in genotypes Waruni and Dhawala was associated with the decrease of hundred seed weight and number of pods per plant, suggesting that genotype variation in flower abscission, fertilization, and the amount and partitioning of net photosynthetic carbon during stress periods may exist.

*3.2. Changes in Ecophysiological Traits in Response to Growth Temperature.* Dhawala showed a slight increase in $A_{sat}$ at 33°C growth temperature (Figure 3(a), Table S1) ($p < 0.05$). The carbon gain per unit carbon loss was increased in Dhawala with increasing temperatures. Even though this genotype showed a marginal increase in the net carbon gain (Figures 3(a)–3(d)), it did not translate to a high yield at high growth temperature (Figure 2(a)). This implies that the genotype Dhawala can acclimate its ecophysiological traits to a possible warm temperature without changing its yield attributes, making it superior to others. Unlike the above

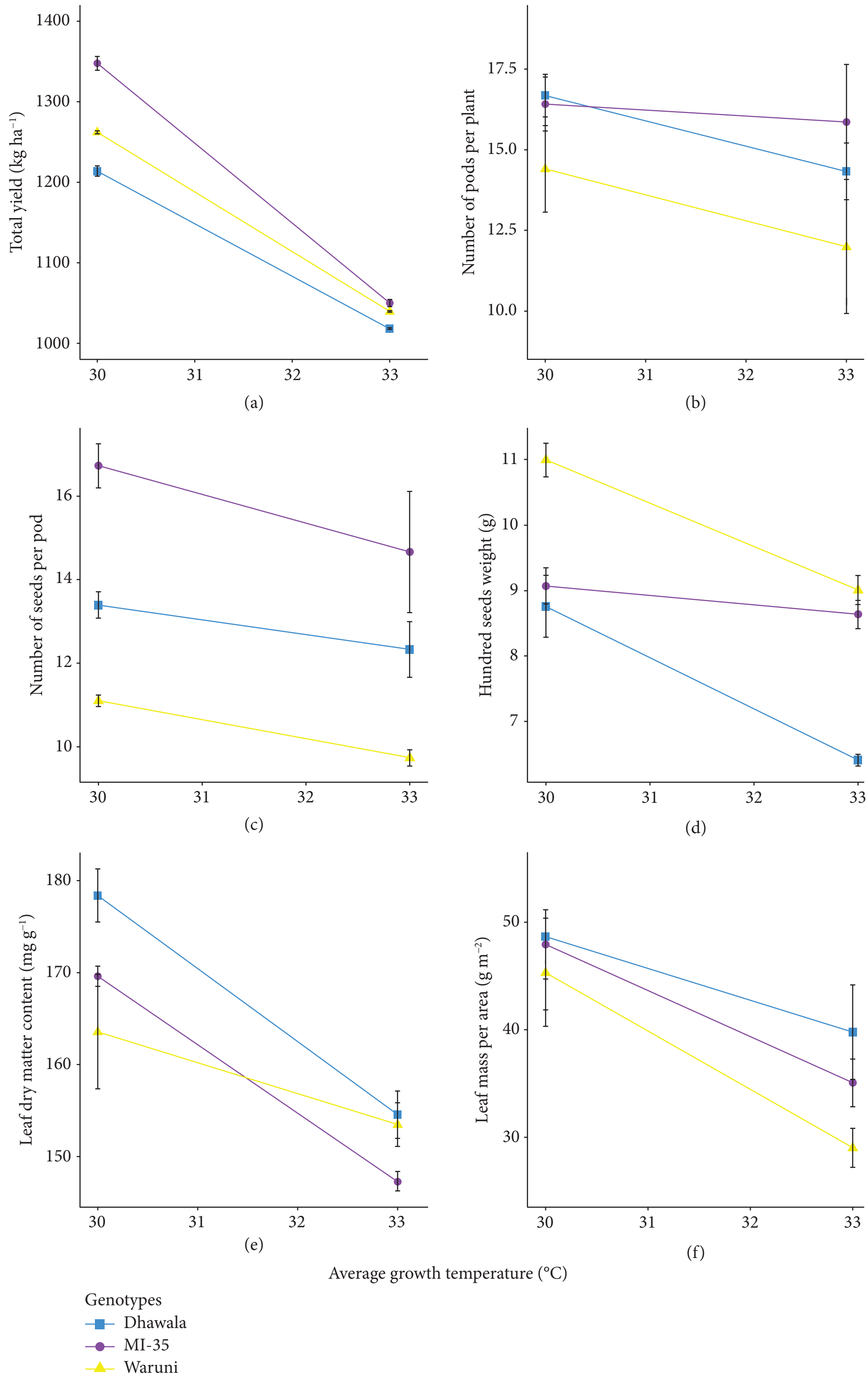


Figure 2: Yield components and leaf traits of three cowpea genotypes (square–Dhawala, circle–MI-35, and triangle–Waruni) grown at two growth temperatures, 30°C and 33°C, in Anuradhapura, Sri Lanka. The panels are (a) total yield (kg·ha$^{-1}$), (b) number of pods per plant, (c) number of seeds per pod, (d) hundred seed weight (g), (e) leaf dry matter content (g·g$^{-1}$), and (f) leaf mass per area (gm$^{-2}$). Whiskers around the points are the standard error of the mean.

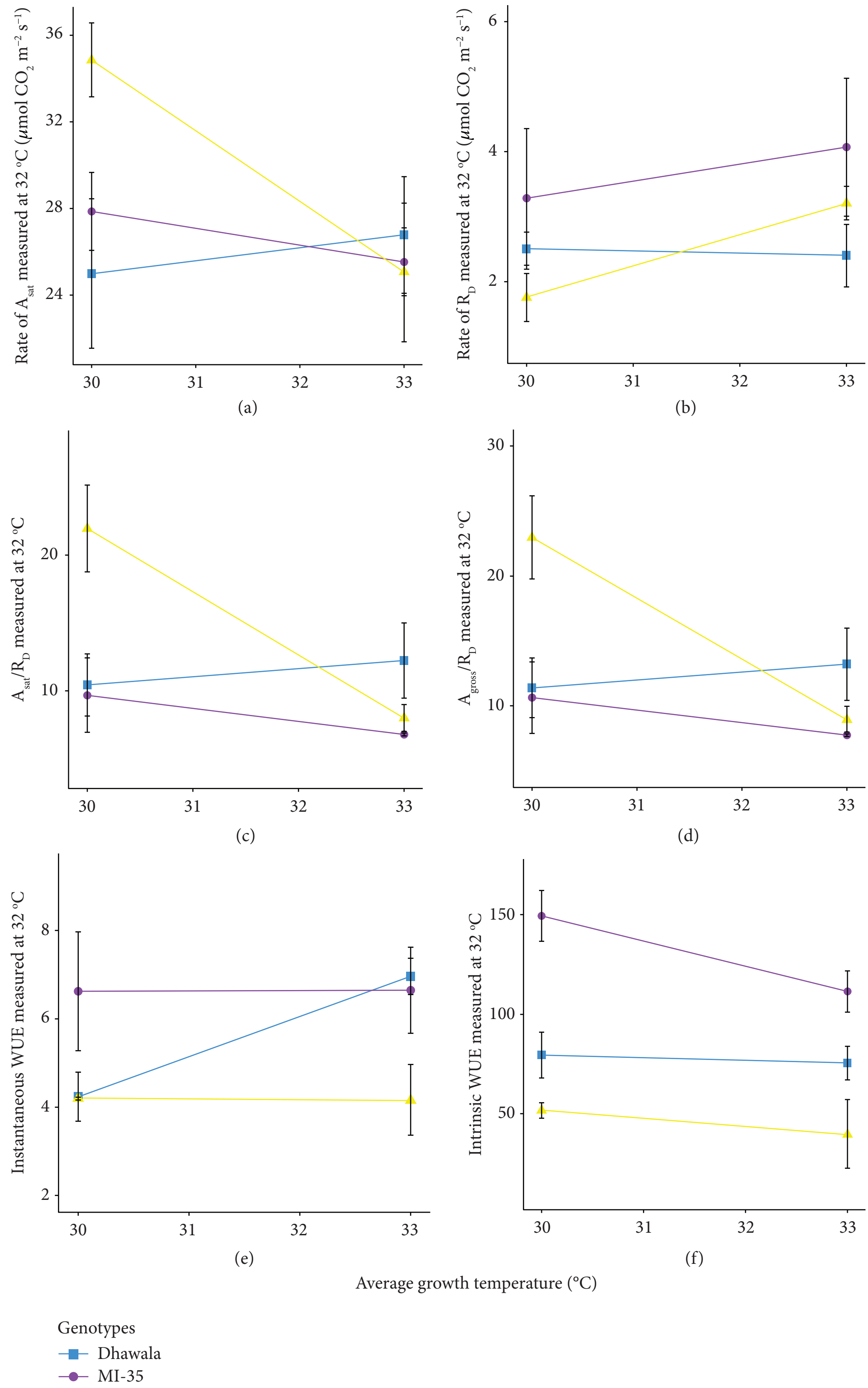


Figure 3: Leaf physiological traits of three cowpea genotypes grown at average daytime growth temperature, 30°C and 33°C, in Anuradhapura, Sri Lanka. (a) Light saturated net photosynthetic rate ($A_{sat}$) at ambient level of $CO_2$ (400 ppm) and photosynthetic photon flux density at 2200 $\mu$mol·m$^{-2}$·s$^{-1}$ measured at 32°C leaf temperature in two growth seasons, (b) rate of dark respiration ($R_D$) measured at ambient level of $CO_2$ (400 ppm) and at and 32°C measurement leaf temperature in two growth seasons, (c) ratio between $A_{sat}$ and $R_D$ at 32°C measurement leaf temperature in two growth seasons, (d) ratio between gross photosynthetic rate ($A_{gross}$) and $R_D$ at 32°C measurement leaf temperature in two growth seasons, (e) ratio between $A_{sat}$ and transpiration rate at 32°C measurement leaf temperature in two seasons, and (f) ratio between $A_{sat}$ and stomatal conductance ($g_s$) at 32°C measurement leaf temperature in two growth seasons. Whiskers around the points are the standard error of the mean.

responses, we also noted that the warming condition did not significantly affect $A_{sat}$, but in dark respiration (Figures 3(a) and 3(b)), thus reducing the carbon gain per unit carbon loss. For instance, in genotype Waruni, the carbon gain per unit carbon loss decreased with increasing growth temperature (Figures 3(c) and 3(d)). A similar trend was also noted in its yield components (Figure 2(a)). Moreover, the MI-35 genotype was drawn to reduce carbon loss to unit carbon gain and yield under warm conditions ($p < 0.05$, $<0.001$; Figures 3(a)–3(d) and 2(a), Table S1). The water use efficiency showed a slight reduction in MI-35 and Waruni, which was not significant. However, the water use efficiency was significantly higher in the warm season than in the cool season (Figures 3(e) and 3(f)). Overall, these results suggest that Dhawala is a better genotype for a warming future than Waruni and MI-35 due to their inferior ecophysiological traits.

## 4. Discussion

In this study, we report the acclimation potential of three cultivated cowpea genotypes to the increase in growth temperature under tropical field conditions in Sri Lanka. When the growth temperature was increased by 3°C from one season to the other, we observed an average decrease in the total yield per hectare by 16%, 17%, and 22%, respectively in Dhawala, Waruni, and MI-35 genotypes (Table 1). These trends were closely associated with the yield components: number of pods per plant, number of seeds per pod, and the hundred seed weight (Figures 2(b)–2(d)). Relative to the potential yield of the genotypes at 27°C growth temperature reported by the Department of Agriculture, Sri Lanka [28], our data from warm grown (33°C) Dhawala, MI-35, and Waruni genotypes showed a yield decline of 31%, 32%, and 35%, respectively.

High-temperature stress causes yield loss in legumes, which is associated with several yield components and physiological processes. It is predicted that a one-degree rise in temperature would reduce the crop yield by at least 10% [8, 10, 29]. High-temperature stress likely reduces crop yields by its influence on the reproductive stage by reducing the numbers of buds, flowers, fruits, pods, and seeds, resulting in marked reductions in yield potential [10, 29]. Temperature fluctuations during seed filling drastically reduce the yield in cowpea [24, 30]. At high temperatures, the magnitude of seed filling is accelerated while reducing the duration of this stage, thereby reducing the overall seed yield. High-temperature stress reduces seed size due to the insufficient accumulation of photosynthates during seed filling [8]. With the increase of 3°C in growth temperature in this study, we noticed that the grain size was reduced (Figure 2(d)) possibly due to the reduced grain filling. In all three genotypes, the leaf mass per area was reduced in the warm season (Figure 2(f)), which is primarily due to the reduced leaf dry matter content (Figure 2(e)).

Although cowpea is bred with the ability to tolerate stress conditions [16, 23], our results suggest that there is a genotype-dependency for this generalization. According to the literature, warm-grown leaves at around 25–35°C have a high heat tolerance of Calvin cycle enzymes, which enables high photosynthetic rates at high temperatures [31–33]. There is an inter-specific variation in the magnitude of change in the photosynthetic rate among different growth temperatures [34, 35]. This suggests that temperature acclimation is a homeostatic response to maintain the photosynthetic rate at different growth temperatures. However, different responses of photosynthetic rate acclimation to increasing growth temperature were observed in trees [32, 36]. Therefore, absolute photosynthetic rates may be regulated to maintain different values in response to the changes in the growth environment [31]. The different magnitudes of acclimation of the photosynthetic rates in our study support this generalization. Furthermore, it is also likely that the thin leaves generated a small fraction of photo-assimilates in the warm season, resulting in low yield, in agreement with previous findings [37, 38].

In this study, we do not overlook the possible changes in plant biomass partitioning with increasing temperature in some legumes [39]. Our generalization of these results could be further verified by evaluating biomass partitioning and radiation use efficiency at the 3°C growth temperature difference. For cowpea, the optimum growth temperature is 30°C [16, 23], and this study was conducted in two consecutive cultivation seasons with an average ambient air temperature of 30 and 33°C, which enabled us to provide a passive warming effect of 3°C relative to the optimum growth temperature of cowpea (Figure 1). For comparison purposes, all ecophysiological traits at both growth temperatures were obtained at a fixed block temperature of 32°C in the measurement chamber of the infrared gas analyzer, which is also the mean annual temperature in Anuradhapura, Sri Lanka, where the study was conducted [40].

The plants grown in the warm season were expected to have been acclimated to the high temperature, rather than to other biotic and abiotic factors in this study. We noticed a wide gap in the mean ambient air temperature difference during the flowering and pod filling stages (Figure 1). Compared to the pre-flowering and flowering stages, the post-flowering stage is more susceptible to elevated temperatures (30 to 35°C) [24, 39]. We did not notice a major fluctuation of pest and disease populations between the two seasons; therefore, the difference in growth temperature should have been a major determinant of variation between the two seasons, which should be indicated by directional changes in ecophysiological traits because of the adjustments happened in physiological traits [41].

Cowpea genotypes with large white seeds have more demand for both cultivation and cooking purposes [42, 43]. White cowpeas contain higher carbohydrate and fiber contents compared to red cowpeas [42, 43]. Dhawala and MI-35 genotypes evaluated in this study have more market demand than the Waruni genotype. However, between Dhawala and MI-35, genotypes, Dhawala has the highest demand due to its large-sized white seeds.

Table 1: Total yields of three cowpea genotypes in two different growth temperatures and average yield potential of three genotypes as reported by the Department of Agriculture, Sri Lanka [28].

| Genotype | Seed colour | Yield at growth temperature | | | Potential yield as per DOASL |
|---|---|---|---|---|---|
| | | 30°C | 33°C | % Decline in warm season | |
| Dhawala | White | $1213.85 \pm 6.4$ | $1018.06 \pm 0.9$ | 16.54 | $1600\,kg{\cdot}ha^{-1}$ |
| Waruni | Red | $1262.04 \pm 1.7$ | $1039.53 \pm 1.0$ | 17.63 | $1650\,kg{\cdot}ha^{-1}$ |
| MI-35 | White | $1347.62 \pm 8.6$ | $1049.95 \pm 4.2$ | 22.09 | $1350\,kg{\cdot}ha^{-1}$ |

## 5. Conclusion

We conclude that there is genotype-dependent variation in the yield components and ecophysiological traits of cultivated cowpea to the variation in growth temperature. Owing to the superior ecophysiological traits, lower reduction in yield potential, and high market preference, we propose that the genotype Dhawala is a better candidate than MI-35 and Waruni in the face of global warming. This genotype could be considered in further breeding programs and included in tropical cropping systems that are vulnerable to global warming. Additional studies are suggested to evaluate the effect of growth temperature on biomass portioning in terms of yield parameters and effect of growth temperature on seed nutrient accumulation cowpea genotypes.

## Data Availability

Summary of the data is available as a supplementary table (Table S1 Wijayaraja et al. Manuscript on Acclimation of cowpea to increasing growth temperature). Whole dataset is available on request.

## Conflicts of Interest

The authors declare that they have no conflicts of interest.

## Authors' Contributions

NG, DAUD, DMD, WCP, LW, DK, IW, MP, and TA contributed to conceptualization. IW, MP, NG, TA, LW, DK, DAUD, DMD, and WCP contributed to data curation. IW, MP, NG, LW, DK, and DAUD performed formal analysis. NG, DAUD, LW, DK, DMD, and WCP provided funding acquisition. IW, MP, TA, NG, DAUD, WCP, and DMD performed investigation. IW, MP, TA, NG, DAUD, WCP, and DMD contributed to methodology. NG and DAUD helped with project administration. NG, DMD, WCP, and DAUD supervised the study. IW, MP, NG, DAUD, LW, and DK helped in visualization. IW, NG, MP, DAUD, LW, and DK wrote the original draft. NG, DAUD, LW, DK, DMD, and WCP reviewed and edited the original draft.

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## Supplementary Materials

Table S1. Summary of yield components and ecophysiological traits of three cowpea genotypes at two growth temperatures in Anuradhapura, Sri Lanka. (*Supplementary Materials*)

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