RESEARCH ARTICLE

Evaluation of photosynthetic efficiency of yam bean (*Pachyrhizus erosus* L.) at saturating photon flux density under elevated carbon dioxide

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Abstract The future CO₂ concentration is projected to reach 900–1000 ppm levels by the end of twenty-first century, pertaining to global climatic changes. Consequences of climate change such as changes in mean climatic conditions, increasing extreme weather events, relentless increase in atmospheric CO₂ concentration and increasing pest damage pose serious threats to agricultural productivity. An experiment was planned to assess the response of yam bean to elevated CO₂, as it is of paramount importance to identify photosynthetically efficient climate-smart crops and varieties to meet future food demand. The net photosynthetic rate (P_n), stomatal conductance (g_s) and intercellular CO₂ (C_i) of yam bean variety, Rajendra Misrikand-1 was recorded under elevated carbon dioxide (400–1000 ppm) and photon flux density (PPFD;

50–2000 $\mu\text{mol m}^{-2} \text{h}^{-1}$) at $30 \pm 2^\circ\text{C}$, 70–80% relative humidity and 0.8–1.2 kPa vapour pressure deficit. The mean P_n rate steadily increased at 200–1000 ppm owing to enhanced intercellular CO₂. The same trend was observed in the case of intercellular CO₂. However, contrasting results were recorded with regard to g_s , which steadily decreased at ascending carbon dioxide concentrations. Further, P_n had a significant ($P < 0.001$) linear correlation with the PPFD ($R^2 = 0.973$). Yam bean was found to be responsive to elevated carbon dioxide as P_n rate at 1000 ppm increased up to 23% relative to 400 ppm.

Keywords Climate change · Elevated carbon dioxide · Intercellular carbon dioxide · Photosynthesis · Stomatal conductance · Yam bean · *Pachyrhizus erosus* L.

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Introduction

The yam bean, *Pachyrhizus erosus* L. (Mexican yam bean) is a legume belonging to the family Leguminosae and subfamily Fabaceae (Papilionaceae), originated in Mexican and Central American regions of Latin America. It is one of the only 15 species with edible tubers among 50,000 edible plants grown in the world (More Sanket et al. 2019). Yam bean is widely cultivated in most southern states of Mexico, El Salvador, Northwestern Honduras and Guatemala (Sørensen 1996). It is commonly called as Misrikand, Kesaru, Sharkaralu or Sankesh in different parts of India. In India, it is mostly grown in North Bihar extending to parts of West Bengal, Assam, Odisha and Eastern Uttar Pradesh (Suresh Kumar et al. 2016). Under optimum agroclimatic conditions, yam bean grows and produces maximum storage root yield within 4 months after sowing (Nedunchezhiyan et al. 2002). The average storage root

yield may vary between 9.1 and 29.1 t ha⁻¹ (Vimala and Nambisan 2011) but improved varieties may yield up to 36–45 t ha⁻¹ (ICAR-CTCRI 2018). Other proximate composition of storage roots, immature pods and seeds are enumerated by Kay (1987) and Sørensen (1996). The storage root of yam bean is usually consumed fresh after removal of the thick, fibrous brown skin and the taste resembles that of Chinese water chestnut (Nedunchezhiyan et al. 2001, 2002; Silva et al. 2016). The storage roots of yam bean germplasm have been reported to contain variable starch (3.4–6.9%), sugar (2.1–4.4%) and dry matter (7.8–15.7%) contents (Vimala and Nambisan 2011). It has a sweet flavor from the oligofructose inulin (also called fructo-oligosaccharide) which is prebiotic. It is very low in saturated fat, cholesterol, and sodium. It is also a good source of Ca, Zn, Fe, Cu, thiamine, riboflavin, niacin and vitamin C.

The global food production in future is challenged by climate change as a result of anthropogenic activities and the climate change cause several effects including increased atmospheric CO₂ concentration, increased risk of extreme weather conditions, pest damage, and changes in average climatic conditions (More Sanket et al. 2017, 2018). According to the IPCC (2007), CO₂ concentrations are projected to reach in the range of 500–1000 ppm at the end of this century. Most of the tuber crops are C₃ plants and increased CO₂ concentration in the atmosphere is known to enhance the growth and productivity of these crops. Enhanced concentration of atmospheric CO₂ for photosynthesis can have profound effects on plant growth and many aspects of plant physiology (Taub 2010; Ravi et al. 2017). Several researchers, with a variety of plant species, have reported increased photosynthetic rates as high as 40% at 475–600 ppm under FACE experiments as compared to the rates under normal CO₂ concentration. At increased CO₂ concentration, plants can maintain high photosynthetic rates with relatively low stomatal conductance which could decrease by an average of 22% (Ainsworth and Rogers 2007). FACE experiments have also shown diminished whole-plant water use by 5–20% under elevated CO₂ (Leakey et al. 2009). Further, Ainsworth (2008) and Long et al. (2006) have reported increment in yield by 12–14% under elevated CO₂ in FACE experiments in various plant species. Net photosynthetic rates in tropical tuber crops under 380–1000 ppm CO₂ varied between 21.4 and 40.3 μmol CO₂ m⁻² s⁻¹ in sweet potato (Ravi and Saravanan 2001; Ravi et al. 2017), between 17.9 and 30 μmol CO₂ m⁻² s⁻¹ in elephant foot yam (Ravi et al. 2018) and between 21 and 50 μmol CO₂ m⁻² s⁻¹ in taro (Ravi et al. 2019). In potato and sweet potato plants, tuber/storage root yield increased significantly up to 1000 ppm and 514–1520 ppm, respectively (Wheeler et al. 1994; Mortley et al. 1996; Czeck

et al. 2012). Yam bean is a unique, tuber producing, tropical legume crop and so different from other legume crops. Furthermore, unlike other crops, in yam bean, the source and sink (tuber) develop simultaneously and it is imperative to understand the photosynthetic response of such crops to elevated CO₂. Because yam bean plants were grown under field conditions, they did not exhibit acclimation to elevated CO₂ as often observed under controlled conditions where light intensity and sink activity are limiting factors. To our knowledge, this is the first study of yam bean response to elevated CO₂ and will help in assessing the suitability of yam bean for high CO₂ environment developing crop simulation models and for genetic improvement of this crop to high CO₂.

Materials and methods

Seeds of yam bean variety Rajendra Mishrikand-1 (RM-1), was sown in the field at 60 cm spacing on ridges prepared 60 cm apart at ICAR-Central Tuber Crops Research Institute, Sreekariyam, Thiruvananthapuram during June–2018. There were three replications and each replication had 16 plants. Farmyard manure (FYM) @ 15 t ha⁻¹ and nitrogen:phosphorus (P₂O₅):potassium (K₂O) at the rate of 80:40:80 kg ha⁻¹ were applied. A full dose of phosphorus, potassium and half dose of nitrogen were applied as basal dose at the time of planting. The remaining half dose of nitrogen was applied 45 days after sowing. Mean temperature, relative humidity, soil moisture, and rainfall during June–September 2018 were 25.9 °C, 86.6%, 19.4% and, 860 mm respectively. The diurnal changes of atmospheric CO₂ in the field indicated a dip from ~ 460–470 ppm at 6.00 AM to ~ 380–390 ppm at 12.00 AM and rise to ~ 400 ppm at 4.00 PM. The field was irrigated to 100% field capacity prior to measurement and plants were maintained under water deficit stress-free conditions. Photosynthetic CO₂ uptake, stomatal conductance, intercellular CO₂ were all recorded in leaves enclosed in the climate-controlled cuvette of LICOR-6400, the portable photosynthetic system under optimum conditions. This instrument has an inbuilt program for setting the desired measurement conditions such as CO₂, PPFD, etc. The relative humidity and vapour pressure deficit during the time of measurements were 70–85% and 0.8–1.2 kPa respectively at 30 ± 2 °C leaf temperature. Measurements were recorded between 2nd and 3rd month after sowing yam bean which is the active growth period reported (Nedunchezhiyan et al. 2002). To avoid error due to temporal variation, measurements were repeated twice and the values averaged for statistical analysis. The net photosynthetic rate (P_n), stomatal conductance (g_s) and intercellular CO₂ (C_i) were measured in the fully mature, healthy, individual leaves in

each plant (4th to 7th leaf) tested with the range of concentrations of CO₂ during 2–3 months after sowing (MAS). Leaves in each plant were tested repeatedly with the range of CO₂ concentrations and PPFD. Yam bean leaves were exposed to elevated carbon dioxide concentrations by enclosing every leaf to 200–1000 ppm CO₂ concentrations. Here, 50% of ambient CO₂ was tested to study the photosynthetic response to low CO₂, both internal and external. First, in order to determine the PPFD required for maximum photosynthetic rate, photosynthetic rates were measured at a broad range of PPFD ranging from 50 to 2000 $\mu\text{mol m}^{-2} \text{h}^{-1}$ in a climate-controlled cuvette of LICOR-6400 portable photosynthesis system. Once, this is determined to be 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, photosynthetic rates and other related parameters at elevated CO₂ were recorded at 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD because the increase in photosynthetic rates above 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was insignificant. At a particular concentration of CO₂, 2–3 readings were recorded at steady state. In this way, many readings were recorded for different leaves in the same plant and for the particular CO₂. Then, the concentration of CO₂ changed to other desired concentration and many readings were recorded for different leaves in the same plants as above. To avoid error due to time of measurement, measurements were repeated at different times in the same plant between 10 and 12 AM. In our experience in measuring photosynthesis in leaves of yam bean, sweet potato, taro, *Amorphophallus* and cassava using this instrument, maximum steady-state photosynthetic rates were attained by 10 min. The enclosure of leaves beyond 10 min resulted in a gradual reduction of rates. Therefore, we recorded all photosynthetic parameters after 10 min enclosure. Recently, Ravi et al. (2017, 2018, 2019) in sweet potato, *Amorphophallus* and taro, respectively, have reported reliability of LICOR-6400 portable photosynthesis system to set the desired CO₂ concentrations and PPFD. The data were analysed statistically with factorial concept and Tukey's post hoc test using SAS/Software Version 9.3, SAS Institute Inc., Cary, NC, USA 2010. Single factor ANOVA was carried out for data analysis. Means comparison was done and significant differences were shown by placing appropriate letters. *P* values were also given.

Results and discussion

The photosynthetic response to the photon flux density

The P_n rate increased steadily due to the increase in PPFD from 50 to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The maximum P_n rate was observed under 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1). P_n Increment rate was found to be less from 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$

Fig. 1 Changes in net photosynthetic rate under different PPFD. The error bars indicate SE

onwards as compared to 50–1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. A significantly positive and linear correlation was observed between P_n and PPFD ($P < 0.001$). Higher PPFD enhanced the photosynthetic efficiency in yam bean. Results are in agreement with those recently reported by Ravi et al. (2017) in sweet potato, Ravi et al. (2018) in elephant foot yam, Ravi et al. (2019) in *Colocasia esculenta* and Pallardy (2008) in fruit trees.

The response of P_n to elevated carbon dioxide

The P_n rate significantly increased with an increase in external CO₂ concentration from 200 to 1000 ppm depicting the positive response of yam bean to elevated carbon dioxide. The differences in P_n rates under elevated carbon dioxide (200–1000 ppm) were statistically significant ($P > 0.001$). The percent of the increase in P_n at 1000 ppm CO₂ as compared to 400 ppm CO₂, was the maximum. However, the percent of increment in P_n rate decreased with every 200 ppm increment of external CO₂ between 400 and 1000 ppm CO₂ (Fig. 2). Several researchers have reported increased photosynthetic rates in leguminous crops. Vu et al. (1997) and Prasad et al. (2005)

Fig. 2 Changes in net photosynthetic rate under different CO₂ concentrations in yam bean. The error bars indicate SE

reported increment of $\sim 33\%$ and 66% photosynthetic rate in soybean at 700 ppm and 1000 ppm, respectively as compared to 350–400 ppm CO_2 . While in chickpea, P_n rate increased by 70% at 550 ppm as compared to 370 ppm CO_2 (Pal and Sangeetha 2009). The elevated CO_2 concentration was responsible for enhanced photosynthetic rates by 12% at 550 ± 60 ppm in mung bean leaf (Hao et al. 2011). Furthermore, increased P_n rates in black gram (78 and 30%) were reflected as a function of enhanced CO_2 concentration (at 700 and 550 ppm) (Sathish et al. 2014). The P_n rate increased by 136–173% in Chinese yam (*Dioscorea opposita* Thunb.) and by 81–118% in rice due to long term exposure to elevated carbon dioxide at 598 ppm relative to 403 ppm (Thinh et al. 2017). In case of tropical root and tuber crops, a similar increase in photosynthetic rate under elevated carbon dioxide has been reported in cassava (Gabriel et al. 2014; Cruz et al. 2014; Rosenthal et al. 2012), sweet potato (Cen and Sage 2005; Ravi et al. 2017), *Amorphophallus* (Ravi et al. 2018) and taro (Ravi et al. 2019). Gleadow et al. (2009) reported that growth and nutritive value of cassava were reduced when grown in elevated CO_2 . The diminished P_n rates at short-term exposure to elevated carbon dioxide is attributed to the factors such as decline in electron transport capacity, capacity of P_i -regeneration from phosphorylated photosynthetic intermediates, RuBP regeneration for Rubisco activity, decline in the activation state of Rubisco and the balance between Rubisco and other processes limiting photosynthesis (Sage et al. 1989; Makino and Mae 1999). Unlike the decline in P_n due to limitations in sink activity and decline in Rubisco activity under long-term exposure to elevated carbon dioxide reported in other crops, the decline in increment of photosynthetic rate recorded under elevated carbon dioxide in the present study is not attributed to acclimation as the source and sink are simultaneously active in yam bean. Furthermore, yam bean plants were grown under field conditions and there was no sink limitation and acclimation.

The response of stomatal conductance (g_s) to elevated carbon dioxide

The stomatal conductance (g_s) under different CO_2 concentrations from 200 to 1000 ppm differed significantly ($P > 0.001$). The g_s in the leaves of yam bean steadily decreased under 200–1000 ppm CO_2 due to increased CO_2 concentrations (Fig. 3). However, the g_s increased by 27% at 600 ppm relative to 400 ppm CO_2 . Extensive literature is available depicting the diminished stomatal conductance (g_s) under elevated carbon dioxide. C_3 plants adapt to increasing atmospheric CO_2 concentrations by reducing transpirational water loss by decreasing stomatal conductance (g_s) and simultaneously increase assimilation rates

Fig. 3 Changes in the stomatal conductance under different CO_2 concentrations. The error bars indicate SE

(Lammertsma et al. 2011). Stomatal closure led by the depolarization of the membrane potential of guard cell might be the possible reason for the realization of such results (Ainsworth and Rogers 2007). Partial stomatal closure and associated decrease in stomatal conductance to H_2O is one of the most important responses to increasing CO_2 . The g_s decreased across various plant species by 21–50% at elevated carbon dioxide (Xu et al. 2016). In soybean, the g_s decreased by 31% at 450–550 ppm CO_2 , 36% at 600–800 ppm CO_2 and 51% at > 850 ppm CO_2 relative to 330–360 ppm CO_2 (Ainsworth et al. 2002). In other experiments with green gram, Hao et al. (2011) reported the decreased g_s (by 32%) at 550 ± 60 relative to 389 ± 40 ppm CO_2 .

In the present study, yam bean plants were grown in ambient CO_2 (~ 390 –400 ppm) and therefore the decrease in g_s in yam bean leaves during short term exposure to elevated carbon dioxide (1000 ppm) is attributed to the partial closure of stomata and not due to a decrease in stomatal density (SD) and the stomatal index (SI). Stomatal opening and closure which regulate stomatal conductance and resistance respectively are affected by the interaction of several factors such as light, air temperature, vapour pressure deficit (VPD) regulated by relative humidity, soil moisture, leaf water potential, and atmosphere and inter-cellular CO_2 concentrations (Ravi 2003; Ocheltree et al. 2014; McAdam and Brodribb 2015; Xu et al. 2016; Merilo et al. 2018). Reduction in stomatal conductance is the general response of plants under elevated CO_2 (Medlyn et al. 2001; Ainsworth and Rogers 2007; Gao et al. 2015) and this may be attributed to the short-term structural plasticity under elevated CO_2 (Xu et al. 2016). In the present study, the mean RH and soil moisture content during the cropping period remained 86% and 19%. The soil had adequate moisture as the yam bean plants were under well-irrigated conditions. Therefore, the short-term decline in g_s in yam bean leaves is exclusively attributed to elevated carbon dioxide (600–1000 ppm) and not due to a decrease in RH and soil moisture.

The response of C_i to elevated carbon dioxide

The intercellular CO_2 concentration (C_i) significantly increased ($P > 0.001$) as the CO_2 concentration increased from 200 to 1000 ppm (Fig. 4). Several studies reported an increase in C_i at elevated carbon dioxide concentrations (Hao et al. 2011). However, the percent of increment in C_i under 400 ppm over 200 ppm, under 600 ppm over 400 ppm, under 800 ppm over 600 ppm and under 1000 ppm over 800 ppm was 59, 69, 26 and 33%, respectively. This indicates that the increment of C_i declined in the leaves of yam bean as the atmospheric CO_2 concentration increased between 200 and 1000 ppm CO_2 . A similar increase in C_i concentration and decline in the increment of C_i in response to short-term exposure to CO_2 between 400 and 1000 ppm have been reported in leaves of sweet potato (Ravi et al. 2017), elephant foot yam (Ravi et al. 2018) and taro (Ravi et al. 2019). Although the P_n rate increased as the external CO_2 concentration increased between 200 and 1000 ppm, the decline in the increment of P_n rate as the external CO_2 concentration increased between 400 and 1000 ppm, resulted in the increase in C_i concentration. Sweet potato plants grown under controlled conditions had greater photosynthetic rate due to increase in C_i from 250 to 560 ppm (Cen and Sage 2005).

Conclusion

Global climate change poses a serious threat to agricultural productivity. Keeping this view, the performance of the RM-1 variety of yam bean was assessed under elevated carbon dioxide in field conditions. A photosynthetic rate was found to be closely related to PPFD as highest P_n rate was observed at the highest PPFD. Yam bean was found to be responsive to elevated carbon dioxide as P_n rate at 1000 ppm increased up to 23% relative to 400 ppm. However, stomatal conductance diminished steadily at the ascending carbon dioxide concentrations. Pertaining to the

Fig. 4 Changes in the intercellular CO_2 under different CO_2 concentrations. The error bars indicate SE

performance of yam bean, it can be said that yam bean is responsive to elevated carbon dioxide and very well suited to thrive under future projected high CO_2 environmental conditions.

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