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National Academy of Agricultural Science (NAAS) Rating : 3.03

Response of photosynthetic pigments and stomatal parameters of Bamboo seedlings to elevated carbon dioxide concentration

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ABSTRACT: *The photosynthetic pigments and stomatal parameters of bamboo seedlings viz. Bambusa tulda, B. nutans, B. balcooa and Dendrocalamus hamiltonii were evaluated under elevated carbon dioxide concentration inside OTC during 2012-13. The results revealed that the chlorophyll-a content, chlorophyll-b content, total chlorophyll content, chlorophyll a:b ratio, chlorophyll stability index, carotenoid content, photosynthetic rate and total dry weight of bamboo seedlings were significantly increased but stomatal frequency, stomatal index and stomatal pore area were significantly decreased with the increase in atmospheric* CO_2 *concentration from 380 ppm to 750 ppm in all four bamboo species tested. During the study the D. hamiltonii was found to be the best performer while B. tulda produced the poorest performance. The interaction effect of* CO_2 *concentration and bamboo species were also found significant during the study.*

Key words: *Chlorophyll content, Dendrocalamus hamiltonii, photosynthetic rate and stomatal frequency*

Carbon dioxide in the atmosphere has been increasing steadily since pre-industrial times from 280 ppm to 395 ppm in 2013 (Annonymous, 3013) and according to IPCC it may reach 550-750 ppm in 2050 (Anonymous, 2007). The recent trend of climate change is considered to be primarily because of increasing atmospheric CO_2 concentration. Therefore, screening out of a crop plant that performs better in such CO_2 enrichment and thus can trap more CO_2 from the atmosphere may provide useful information for an effective climate mitigation strategy. Efforts to thoroughly study the role of plants in climate change mitigation are increasing and it is obvious that bigger the plant, the more CO_2 it absorbs. Bamboo is known for its high ability to capture and sequester atmospheric carbon in a similar way that trees do (Lou *et al.*, 2010). Bamboos as C_3 plants have the potentiality to increase net primary productivity at CO_2 enriched atmosphere (Korner *et al.*, 2007). The bamboo (*Fargesia rufa* Yi) significantly increases the net photosynthetic rate, carbohydrates content like sucrose, sugar, starch and non-structural carbohydrates and decreases stomatal conductance at CO, environment (Li *et al.*, 2013).Therefore, the present study was carried out to evaluate the variation in photosynthetic pigments and stomatal parameters in seedlings of four most important bamboo species at elevated level of carbon dioxide concentration.

MATERIALS AND METHODS

The study was conducted during 2012-13 in Open Top Chamber (OTC) of Assam Agricultural University, Jorhat, Assam. The experimental design was FCRD with three replications. Four concentrations of CO_2 were selected *viz.* C_1: Ambient, C_2: 380 ppm, C_3: 550 ppm and C_4: 750 ppm. The average atmospheric CO_2 concentration at the experimental site was 380 ppm and based on IPCC prediction the CO_2 concentrations were maintained at 380, 550 and 750 ppm inside the OTC. One year old uniform sized bamboo seedlings of *Bambusa tulda* (S_1), *B. nutans* (S_2), *B. balcooa* (S_3) and *Dendrocalamus hamiltonii* (S_4) were collected from the Rain Forest Research Institute, Jorhat and planted in earthen pots (Choudhury *et al.*, 2015). On 1st August, 2012 seedlings were grouped into four sets containing three randomly selected seedlings of each species to get twelve seedlings per set. One set of seedlings was kept in an open place and considered as C_1 (ambient)

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seedlings. Likewise other three sets were kept inside three different OTCs and were considered as C_2, C_3 and C_4 seedlings. The concentrations of CO_2 in OTCs were maintained accordingly through out the period of study (six months) with computerized control unit of OTC. The evaluations were made after six month of treatment exposure in second week of January, 2013. Observation were taken at ten representative third leaves from the tip of main stem or branches of each bamboo seedling and the average values were recorded. Parameters were evaluated following standard methods *viz.* Chlorophyll content (Hiscox and Israelstam, 1979), CSI (Chetty *et al.*, 2002) carotenoid content (Hartmut and Claus, 2001), stomatal frequency & stomatal index (Royer, 2001) and stomatal pore area (Pompelli *et al.*, 2010).The photosynthetic rates of bamboo leaf were measured with the help of Portable Photosynthetic System, Model PP System 2, USA. The seedlings were carefully uprooted on 19th January, 2013 washed repeatedly to remove all debris and were then oven dried at 70°C till the constant weight and then their weights were measured with electronic balance and the average value was considered as the dry weight of a seedling.

RESULTS AND DISCUSSION

The result revealed that at the onset of expiriment CO_2 concentration produced no significant effect on seedling height and seedling girth of bamboo species however, they varied significantly in different species (Table 1). The S_1 (*Bambusa tulda*) maintained the tallest seedling followed by S_4 *(Dendrocalamus hamiltonii)* and S_2 (*Bambusa nutans*) and the shortest seedlings were found in S_3 (*Bambusa balcooa*). The seedling girth was highest in S_4 followed by S_3 and S_2 and it was lowest in S_1. Likewise, there was a gradual but significant increment in chlorophyll-a, chlorophyll-b, total chlorophyll and carotenoid content while reduction in chlorophyll a:b ratio in leaf of bamboo seedlings with the increase in CO_2 concentration from 380 ppm to 750 ppm in all four bamboo species tested. The highest chlorophyll-a (2.12 mgg^{-1} fw), chlorophyll-b (1.13 mgg^{-1} fw), total chlorophyll content (3.25 mgg^{-1} fw) and carotenoid content (0.5506 mgg^{-1} fw) of bamboo leaf were found at 750 ppm CO_2 concentration followed by 550 ppm. On the other hand the lowest chlorophyll-a (1.77 mgg^{-1} fw), chlorophyll-b (0.82 mgg^{-1} fw), total chlorophyll content (2.59 mgg^{-1} fw) and carotenoid content (0.5081mgg^{-1} fw) were recorded at 380 ppm CO_2 concentration followed by control. Among the species, S_4 maintained significant superiority in terms of chlorophyll-a, chlorophyll-b, total chlorophyll and carotenoid content of leaf over other three species at all the concentration of CO_2. At 750 ppm CO_2 concentration S_4 maintained the highest chlorophyll-a (2.34 mgg^{-1} fw), chlorophyll-b (1.20 mgg^{-1} fw), total chlorophyll (3.54 mgg^{-1} fw) and carotenoid (0.5706 mgg^{-1} fw) content followed by S_3, S_2 while S_1 maintained the lowest chlorophyll-a (1.93 mgg^{-1} fw), chlorophyll-b (1.08 mgg^{-1} fw), total chlorophyll content (3.01 mgg^{-1} fw) and carotenoid (0.5349 mgg^{-1} fw) content at the same CO_2 concentration. The highest chlorophyll a:b ratio of bamboo leaf (2.41) was found in control seedling followed by 380 ppm (2.15), 750 ppm (1.88) and the lowest chlorophyll a:b ratio (1.86) was found at 550 ppm CO_2 concentration. Among the species S_4 maintained the significant superiority over other bamboo species with highest chlorophyll a:b ratio (2.53) in leaf at control.

Similarly, the higher photosynthetic rates were recorded in bamboo seedlings exposed to CO_2 enrichment (Table 2). The observed higher photosynthetic pigments content in bamboo exposed to CO_2 enrichment could be due to internal adjustment of the photosynthetic tissues to trap more CO_2 from the external environment to keep the photosynthetic rate higher at such modified environment. Again, higher chlorophyll a:b ratio might help the S_4 species to maintain superiority over other species by carrying out photosynthesis and dry matter accumulation more efficiently, as the higher ratio indicates relatively more primary photosynthetic pigment (chlorophyll-a) than secondary pigments (chlorophyll-b and others). Again, the chlorophyll synthesising genes might be activated by CO_2 enrichment to keep pace with the increased level of photosynthetic rate. Being a C_3 plant, the rate of photosynthesis in bamboo increases with the increase in CO_2 concentration and to support this higher rate the synthesis of photosynthetic pigments might also increase. Carotenoid might support to harness maximum light energy to convert more amount of CO_2 in to sugar in CO_2 rich environment. The higher carotenoid content might also help to protect the photosynthetic apparatus from photo-oxidation and thereby increased the observed rate of photosynthesis. Li *et al*. (2013) also registered higher chlorophyll content in dwarf bamboo (*Fargesia rufa* Yi) exposed to elevated CO_2 concentration. Many earlier workers reported that because of the physiological adustment like higher photosynthetic rates, carbon gain and water relations specially in CO_2 enriched environment bamboo could perform dominant role in global climate change mitigation strategies (Davina *et al.*, 2013 and Grombone-Guaratini *et al.*, 2013).

The highest 41.01% chlorophyll stability index (CSI) was found in bamboo seedling grown in open condition (control). Although, inside the OTC, the CSI significantly increased with the increase in CO_2 concentration from 380 ppm to 750 ppm in all four bamboo species (Table 1). So, the highest 40.77% CSI was recorded with 750 ppm followed by 550 ppm (40.18%) and the lowest CSI (39.33%) was recorded at 380 ppm. A significant interaction effect of CO_2 concentration and species was also recorded. During the investigation 10-15% less light intensity was observed inside the OTC than outside open areas. Therefore, seedlings grown in OTC received less light intensities compared to seedlings grown in open field (control). Probably for this reason, seedlings inside OTC were relatively tender, susceptible to heat hence the CSI of such seedlings were found to be lower than seedlings grown under full sunlight (control).

The study also revealed that with the increase in CO_2 concentration there was significant reduction in stomatal parameters *viz.* stomatal frequency, stomatal index, pore area of single stomata and per cent pore area of bamboo leaf (Table 2). The higher number of stomata (263.15 mm^{-2}), stomatal index (17.77%), pore area of single stomata (680.81 μm^2) and per cent pore area of bamboo leaf (18.10%) were recorded at 380 ppm CO_2 and the values of these traits were lowest (203.01 mm^{-2}, 14.01%, 512.80 μm^2 and 10.54% respectively) at 750 ppm followed by 550 ppm CO_2 concentration with the average values of stomatal frequency (210.73 mm^{-2}), stomatal index (14.98%), pore area of single stomata (520.72 μm^2) and per cent pore area of bamboo leaf (11.10%). Among the species S_4 produced the highest number of stomata (301.27 mm^{-2}), stomatal index (21.97%), pore area of single stomata (806.85 μm^2) and stomatal pore area (24.31%) in bamboo leaf at 380 ppm CO_2. In contrast S_1 maintained the lowest number of stomata (181.19 mm^{-2}), stomatal index (11.65%), pore area of single stomata (417.14 μm^2) and stomatal pore area (7.56%) of bamboo leaf at 750 ppm CO_2. A significant interaction effect was also noticed in these aspects. This decrease in stomatal parameters of bamboo leaf at higher CO_2 concentration may help the plant to retain more water in leaf without hampering the gaseous exchange and

Table 1

Seedling height, girth, chlorophyll-a, chlorophyll-b, total chlorophyll content, Chl-a:Chl-b ratio, chlorophyll stability index (CSI) and carotenoid content in leaves of different bamboo seedlings at various CO_2 concentration levels

CO_2 Concentration	*Bamboo species*	*Seedling height and girth at the onset of treatments*		*Chl-a ($mgg^{-1}fw$)*	*Chl-b ($mgg^{-1}fw$)*	*Total Chl ($mgg^{-1}fw$)*	*Chl-a:Chl-b ratio*	*CSI (%)*	*Carotenoid ($mgg^{-1}fw$)*
		height (cm)	*girth (cm)*						
Control	S_1	130.67	3.02	1.77	0.75	2.52	2.36	41.65	0.5034
	S_2	95.37	3.22	1.83	0.77	2.60	2.38	43.19	0.5117
	S_3	56.42	4.51	1.85	0.78	2.63	2.37	41.57	0.5128
	S_4	126.87	5.27	2.05	0.81	2.86	2.53	37.62	0.5237
	Mean	**102.33**	**4.01**	**1.88**	**0.78**	**2.65**	**2.41**	**41.01**	**0.5129**
380 ppm	S_1	131.24	3.01	1.65	0.80	2.45	2.06	40.87	0.4995
	S_2	94.73	3.20	1.69	0.81	2.50	2.09	40.93	0.5016
	S_3	56.32	4.50	1.77	0.82	2.59	2.16	40.15	0.5119
	S_4	127.87	5.25	1.95	0.86	2.81	2.27	35.36	0.5193
	Mean	**102.54**	**3.99**	**1.77**	**0.82**	**2.59**	**2.15**	**39.33**	**0.5081**
550 ppm	S_1	129.73	3.04	1.88	1.06	2.94	1.77	41.05	0.5231
	S_2	96.86	3.29	1.95	1.08	3.03	1.81	42.33	0.5337
	S_3	54.73	4.60	2.11	1.10	3.21	1.92	40.87	0.5461
	S_4	126.96	5.14	2.27	1.18	3.45	1.92	36.45	0.5517
	Mean	**102.07**	**4.02**	**2.05**	**1.11**	**3.16**	**1.86**	**40.18**	**0.5387**
750 ppm	S_1	130.52	3.05	1.93	1.08	3.01	1.79	41.48	0.5349
	S_2	95.89	3.32	2.00	1.09	3.09	1.83	42.97	0.5382
	S_3	57.35	4.54	2.20	1.14	3.34	1.93	41.35	0.5588
	S_4	127.89	5.26	2.34	1.20	3.54	1.95	37.28	0.5706
	Mean	**102.91**	**4.04**	**2.12**	**1.13**	**3.25**	**1.88**	**40.77**	**0.5506**
CD 0.05	Conc.	NS	NS	0.03	0.01	0.04	0.03	0.24	0.0040
	Species	0.88	0.19	0.03	0.01	0.04	0.03	0.24	0.0040
	Interaction	NS	NS	0.07	0.02	0.08	0.05	0.49	0.0081
CD 0.01	Conc.	NS	NS	0.04	0.02	0.05	0.03	0.32	0.0053
	Species	1.16	0.25	0.04	0.02	0.05	0.03	0.32	0.0053
	Interaction	NS	NS	0.09	0.03	0.11	0.07	0.64	0.0106

Table 2
Stomatal frequency, stomatal index, stomatal pore area, photosynthetic rate and dry weight of bamboo seedlings at various CO_2 concentration levels

CO_2 Concentration	*Bamboo species*	*Stomatal frequency (No mm^{-2})*	*Stomatal index (%)*	*Stomatal pore area*		*Photosynthetic rate (µmole CO_2 $m^{-2}S^{-1}$)*	*Dry weight of seedling (kg)*
				Single stomata (µm^2)	*Per cent pore area*		
Control	S_1	229.33	14.74	597.28	13.70	12.85	0.2526
	S_2	243.67	15.36	643.52	15.68	13.06	0.2451
	S_3	261.53	17.29	650.27	17.01	15.35	0.4428
	S_4	296.48	21.21	796.31	23.61	17.21	0.4622
	Mean	**257.75**	**17.15**	**671.85**	**17.50**	**14.62**	**0.3507**
380 ppm	S_1	235.16	15.06	610.26	14.35	12.61	0.2254
	S_2	246.55	15.89	648.64	15.99	12.75	0.2084
	S_3	269.61	18.14	657.48	17.73	15.02	0.3752
	S_4	301.27	21.97	806.85	24.31	16.56	0.4059
	Mean	**263.15**	**17.77**	**680.81**	**18.10**	**14.24**	**0.3038**
550 ppm	S_1	187.42	12.28	434.15	8.14	13.21	0.4497
	S_2	198.29	13.14	501.23	9.94	14.33	0.4355
	S_3	211.37	15.21	549.16	11.61	16.05	0.7374
	S_4	245.83	19.29	598.35	14.71	18.39	0.7558
	Mean	**210.73**	**14.98**	**520.72**	**11.10**	**15.50**	**0.5946**
750 ppm	S_1	181.19	11.65	417.14	7.56	13.17	0.4800
	S_2	186.23	12.18	498.27	9.28	14.29	0.4696
	S_3	208.28	14.36	543.67	11.32	15.98	0.7527
	S_4	236.32	17.85	592.12	13.99	18.35	0.7716
	Mean	**203.01**	**14.01**	**512.80**	**10.54**	**15.45**	**0.6185**
CD 0.05	Conc.	2.33	0.13	18.19	0.85	0.22	0.0274
	Species	2.33	0.13	18.19	0.85	0.22	0.0274
	Interaction	4.67	0.25	36.37	1.70	0.44	0.0547
CD 0.01	Conc.	3.07	0.16	23.90	1.12	0.29	0.0360
	Species	3.07	0.16	23.90	1.12	0.29	0.0360
	Interaction	6.13	0.33	47.80	2.24	0.57	0.0719

photosynthetic rate. This suggests that whatever amount of CO_2 entered the leaf with partially open stomata at such elevated CO_2 concentrations was sufficient to keep the photosynthetic rate high. Therefore, the bamboo seedlings may opt to reduce water loss by partially closing the stomata because at that situation water may be the liming factor rather than CO_2. Grombone-Guaratini *et al.* (2013) ; Li *et al.* (2013) and Thokchom & Yadava (2015) also reported that high CO_2 concentration lowered stomatal conductance and increased water use efficiency of bamboo.

The photosynthetic rate of bamboo seedlings significantly increased when CO_2 concentration increased from 380 ppm to 550 ppm but beyond that (750 ppm) the photosynthetic rate reduced however, it was non-significant. The highest photosynthetic rate (15.50 µmole CO_2 m^{-2} S^{-1}) was noticed at 550 ppm CO_2 followed by 750 ppm (15.45µmole CO_2 m^{-2} S^{-1}) while the same was lowest (14.24 µmole CO_2 m^{-2} S^{-1}) at 380 ppm. Again S_4 maintained the highest photosynthetic rate (18.39 µmole CO_2 m^{-2} S^{-1}) at 550 ppm CO_2 concentration while the same was lowest in S_1 (13.21 µmole CO_2 m^{-2} S^{-1}). A significant interaction effect of CO_2 concentration and bamboo species was also noticed. The higher photosynthetic rate with CO_2 enrichment might be due to internal adjustment mechanism of photosynthesising tissues of bamboo leaf to trap more CO_2 from the modified external environment and to fix them photosynthetically at a faster rate. It is expected that being C_3 plants, the bamboo seedlings increased the rate of photosynthesis at elevated CO_2 concentration. Similarly, De Souza *et al.* (2008) found that sugarcane grown in OTC with 720 ppm CO_2 had 30% more photosynthesis, 17% more plant height, 40% more biomass accumulation and 29% more sucrose content compared to sugarcane grown with 370 ppm CO_2. Sugarcane grown at 720 ppm CO_2 showed up regulation of 22 genes. These genes were mainly related to photosynthesis and development of the plant like genes for PSI reaction centre subunit N, PSII protein K, G-6-P dehydrogenase, glutamate tRNA ligase, auxin independent growth promoter, sugar transporter (De Souza *et al.*, 2008).

The slight reduction in photosynthetic rate of bamboo leaf at 750 ppm CO_2 might be because of down regulation of photosynthetic genes due to feedback inhibition mechanism at such a higher CO_2 concentration which might not have achieved at 550 ppm CO_2 concentration. Pandurangam *et al.* (2006) also found that the content of main photosynthetic enzyme Rubisco was reduced in wheat leaf exposed to CO_2 enrichment (650 ± 50 ppm). Grombone-Guaratini *et al.* (2013), Korner *et al.* (2007), Li *et al.* (2013) and Zhihong *et al.* (2011) also observed that the net photosynthetic rate in bamboo increased with increased CO_2 concentrations. In our study the highest dry weight of bamboo seedling (0.6185 kg) was found at 750 ppm CO_2 concentration followed by 550 ppm (0.5946 kg) while the same was lowest (0.3038 kg) at 380 ppm CO_2. Again S_4 produced the heaviest bamboo seedlings (0.7716 kg) and S_2 produced the lightest seedlings (0.4696 kg) at 750 ppm. In earlier communication we reported that CO_2 enrichment increased the leaf weight, branch weight, main stem weight, rhizome weight and total above ground biomass of bamboo seedlings (Choudhury *et al.*, 2015). Therefore, with higher photosynthetic rate, efficient partitioning and accumulation of dry matter in the different parts of bamboo seedling finally led to the observed heavier seedlings with CO_2 enrichment. The *Dendrocalamus hamiltonii* is found to be the most prominent one among the species studied. The study finally, reveals a positive influence of CO_2 enrichment on photosynthetic pigments and stomatal parameters of bamboo seedlings. This positive respond of all four bamboo species to CO_2 enrichment certifies bamboo as an efficient crop plant that could be recommended for an effective climate mitigation strategy.

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