# Influence of Elevated $CO_2$ Concentration on Photosynthesis and Biomass Yields in a Tree Species, *Gmelina Arborea* Roxb

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**Abstract**: The present study dissects out the $CO_2$ fertilization effects on photosynthetic gas exchange characteristics, key responses of photosynthetic and carbohydrate metabolizing enzymes and overall plant growth performance in a fast growing tree species, *Gmelina arborea* Roxb (*Verbenaceae*). The main objective of this investigation was to unravel and evaluate the role of elevated $CO_2$ on tree photosynthesis and productivity. *Gmelina* plants were grown under ambient (360 μmol $mol^{-1}$) and $CO_2$-enriched conditions (460 μmol $mol^{-1}$) in open top chambers for two marked growth seasons, subsequently for three years. The leaf gas exchange characteristics and associated biochemical measurements were carried out at regular intervals. *Gmelina* plants were harvested and growth parameters were measured at the end of two growth seasons for three consecutive years. *Gmelina* plants significantly responded to $CO_2$ enrichment. *Gmelina* plants grown under elevated $CO_2$ showed 52% more plant biomass compared with those grown under ambient $CO_2$. We conclude that fast growing tree species like *Gmelina,* exhibiting high $CO_2$-mediated photosynthetic up-regulation, can be used as potential tree species for efficient carbon sequestration under predicted future climate change scenario.

**Keyword:** Biomass yields ; Elevated $CO_2$ ;*Gmelina arborea*; Photosynthesis

## Introduction

Atmospheric $CO_2$ is rising rapidly and the options for slowing the $CO_2$ largely require reductions in industrial $CO_2$ emissions or through efficient carbon sequestration. Forests cover ~43% of the earth's surface, account for some 70% of terrestrial net primary production (NPP) and are being bartered for carbon mitigation. In this scenario, it is critically important to study the impact of elevated atmospheric $CO_2$ on growth and productivity of forest tree species (Prentice *et al*., 2001; IPCC, 2007). The exponential increase of $CO_2$ in the atmosphere should theoretically stimulate photosynthesis due to enhanced rubisco carboxylation, leading to efficient $CO_2$ sequestration (Long *et al*., 2004). However, many plant species grown at elevated $CO_2$ exhibit an acclimatory down regulation associated with decreased photosynthetic potential (Davey *et al*., 2006). The objective of our study was to address the photosynthetic productivity in *Gmelina arborea,* a fast growing economically important tropical forest tree species during the marked growth seasons under $CO_2$-enriched atmosphere. We were specifically interested to investigate the physiological and biochemical changes associated with photosynthesis as well as to understand the role of key enzymes of photosynthetic carbon metabolism in this tree species grown under high $CO_2$ environment.

## Materials and Methods

*Gmelina* plants were grown for two marked growth seasons subsequently for three years (2006 to 2008) under ambient (360 μmol $mol^{-1}$) and $CO_2$-enriched (460 μmol $mol^{-1}$) atmosphere in open top chambers. Leaf gas exchange characteristics and associated biochemical measurements were carried

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out at regular intervals. The rate of leaf gas exchange was measured using a portable infrared $CO_2/H_2O$ gas analyzer (IRGA) (LC Pro+, ADC Bioscientific Ltd. U.K.) equipped with a broad leaf chamber. The gas analyzer was used to measure instantaneous net photosynthetic rates ($P_n$; μmol $m^{-2}$ $s^{-1}$), stomatal conductance to $CO_2$ ($g_s$; mol $m^{-2}$ $s^{-1}$) and transpiration rates ($E$; mmol $m^{-2}$ $s^{-1}$) periodically during each growing season between 10:00–11:00 h solar time. Instantaneous water use efficiency ($WUEi = P_n/E$ mmol $CO_2$ $mol^{-1}$ $H_2O$) was also calculated. Extraction of RuBPcase and its activity measurements were performed according to Cheng and Fuchigami (2000). The activity of carbonic anhydrase (CA) in the leaf extracts was determined by following the time-dependent decrease in pH from 8.3 to 7.3 according to Wilbur and Anderson (1948). FBPase (Zimmerman *et al.*, 1978), SPsynthase (Huber, 1981), Hexokinase (Martinez-Barajas and Randall, 1998) and Sedheptulose 1,7 bisphosphatase (Lanzetta *et al.*, 1979) activities were determined according to standard protocols. In each year, all the plants in ambient and elevated OTC's were harvested to obtain growth and yield measurements at the end of two growing seasons.

## Results and Discussion

$CO_2$ enrichment had a profound influence on the gas exchange physiology of young *Gmelina* when compared to its counterparts grown at ambient $CO_2$ concentration. The $P_n$ of *Gmelina* grown under high $CO_2$ atmosphere showed a significant increase in $P_n$ ($p < 0.05$) of ~32% compared to ambient $CO_2$-grown plants. In anomaly to $P_n$, the *gs* and *E* showed a decreasing trend in the plants under high $CO_2$. Young *Gmelina* plants showed a significant upsurge in *Pn* in the interim enriched $CO_2$ exposure. Increased $CO_2$ concentrations can boast the rates of carboxylation sites of rubisco and concomitantly increase the *Pn* of $C_3$ plants. A time dependent photosynthetic down regulation under elevated $CO_2$ has also been observed in many plants, on account of diffusion limitation of $CO_2$, internal $CO_2$ concentration (*Ci*), availability of the light and sink capacity for photosynthates resulting in curtailment of dark reaction capacity in processing $CO_2$ (Norby *et al.*, 2001; Oren *et al.*, 2001; Ainsworth *et al.*, 2004). The relationship between the $P_n$ and *Ci* for the ambient and elevated $CO_2$ grown plants were shown in Fig. 1A. Elevated $CO_2$ atmosphere induced a positive correlation between *Pn* and *Ci* ($r^2 = 0.71$; $p < 0.001$); however, the correlation between *Pn* and *Ci* under ambient conditions was comparatively weak ($r^2 = 0.46$; $p < 0.10$). The relationship between *gs* and *Ci* showed positive correlation under ambient conditions ($r^2 = 0.41$ $p < 0.10$), where as the correlation was found to be negative in plants grown under elevated $CO_2$ ($r^2 = –0.65$ $p < 0.001$) (Fig. 1B). The $CO_2$ exchange between the plants and its atmosphere mainly occurs through the stomata and *gs* is one of the major limitations in carbon assimilation, particularly when plants are grown under elevated $CO_2$ (Jensen, 2000; Anderson *et al.*, 2001; Beedlow *et al.*, 2004; Ainsworth and Rogers, 2007). A down drop in the *gs* was observed under high $CO_2$ atmosphere mainly due to escalation in the *Ci* as the stomata respond to *Ci* through the guard cells (Paoletti and Grulke, 2005). The decrease in the *gs* had no effect on the *Pn* in young *Gmelina*. The subsidence in photosynthetic acclimation despite the decrement in *gs* was believed to be due to accelerated internal photosynthetic activity as the stomata were found to limit the *Pn* particularly when *Ci* is saturating (Farquhar and Sharkey, 1982; Noormets *et al.*, 2001; Sage, 2002; Herrick *et al.*, 2004; Paoletti and Grulke, 2005).

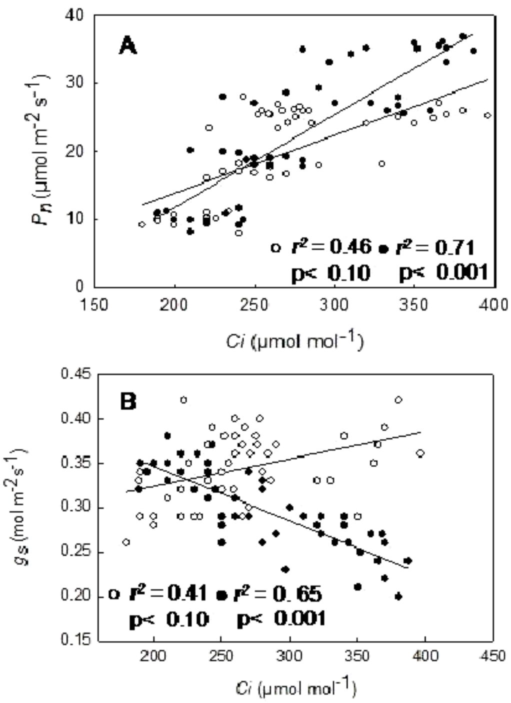


**Fig. 1** Relationship between photosynthetic rates ($P_n$) and internal $CO_2$ concentration (*Ci*) (A), between stomatal conductance (*gs*) and internal $CO_2$ concentration (*Ci*) (B) in young *Gmelina arborea* grown under ambient and elevated $CO_2$ concentrations (○ ambient; ● elevated).

Changes in biochemical indices were recorded at regular intervals during 120 days of exposure to elevated $CO_2$. Initial and total rubisco activity of the leaf samples in *Gmelina* grown under ambient and elevated $CO_2$ were shown in Table 1. Initial and total rubisco activity showed a progressive enhancement during 120 days of treatment. *Gmelina* plants grown under elevated $CO_2$, showed ~ 48% ($p < 0.05$) and ~ 44% ($p < 0.05$) higher initial and total activity, respectively, compared to the plants grown under ambient $CO_2$ (Table 1). CA activity was significantly higher (61% $p < 0.05$) in plants under elevated $CO_2$ when compared with ambient $CO_2$-grown plants (Table 1). It has been proposed that enzymatic processes like modulation of rubisco activity and expression of certain other key photosynthetic enzymes probably play a important role in influencing the guard cell responses to *Ci*- saturation and prevention of down regulation of *Pn* in young tree species under high $CO_2$ atmosphere (Warren and Adams, 2004; Coleman, 2000; von Caemmerer and Quick, 2000; Messinger *et al*., 2006). Internal $CO_2$ concentrations (*Ci*) influence the rate of $CO_2$ fixation in the chloroplasts, where photosynthetic carbon reduction cycle is exclusively located, but the initial assimilation of $CO_2$ takes place in the mesophyll cells (Li *et al*., 2004). This initial assimilation of *Ci* is catalysed by the enzyme CA which plays an important role in accelerating carbon assimilation by catalyzing the reversible interconversion of $CO_2$ and $HCO_3^-$ and preventing the *Ci* saturation (Coleman, 2000). In this study, *Gmelina,* grown under the high $CO_2$ atmosphere showed a dynamic increase in the activity of the CA. Very little is known about increases in CA activity in plants grown under elevated $CO_2$ (Sicher *et al*., 1994). The increase in the *Ci* and inturn the radical increase in the activity of the CA might lead to upsurge in the rubisco activity. The rubisco activity in *Gmelina* leaves grown under enriched $CO_2$ was significantly high at 120 DAP followed by absonant increase in *Pn* when compared to the plants grown under ambient $CO_2$. The activities of key carbohydrate metabolising enzymes like FBPase, SPsynthase and hexokinase were also significantly high in the plants grown under high $CO_2$ atmosphere compared to those grown under ambient $CO_2$.

Growth and biomass of *Gmelina* grown under elevated $CO_2$ were significantly high compared with those grown in ambient $CO_2$ as evidenced by the harvest data (Table 2). Elevated $CO_2$ atmosphere persistently enhanced the growth in *Gmelina.* All the growth characteristics including plant height, number of branches, internodes, intermodal distance, aerial biomass and plant biomass increased significantly in the plants grown under high $CO_2$ suggesting that *Gmelina* plants have greater capacity for carbon accumulation.

**Table 1** Effect of elevated $CO_2$ on key photosynthetic enzyme activities.

| Enzyme | Ambient $CO_2$ | Elevated $CO_2$ | |
|---|---|---|---|
| RUBPcase initial activity μmol $mg^{-1}$ protein $h^{-1}$ | 22.2±3.2 | 32.6±2.8 | *** |
| RUBPcase total activity μmol $mg^{-1}$ protein $h^{-1}$ | 36.2±2.8 | 47.8±3.7 | ** |
| Carbonic anhydrase Units $mg^{-1}$ protein | 18.0±1.8 | 29.5±2.6 | *** |
| FBPase activity μmol $mg^{-1}$ protein $h^{-1}$ | 42.3±1.7 | 78±3.5 | *** |
| SPsynthase activity μmol $mg^{-1}$ protein $h^{-1}$ | 28.3±2.1 | 36±3.6 | ** |
| Hexokinase μmol $mg^{-1}$ protein $h^{-1}$ | 7.4±2.3 | 13.5±4.7 | *** |
| Sedheptulose 1,7 bisphosphatase μmol $mg^{-1}$ protein $h^{-1}$ | 2.8±0.9 | 2.7±0.7 | ns |

**Table 2** Growth and Biomass yields of *Gmelina* grown elevated $CO_2$ atmosphere.

| **Character** | **Ambient $CO_2$** | **Elevated $CO_2$** | |
|---|---|---|---|
| Plant height (cm) | 209.45±2.12 | 359.92±2.78 | *** |
| Basal Diameter (cm) | 13.21±0.59 | 28.40±0.80 | *** |
| Number of Branches | 26.20±0.72 | 44.20±1.19 | *** |
| Relative plant height growth rate RHGR (g $day^{-1}$) | 2.97±0.45 | 4.08±0.72 | ** |
| Leaf size expansion rate | 3.89±0.57 | 9.75±1.02 | *** |
| Root weight (kg) | 3.96±0.89 | 5.97±0.85 | ** |
| Aerial biomass (kg) | 25.67±2.32 | 37.67±2.98 | ** |
| Plant biomass (kg) | 29.63±1.67 | 43.64±3.12 | *** |

Plant height was ~82% ($p < 0.001$) more in plants grown under high $CO_2$ than those grown under ambient condition (Table 2). The total shoot length constituting the length of main stem and branches together was ~77% ($p < 0.001$) more in high $CO_2$ grown plants. $CO_2$ treatment had a notable effect on the aerial biomass accumulation (~41% $p < 0.05$) and in turn on the total plant biomass (~47% $p < 0.05$) (Table 2). We noticed that increased number of branches resulted in greater crown size and structure of *Gmelina* under high $CO_2$ atmosphere. Profuse root growth and more number of secondary and tertiary roots in *Gmelina* under elevated $CO_2$ also shows the varied sink-source status of *Gmelina* plants. We demonstrate a strong and sustained photosynthetic enhancement in *Gmelina* plants grown under $CO_2$-enrichment and our data propound that *Gmelina* can be a potent trees species for efficient carbon sequestration corresponding to its rapid growth and high sink demand with no acclimatory responses.

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