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Photosynthetic response of sweet potato (*Ipomoea batatas*) to photon flux density and elevated carbon dioxide

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ABSTRACT

The continuous rise in the atmospheric CO_2 due to anthropogenic activities is likely to benefit crop species with C_3 photosynthetic pathway by enhancing photosynthetic efficiency and crop productivity. This is particularly important in the context of climate change and food security of ever increasing population amidst scarcity of natural resources. In the search of photosynthetically efficient climate smart genotypes. In the present study, the net photosynthetic rate (*Pn*), stomatal conductance (g_s) and intercellular CO_2 (*Ci*) was studied in twelve contrasting sweet potato genotypes, viz. Sree Arun, Sree Badhra, Sree Kanaka, Kanhangad, Pusa Safed, Pusa Red, Kisan, Gouri, Sankar and ST-13, S-1464 and S-1466 under ambient (400 ppm) and eCO_2 (eCO_2) (600, 800 and 1000 ppm) and the *Pn* at photosynthetic photon flux densities (PPFDs), viz. 200, 400, 600, 800, 1000, 1200 and 1500 µmol/m^2/h at 30ºC and 400 ppm CO_2 using portable photosynthesis system. The maximum *Pn* of ten sweet potato genotypes was recorded at PPFD of 1500 µmol/m^2/s and the increase in *Pn* at PPFDs above 1000 µmol/m^2/s were insignificant. The *Pn* steadily increased due to short-term (ten minutes) exposure at eCO_2 concentrations between 400 ppm and 1000 ppm in twelve sweet potato genotypes. The sweet potato genotypes had the average *Pn* of 26.30, 33.41, 38.02 and 40.32 µmol/m^2/s at 400, 600, 800 and 1000 ppm CO_2 respectively. However, the per cent of increment in *Pn* at eCO_2 significantly declined (average 5.98%) at CO_2 concentrations above 800 ppm. The genotypes Gouri, Sankar, Sree Arun, and S1466 had 61.00 – 74.3% hike in *Pn* at eCO_2 (1000 ppm) as compared to ambient CO_2 (400 ppm). The per cent increment in *Pn* significantly decreased at CO_2 concentrations above 600 ppm. The differences in *Pn* were statistically significant across sweet potato genotypes and CO_2 concentrations (P>0.001), whereas the *Pn* had a quadratic relation with the increase in CO_2 concentration (R^2=0.603). The g_s steadily decreased at eCO_2 concentrations. The sweet potato genotypes had the average g_s of 0.606, 0.508, 0.431, 0.376 mol H_2O/m^2/s at 400, 600, 800 and 1000 ppm CO_2 respectively. The per cent of decrease in g_s at eCO_2 significantly increased (average 38.33%) at 1000 ppm CO_2. The differences in g_s were statistically significant across sweet potato genotypes and CO_2 concentrations (P>0.001). The sweet potato genotypes had the average *Ci* of 271.50, 405.20, 543.00, and 684.00 µmol CO_2/mol air at 400, 600, 800 and 1000 ppm CO_2 respectively. However, the per cent of increment in *Ci* at eCO_2 significantly declined (average 25.70%) at CO_2 concentrations above 600 ppm. The differences in *Ci* were statistically significant across sweet potato genotypes and CO_2 concentrations (P>0.001), whereas the *Pn* had a quadratic relation with the increase in *Ci* (R^2=0.504). The interaction effect of genotypes and CO_2 concentration on *Ci*, *Pn* and g_s was insignificant. The differences in the total chlorophyll and protein content in the leaves of sweet potato genotypes were statistically significant. Nevertheless, the gas exchange parameters were not influenced by the total chlorophyll and protein content.

Key words: Climate change, ECO_2, Intercellular CO_2, Photosynthesis, Stomatal conductance, Sweet potato

The relentless increase in CO_2 concentration in the atmosphere since 1950 after industrial revolution due to anthropogenic activities of human is the major concern of global climate change. The atmospheric CO_2 has been estimated to remain at ~280 ppm before 1750 and then steadily increased to ~400 ppm at present and is expected to increase to 700-900 ppm by the end of the 21st century (IPCC 2001, Teng *et al*. 2006). During the past five years between 2010 and 2015 the average rate of raise in global CO_2 was 2.32 ppm per year and at this rate global atmospheric CO_2 is expected to reach between 472 and 567 ppm by 2050 (climate.nasa.gov/climate_resources/24).

Sweet potato [*Ipomoea batatas* (L.) Lam.] is a C_3 plant and previous studies indicated that the net photosynthetic

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rate (*Pn*) of field grown six sweet potato genotypes varied between 21.4 and 23.7 µmol $CO_2/m^2/s$ (Ravi and Saravanan 2001) and the rates saturated at 600 µmol/m^2/s photon flux density (PPFD) at ambient CO_2 concentration (~330 ppm) (Mortley *et al*. 1996, Ravi and Saravanan 2001). The rise in CO_2 concentration of the atmosphere is an important change which can effectively influence the productivity of the crop plants. CO_2 can affect plant function mainly through its direct effect on photosynthesis and stomatal physiology. C_3 plants respond to eCO_2 significantly. This is because, first, the photosynthetic enzyme Ribulose biphosphate carboxylase (Rubisco) has a low affinity for CO_2 on carboxylation and this reaction is not saturated at the current CO_2 concentration. Therefore, the carboxylation of Rubisco will respond to rising CO_2. Second, because photorespiration (*Pr*) decreases the net efficiency of photosynthesis by 20-50% depending on temperature, and rising CO_2 50% reduces the oxygenase (photorespiration) reaction of Ribulose Biphosphate Carboxylase/Oxygenase (Rubisco) enzyme as CO_2 competes with O_2 (Lawlor and Mitchell 2000). The photosynthetic rates of C_3 plants were approximately doubled when plants were exposed to 700 when compared to 380 ppm (Ainsworth and Long 2005). Although, sweet potato being a C_3 plant has the advantage of responding positively to an increase in atmospheric CO_2, limited studies have been conducted under controlled conditions on the photosynthetic response of sweet potato to CO_2 concentrations. Under controlled conditions, sweet potato photosynthetic rate increased due to increase in *Ci* from 250 to 560 ppm and the response was temperature dependant (Cen and Sage 2005). The *Pn* increased at the rate of 0.056 µmol $CO_2/m^2/s$ per 1 ppm rise in CO_2 at 34°C and at the rate of 0.048 µmol $CO_2/m^2/s$ per 1 ppm rise in CO_2 at 38°C. Sweet potato tuber yield per plant increased significantly (41.3 g/plant) due to rise in CO_2 concentration from 363 ppm to 514 but further rise in CO_2 did not significantly increase tuber yield. Under high photon flux density (PPFD), leaf carboxylation rate is linked with the availability of CO_2 and increasing CO_2 concentration positively influences the *Pn* and yield. In potato, tuber yield increased up to 1000 ppm (Wheeler *et al*. 1994). Yields of many crops (wheat, rice, maize, soybean, cotton, castor bean, vegetable crops) have significantly increased at eCO_2 concentrations (Reddy and Hodges 2000, Prasad *et al*. 2005, Chowdhury *et al*. 2005, De Souza *et al*. 2008, Vanaja *et al*. 2008, Razzaque *et al*. 2009, Singh and Jasrai 2012, O'Leary *et al*. 2015, Zhang *et al*. 2015). Sweet potato storage root yield has been reported to increase up to 750 ppm CO_2 (Mortley *et al*. 1996). Czeck *et al*. (2012) reported a significant increase in both above- and below-ground biomass at eCO_2 (1520 ppm) in sweet potato. The above-ground dry biomass increased by 43% for the organic source of nutrients and by 31% for the inorganic source of nutrients at eCO_2. The below-ground biomass increased by 61% in the organic treatment and 101% increase in the inorganic treatment, appreciably greater than the above-ground biomass, attributing the importance of root crops under high CO_2 environment. Understanding genotypic responses to eCO_2 is therefore essential to identify traits for breeding varieties for changing climate. The present paper reports the photosynthetic response of 12 field grown sweet potato genotypes to eCO_2 and PPFD.

MATERIALS AND METHODS

Twelve contrasting sweet potato genotypes, viz. Sree Kanaka, Sree Badhra, Sree Arun, Kanhangad, Pusa Safed, Pusa red, Kisan, Gouri, Sankar, ST-13, S-1464 and S-1466 were grown under irrigated conditions during June- August 2016 in the farm of ICAR-Central Tuber Crops Research Institute (CTCRI), Thiruvananthapuram. There were three replications and each replication had 10 plants. N: P_2O_5 and K_2O were applied @ 75:25:75 kg/ha as per the package of practices recommended by ICAR-CTCRI. Plants were grown under open sunlight conditions with ≈12 hours sun light per day under ≈1700 µ mol m^2/h at 30°C ± 2°C during day time and 23°C ± 1°C during night time. The diurnal changes of atmospheric CO_2 in the field indicated a dip from ~470 ppm at 6.00 AM to ~380 ppm at 12.00 AM and ~400 ppm at 4.0 PM.

The net photosynthetic rate (*Pn*), stomatal conductance (g_s) and sub-stomatal/intercellular CO_2 (*Ci*) under short-term exposure (10 minutes) to CO_2 concentrations, viz. 400, 600, 800, 1000 ppm at 30°C and 1500 µ mol m^2/h photosynthetic photon flux density (PPFD), and the *Pn* at different PPFDs, viz. 200, 400, 600, 800, 1000, 1200 and 1500 µ mol/m^2/h at 30°C and 400 ppm CO_2 were recorded in the leaves in the controlled-climate cuvette using a LI6400 portable photosynthesis system. The aforementioned parameters were recorded in the 5th to 10th leaf during 2nd month after planting. In the leaves the total chlorophyll content was estimated according to Lichtenthaller (1987) and the total protein content according to Bradford (1966). The data were statistically analysed using SAS/Software Version 9.3, SAS Institute Inc., Cary, NC, USA 2010.

RESULTS AND DISCUSSION

The Pn response to photosynthetic photon flux density

In the present study, the *Pn* was recorded in the leaves of 12 sweet potato genotypes during short-term (10 minutes) exposure to CO_2 concentrations, viz. 400, 600 800 and 1000 ppm at 30°C and 1500 µmol/m^2/s PPFD inside the controlled-climate cuvette in a portable photosynthesis system. The *Pn* of 12 sweet potato genotypes steadily increased due to increase in PPFD from 200 to 1500 µmol/m^2/s (Fig 1). The differences in *Pn* among 12 sweet potato genotypes were statistically significant across varieties and PPFDs (P<0.001). However, the interaction effect of genotypes and PPFDs on *Pn* was insignificant. Although maximum *Pn* of 12 sweet potato genotypes was recorded at PPFD of 1500 µmol/m^2/s, the increase in *Pn* at PPFDs above 1000 µmol/m^2/s were insignificant.

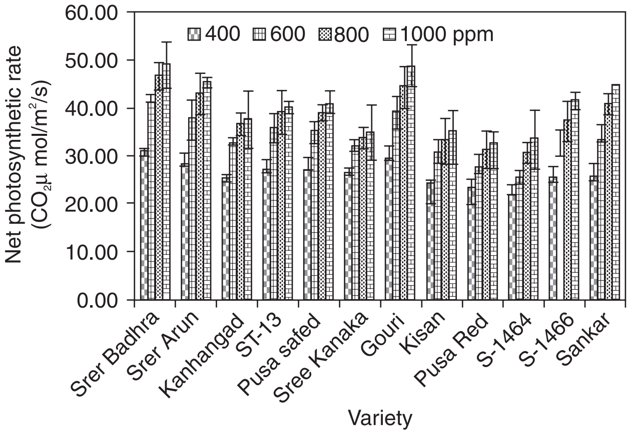

Fig 1 Changes in net photosynthetic rate under different CO_2 concentrations. The error bars indicate St. Dev.

The Pn response to eCO_2

The *Pn* steadily increased due to increase in CO_2 concentration from 400 ppm to 1000 ppm in the leaves of 12 sweet potato genotypes studied (Fig 2). At 400 ppm CO_2, *Pn* varied from 21.77 µmol/m^2/s in the genotype S-1464 to 30.98 µmol/m^2/s in the genotype Sree Badhra. At 600 ppm CO_2, *Pn* varied from 25.53 µmol/m^2/s in the genotype S-1464 to 41.01 µmol/m^2/s in the genotype Sree Badhra. At 800 ppm CO_2, *Pn* varied from 30.73 µmol/m^2/s in the genotype S-1464 to 46.76 µmol/m^2/s in the genotype Sree Badhra. At 1000 ppm CO_2, *Pn* varied from 32.40 µ mol/m^2/s in the genotype Pusa Red to 48.95 µmol/m^2/s in the genotype Sree Badhra. The per cent of increment in *Pn* at 600 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (17.20%) in the variety Pusa Red and the genotype S-1464 and the maximum in the genotype Sree Arun (33.70%). The per cent of increment in *Pn* at 800 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (27.00%) in the genotype Sree Kanaka and the maximum in the genotype Sankar (59.40%). The per cent of increment in *Pn* at 1000 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (31.10%) in the genotype Sree Kanaka and the maximum in the genotype Sankar (74.30%). In the present study, the average *Pn* of 12 sweet potato genotypes increased by 53.85% at 1000 ppm CO_2 as compared to 400 ppm CO_2.

The differences in *Pn* were statistically significant across sweet potato genotypes and CO_2 concentrations (P>0.001). However, the interaction effect of genotypes and CO_2 concentrations on *Pn* was insignificant, whereas the *Pn* had a quadratic relation with the increase in CO_2 concentration (R^2=0.603) (Fig. 3). ECO_2 increased the *Pn* by ~54% in rice and ~33% in soybean at 700 ppm as compared to 350 ppm CO_2 (Vu *et al*. 1997), by 45% in sunflower at 700 ppm as compared to 350% (Tezara *et al*. 2002), by ~48% at 800 ppm as compared to 400 ppm in C_3 plants (Allen and Prasad 2004), by 66% in soybean at 1000 ppm as compared to 400 ppm CO_2 (Prasad *et al*. 2005), by 22 and 9% at 700 and 450 ppm as compared to 350 ppm CO_2 in cotton (Reddy *et al*. 2005), by 30-60% at 720 ppm as compared to 370 ppm CO_2 in sugarcane (de Souza *et al*. 2008), by ~70% at 550 ppm as compared to 370 ppm CO_2 in chickpea (Madan Pal and Sangeeta 2009). Compared to 389±40 ppm CO_2, eCO_2 increased the *Pn* by 11.7% at 550 ±60 ppm in mung bean leaf (Hao *et al*. 2011). The *Pn* significantly increased by 78% and 30% at 700 and 550 ppm CO_2 as compared to 390 ppm CO_2 in black gram under long-term exposure (Sathish *et al*. 2014). Compared to 380 ppm CO_2, eCO_2 significantly increased the net photosynthetic rate at 700 ppm in sunflower leaf under long-term exposure (Vanaja *et al*. 2011). In oats (*Avena sativa*), *Pn* significantly increased by 21-61% under long-term exposure to 600±50 ppm CO_2 as compared to 360 ppm CO_2 (Bhatt *et al*. 2010). In rice (*Oryza sativa*) the *Pn* was significantly enhanced by 53-66% at eCO_2 (660 ppm) CO_2 as compared to 330 ppm. Similarly, the *Pn* was significantly enhanced by 48-94% under long term exposure to eCO_2 700 ppm CO_2 as compared to 350 ppm in soybean (Vu *et al*. 1997). The *Pn* significantly increased in maize under long-term exposure to eCO_2 at 450 and 550 ppm CO_2 as compared to 390 ppm (Meng *et al*. 2014). Long-term exposure to eCO_2 (570±50 ppm CO_2) increased the *Pn* by 24.2 and 25.4% compared with ambient CO_2 (~360 ppm CO_2) and field grown rice plants (Razzaque *et al*. 2009). Long-term exposure to eCO_2 increased the *Pn* during flowering by 46 and 104%, while that during pod maturation by 23 and 14% than that in ambient CO_2 and field conditions, respectively in mung

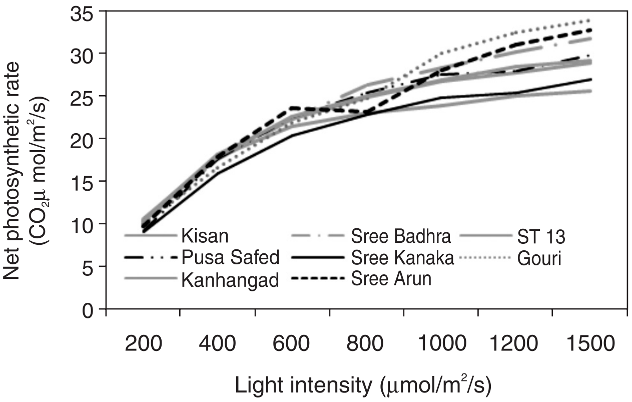

Fig 2 Changes in net photosynthetic rate under different PPFD

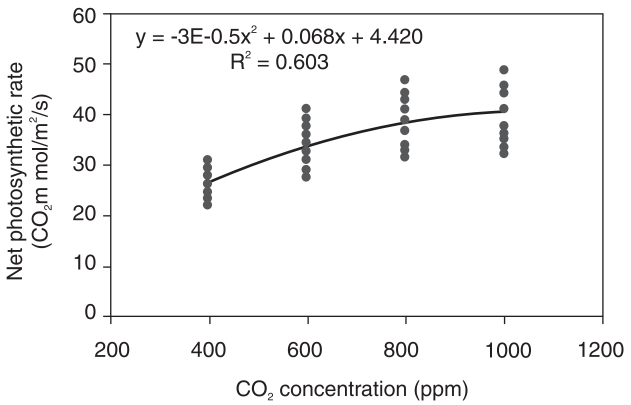

Fig 3 Statistical relation between the net photosynthetic rate and CO_2 concentration.

bean plants (Chowdhury *et al*. 2005). Long term exposure to eCO_2 (550 ppm) significantly enhanced photosynthetic rate in rice as compared to 370 ppm (Sujatha *et al*. 2008). The *Pn* of wheat leaves had 31% enhancement under long-term exposure to 550 ppm CO_2 than at 380 ppm (Nie *et al*. 1995). In the case of soybean, CO_2 enrichment between 550 and 700 ppm increased photosynthesis by up to ~30% (Bernacchi *et al*. 2005, Prior *et al*. 2011). Photosynthesis under eCO_2 (700 ppm) increased by 50, 60 and 78% under short term (>1 week) exposure and by 14, 13 and 42% under long term exposure in barley, cotton and soybean respectively (Ratnakumar *et al*. 2011).

In the present study, the per cent increment in *Pn* in the leaves of twelve sweet potato genotypes steadily declined with an increase in CO_2 concentration between 600 ppm to 1000 ppm. The per cent of increment in the *Pn* at 600 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (17.20%) in the genotypes Pusa Red and S-1464 and the maximum in the genotype Sree Arun (33.70%). The per cent of increment in *Pn* at 800 ppm CO_2 as compared to 600 ppm CO_2 declined to the minimum (5.44%) in the genotype Sree Kanaka and the maximum in the genotype Sankar (22.59%). The per cent of increment in *Pn* at 1000 ppm CO_2 as compared to 800 ppm CO_2 was negligible and varied from the minimum (1.94%) in the genotype Kanhangad to the maximum in the genotype S-1466 (11.62%). The canopy photosynthesis of cotton plants gradually increase with increase in CO_2 above 350 ppm and reached maximum at 700 ppm and there was no further increase at 900 ppm (Reddy *et al*. 2005). Similarly, the canopy photosynthetic rates increased with increasing CO_2 from 160 to 500 ppm, but saturated at 500 ppm in rice (Baker *et al*. 1990). The decrease in increment of *Pn* at short-term exposure to eCO_2 is attributed to the factors such as decline in electron transport capacity, capacity of *Pi*-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). Furthermore, unlike the decline in *Pn* due to limitations in sink activity and decline in Rubisco activity under long-term exposure to eCO_2 reported in other crops, the decline in increment of photosynthetic rate recorded under eCO_2 in the present study is not attributed to acclimation as the source and sink are simultaneously active in sweet potato. The total chlorophyll content in the leaves of 12 sweet potato genotypes varied from the minimum (3.18 mg/g fresh leaf) in the genotype S-1464 to the maximum (25.64 mg/g fresh leaf) in the genotype Pusa Red. The differences in the total chlorophyll content in the leaves of sweet potato genotypes were statistically significant. Nevertheless, the *Pn* had no definite correlation with the total chlorophyll content. Some studies reported that the long-term exposure of leaves to eCO_2 had decreased or increased or had no effect on the total chlorophyll content (Bhatt *et al*. 2010, Singh and Jasrai 2012).

The g_s response to eCO_2

The g_s in the leaves of 12 sweet potato genotypes steadily decreased due to an increase in CO_2 concentration from 400 ppm to 1000 ppm (Fig 4). At 400 ppm CO_2, g_{sw} varied from the minimum 0.425 mol $H_2O/m^2/s$ in the genotype Kanhangad to a maximum 0.967 mol $H_2O/m^2/s$ in the genotype Kisan. At 600 ppm CO_2, g_s varied from the minimum 0.268 mol $H_2O/m^2/s$ in the genotype Sankar to the maximum 0.899 mol $H_2O/m^2/s$ in the genotype Kisan. At 800 ppm CO_2, g_s varied from the minimum 0.233 mol $H_2O/m^2/s$ in the genotype Sankar to a maximum 0.893 mol $H_2O/m^2/s$ in the genotype Kisan. At 1000 ppm CO_2, g_s varied from the minimum 0.203 mol $H_2O/m^2/s$ in the genotype S-1466 to a maximum 0.591 mol $H_2O/m^2/s$ in the genotype Kisan. The per cent of decrease in g_s at 600 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (1.70%) in the genotype Sree Badhra and the maximum in the genotype Sankar (39.81%). The per cent of decrease in g_s at 800 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (8.52%) in the genotype S-1464 and the maximum in the genotype Sankar (47.59%). The per cent of decrease in g_s at 1000 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (11.39%) in the genotype S-1464 and the maximum in the genotype S-1466 (56.90%). The per cent of decrease in g_s at 600 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (1.70%) in the genotype Sree Badhra and the maximum in the genotype Sankar (39.81%). The per cent of decrease in g_s at 800 ppm CO_2 as compared to 600 ppm CO_2 was greater in genotypes Sree Badhra, Sree Arun, Gouri and Kisan (5.43% to 22.90%). The per cent of decrease in g_s at 1000 ppm CO_2 as compared to 800 ppm CO_2 was lesser and varied from the minimum (3.14%) in the genotype S-1464 to the maximum in the genotype Kanhangad (16.45%) except the genotypes Sree Kanaka and ST-13. The differences in g_s were statistically significant across sweet potato genotypes and CO_2 concentrations (P>0.001). However, the interaction effect of genotypes and CO_2 concentration on g_s is insignificant. Many studies reported a decrease in stomatal conductance (g_s) under eCO_2. During the short term exposure to eCO_2, stomatal aperture generally decreases in response to high CO_2

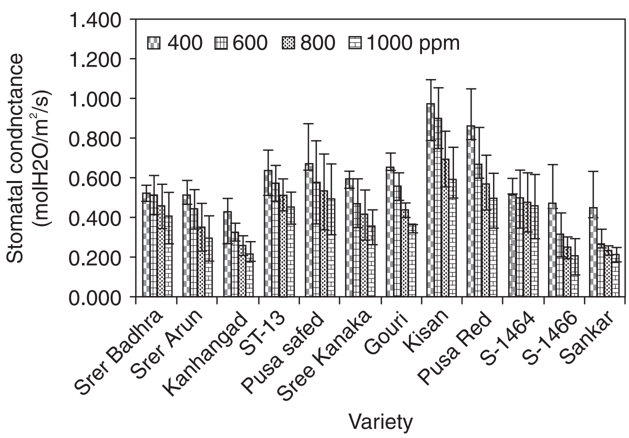

Fig 4 Changes in the stomatal conductance under different CO2 concentrations. The error bars indicate St. Dev.

due to depolarization of the membrane potential of guard cells and stomatal closure (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. In a recent review, g_s has been reported to be reduced by 21-50% at eCO_2 across plant species (Xu *et al*. 2016). The g_s decreased by 32% in cotton leaves under long term exposure to eCO_2 (65 Pa CO_2) than at 35 Pa CO_2 (Harley *et al*. 1992). The g_s decreased by 31% at 450-550 ppm CO_2, 36% at 600-800 ppm CO_2 and 51% at > 850 CO_2 with respect to 330-360 CO_2 in soybean (Ainsworth *et al*. 2002). The g_s decreased, on average, by 37% in eCO_2 at 720 ppm as compared to 370 ppm in sugarcane (De Souza *et al*. 2008). ECO_2 (700 ppm) decreased the g_s of individual leaves by 43% at 26°C, 45% at 31°C, and 20% at 36°C as compared to 350 ppm in cotton (Reddy *et al*. 2005). In the leaves of sunflower, the g_s decreased by ~50% at 700 ppm as compared to 350 ppm CO_2 (Tezara *et al*. 2002). Compared to 389±40 ppm CO_2, eCO_2 decreased g_s by 32% at 550±60 ppm in greengram leaf (Hao *et al*. 2011). The g_s significantly decreased in sunflower at 700 ppm CO_2 as compared to 380 ppm (Vanaja *et al*. 2011). In the leaves of *Arabidopsis thaliana* grown in ambient CO_2 (350 ppm) and measured at 700 ppm, the g_s decreased by ~25% as compared to 350 ppm because of partial stomatal closure CO_2 (Teng *et al*. 2006). In the leaves of *Arabidopsis thaliana* grown in eCO_2 (700 ppm) the g_s decreased by ~25% at 700 ppm as compared to 350 ppm CO_2 because of 19 and 14% decrease in stomatal density (SD) on the adaxial and abaxial surfaces of leaves and 12 and 9% decrease in stomatal index (SI) on the adaxial and abaxial surfaces of leaves (Teng *et al*. 2006). In the present study, sweet potato plants were grown in ambient CO_2 (400 ppm) and therefore the decrease in g_s in sweet potato leaves during short term measurements at eCO_2 (600, 800 and 1000 ppm) as compared to 400 ppm is attributed to partial closure of stomata and not due to a decrease in SD and the SI.

The Ci response to eCO₂

The *Ci* in the leaves of 12 sweet potato genotypes steadily increased due to an increase in CO_2 concentration from 400 ppm to 1000 ppm. At 400 ppm CO_2, *Ci* varied from 192.40 μmol CO_2/mol air in the genotype S-1466 to 294.10 μmol CO_2/mol air in the genotype Pusa Safed. At 600 ppm CO_2, *Ci* varied from 290.50 μmol CO_2/mol air in the genotype S-1466 to 446.50 μmol CO_2/mol air in the genotype Pusa Red. At 800 ppm CO_2, *Ci* varied from 367.60 μmol CO_2/mol air in the genotype S-1466 to 611.30 μmol CO_2/mol air in the genotype ST-13. At 1000 ppm CO_2, *Ci* varied from 437.90 μmol CO_2/mol air in the genotype S-1466 to 781.80 μmol CO_2/mol air in the genotype ST-13. In the present study, although, the g_s significantly decreased at eCO_2 levels between 600 and 1000 ppm, the decline in the increment of net photosynthetic rate due to increase in CO_2 resulted in high intercellular CO_2 concentrations which in turn sustained greater net photosynthetic rates at these eCO_2 as compared to 400 ppm CO_2. Several studies reported greater *Ci* at eCO_2 levels. Compared to 389±40 ppm CO_2, eCO_2 increased the Ci by 9.8% at 550 ±60 ppm in greengram leaf (Hao *et al*. 2011). The per cent of increment in *Ci* at 600 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (44.10%) in the genotype Pusa Red and the maximum (68.40%) in the genotype S-1466. The per cent of increment in *Ci* at 800 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (71.40%) in the genotype Sankar and the maximum (133.10%) in the genotype S-1464. The per cent of increment in *Ci* at 1000 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (117.80%) in the genotype Sankar and the maximum (206.00%) in the genotype S-1464. The per cent of increment in *Ci* at 600 ppm CO_2 as compared to 400 ppm CO_2, was the minimum (44.10%) in the genotype Pusa Red and the maximum (68.40%) in the genotype S-1466. The per cent of increment in *Ci* at 800 ppm CO_2 as compared to 600 ppm CO_2 declined to the minimum (26.50%) in the genotype S-1466 and the maximum (38.40%) in the genotype S-1464. The per cent of increment in *Ci* at 1000 ppm CO_2 as compared to 800 ppm CO_2 further declined to the minimum (19.1%) in the genotype S-1466 and the maximum (28.20%) in the genotype Pusa Red. Although eCO_2 significantly decreased the g_s, the eCO_2 was adequate to sustain the *Ci* at high levels which resulted in the decreased *Pr* and increased *Pn*. The differences in *Ci* were statistically significant across genotypes and CO_2 concentrations (P>0.001). However, the interaction effect of genotypes and CO_2 concentrations on *Ci* was insignificant. Statistically the net photosynthetic rate had a binomial relation with the *Ci* (R^2=0.504) (Fig 5) and is in agreement with Hikosaka *et al*. (2005).

The total protein content in the leaves of 12 sweet potato genotypes varied from the minimum (4.50mg/100mg fresh leaf) in the genotype Pusa Red to the maximum (8.75 mg/100g fresh leaf) in the genotype Sree Badhra. The differences in the total protein content in the leaves of sweet potato genotypes were statistically significant. Nevertheless, the *Pn* had no definite correlation with the total protein content. Several reports indicate that long term exposure to eCO_2 had decreased or increased or had no change on the soluble protein content in the leaves (Bhatt *et al*. 2010). Long-term exposure to eCO_2 reduced Rubisco content by

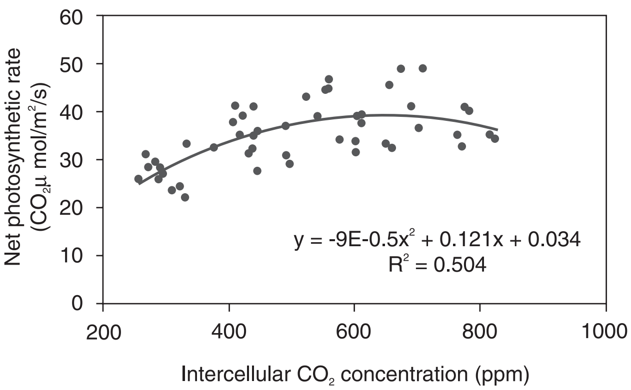

Fig 5 Statistical relation between net photosynthetic rate and intercellular CO_2 concentrations

22% in rice and 8% in soybean (Vu *et al*. 1997). Long term exposure to eCO_2 had no significant effect on Rubisco content in the leaves of *Chenopodium album*, *Phaseolus vulgaris*, *Solanum tuberosum*, *Solanum melongena*, and *Brassica oleracea* (Sage *et al*. 1989). Long-term growth of *Arabidopsis* at high CO_2 (1000 ppm) resulted in a ~35–40% decrease in the expression of Rubisco protein and in the transcript of *rbcL*, the gene encoding the large subunit of Rubisco, and 60% decline in mRNA of *rbcS*, the gene encoding the small subunit of Rubisco (Cheng *et al*. 1998).

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