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Season and genotype effect on whole plant water use efficiency of coconut (*Cocos nucifera* L.) seedlings grown in a hydroponic system

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ABSTRACT

A study was conducted to understand the influence of climatic factors on nutrient use, and whole plant water use efficiency (WUE) of hydroponically grown coconut seedlings. Two dwarf (Chowghat green dwarf, CGD and Malayan yellow dwarf, MYD) and two tall (Kalpa Pratibha, KP and Kalpatharu, KT) coconut genotypes were grown in triplicates and their water use, and biomass production were measured and WUE was analyzed across summer, monsoon and winter seasons, characterized with distinct climatic variability. In comparison to monsoon, during summer the morning temperature was (6 ℃) high, and relative humidity (RH) was low during summer resulting in two folds increase in vapour pressure deficit on leaf surface (VPDL). Increasing VPDL had direct influence on water consumption of the plant per day which was significantly high during summer (3.14 L) compared to monsoon (1.83 L), but the difference in biomass gain was not significant. This had led to a weakly negative [$R^2(144) = 0.12$, $p < .0001$] relation between water use and WUE, the WUE was only 3.35 g L^{-1} during summer as against 6.6 g L^{-1} of monsoon. The response of genotypes to increasing VPDL was also significantly different. The sensitive stomata of talls could conserve water and maintain significantly high WUE while insensitive stomata of dwarfs allowed greater water loss without a concomitant increase in biomass resulted in low WUE. The early photosynthetic light saturation at 1400 μ mole photon m^{-2} s^{-1} might have also contributed to low biomass production in dwarfs. This study divulges that, at high temperature and low humidity in general, coconut WUE is low and especially dwarfs are not suitable for those regions with dry weather or regions expected to become dry under future climate scenario.

1. Introduction

Coconut (*Cocos nucifera* L.) is an economically important palm grown in the tropical and sub-tropical regions. The crop is cultivated in more than 94 countries across the world in an area of 12.28 M ha producing 67.04 billion nuts with a productivity of around 6000 nuts ha^{-1} (ICC, 2019). India, with an area of 2.1 million ha and production of 2.73 million ton copra equivalent, occupies third place in area and second place in production after Indonesia and the Philippines. Coconut growing and processing empower the livelihood of around 80 million people (Omont, 2001). Traditionally, coconut cultivation relied upon products such as copra and coconut oil and to some extent on coir-based industries. The nutraceutical and functional food potential of coconut and its value added products *viz*., virgin coconut oil (Joshi et al., 2020; Ramesh et al., 2021), coconut inflorescence sap or *Kalparasa* (Asghar et al., 2020; Hebbar et al., 2015; Gopal et al., 2021), coconut sugar (Hebbar et al., 2020, 2022a) etc., have further renewed interest in coconut. Consequently, a steady annual increment in the production of coconut and coconut products is being witnessed during the last decade. Nevertheless, the global coconut production, during the same period, has either decreased or stagnated due to frequent and severe weather extremities like drought and flood, numerous pests and diseases infestation (OECD/FAO, 2017) causing a discrepancy in the demand and supply of coconut products.

Climate variables such as temperature, precipitation, and humidity have enormous impact on the growth, development and geographical

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Abbreviations: APCC, The Asian and Pacific Coconut Community; CGD, Chowghat Green Dwarf; E, Transpiration rate; g_s, Stomatal Conductance; KP, Kalpa Pratibha; KT, Kalpatharu; MYD, Malayan Yellow Dwarf; PAR, Photosynthetically Active Radiation; P_n, Net Photosynthetic Rate; Ppm, Parts Per Million; RH, Relative Humidity; VPD, Vapour Pressure Deficit; VPDL, Vapour Pressure Deficit on Leaf surface; WUE, Water Use Efficiency.

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distribution of coconut (Kumar et al., 2009; Hebbar et al., 2013, 2022b). Coconut palms grow well in warm weather with abundant sunshine and a mean annual temperature of 27 ℃ (Murray, 1977). Temperature conditions above 34 ℃ not only reduces the growth of seedlings (Hebbar et al., 2013), but also causes poor nut set in adult palms (Ranasinghe et al., 2015; Samantha et al., 2013) due to reduced pollen germination (Hebbar et al., 2018) and pollen tube growth through the style (Hebbar et al., 2020a). In India, west coast region is the predominant coconut cultivation area where the rainfall is high (>2000 mm) and summer T_{max} reaches as high as 36°C. On the other hand, east coast is characterized with low rainfall (~1000 mm) and T_{max} during summer is high and reaches around 43°C. In south interior regions T_{max} is as high as 38°C and the relative humidity (RH) is low during summer (around 40%). The adverse effects of high temperature are further exacerbated under low RH conditions. RH less than 60% is detrimental to the coconut as it causes water imbalance due to the excessive transpiration (Ochs, 1977). Solar radiation incidence of 300-900 W m^{-2} and sunshine duration of 2000 h, RH between 60-–90%, and mean annual rainfall above 1500 mm, that is fairly well distributed, are the suitable climatic factors for coconut (Ohler, 1999; Rajagopal et al., 1996).

Plants under high temperature and low humidity experience vapor pressure deficit (VPD), which is an increasingly important driver of plant functioning in terrestrial biomes (Grossiord et al., 2020). In general stomatal conductance declines under high VPD and transpiration increases in most species up until a given VPD threshold, leading to a cascade of reactions including reduced photosynthesis and growth, and higher risks of carbon starvation and hydraulic failure (Gomes et al., 2002; Gomes and Prado, 2007; Kasturibai et al., 1988). The leaf level response of stomatal regulation, net photosynthetic rate (*Pn*), transpiration rate (*E*) and the intrinsic WUE to VPD caused by factors such as light, temperature and RH are well documented in many crops including coconut (Forotaghe et al., 2021; Serri et al., 2021). However, in most of the studies there was less obvious or perceptible direct relationship between *Pn*, stomatal conductance (g_s), WUE and changes in climate parameters (Polley, 2002) due to insufficient understanding of growth response to a change in temperature and the rate of water use by the plant canopy for a given species (Polley, 2002). Hence, estimating growth and water use response of a genotype to the host of climatic

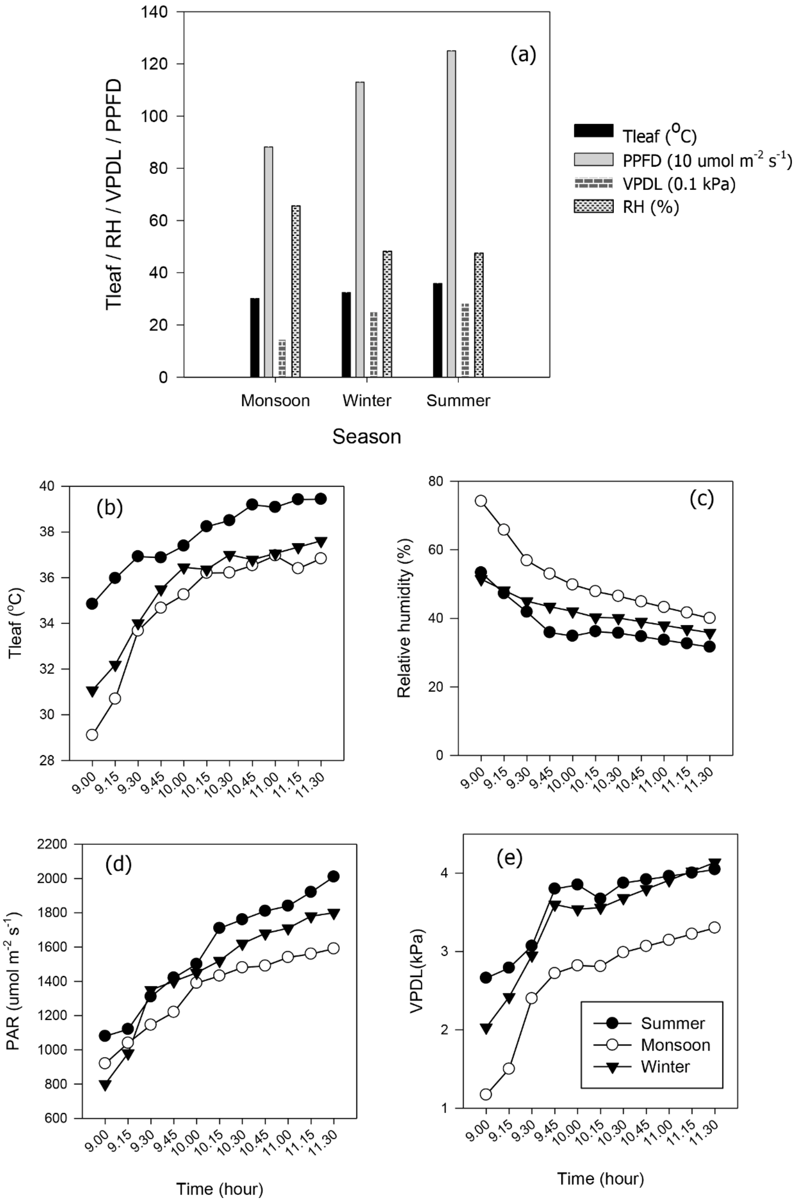


Fig. 1. Average leaf temperature (Tleaf), relative humidity (RH), photosynthetically active radiation (PAR) and vapor pressure deficit of leaf (VPDL) of the coconut seedlings ($n = 3$) during monsoon, winter and summer (a) and diurnal variations of Tleaf (b), RH(c), PPFD (d) and VPDL (e) during monsoon, winter and summer.

factors at the canopy level warrants a methodology to quantify the periodic accumulation of dry matter and the water use in the canopy.

In normal soil or field grown plants it would be difficult to make periodic quantification of biomass gain and water use and hence, for this study coconut seedlings grown in a hydroponic system, which was standardized earlier (Hebbar et al., 2021), was utilized. The data collected were classified under summer, monsoon and winter seasons and analyzed to quantify the effect of climatic factors on water uptake and biomass gain. Further, the genotypic influence on biomass gain and water use across the seasons was determined involving two dwarfs (Chowghat green dwarf, CGD and Malayan yellow dwarf, MYD) and two talls (Kalpa Pratibha, KP and Kalpatharu KT).

2. Material and methods

2.1. Study site

Experiment was conducted in an open facility at the farm of ICAR-Central Plantation Crops Research Institute (ICAR-CPCRI), Kasaragod, Kerala, India. The experimental site is located at 12° 18’ N latitude and 75° E longitude, and at an altitude of 10.7 m above mean sea level. The leaf temperature (Tleaf), RH, photosynthetically active radiation (PAR) and vapour pressure deficit of leaf (VPDL) of the plants during experimentation was recorded at regular monthly intervals in the forenoon (9.00 am to 11.30 AM) using portable photosynthesis system (LI-COR 6400XT, LI-COR, Lincoln, NE, USA) and the data is presented in Fig. 1. The seedlings were grown under open ambient condition and a provision was made to place a transparent polythene cover over the seedlings to protect the seedlings from rain. The experimental site has three distinct seasons *viz.* summer (March, April and May), monsoon (June, July and August) and winter (November, December, January and February) with a characteristic temperature, humidity and PAR profiles (Hebbar et al., 2020a).

2.2. Plant material

Two popular dwarf coconut varieties, Chowghat Green Dwarf (CGD) and Malayan Yellow dwarf (MYD) and two tall varieties, Kalpa Pratibha (KP) and Kalpatharu (KT), were chosen. The coconut seedlings were grown in polythene bags at ICAR-CPCRI farm and one year old uniform, healthy seedlings were selected and transplanted to hydroponic system on 31st, June 2017. After taking out the seedlings from polythene bag, the protruding roots surrounding the nut were cut; the nut was thoroughly washed off the soil before the plant was transplanted to the hydroponic system.

2.3. Growth conditions

Hydroponics was used to investigate the influence of season and genotype on water use, biomass gain and nutrient use of coconut seedlings. The growth conditions of coconut in the hydroponic system are described in Hebbar et al. (2021). Briefly, large plastic drums of 100 L capacity were used to grow the seedlings for the first 8 months (Supplementary Fig. 1) and later the seedlings were shifted to large drums of 300 L capacity (Supplementary Fig. 2). The drums having 100 L and 300 L capacity were filled with 60 L and 250 L of water, respectively enriched with full strength Hoagland’s nutrient solution (pH 5.8). A Hoagland’s solution had the following nutrient composition of which macronutrients (in mM) were: KNO_3 (5); Ca $(NO_3)_2$. $4H_2O$ (4); $MgSO_4.7H_2O$ (1); KH_2PO_4 (2); and the micronutrients were KCl (0.05); H_3BO_3 (0.025); $MnCl_2$ (0.002); $ZnSO_4$ (0.002); $CuSO_4$ (0.0005); Na_2MoO_3 (0.0001) and Fe-Na-EDTA (0.064). Seedlings removed from the polybag were washed and roots were trimmed. The seedlings were inserted into a drum containing Hoagland’s solution through a hole bore at the center of upper lid in such a way that nut and roots remain immersed in water while shoot and leaves were above the lid. The plastic ropes inserted through nut exocarp and fastened to the small holes made at the periphery of the lid, ensured upright plant stand as well as allowed the positioning of nut and roots with respect to water level in the drum (Supplementary Fig. 1 and 2). Additionally, plants tied to the poles above the pot level made them stand firm and resisted fall due to wind. Each pot or drum contained a single seedling. A 1.5 HP compressor, which pumped the air to a mainline and through a micro tube, connected to each pot ensured continuous and adequate aeration to the plants. The outer surface of the drums was painted black to prevent the entry of sunlight and to avoid the growth of algae in the nutrient medium. The seedlings were acclimatized to grow and stabilize in the nutrient solution for another six months (Supplementary Fig. 1 and 2).

After six months of stabilization in hydroponics, two year old seedlings of uniform health (both roots and above ground parts) were selected on 1st January 2018 to investigate the water use, biomass gain and nutrient use. For each genotype, the observation was recorded from three plants. The nutrient solution in the drums was renewed after every 15 days and the pH of fresh solution was maintained at 5.8 by adding either sodium hydroxide (NaOH) or hydrochloric acid (HCl) (Kargbo et al., 2019). While replenishing the nutrient solution, the residual water in the drum, fresh weight of the seedlings, leaf area, collar girth and plant height were measured. In the residual water, the nutrient content was estimated during few measurements. The observation was continued for a period of one year till 31st December 2018. During the course of the experiment, at monthly intervals physiological observations were recorded. At the end of the experiment, leaf, stem, and root samples were harvested for estimation of dry biomass accumulation. Physiological measurements were made on the middle leaflets of the topmost fully opened leaf in a randomized way.

2.4. Growth measurements

Plant height was recorded from plant base to the highest point of the fully opened leaf. The circumference of the stem, just above the attachment of nut, was measured at a fixed point using measuring tape and expressed in centimeters as the collar girth. Length and width of each fresh leaf was measured to calculate the whole plant leaf area using the linear regression equation [$y = 3.9325 + 0.7044x$, where y=area of the leaflet; x = length X breadth at the broadest position of the leaflet] developed by Mathes et al. (1989). To measure the fresh biomass, the whole seedling was lifted from the pot, allowed to drain the excess water on the roots, dried using paper towel and placed on a weighing balance of 100 kg capacity. Leaf area, collar girth and fresh weight of the plant were recorded every 15 days. At the end of the experiment, seedlings were separated into root, shoot and leaf, oven dried at 65 °C for two days and dry weights were recorded to calculate the total dry biomass production. The moisture content of root, shoot and leaf was estimated at the beginning and end of the experiment so as to calculate average moisture content of seedlings in order to convert fresh weight biomass obtained at regular intervals into dry weight biomass.

2.5. Physiological measurements

Process parameters *viz.* net photosynthetic rate (P_n), stomatal conductance (g_s) and transpiration (E) were measured using a portable photosynthesis system (LI-COR 6400XT, LI-COR, Lincoln, NE, USA). Measurements were made in triplicates at a fixed light intensity of 1000 μmol m^{-2} s^{-1} during summer, monsoon and winter seasons. Pn-PAR curves were obtained using the LI-COR 6400-XT photosynthetic system for the tall and dwarf genotypes. Measurements were made between 9:00–11:30 h on a sunny day. For every measurement, PAR was set at 2400, 2200, 2,000, 1,800, 1,600, 1,400, 1,200, 1,000, 800, 600, 400, 200, 100 and 50 µ mol (photon) m^{-2} s^{-1} by artificial Li-6400-XT LED radiation source to measure *Pn* under different light intensities. For each PAR, the measurement time was controlled to 180 s and the photosynthetic parameters such as *Pn*, g_s and *E* were recorded automatically by the instrument. During the measurement, the flow rate of air in the measuring chamber was about 500 µ mol s^{-1}, the atmospheric CO_2 concentration was maintained at 400 ± 10 µ mol s^{-1}, the temperature of the leaf chamber was 30 ± 3°C, and the relative humidity was 50 ± 5%. Physiological measurements were made as stated above and *Pn*, g_s and E-PAR curves for each genotype were drawn based on the measured data.

2.6. Nutrient analysis

Freshly prepared hydroponics solution and the residual water in the drum, every 15 days, were collected in polyethylene bottles for analysis of the macro and micronutrients. Samples were stored in a refrigerator at 4°C until analysis. The pH was determined using a Eutech multiparameter model PC2700. The Na$^+$ and K$^+$ contents were determined using flame photometer (Elico CL378) (Williams and Twine, 1960). Nitrogen content was determined by Kjeldahl distillation method (Bremner and Keeney, 1965). Determination of PO_4^{3-} content was carried out following ascorbic acid spectrometric method (APHA, 2005, 4500-P, E. Ascorbic Acid Method). Calcium and magnesium contents were determined by following Versenate titration method (Hesse, 1971). Micronutrients *viz*., Fe^{2+}, Mn^{2+}, Zn^{2+} and Cu$^+$ contents were determined using atomic absorption spectrophotometer (ICE 3300, Thermo Fisher Scientific). The differences in the initial and residual nutrient contents in the drum yielded the nutrient use by the plant. The nutrient uptake per unit water quantity during summer, monsoon and winter for different genotypes was calculated from the nutrient use and total water uptake data. Similarly, ratio of the nutrient use and the biomass gain was calculated to compute the nutrient required to produce a unit biomass across the seasons and genotypes.

2.7. Statistical analysis

There were four genotypes and three seasons and each genotype had three replications. The water use, nutrient use, biomass gain and WUE data were analyzed using two way analysis of variance (ANOVA) of repeated measures and the treatment means were compared by Duncan's multiple – range test ($P \leq 0.05$) using the statistical software SAS 9.3.

3. Results

3.1. Seasonal variations in climate

Fig. 1a shows the Tleaf, RH, PAR and VPDL of the experimental site during morning hours (~9.30 AM) which varied significantly during summer, winter and monsoon. Temperature, PAR and VPDL which were 30°C, 880 µmol m^{-2} s^{-1} and 1.45 kPa, respectively during monsoon had increased by 6°C, 366 µ mol m^{-2} s^{-1} and 1.39 kPa during summer while the RH which was 65% during monsoon got reduced to 47% during summer. The temperature, PAR and VPDL during winter were intermediate compared to that observed during monsoon and summer while RH during winter was on par with summer. Fig. 1b, c, d, e shows the diurnal pattern of plant Tleaf, RH, PAR and VPDL during the forenoons of summer, monsoon and winter. During morning hours, there was a steep rise in temperature which rose to 38.5, 37.0 and 36.0°C at 10.30 AM, during summer, winter and monsoon seasons, respectively (Fig. 1b). Further increase in temperature was gradual. The corresponding decline in RH during the same period was 36, 40 and 47% at 10.30 AM, respectively (Fig. 1c). PAR increased to 1480, 1620 and 1760 at 10.30 am and 1590, 1800 and 2010 at 11.30 AM respectively (Fig. 1d). VPDL got raised to 2.99, 3.87 and 3.80 at 10.30 AM, respectively (Fig. 1e).

3.2. Water use, biomass gain and WUE

Per day water use, biomass gain and WUE of coconut seedlings across the months were depicted in Fig. 2a. Coconut seedlings consumed around 2.2 L water per day. The consumption was significantly high during the month of May (2.8 L), followed by December (2.15 L) and was the least during August (1.62 L). During the same period, the mean monthly biomass gain was 13.08, 9.68 and 14.17 g, but it was not significant. However, the corresponding WUE, which were 4.67, 4.56 and 8.74 g L^{-1}, respectively, was significantly different. The effect of season and genotypes are presented in Table 1 and Fig. 2b, c and d. Both the season ($p < 0001$) and genotypes ($p < 0001$) exerted significant effect on water use (Table 1 & Fig. 2b). Water use was high during summer (3.34 L) followed by winter (2.63 L) and was the least during monsoon (1.84 L). Across the genotypes, water use was high for KP (3.01 L per day), followed by KT and MYD (around 2.5 L) and was the least for CGD (2.05 L). Genotypic and season effect was significant ($p = .0018$) though it was less variable during monsoon and winter, but it was highly variable during summer (Fig. 2b). During summer, water consumption of tall genotypes (KP and KT 3.83 and 3.45 L, respectively) was 16% more water than the dwarfs (CGD and MYD 2.99 and 3.11 L, respectively). Across the seasons, KP exhibited high water uptake compared to other genotypes.

Unlike the water use, the effect of season on biomass gain was not significant. It was 12.19, 12.02 and 12.02 g during winter, monsoon and summer, respectively (Table 1 & Fig. 2c). The genotypic effect, on the other hand, was significant ($p < 0001$). Biomass accumulation was high for talls KP (14.37g) and KT (13.90 g) compared to the dwarfs [MYD (10.98 g) and CGD (7.62g)]. The interaction effect of genotype and season was significant ($p = 0.042$) (Table 1). The variability was more significant during summer as talls accumulated 58% more biomass than the dwarfs. Low water use during monsoon, without a considerable change in biomass accumulation across the seasons resulted in significantly ($p < 0001$) high WUE during monsoon (6.60) compared to winter (4.45), and summer (3.35 g L^{-1}) (Table 1 & Fig. 2c). WUE was significantly high for talls [KT (5.68 g L^{-1}) and KP (4.99 g L^{-1})] compared to dwarfs MYD [(4.45 g L^{-1}) and CGD (4.02 g L^{-1})]. As with water use and biomass gain, genotypic variation for WUE was less during monsoon and winter while it was high during summer. WUE of talls, KP and KT were 4.16 and 4.32 g L^{-1}, respectively during summer was 50% higher than dwarfs namely CGD and MYD that were 2.19 and 2.08 g L^{-1}, respectively.

3.3. Correlation between water use, biomass gain and WUE

A significant correlation was observed among the water use, biomass gain and WUE (Fig. 3). Between water use and biomass gain the correlation was moderately positive [R^2=0.47, $p < 00001$] (Fig. 3a). On the other hand, the relation was weakly negative between water use and WUE [$R^2 = 0.12$, $p < 0001$] (Fig. 3b) while it was weakly positive between biomass gain and WUE [$R^2 = 0.17$, $p < 0001$] (Fig. 3c).

3.4. Morphological response

Leaf area (LA) expansion was on an average 374 cm^2 day^{-1} which was significantly high during monsoon (489 cm^2) followed by summer (321 cm^2) and winter (313 cm^2) (Fig. 4a) Genotypic influence was significant ($p < 0001$). LA expansion was high for talls *viz*., KP (551 cm^2) and KT (422 cm^2) followed by MYD (265 cm^2) and was the least for CGD (257 cm^2). Across the seasons, high LA expansion was recorded for all the genotypes during monsoon followed by LA expansion in talls during summer, and in dwarfs during winter. Collar girth (CG) expansion was 1.21 mm day^{-1}. Season did not significantly influence the CG expansion (Fig. 4b). Amongst the genotypes, CG was high for KP (1.38 mm day^{-1}) followed by MYD (1.25 mm day^{-1}), KT (1.22 mm day^{-1}) and was the least for CGD (0.98 mm day^{-1}). Plant height increment per day was 3.7

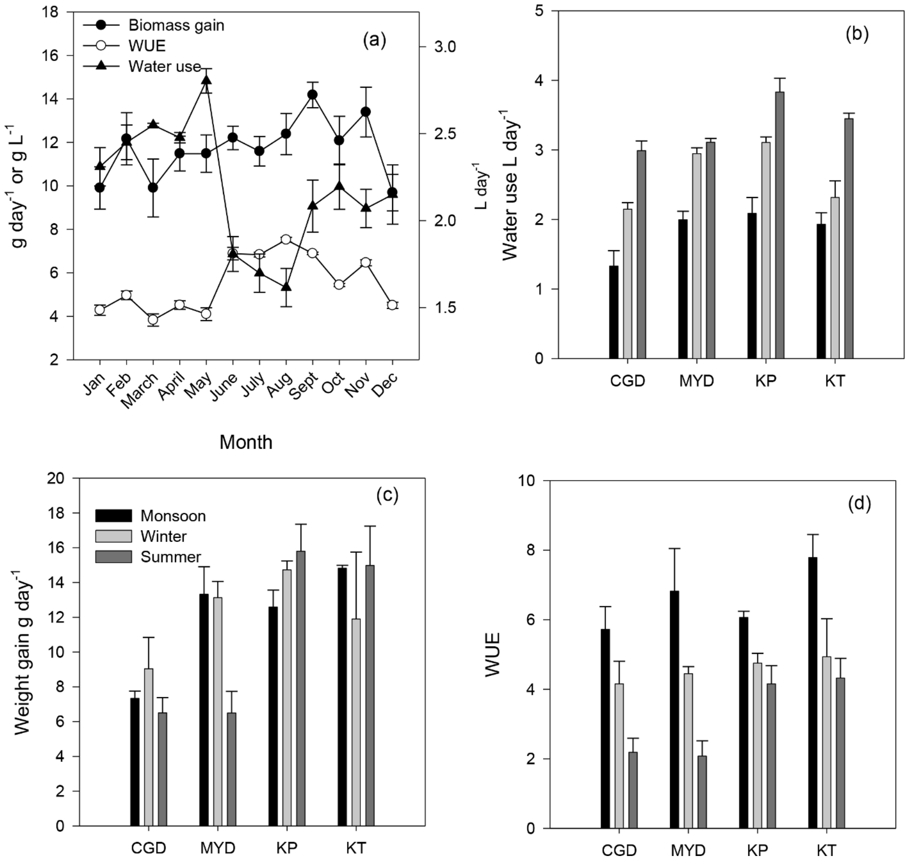


Fig. 2. Water use (L day^{-1}), biomass gain (g day^{-1}) and WUE (g L^{-1}) of two year old coconut seedlings grown in hydroponics. (a) Comparison of mean monthly data on water use [LSD (0.05) 0.713, $n = 12$], biomass gain (non-significant) and WUE [(LSD (0.05) 1.52]. Seasonal influence on water use (b), biomass gain (c) and WUE (d) across coconut genotypes during summer, monsoon and winter. Vertical line on the bar indicate ±SE ($n = 3$). LSD for the comparison of means-water use [Genotype-G (0.26, $p < 0001$); Season-S (0.23, $p < 0001$); GxS ($p = .0018$)]; biomass gain [Genotype-G (0.29, $p = .0001$); Season-S (NS); GxS ($p = .05$)] and WUE [Genotype-G (1.08, $p = .04$); Season-S (.94,$p < 0001$); GxS (NS)].

Table 1

Water use (L day^{-1}), biomass gain (g day^{-1}) and WUE (g L^{-1}) of two year old coconut seedlings of variety CGD, MYD, KP and KT across the various seasons *viz.*, monsoon, winter and summer. LSD represents least significant difference between treatment means at 5%. Different letter in each column after mean value are significantly different at 5% level according to Duncan's multiple range test. NS is non-significant.

						LSD at 5%		
	CGD	MYD	KP	KT	Mean	Genotype	Season	G x E
Water use								
Monsoon	1.33	2.00	2.09	1.93	1.84c	0.27	0.23	0.19
Winter	2.15	2.95	3.11	2.32	2.63b	$p < 0001$	$p < 0001$	$p = .0018$
Summer	2.99	3.11	3.83	3.45	3.34a			
Mean	2.16c	2.69b	3.01a	2.57b				
Weight gain								
Monsoon	7.34	13.32	12.58	14.83	12.01a	2.76	NS	2.39
Winter	9.03	13.12	14.72	11.89	12.19a	$p < 0001$	$p < 51$	$p < 042$
Summer	6.50	6.49	15.79	14.98	10.94a			
Mean	7.62c	10.97b	14.36a	13.90a				
Water use efficiency								
Monsoon	5.72	6.82	6.06	7.79	6.59a	1.08	0.94	NS
Winter	4.16	4.44	4.75	4.94	4.57b	$p < 04$	$p < 001$	$p < 57$
Summer	2.19	2.08	4.16	4.32	3.18c			
Mean	4.02b	4.45ab	4.99ab	5.68a				

cm which was significantly high during monsoon (4.4 cm) followed by summer (3.97cm) and winter (2.79 cm) (Fig. 4c). The increment was high for KP (5.23 cm) followed by KT (4.95cm), MYD (2.3cm) and CGD (2.4 cm). Thus, genotypes KP and KT showed more LA expansion and plant height increment during monsoon and summer seasons.

3.5. Response of Pn, g_s and E to PAR

The response of coconut seedlings to PAR was studied from 50 to 2400 μ mol m^{-2} s^{-1} (Fig. 5). The response of *Pn* to PAR followed an asymptotic or exponential model-like curve, wherein *Pn* showed rapid increase concurrent with the PAR values up to 800 μ mol m^{-2} s^{-1}, but a complete saturation was reached at 1600 μ mol m^{-2} s^{-1}(Fig. 5a). A similar trend, however with less initial increment, was observed for *gs* and *E* and reached saturation at 1400 μ mol m^{-2} s^{-1}. At low PAR of 100 μ mol m^{-2} s^{-1} *Pn* was negligible; still there was considerable stomatal conductance (0.08 mol m^{-2} s^{-1}) and transpiration. *Pn* response of genotypes to PAR was significant ($p < 0001$). At low light intensity of 100 μ mol m^{-2} s^{-1}, *Pn* of CGD and MYD was 1.50 and 2.06 μ mol m^{-2} s^{-1}, respectively while it was nil for KP and KT (Fig. 5b). It increased to 5.44, 7.82, 6.08 and 7.07μ mol m^{-2} s^{-1} for CGD, MYD, KP and KT, respectively at 800 μ mol m^{-2} s^{-1}. Further a maximum *Pn* of 6.76 (CGD), 7.96

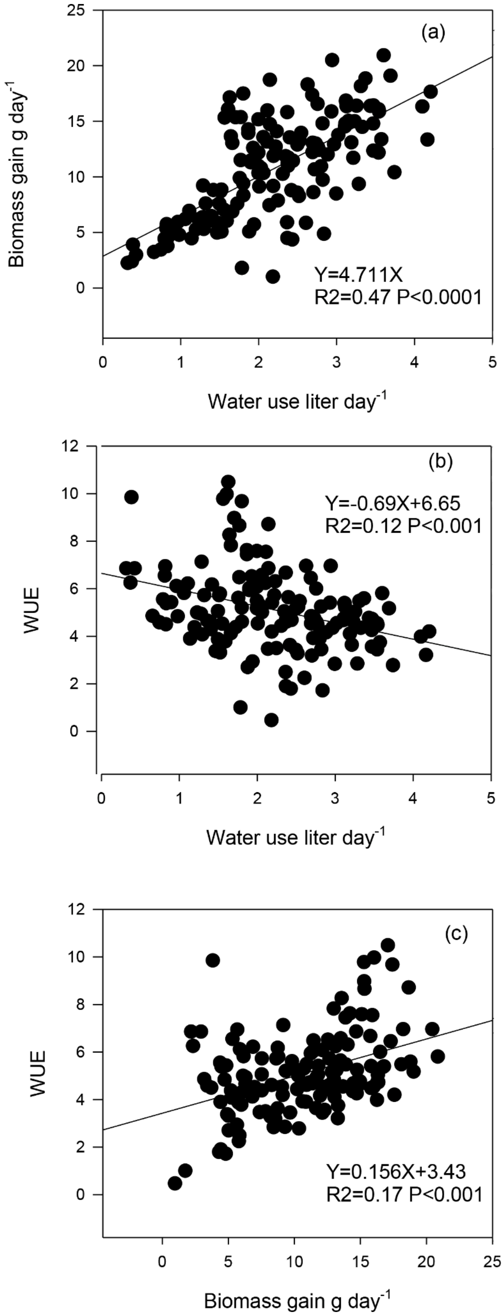


Fig. 3. Correlation between (a) water use vs. biomass gain per day, (b) water use vs. WUE (g L^{-1}) and (c) biomass gain vs. WUE (n = 144).

(MYD), 7.11 (KP) and 7.98 (KT) μ mol m^{-2} s^{-1} was reached at a PAR of 1400, 1200, 2400 and 1600 μ mol m^{-2} s^{-1}, respectively.

Stomatal conductance (g_s) was significantly high in MYD and KT followed by KP and was the least for CGD (Fig. 5c). At low PAR of 100 μ mol m^{-2} s^{-1}, *gs* was 0.13, 0.11, 0.08 and 0.03 for MYD, KT, CGD and KP, respectively whereas at a PAR of 800 *gs* of the genotypes increased to 0.13, 0.15, 0.11 and 0.13, respectively. Beyond that there was steady increase for MYD and KT but not for KP and CGD. The response trend of E was similar to that of *gs* (Fig. 5d). At PAR, 100 m mol m^{-2} s^{-1}, E was 2.27, 2.99, 2.14 and 1.07 for CGD, MYD, KT and KP, respectively. At PAR, 800 μ mol m^{-2} s^{-1} E values of the genotypes increased to 3.17, 3.77, 3.36 and 4.11, respectively.

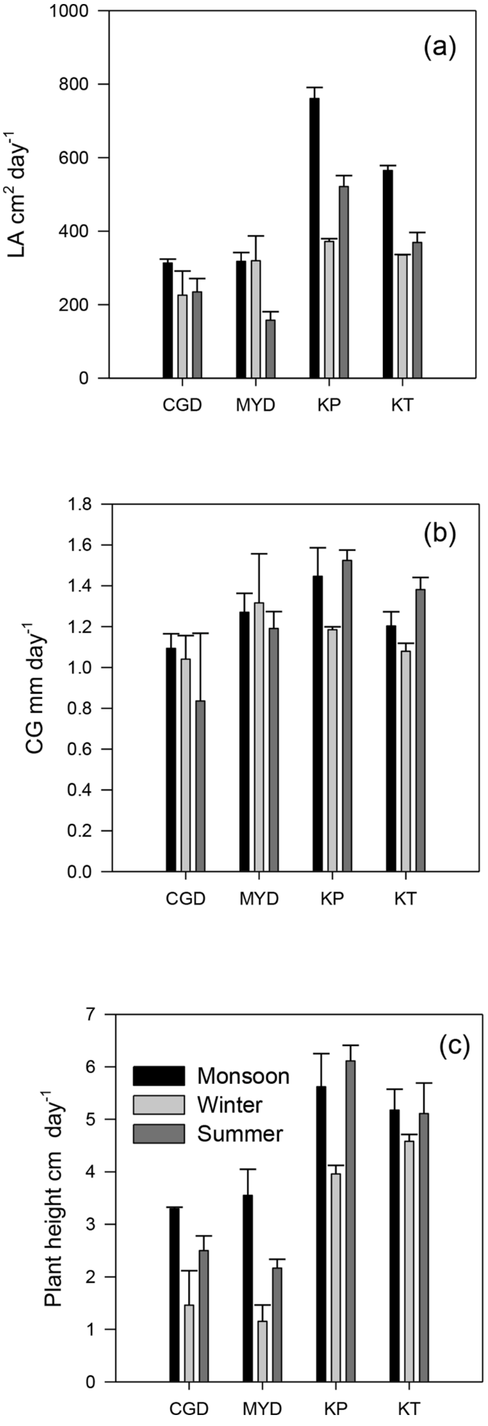
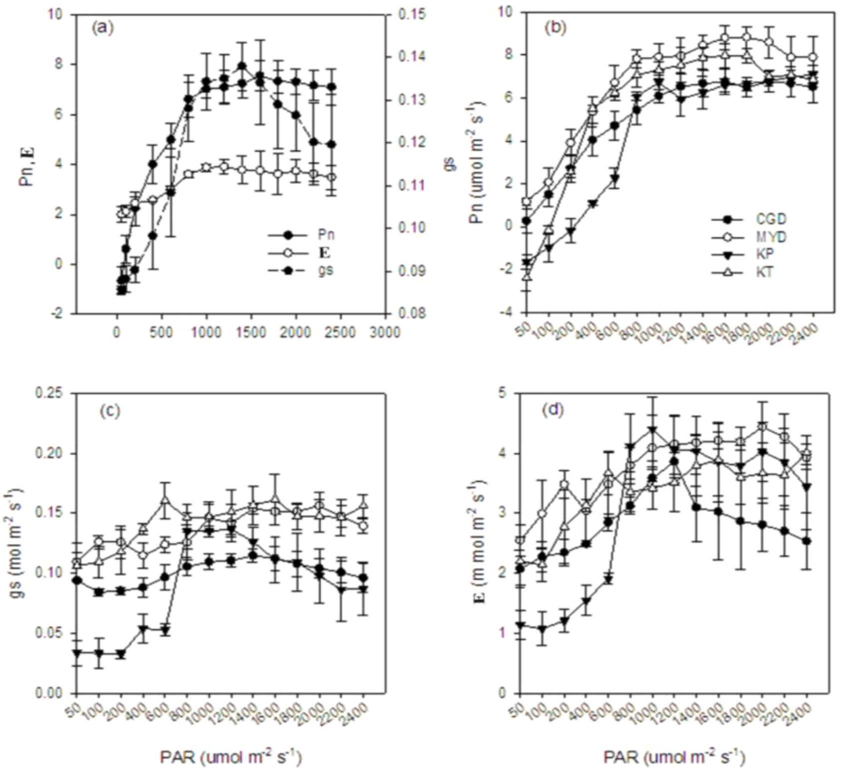


Fig. 4. Seasonal influence on morphological characters of two year old coconut seedlings of CGD, MYD, KP and KT grown in hydroponics; (a) Leaf area per day (LA day^{-1}) (b) collar girth (CG day^{-1}) (c) and plant height (pht day^{-1}). Vertical line indicate ±SE (n = 8). LSD at 5% (0.05) for comparison of mean values of genotypes for LA (40.76), CG (0.153) and pht (0.54).

3.6. *Relation between VPDL and gs*

The relationship between VPDL and *gs* was significant and it was moderately negative [R^2=0.485, $p < 00001$] (Fig. 6a). *gs* was 0.2, 0.15 and 0.07 mole m^{-2} s^{-2} at VPDL of 1.5, 2.5 and 3.5, respectively. However, the relationship was weakly positive for dwarfs CGD [$R^2 = 0.147$, $p < 001$] (Fig. 6b) and MYD [R^2= 0.07, $p = 0.039$] (Fig. 6c) while it was moderately negative for KP [R^2=0.160, p = 0.0016] (Fig. 6d) and



Fig, 5. Net photosynthetic rate (P_n) (μ mol m^{-2} s^{-1}), stomatal conductance (g_s) (mol $m^{-2}s^{-1}$) and transpiration (E) (m mol $m^{-2}s^{-1}$) versus photosynthetically active radiation (PAR) of two years old coconut seedlings grown in a hydroponics system (a). Vertical lines indicate ±SE ($n = 12$). Influence of PAR on P_n (b), g_s (c) and E (d) of coconut genotypes CGD, MYD, KP and KT. Vertical lines indicate ±SE ($n = 3$). LSD at 5% (0.05) for mean comparison across genotypes for Pn (0.42); gs (0.009) and E (0.32).

strongly negative for KT [R^2=0.706, $p < 0001$](Fig. 6e).

3.7. Nutrient uptake per liter water

The nutrient use pattern was significantly different across the genotypes for all the nutrients except for P and K (Table 2). Coconut seedlings exhibited highest nutrient extraction for N (241 ppm) followed by K (193 ppm), Ca (151 ppm), P (66 ppm), Mg (26.7 ppm) etc. Among the genotypes, N extraction was the highest for CGD (294 ppm), followed by KP (246 ppm) and was on par with that of MYD (218 ppm) and KT (206 ppm). Almost similar trend was observed for the uptake of Ca, Mg, Mn, Fe, Zn and Cu with the highest uptake recorded by CGD followed by KP for Ca and Mg and for the rest of the nutrients it was on par across the genotypes. Season had significant influence on the nutrient uptake. Nutrient uptake rate was significantly high (almost two folds) during monsoon than that of summer and winter. During summer and winter it was on par.

3.8. Nutrient uptake per unit biomass

Coconut seedlings, to produce a unit biomass, have used N (57 ppm), followed by K(44 ppm), Ca (38 ppm), P (15 ppm), Mg (6.4 ppm), Mn (0.02 ppm), Fe (1.01 ppm), Zn (0.03 ppm) and Cu (0.02 ppm) (Table 2). Genotypic influence for the use efficiency was significant for N ($p = 0.45$), P ($p = 0.02$) and Zn ($p = 0.04$) and for the rest of the nutrients it was on par. Nutrient requirement to produce a unit biomass was high for CGD and MYD while it was significantly low for KP and KT. The seasonal influence was significant for use efficiency of N ($p = 0.047$), P ($p = 0.0006$), K($p = 0.045$), Ca ($p = 0.04$). Nitrogen and K requirement was high during summer followed by winter and low during monsoon, P and Ca requirement was high during winter followed by monsoon and low during summer.

4. Discussion

As the objective of the present study was to understand the influence of climatic factors on water and nutrient uptake, biomass production and WUE at the whole plant level of coconut seedlings, hydroponic system was designed and adopted to measure the above parameters during three seasons (summer, monsoon and winter) characterized with distinct climatic features. Hydroponic system not only enabled the quantification of water use by plants accounting for transpiration alone, which otherwise in soil grown plants includes evaporation (Hatfield and Dold, 2019), but also facilitated the recording of biomass gain at periodic intervals. It also eliminates the confounding effects of high temperature induced water deficit usually experienced in soil grown plants of semi-arid tropics (Bloomfield et al., 2019). Coconut seedlings grown in hydroponic system of one strength Hoagland solution exhibited normal growth and it was comparable to the potted seedlings of similar age raised in soil (Hebbar et al., 2013). Climatic factors play an important role in the growth and development of the plants. In order to assess the impact of climate on coconut seedling growth, water and nutrient uptake and biomass gain were recorded during monsoon, winter and summer seasons with distinct temperature, humidity and PAR. At the experimental site, on a typical summer day T_{max} at 9.30 am was 34°C which is 4 and 6°C higher than winter and monsoon respectively. During the same period RH of summer and winter season was around 53% as against 73% in monsoon. The increasing temperature and decreasing RH have increased VPDL during summer (2.66 kPa) compared to monsoon (1.17 kPa) which is in conformity with earlier findings (Will et al., 2013). Moreover, the number of days with T_{max}>30°C in a month is more in summer and winter (28 to 29 days) compared to monsoon (4 to 6 days). PAR was also high during summer and winter compared to monsoon. Thus, hydroponically grown coconut seedlings were exposed to distinct climatic factors during summer, monsoon and winter. Further, two dwarf (CGD and MYD) and two tall (KP and KT) genotypes grown, have allowed us to determine the genotypic response to climatic factors.

Coconut seedlings grown in hydroponic system consumed on an average 2.2 L water and produced 11 g biomass per day resulting in 5 g L^{-1} WUE which is reasonably high compared to the soil grown coconut seedlings of similar age (Hebbar et al., 2016) or other crops like cocoa

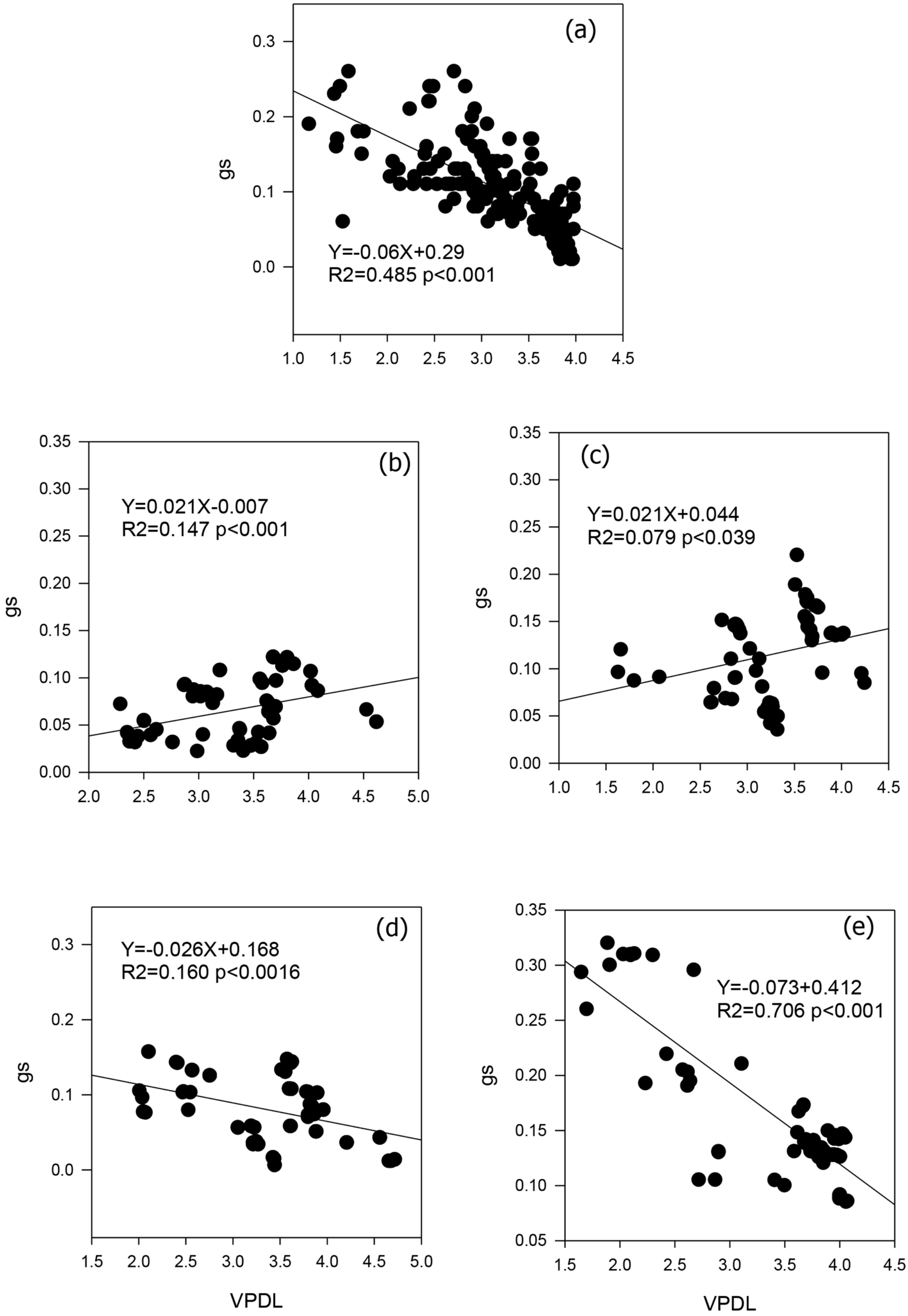


Fig. 6. Relation between vapor pressure deficit of leaf (VPDL, kPa) versus stomatal conductance (*gs*, mol $m^{-2}s^{-1}$) of two year coconut seedlings grown in hydroponic system across the genotypes (n = 159) (a); and for CGD (n = 73) (b); MYD (n = 68) (c); KP (n = 67) (d); and KT (n = 76) (e).

Table 2

Genotype and season (summer, monsoon and winter) influence on nutrient use (ppm g^{-1} biomass) and nutrient uptake (ppm L^{-1} water) of two year old coconut seedlings grown in hydroponics. Data are mean value of 3 replicates. LSD represents least significant difference between treatment means at 5%. Different letter in each column after mean value are significantly different at 5% level according to Duncan's multiple range test. NS is non-significant.

Nutrient use ppm g^{-1} biomass									
Genotype	N	P	K	Ca	Mg	Mn	Fe	Zn	Cu
CGD	84.23a	19.27a	55.48a	59.6a	11.53a	0.0257a	1.675a	0.0483a	0.0255a
MYD	56.93ab	17.16ab	48.83a	35.0a	5.78a	0.0164a	1.015a	0.0236b	0.0159a
KP	47.92b	12.89bc	36.23a	29.8a	4.20a	0.0112a	0.711a	0.0254b	0.0124a
KT	40.36b	12.06c	35.35a	27.8a	4.20a	0.0097a	0.658a	0.0214b	0.0122a
Season									
Summer	74.82a	10.32c	53.70a	26.2b	4.09a	0.0106a	0.615a	0.0319a	0.0124a
Monsoon	41.37b	15.31b	30.24b	32.5ab	5.88a	0.0138a	0.855a	0.0269a	0.0145a
Winter	55.88ab	20.42a	47.98ab	55.5a	9.31a	0.0230a	1.575a	0.0302a	0.0225a
LSD at 5%									
Gen	33.9 ($p = .045$)	4.71 ($p = .02$)	NS	NS	NS	NS	NS	0.02($p = .04$)	NS
Season	29.3 ($p = .047$)	4.08($p = .0006$)	19.2 ($p = .045$)	26.3($p = .04$)	NS	NS	NS	NS	NS
G X S	NS	NS	NS	NS	NS	NS	NS	NS	NS
Nutrient Uptake ppm L^{-1} water									
CGD	293.7a	71.8a	179.9a	185.6a	35.37a	0.078a	4.77a	0.169a	0.084a
MYD	218.6b	65.4a	197.8a	130.0b	19.52c	0.060b	3.73b	0.104b	0.060b
KP	246.4ab	66.6a	191.4a	153.3ab	29.79ab	0.058b	3.43b	0.109b	0.062b
KT	206.2b	59.7a	204.4a	134.8ab	22.02bc	0.051b	3.56b	0.130b	0.063b
Season									
Summer	179.3b	45.4b	132.9b	112.3b	22.53b	0.046b	2.73b	0.136b	0.055b
Monsoon	373.6a	102.3a	323.8a	217.7a	39.21a	0.092a	5.69a	0.180a	0.098a
Winter	170.7b	50.0b	123.4b	122.8b	18.28b	0.047b	3.20a	0.068c	0.050b
LSD at 5%									
Gen	51.6($p = .01$)	NS	NS	50.2 ($p = .02$)	7.9($p = .004$)	0.01($p = .006$)	0.67($p = .003$)	0.04($p = .009$)	0.01 ($p = .002$)
Season	44.7($p < p < 0001$)	13.28 (<.0001)	43.8 ($p < 0001$)	43.4($p = .0003$)	6.9($p < 0001$)	0.01($p < p < 0001$)	0.58($p < 0001$)	0.03($p < p < 0001$)	0.01($p < 0001$)
G X S	NS	NS	NS	NS	NS	0.009($p = .03$)	0.53($p = .008$)	NS	0.009($p = .002$)

(Santos et al.,2014; Hebbar et al.,2020b), groundnut (Hebbar et al., 1994; Hubick et al., 1986; Wright et al., 1994), wheat (Shi et al.,2014; Guan et al., 2015), sorghum (Donatelli et al., 1992) and soybean (Mian et al., 1996; Hufstetler et al., 2007). It could be attributed to the hydroponic set up as the water use herein fully accounts for water loss through transpiration devoid of any evaporation. The genotypes and the seasons had significant influence on water use and WUE but seasonal influence was non-significant on biomass gain. In coconut, the relationship between water use and WUE was negative [$R^2(144)= 0.12, p < 0001$], hence, summer with high water use (3.14 L) exhibited low WUE (3.35 g L^{-1}), while monsoon with low water use (1.83L) exhibited relatively high WUE (6.6 g L^{-1}). This is contrary to the accepted hypothesis that plant productivity increases with an increase in water use and therefore increased water use would increase WUE (Hatfield and Dold, 2019). In field crops like maize increased WUE could be achieved by increasing productivity without change in water use (Basso and Ritchie, 2018). On the contrary, in our experiment in coconut during summer WUE declined due to considerable increase in water use without a concomitant increase in biomass gain. It suggests that the atmospheric conditions are of utmost importance in determining absolute relations between water consumption and biomass productivity of coconut (Ehleringer et al., 1993). It was further evident from our study that at the level of whole plant, the relation between water use and biomass gain was only moderate in coconut [$R^2(144)=0.47, p < 00001$] which otherwise is highly linear in several species (Hanks, 1983; Arkley, 1963; Bierhuizen and Slatyer, 1965; Trout and DeJonge 2017; Bhattacharya 2021; Gan et al., 2021). However, the scientific advances and the experimental evidences to improve our comprehension of the behavior of WUE of perennial plants, to different climatic conditions remain obscure.

The interaction effect of season and genotype was significant on water use, biomass gain and WUE. Across the genotypes it was less variable during monsoon while in summer talls (KP and KT) exhibited significantly high water use, biomass production and WUE compared to the dwarfs (CGD and MYD). WUE during summer was 33% and 65% less for talls and dwarfs compared to monsoon. Water use of both talls and dwarfs increased by 81 % and 90%, respectively but on the other hand biomass increased in talls by 13% while it was sensitive in dwarfs and reduced by 31% from monsoon season. It implies biomass production is the major limitation in dwarfs during summer for the decreased WUE. Thus it is apparent that during hot season, climatic factors have profound influence on water use and biomass production of dwarf coconut genotypes. The increased water use both in dwarfs and talls with only positive response to biomass production in talls during summer suggests that both stomatal and non stomatal factors might be involved in physiological response of coconut to climatic factors.

Stomatal conductance is strongly driven by VPD, which besides increasing the atmospheric demand for evapotranspiration (Monteith, 1965; Penman, 1948) reduces the stomatal conductance through stomatal closure in many crops (Damour et al., 2010; Medlyn et al., 2011; Lahive et al., 2019) including in coconut (Gomes et al., 2002; Gomes and Prado, 2007; Kasturibai et al., 1988). In coconut, VPDL during summer was two folds high than that of monsoon and considerably high during winter, which had a significant moderate negative relation with *gs* [$R^2(159)=0.45, p < 00001$] confirming stomatal closure at high VPDL in coconut. However, most surprisingly the relation was weakly positive for both dwarfs CGD [$R^2(73)=0.15, p < 001$] and MYD [$R^2(68)=0.079, p = 0.039$] while it was weakly negative for KP [$R^2(67)=0.16, p = .0016$] and strongly negative for KT [$R^2 (76)=0.71, p < 0001$] suggesting stomata was insensitive to high VPDL in dwarf while in talls stomata remained highly sensitive. This explains at the leaf level, stomata of talls have evolved to optimally regulate the exchange of water and carbon dioxide and tend to partially close in response to increased atmospheric dryness (Ball et al., 1987; Katul et al., 2009; Medlyn et al., 2011). However, this leaf level regulation of water conservation and biomass production might have been compensated by large leaf area in talls and hence they had greater water use and biomass production than the dwarfs at all seasons. As observed in coconut dwarfs, increasing VPD increased E but decreased *Pn* in cocoa (Baligar et al., 2008).

In addition to VPD, Tleaf and RH, the photosynthesis and biomass production of plants is also controlled by radiation (Anthoni et al., 1999; Dolman et al., 2002). Plants are sensitive to both low and high radiation. In coconut, PAR response on *Pn, gs* and *E* was a asymptotic or exponential model like curve, linear up to photosynthetic photon flux density (PPFD) of 800 μ moles photon m^{-2} s^{-1} while light saturated maximum rate of *Pn* reached at an interception of around 1200-1400 for dwarfs and 1600 to 2400 μ moles photon m^{-2} s^{-1} for talls beyond this *Pn* declined. Earlier workers have recorded light saturation at 1400 to 1600 μ moles photon m^{-2} s^{-1} for coconut (Jayashekar et al., 1996). The PAR of experimental site reached above 1400 μ moles photon m^{-2} s^{-1} at 10.30 AM itself both during winter and summer suggests that high PAR observed during summer might have limited the biomass production in dwarfs in spite of having high *gs*. Thus, the insensitive stomata to high VPDL and low light saturation of maximum rate of *Pn,* make the dwarfs more vulnerable to summer or extreme weather while talls had wider adaptability.

As with WUE, the nutrient uptake and use efficiency in coconut was significantly influenced by the season. Despite the increasing water uptake during summer and winter the nutrient uptake per liter was quite low whereas the uptake was almost two folds high during monsoon, when water uptake was low suggesting uptake of nutrients in coconut is well regulated. The nutrient assimilation was high during monsoon compared to summer. To produce a g biomass, N, P, K, Ca requirements of plants during summer and monsoon were 73, 54, 20 and 56 and 41, 30, 15, 32 respectively. The greater water uptake was positively correlated with the nutrient uptake during summer and winter, as corroborated by the linear relationship between the rate of transpiration and the uptake rates of nitrogen, phosphorus, and potassium (Novak and Vidovic, 2003). The mass flow of nutrients such as N, Ca, Mg, and S to root surfaces is attributed to transpirational water uptake by the plant (Havlin et al., 2005). Amongst the genotypes, dwarfs required significantly high quantum of nutrients to produce per unit biomass compared to the talls.

5. Conclusions

This investigation proves that climatic factors significantly influence the water use and nutrient use of coconut seedlings without a significant change in biomass gain causing an appreciably low WUE during summer while WUE was quite high during monsoon. Amongst the genotypes, the talls (KP and KT) showed high WUE during summer due to better regulation of stomata and biomass gain, despite exhibiting high water use and biomass on account of large leaf area. In dwarfs (CGD and MYD), the insensitive stomata led to increased water loss, however their limited biomass production could be attributed to their sensitivity to high PAR. Dwarf genotypes exhibit low light saturation compared to the talls contributing to their low WUE. Dwarfs also display less nutrient use efficiency, compared to talls, suggesting that dwarfs (CGD and MYD), are not suitable for regions with high temperature, low humidity and high radiation while talls (KP and KT) had wider adaptability to environmental extremes.

Supplementary materials

All data generated or analyzed during this study are included within this published article and its supplemental information files.

CRediT authorship contribution statement

K.B. Hebbar: Conceptualization, Methodology, Formal analysis, Resources, Project administration, Supervision, Writing – original draft, Writing – review & editing. **S. Kannan:** Investigation, Validation, Data curation. **S. Neenu:** Investigation, Validation, Data curation. **Abhin Sukumar. P:** Investigation, Validation, Data curation. **S.V. Ramesh:** Investigation, Validation, Data curation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2022.111198.

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