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Assessment of photosynthetic efficiency of greater yam and white yam subjected to elevated carbon dioxide

Velumani Ravi[1], Sanket J. More[1],*, Saravanan Raju[1], R. Muthuraj, Suja G

Division of Crop Production, ICAR-Central Tuber Crops Research Institute, Sreekariyam P.O., Thiruvananthapuram, Kerala, India

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ABSTRACT

Carbon dioxide concentration is likely to increase by 2−2.5 fold by the end of 21st century from its current level of 400 ppm due to anthropogenic activities mediated climate change. As yam is an important food and nutrition security crop, it is of paramount importance to assess the effect of climate change on the physiological processes especially photosynthetic efficiency to identify the climate-smart varieties to meet the future food demand. The aim of this experiment was to assess the net photosynthetic rate, stomatal conductance, intercellular CO_2, transpiration and physiological water use efficiency of seven yam varieties subjected to 400 ppm (ambient), 600, 800 and 1000 ppm (elevated carbon dioxide concentration). All the parameters were found significant at $P<0.001$. The mean photosynthetic rate increased significantly increased at 400−1000 ppm and no down-regulation was observed. Similar trend was observed in case of intercellular CO_2 and physiological water use efficiency ($WUE_{instantaneous}$ and $WUE_{intrinsic}$). However, stomatal conductance increased significantly up to 800 and decreased at 1000 ppm. Contrasting results were recorded with regard to transpiration, which steadily decreased at ascending carbon dioxide concentrations. Further, photosynthesis rate had a significant ($P<0.001$) positive linear correlation with the elevated carbon dioxide ($R^2 = 0.783$) and intercellular CO_2 concentration ($R^2=0.763$). White yam and greater yam were found to be responsive to elevated carbon dioxide as photosynthetic rate at 1000 ppm increased up to ~68% in comparison to 400 ppm.

1. Introduction

White yam (*Dioscorea rotundata* Poir.) and greater yam (*Dioscorea alata* L.) are important species of *Dioscorea* genus belonging to the family Dioscoreaceae. *D. alata* is mostly confined to tropical and subtropical countries whereas, *D. rotundata* is the main species of the West African region (Britannica, 2021). The total production of yams increased by 4−5 folds from 17.4 million tonnes (1970) to 74.3 million tonnes in 2019 at an average annual rate of 3.41%. About 95% of the total white and greater yam in the world is produced and consumed in West African counties, Nigeria, Ivory Coast and Ghana (FAOSTAT, 2019). Yams serve as a staple food (either in primary or secondary form) and principal source of income for millions of the marginal and poor farmers confined to the tropical and subtropical regions of Africa, Asia, the Caribbean and Latin America (FAOSAT, 2019). According to Padhan and Panda (2020) yams are one of the potential crops to ensure global food and nutrition security as they are the storehouse of carbohydrates. They are reliable food security crop relating to 'Climate-Resilience' (ability to produce considerable yield in challenging environments) (Mukherjee et al., 2019). Under the least developed countries yams can provide more protein per hectare per year than maize, rice, sorghum or even soybean along with a contribution of about 200 dietary calories per person per day to 300 million people (Obidiegwu et al., 2020). Amongst all the root and tuber crops, yams are highly nutritious in terms of protein (FAO, 1990) and bioactive compounds (Iwu et al., 1990; Bhandari et al., 2003).

Future demand of yam is expected to be higher under the pressure of continuous population growth and changing agro-climate. The global yams market is projected to register a CAGR of 3.5% during the forecast period 2020−2025 (BUSINESS WIRE, 2021). Srivastava et al. (2012) reported ~18−48% yield reduction in yam tuber yield as an effect of the projected climate variables and CO_2 which could be of great concern. As mentioned earlier, the area under cultivation has increased steadily but the productivity has not increased significantly over the years (FAOSTAT, 2019). Although, yam breeding programme are aimed at increasing productivity by developing and deploying end-user preferred varieties with higher yield, greater resistance to pests and diseases and improved quality (Darkwa et al., 2020; IITA, 2021) but progress has been hindered by polyploidy, negative flowering traits, low propagation rate and interspecific genetic barriers, taking long period to release a new variety (Lopez-Montes et al., 2013).

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* Corresponding author.
E-mail address: sanketmore1818@gmail.com (S.J. More).
[1] Contributed equally and are co-first authors.

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Yam plants exhibited four growth phases including shoot growth and tuber bulking (Ferguson 1977; Suja et al., 2005; Sunitha et al., 2020). The four different growth phases identified in the generalized growth cycle of yam plants included the first phase starting from emergence to about six weeks where profuse root system development occurs with vine elongation, second phase, with development of foliage which lasts up to the tenth week, the third phase coinciding with tuber development and the last senescence phase (Onwueme and Charles 1994). The exact duration of all these growth phases during its life cycle varies with yam species, varieties and the climatic conditions. Yam plants exhibited a complex shoot structure with primary, secondary and tertiary branches. Ferguson (1977) based on changes in dry matter content in tuber described four growth phases in greater yam (*Dioscorea alata*) which included initial establishment of I phase between 1st and 13th week, a slow tuber growth of II phase between 13 and 19 weeks, a rapid tuber growth of III phase between 19 and 32 weeks and final IV phase of slow and negligible tuber growth between 32 and 36 weeks. In this study, weight of both fresh and dry tuber mass was slow between 1st and 19th weeks, steadily increased between 19th and 31st weeks (5th −10th month), and thereafter declined. Similar pattern of tuber growth was also recorded in lesser yam (*D. esculenta*) varieties (Ferguson et al., 1969; Enyi 1972,1973). Suja et al. (2005) described four growth phases in greater yam and lesser yam varieties, and in both tall and dwarf varieties of white yam (*D. rotundata*). Here, the canopy establishment of I phase occurred between 3rd and 4th month, II phase of initial tuber development occurred between 4th and 5th month, III phase of tuber enlargement occurred between 5th and 6th month and IVth phase of tuber maturation occurred between 6th and 7th month. In lesser yam, Crop Growth Rate (CGR) steadily increased and was highest at IVth phase whereas, CGR peaked at II phase in tall white yam variety and during III phase in greater yam and dwarf white yam varieties. The Leaf Area Index (LAI) was highest at 5th month after planting (MAP) in greater yam and lesser yam varieties whereas highest LAI was recorded at 6th MAP in white yam varieties (Suja et al., 2000, 2005). In their study, total dry matter accumulation steadily increased between 3rd and 7th MAP whereas dry matter partitioning steadily and rapidly increased after 4−5 months depending upon variety till 7 months (Suja et al., 2000). Goenaga and Irizarry (1994) recorded highest LAI and leaf dry mass per plant at 140−150 DAP which plummeted thereafter in a greater yam cultivar. In their study, weight of vine dry mass was highest during 160−170 days. The weight of tuber dry mass began to increase after 90 days and steadily increased up to 210 days. Partitioning of dry matter to leaves increased steadily up to 100 days, and to vines steadily increased up to 120 days which in both cases declined thereafter whereas partitioning of dry matter to tubers steadily increased after 130 days till 120 days. Enyi (1972) reported highest LAI as well as leaf area per plant in a lesser yam variety at 5 MAP. Tuber initiated in 83−88 days after planting and active tuber growth was reported to occur between 6 and 8 MAP which plummeted thereafter till 9th MAP in two varieties of greater yam (Sunitha et al., 2020).

There has been a remarkable growth in the food grain production in the last 5 decades but photosynthetic efficiency still remains stagnant (Zhu et al., 2010). Improving the photosynthetic efficiency will play a key role in meeting the future food demand (Milgani et al., 2021). With the various modern approaches yield could be increased up to 40% by enhancing the photosynthetic efficiency (Simkin et al., 2019). The quantum of enhancement in photosynthesis and in turn the yield will majorly be depend upon the synergism between source-sink tissues for carbon accumulation and their effective utilisation (Ruiz-Vera et al., 2021). Acclimation or down-regulation of photosynthesis because of limited sink capacity is one of major concerns, especially in the C_3 crops. Similar effects have been observed when C_3 and C_4 plant species were exposed to elevated carbon dioxide (ECO_2) conditions (Long et al., 2006; Vanaja et al., 2011; Jobe et al., 2020). Based on ^{13}C content in the leaves of 7 tropical food yam species and 27 genotypes including greater yam, lesser yam and white yams, Cornet et al. (2007) concluded that yams exhibit C_3 photosynthetic pathway.

Burning of the fossil fuels and other human activities are responsible for the global warming causing remarkable alteration in the global mean surface temperature, carbon dioxide concentration, rainfall pattern and occurrence of extreme climatic events such as drought, high temperature stress, salinity and flood (Aggarwal et al., 2019). Increased CO_2 concentration is also one of the consequences of global climate change. Global CO_2 concentration is rising steadily and is projected to reach 700−1000 ppm at the end of this century (IPCC, 2007, 2013, 2014; NASA, 2021). And hence, researchers' keen focus is on estimating the CO_2 fertilization effects on the yield and quality under current and projected CO_2 concentrations. According to Ainsworth and Long (2020) based on a meta-analysis on 186 independent studies with 18 C_3 crops, reported 18% higher yield, whereas no yield improvement was noted in C_4 crops except with concurrence of abiotic stresses under +200 ppm above ambient. Several attempts have been made to study the effect of eCO_2 by employing OTC and FACE facility under field, greenhouse or controlled conditions in C_3 (Erbs et al., 2015 in wheat and barley; Blandino et al., 2020 in wheat) or C_4 crops (Erbs et al., 2015 in maize) including important tuber crops potato (Lee et al., 2020), sweet potato (Ravi et al., 2017; Runion et al., 2018), cassava (Ruiz-Vera et al., 2021; Ravi et al., 2021) and elephant foot yam (Ravi et al., 2018). Although yam (*Dioscorea* spp.) being an important C_3 and food security crop (Padhan and Panda, 2020), no studies have been conducted in this regards except by Thinh et al. (2017) on Chinese yam in Japan.

Yam being an important food security crop, it is utmost important to assess the crop performance under ECO_2. Furthermore, very limited scientific knowledge is available with regard to the photosynthetic responses of yam under eCO_2 conditions. In the current experiment, we have reported the photosynthetic responses of 3 white yam and 4 greater yam improved varieties subjected to eCO_2.

2. Materials and methods

2.1. Planting material and experimental details

Present experiment was conducted at Block-I of ICAR-Central Tuber Crops Research Institute, Sreekariyam, Thiruvananthapuram, Kerala, India (N8° 32′ 43.4″, E76° 54′ 53.5″). Tuber pieces of worth 300−500 gm weight of seven improved varieties (4 white yam and 3 greater yam; Table 1) were planted during April-2019 at 90 × 90 cm planting distance in the open pits of 45 × 45 × 45 cm. Three fourth of the pits were filled with top soil and well decomposed farm yard manure and were reformed into a mount by covering them with the soil. All plants were supplemented with farm yard manure (10−12.5 t ha^{-1}) as basal dressing before planting followed by a fertilizer dose of nitrogen:phosphorus (P_2O_5):potassium (K_2O) at the rate of 80:60:80 kg ha^{-1}. Half of the nitrogen (~87 kg of urea), full dose of phosphorous (~375 kg of single superphosphate) and half dose of potash (~67 kg of muriate of potash) were applied within a week after sprouting. Whereas, the remaining nitrogen and potash were applied one month after the first application. Plant protection measures and other crop husbandry practices were followed as explained by Ravindran et al. (2013). Water stress free conditions were maintained by irrigating the field at 100% field capacity on a regular basis. The relative humidity and vapour pressure deficit during the time of measurements remained between ~72 to 85% and ~0.92 to 1.37 kPa, respectively, at 33 ± 2 °C leaf temperature.

2.2. Measurement of photosynthetic efficiency

For measuring photosynthetic response of yam varieties to eCO_2, the crop growth stage and leaf age were determined based on leaf

Table 1
Details of the variety used to study the effect of elevated carbon dioxide.

Sl. No.	Name	Special features
White yam		
1.	Sree Dhanya	Dwarf type with bushy appearance (30 cm height and 50–60 cm diameter), high yielding variety, 9 months duration
2.	Sree Haritha	Trailing type, high yielding variety with smooth tuber surface and good cooking quality, starch 20–22% (FW)
3.	Sree Priya	Trailing type, high yielding variety with smooth tuber surface and good cooking quality, starch 20–21% (FW)
4.	Sree Swetha	Dwarf type with bushy appearance (30 cm height and 50–60 cm diameter), high yielding variety
Greater yam		
5.	Sree Karthika	Trailing type, high yielding selection with good cooking quality and shelf-life, 9 months duration
6.	Sree Nidhi	Trailing type, high yielding selection with no browning when cooked, tolerant to anthracnose disease
7.	Sree Shilpa	Trailing type, high yielding selection with good cooking quality and shelf-life, 8 months duration

area development and tuber growth characteristics of yam varieties (Chapman 1965; Enyi 1972, 1973; Ferguson 1977; Goenaga and Irizarry 1994; Suja et al., 2000, 2005; Sunitha et al., 2020). Measurements were recorded in photosynthetically active leaves exposed to solar radiation between 9 and 11 AM and during active shoot growth (3–5 months) and tuber bulking phase (5–8 months). The leaf life of yam varieties in the present study varied between 150 and 180 days. Nevertheless, the leaves had high photosynthetic rates between 30 and 120 days and thereafter little declined. Therefore, 30 to 60 days old fully expanded, healthy, and turgid leaves were selected for measurements. Measurements were repeated 2 to 3 times to avoid the error due to temporal variation. Leaves were selected randomly from primary, secondary and tertiary branches to represent overall variability. Leaf gaseous exchange parameters viz; photosynthetic efficiency (P_n; μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s; mmol H_2O m^{-2} s^{-1}), trasnspiration (E; mmol H_2O m^{-2} s^{-1}), intercellular CO_2 (C_i; ppm), intrinsic water use efficiency (P_n/g_s; μmol CO_2 H_2O mol^{-1}) and instantaneous water use efficiency (P_n/E; μmol CO_2 H_2O mol^{-1}) were measured at four different CO_2 concentrations viz., 400, 600, 800 and 1000 ppm on the fully expanded intact mature leaf under full sunlight conditions. For measurements, a single leaf, every time was enclosed for 10 min in the climate-controlled cuvette of LICOR-6400XT portable photosynthetic system (LI-COR Environmental, Lincoln, Nebraska, U.S.A.). Climate-controlled cuvette of LICOR-6400XT is meant for the ambient air and leaf temperature flow along with optimum PAR irradiance and atmospheric CO_2 concentration around the leaf. CO_2 concentration can be adjusted/modified/elevated at the desired level by running a inbuilt programme as well as with the help of refillable CO_2 cartridge installed inside CO_2 injector system. Healthy and mature leaf of each plant remaining intact with the plant was first exposed to 400 ppm CO_2 concentration and eventually the same leaf was exposed to 600, 800 and 1000 ppm CO_2 concentrations, respectively, by keeping the climate-controlled cuvette of the portable LICOR-6400XT system. At a particular CO_2 concentration, many readings were recorded at steady state at 30–60 s intervals. Likewise, many readings were recorded for different leaves on the same plant at the particular CO_2 concentration. Leaf temperature was maintained at 25 °C, PAR at 1500 μmol m^{-2} s^{-1}, and relative humidity at 80%. As observed during the series of experiments with sweet potato (Ravi et al., 2017), *Amorphophallus* (Ravi et al., 2018), taro (Ravi et al., 2019), yam bean (Ravi et al., 2020) and cassava (Ravi et al., 2021), it takes approximately 10 min to reach a maximum steady-state photosynthetic rate and exposure of leaves beyond 10 min resulted in the reduction of rates. Hence, at least 10 min was allowed for a steady-state condition in order to obtain the optimum gaseous exchange data. Reliability of LICOR-6400XT portable photosynthesis system to set the desired CO_2 concentrations and PPFD was reported in these experiments under field conditions.

2.3. Statistical analysis

Statistical analysis was performed by using SAS/Software Version 9.3, SAS Institute Inc. (Cary, NC, USA 2010). CO_2 concentration and varieties were considered as fixed effects, while blocks were considered as random effect. Means were compared by adopting Tukey's post hoc test when the main effect of CO_2 concentration and varieties were significant.

3. Results and discussion

3.1. Statistical analysis

A one-way ANOVA was performed to compare the effect of four different carbon dioxide concentration (ECO_2), seven varieties and their interaction. A one-way ANOVA revealed that there was a statistically significant difference in variety ($P<0.001$), ECO_2 ($P<0.001$) and their interaction ($P<0.001$) (Table 2). Tukey's post hoc test for multiple comparisons found that the mean value of mean photosynthesis, stomatal conductance, intercellular carbon concentration, transpiration and vapour pressure deficit (VpdL) was significantly different ($P<0.01$) between ECO_2, variety and their interactive effect (Table 3).

3.2. Photosynthetic efficiency

Researchers are concerned over the responses of crops to ECO_2, as carbon dioxide is predicted to increase significantly over the years (Thompson et al., 2017). Yam is an important food security crop (Pradhan and Panda 2020) and hence it is critical to assess the effect of ECO_2 on photosynthetic efficiency. Photosynthetic rates increased at ECO_2 concentration with no down-regulation. Mean photosynthetic rate of seven yam varieties remained as 18.99, 26.35, 29.54 and 31.95 at 400, 600, 800 and 1000 ppm, respectively, but the magnitude of that increase differed amongst varieties. Sree Priya recorded the highest photosynthetic responses across all the concentrations, while Sree Haritha exhibited the lowest mean photosynthetic rates (Fig. 1). Notable increase in photosynthesis rate was observed at 600 ppm (~28%) in comparison to 400 ppm, whereas the same increased by 10.81% at 800 in comparison to 600 ppm and by 7.53% at 1000 ppm in comparison to 800 ppm. It can be said that yam is more responsive to 600–800 ppm as compare to 400 ppm in regards to the photosynthesis. Statistically, the net photosynthetic rate had a significant ($P<0.001$) linear relation with ECO_2 and C_i (R^2 = 0.783 and 0.763) (Fig. 2).

Stomata are the critical gateway for the entry of CO_2 inside plants. ECO_2 significantly impacted g_s at various magnitudes (Fig. 1). Mean g_s was increased at 600 and 800 ppm followed by down-regulation at 1000 ppm as compared to 400 ppm. g_s rate at 400 and 1000 ppm remained almost same with reduction of 1.3% at 1000 ppm. On the other hand, g_s increased by ~30 and ~37% at 600 and 800 ppm in comparison to 400 ppm. Sree Nidhi exhibited the lowest g_s rate at 600 and 800 ppm, whereas Sree Karthika exhibited the highest rate at 600 and 800 ppm. C_i increased significantly under ECO_2 across all

Table 2
One way analysis of variance of CO_2 concentrations, variety and their interaction.

Parameters	df	Sum Sq.	Mean Sq.	F value	Probability level
Variety (V)	6	4353.014	725.5024	71.0224	<0.001
CO_2	3	21,488.68	7162.893	701.2052	<0.001
V x CO_2	18	971.5458	53.9748	5.2838	<0.001

Table 3
Mean comparison of seven yam varieties subjected to elevated carbon dioxide.

Variables	CO_2 conc.	No. of observations	P_n	g_s	C_i	E	VpdL
White Yam							
Sree Dhanya	**400**	$n = 52$	17 ± 0.42^{p}	0.74 ± 0.081^{eg}	340 ± 12^{mn}	3.5 ± 0.25^{j}	0.7 ± 0.082^{hij}
	600	$n = 33$	25 ± 0.3^{jklm}	0.89 ± 0.1^{bdef}	500 ± 8.6^{kl}	5 ± 0.16^{efg}	1 ± 0.12^{dg}
	800	$n = 24$	30 ± 0.93^{cf}	1.2 ± 0.17^{ab}	690 ± 13^{fg}	4.9 ± 0.1^{efh}	0.88 ± 0.14^{efgi}
	1000	$n = 32$	33 ± 0.7^{c}	1.1 ± 0.1^{acd}	890 ± 11^{ab}	5 ± 0.2^{efg}	0.79 ± 0.11^{fgj}
Sree Haritha	**400**	$n = 27$	16 ± 0.23^{p}	1.1 ± 0.065^{ad}	360 ± 6.1^{m}	4.7 ± 0.13^{fhi}	0.48 ± 0.023^{j}
	600	$n = 36$	24 ± 0.38^{klm}	1.2 ± 0.04^{ab}	540 ± 1.2^{j}	5.1 ± 0.063^{efg}	0.5 ± 0.021^{j}
	800	$n = 14$	26 ± 0.33^{hil}	0.95 ± 0.048^{aef}	720 ± 4.8^{ef}	5 ± 0.052^{defhi}	0.59 ± 0.045^{hij}
	1000	$n = 15$	30 ± 0.59^{cfg}	0.77 ± 0.074^{bdegh}	890 ± 6.5^{ab}	5 ± 0.18^{defh}	0.75 ± 0.066^{fgj}
Sree Priya	**400**	$n = 12$	22 ± 0.34^{ln}	0.67 ± 0.041^{degi}	320 ± 4.6^{mn}	7.3 ± 0.1^{ab}	1.2 ± 0.082^{bcdf}
	600	$n = 16$	31 ± 0.29^{cf}	0.81 ± 0.033^{bdeg}	500 ± 3.7^{jl}	7.1 ± 0.13^{ab}	0.95 ± 0.048^{dgi}
	800	$n = 22$	37 ± 0.47^{ab}	0.65 ± 0.025^{ei}	$660 \pm 4.4\ g^{h}$	6.5 ± 0.077^{ac}	1.1 ± 0.041^{cdg}
	1000	$n = 15$	39 ± 0.71^{a}	0.66 ± 0.042^{cegi}	850 ± 8.7^{bc}	6.8 ± 0.23^{ac}	1.1 ± 0.05^{cdg}
Sree Swetha	**400**	$n = 38$	19 ± 0.37^{no}	0.71 ± 0.02^{egh}	330 ± 1.5^{mn}	6.9 ± 0.077^{ab}	1 ± 0.03^{dg}
	600	$n = 24$	26 ± 0.53^{ik}	0.62 ± 0.027^{ei}	500 ± 3.3^{kl}	7 ± 0.18^{ab}	1.2 ± 0.04^{cde}
	800	$n = 17$	31 ± 0.71^{cf}	$0.45 \pm 0.019\ g^{i}$	640 ± 5.1^{hi}	7.4 ± 0.25^{a}	1.7 ± 0.021^{a}
	1000	$n = 19$	31 ± 0.58^{cde}	$0.43 \pm 0.0088\ g^{i}$	830 ± 4.1^{cd}	6.9 ± 0.11^{ab}	1.6 ± 0.0072^{ab}
Greater yam							
Sree Karthika	**400**	$n = 30$	18 ± 0.55^{op}	0.58 ± 0.025^{fgi}	330 ± 2.2^{mn}	4.9 ± 0.16^{efh}	0.89 ± 0.03^{efgi}
	600	$n = 28$	26 ± 0.77^{hik}	1.1 ± 0.1^{ad}	520 ± 4.8^{jk}	4.8 ± 0.15^{fhi}	0.58 ± 0.053^{ij}
	800	$n = 34$	29 ± 0.6^{dfgh}	1.3 ± 0.099^{a}	720 ± 4.3^{e}	6.1 ± 0.24^{bcd}	0.61 ± 0.047^{ij}
	1000	$n = 15$	31 ± 1.1^{cfg}	1 ± 0.044^{ae}	910 ± 4.5^{a}	6.3 ± 0.063^{acd}	$0.69 \pm 0.036\ g^{j}$
Sree Nidhi	**400**	$n = 6$	20 ± 0.43^{mnp}	0.54 ± 0.0026^{degi}	310 ± 1.8^{mn}	7.9 ± 0.16^{a}	1.5 ± 0.029^{ad}
	600	$n = 21$	28 ± 0.93^{fij}	$0.44 \pm 0.025\ g^{i}$	460 ± 3.2^{l}	5.6 ± 0.26^{cf}	1.3 ± 0.016^{ad}
	800	$n = 23$	$27 \pm 0.38\ g^{ik}$	0.31 ± 0.017^{i}	610 ± 6.6^{i}	3.8 ± 0.18^{ij}	1.3 ± 0.02^{bcd}
	1000	$n = 19$	32 ± 0.79^{cd}	0.33 ± 0.014^{hi}	800 ± 4.9^{d}	3.9 ± 0.13^{hj}	1.2 ± 0.012^{cde}
Sree Shilpa	**800**	$n = 34$	28 ± 0.67^{efi}	$0.46 \pm 0.027\ g^{i}$	$660 \pm 4.5\ g^{h}$	$4.5 \pm 0.18\ g^{hi}$	1 ± 0.026^{dg}
	400	$n = 27$	19 ± 0.5^{np}	$0.5 \pm 0.025\ g^{i}$	310 ± 2.6^{n}	6.5 ± 0.2^{ac}	1.4 ± 0.031^{ac}
	600	$n = 28$	26 ± 0.56^{il}	0.61 ± 0.037^{ei}	490 ± 5.1^{kl}	5.8 ± 0.2^{ce}	1 ± 0.043^{dg}
	1000	$n = 16$	33 ± 0.83^{bc}	0.49 ± 0.034^{fgi}	830 ± 11^{cd}	4.7 ± 0.25^{efhi}	1 ± 0.021^{cdgh}
***P*-value**	**Variety (V)**		<0.01	<0.01	<0.01	<0.01	<0.01
	CO_2		<0.01	<0.01	<0.01	<0.01	0.24
	V x CO_2		<0.01	<0.01	<0.01	<0.01	<0.01

Note: Values with similar letters are statistically non-significant.

the concentrations. Mean C_i concentration at 400–1000 ppm remained at 328.67, 507.85, 655.19 and 863.77 ppm, respectively, with an increase up to 1.5–2.6 fold. The extent of increase under ECO_2 diverged significantly amongst cultivars (Fig. 1). When averaged over the concentrations and varieties, mean E decreased significantly across ECO_2 concentration at the extent of −1.9 to −8%. Mean

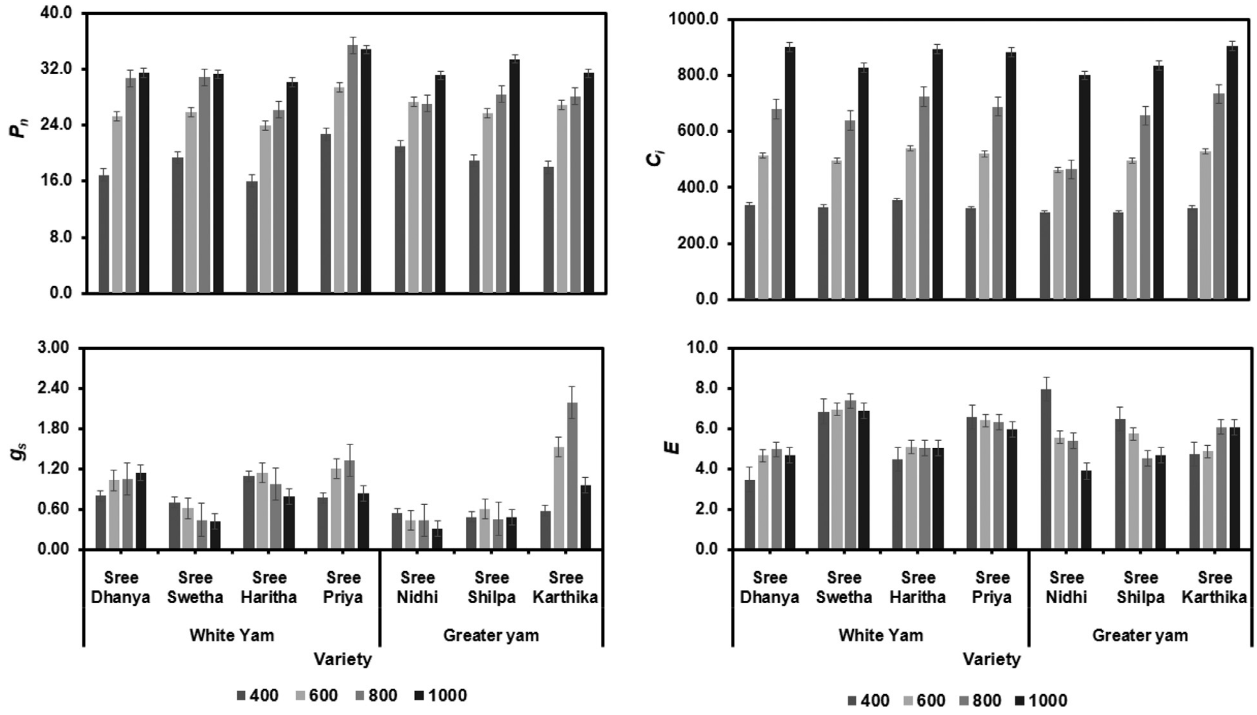

Fig. 1. Effect of elevated CO_2 on net photosynthesis, intercellular carbon concentration, stomatal conductance and transpiration in white yam and greater yam. The error bars indicate SE.

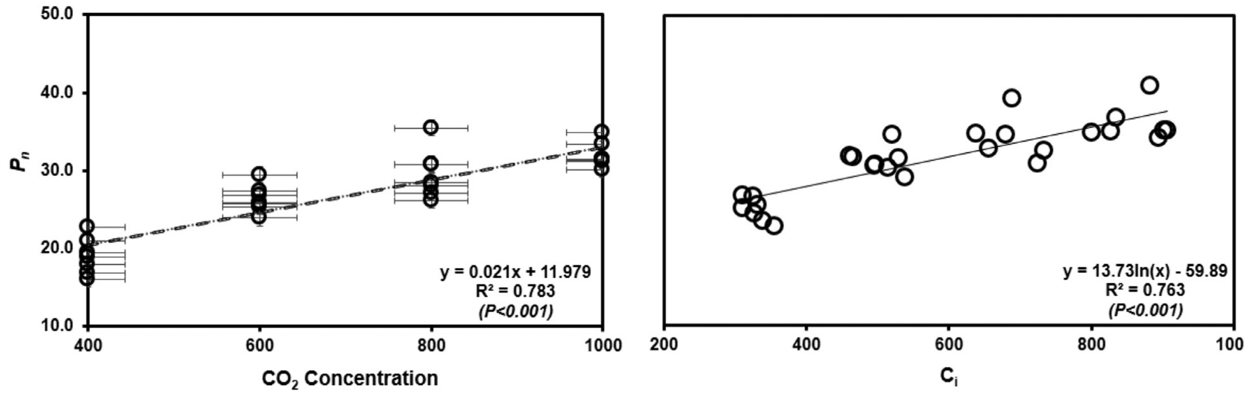

Fig. 2. Statistical relation between the net photosynthetic rate with CO_2 concentration and intercellular carbon concentration in white yam and greater yam. The error bars indicate SE.

E concentration at 400−1000 ppm recorded to be 5.81, 5.74, 5.70 and 5.33, respectively (Fig. 1). Intrinsic water use efficiency ($WUE_{intrinsic}$) and instantaneous water use efficiency ($WUE_{instantaneous}$), were significantly increased under elevated CO_2 (Fig. 3). $WUE_{intrinsic}$ consistently increased under ECO_2 by 16, 43 and 88, under 600, 800 and 1000 ppm CO_2, respectively, as compared to 400 ppm CO_2. Similar trend was observed with respect to instantaneous water use efficiency, which increased at the extent of 38, 53 and 80% at 600, 800 and 1000 ppm, respectively.

This study is planned because very little attention is given to this underutilised crop. Though it is an underutilised crop, it is a very critical ingredient to alleviate the poverty and malnutrition (More et al., 2019). To the best of our knowledge, no study has been done in yams with respect to elevated CO_2 except by Thinh et al. (2017) in Chinese yam. We have considered studying two economically and nutritionally important species viz, *D. rotundata* Poir. and *Dioscorea alata* L. (Obidiegwu et al., 2020). We exposed yam leaves to short term (10−15 min.) elevated carbon dioxide concentration conditions to assess the performance of photosynthetic efficiency which we hypothesised that ECO_2 would prevent the down-regulation of yam photosynthesis. Results were expected as such because yam has a higher sink capacity, biological efficiency and yield potential (Diby et al., 2009). Though, plants were exposed to a very short period under field conditions, our results are in line with the results reported by other researchers performed under FACE and OTC conditions for longer exposure.

Numerous reports are available referring to the positive effect of ECO_2 on plant growth and physiological processes (Zinta et al., 2014; Dong et al., 2018; Soares et al., 2019). As a matter of fact, plant type (C_3, C_4 and CAM) is the determinant factor for the quantum of the stimulation of photosynthetic efficiency under higher CO_2 concentration (Xu et al., 2015; Boretti and Florentine, 2019). These differences are further likely to be intensify with the environmental conditions, water-nutrient availability and crop husbandry practices (Xu et al., 2015). For instance, legumes, root and tuber crops are likely to achieve higher yield than cereals under elevated CO_2 conditions (Ainsworth and Long, 2020). In Japan, Chinese yam plants were exposed to 600 ppm CO_2 concentration and two temperature regimes (low and high) for 40−45 days grown in temperature-gradient chambers. Net photosynthetic rate was significantly higher under ECO_2 than under ambient CO_2 in both temperature regimes (Thinh et al., 2017). In a series of experiments on major and minor tropical tuber crops, exposing plants to 1000 ppm for a short period significantly increased the photosynthetic rates (sweet potato +53%, Ravi et al., 2017; elephant foot yam +66%, Ravi et al., 2018; taro +113%, Ravi et al., 2019; yam bean +23%, Ravi et al., 2020; cassava +23%, Ravi et al., 2021).

In current experiment, ECO_2 significantly impacted the gaseous exchange capacity. Photosynthesis and intercellular carbon dioxide concentration increased significantly and no down-regulation was observed at the highest concentration. Contrastingly, g_s increased up to 800 ppm followed by down-regulation at 1000 ppm. Transpiration rate reduced minutely as the CO_2 concentration increased. Whereas, C_i and $WUE_{intrinsic}$ increased at each CO_2 level without any down-regulation. These variables interacted significantly across all the concentrations and varieties indicating differential varietal responses to CO_2 enrichment. Alteration in photosynthetic responses to ECO_2 in C_3 and C_4 crops have been reported by Allen and Prasad (2004) and Vanaja et al. (2011) under various CO_2 concentrations. In soybean, photosynthesis enhanced by up to 30% at 550−700 ppm, whereas

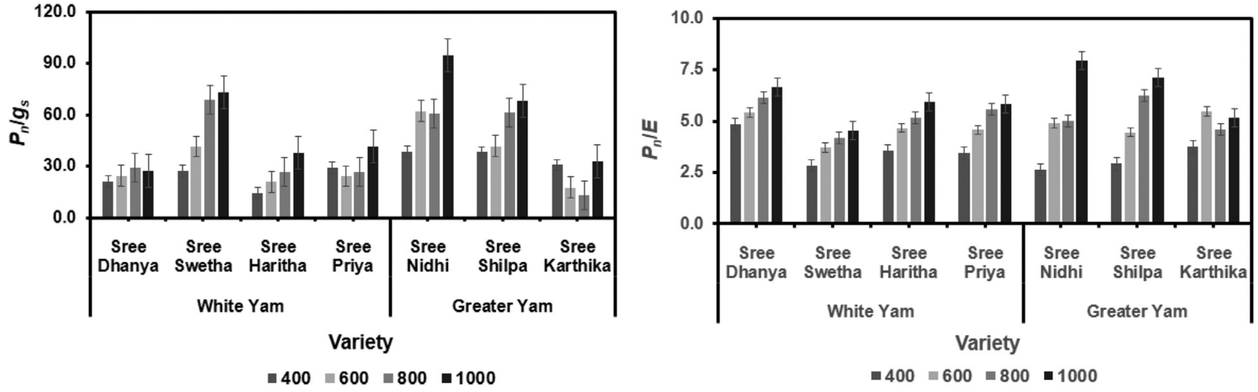

Fig. 3. Effect of elevated CO_2 on intrinsic (P_n/gs) and instantaneous water use efficiency (P_n/E) in cassava. The error bars indicate SE.

the same increased by 50−60% in barley and cotton (Bernacchi et al., 2005; Prior et al., 2011; Ratnakumar et al., 2011). Positive trend with respect to photosynthesis and biomass accumulation was also reported in tuber crops viz; potato (Aien et al., 2014), sweet potato (Ravi et al., 2017) and cassava (Ruiz-Vera et al., 2021). There are some reports in cassava showing acclimation or down-regulation of photosynthesis at higher CO_2 concentrations. For instance, Gleadow et al. (2009) and Cruz et al. (2016) reported down-regulation of photosynthesis rate at 550−710 ppm and 750 ppm, respectively. Recently, Ravi et al. (2021) reported similar findings in cassava with the increment in P_n at 600−800 ppm followed by the down-regulation at 1000 ppm. It is clear that crops' responses to ECO_2 are subject to the plant species/variety under study and the growing/experimental conditions.

C_3 crops are biologically less efficient as compared to C_4 and CAM crops (Wang et al., 2012) and hence show more positive response to ECO_2 condition (Xu et al., 2015). That is likely because of relatively abundant availability of CO_2 for photosynthesis in comparison to ambient conditions along with the absence of feedback inhibition (Xu et al., 2015). However, the exposure time to ECO_2 (short or long) is the most critical decisive factor for up-regulation or down-regulation of photosynthesis. Because short-term exposure enhances the P_n rate whereas long term exposure may cause photosynthetic acclimation or the down-regulation of the photosynthetic apparatus (Ainsworth and Rogers, 2007; Sanz-Saez et al., 2013). Photosynthesis stimulation under ECO_2 is achieved by up-regulating the carboxylation of RuBP in concurrence with inhibition of the oxygenation of RuBP, inhibition of photorespiration and higher sink demand (Bowes, 1991; Long, 1991; Ainsworth and Rogers, 2007; Kane et al., 2013; Moroney et al., 2013; Xu et al., 2015; Forbes et al., 2020).

Increased photosynthesis along with the reduced stomatal conductance are the general (but not universal) responses of cassava under ECO_2. Carbon enriched environments increases the carbon flux inside the leaf without much increment in stomatal conductance (Xu et al., 2016). Some species are known to reduce the stomatal density to limit the water loss in accordance with maintenance of optimum photosynthetic rates and WUE (Franks and Farquhar, 2007; Franks et al., 2009; Lammertsma et al., 2011; Garrison et al., 2021). Reduced stomatal activity could limit the carbon assimilation rate in plants, but enhances the WUE and productivity which is an advantage in the context of climate change where water deficit stress episodes are likely to increase (Leakey et al., 2009; Sreeharsha et al., 2015; Xu et al., 2016). Plant species moderate the stomatal responses in order to maintain the balance between CO_2 enrichment and water loss in the form of transpiration to achieve optimum productivity (Gray et al., 2000; Haworth et al., 2013; Lawson et al., 2014). Reduced stomatal activity under carbon enriched environments is further driven by reduced stomatal density, greater depolarization of guard cells caused by decreased K^+ ion, cytosolic Ca^{2+}, Cl^- and malate (Mal^{2-}), cytosolic zeaxanthin level and the pH value of guard cells (Schroeder et al., 2001; Fujita et al., 2013; Lawson et al., 2014; Xu et al., 2016). Contrastingly, inverse to the general notion that g_s is reduced under ECO_2, research results of Purcell et al. (2018) revealed that under certain environmental conditions, g_s can increase in response to elevated CO_2 based on model predictions (data from 51 FACE experiments concerning the effect of elevated CO_2 on plant stomatal conductance (g_s) in different plant species were considered).in current experiment also g_s increased up to 800 ppm followed by a down-regulation at 1000 ppm.

Increment of C_i under ECO_2 is well established, as found in the current experiment. When yam varieties were subjected to ECO_2, C_i also enhanced, as reported by Fernandez et al. (2002), Gleadow et al. (2009), Rosenthal et al. (2012) and Cruz et al. (2014) in cassava; Ravi et al. (2017) in sweet potato; Ravi et al. (2018) in elephant foot yam; Ravi et al. (2019) in taro and Ravi et al. (2020) in yam bean. Higher carbon assimilation and lower g_s and E under ECO_2 attributed the increased $WU_{Eintrinsic}$ and $WUE_{instantaneous}$. Increased WUE was resulted mainly due to lower transpiration mediated by restricted stomatal activity rather than increased carbon assimilation. Results corroborated with Fernandez et al. (2002), Rosenthal et al. (2012), Cruz et al. (2014) and (2016) in cassava under ECO_2. The higher WUE observed in cassava plants measured at elevated CO_2 was due to a direct effect of CO_2 on P_n (increase), rather than to a decrease in g_s (Fernandez et al., 2002).

Yam is biologically efficient crop with yield potential up to 50−70 t ha^{-1} (Irizarry and Rivera, 1993; Diby et al., 2009; Ruttanaprasert et al., 2019). We are of strong opinion that yam can produce even higher than these levels followed with scientific crop husbandry practices and adoption of improved varieties. Yam is consumed for its starchy tubers (More et al., 2019) and tuber bulking and canopy development take place simultaneously during early growth period (2−5 months after planting) (Ferguson 1977). Carbon assimilation capacity and pattern and extent of translocation of carbohydrates towards various growing organ especially towards tubers are the critical factors to determine the tuber and starch yield potential. As yams are potentially highly productive, it is expected to exhibit positive responses towards elevated CO_2 environments to support high sink demand.

4. Conclusion

Photosynthetic responses of seven varieties of yam (three of greater yam and four of white yam) were assessed under elevated carbon dioxide conditions exposed for short period. Net photosynthesis, intercellular carbon concentration, $WUE_{intrinsic}$ and $WUE_{instantaneous}$ increased consistently when exposed to 600, 800 and 1000 ppm in comparison to ambient concentration (400 ppm). Stomatal conductance enhanced till 800 ppm and decrease eventually, whereas transpiration decreased consistently across all concentrations to optimize the water use efficiency. Results from this experiment revealed that yam is a suitable crop in the context of climate change.

Declaration of Competing Interest

The authors declare that there is no conflict of interest regarding the publication of this article

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