



# Responses of Grass Species to Elevated CO<sub>2</sub> – A Review of Three Decades of Research and Future Direction

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## ABSTRACT

Rising atmospheric carbon dioxide accelerates growth and modifies physiological responses in plants. Over the last 40 years, the global scientific community had taken up initiatives to make out the role of plants in capturing and storing atmospheric carbon dioxide. This review consolidates the research of the past three decades on the responses of grass species to elevated levels of CO<sub>2</sub>. An enhancement in intercellular CO<sub>2</sub> concentration, water use efficiency, photosynthesis, total non-structural carbohydrates, and total biomass was noticed in grass species under controlled growth systems supplied with varying levels of CO<sub>2</sub>. Each of these responses reflects the potency of grasses to survive and store ample carbon in CO<sub>2</sub>-enriched environments. Reduction in stomatal conductance, transpiration rate, and total nitrogen concentration was in effect positive responses, in connection with the acclimatization of plants at CO<sub>2</sub>-enriched environments. This review ascertains that in experimental microclimatic environments with varying CO<sub>2</sub> regimes or varying treatment duration, grasses show positive growth responses. Thus it illustrates the efficient atmospheric carbon sequestration of grasses irrespective of their photosynthetic pathway (whether C<sub>3</sub>/C<sub>4</sub>).

## INTRODUCTION

Over the last 50 years, an amplified global temperature scenario was caused by increased greenhouse gas emissions (Khan 2017), primarily from carbon dioxide (CO<sub>2</sub>). Considering the present levels of atmospheric carbon dioxide and its hazardous effects on climate and ecosystems, there is a pressing need to develop technologies for their capture and storage. A recent report of the Intergovernmental Panel on Climate Change (IPCC 2018) set forth the urgent need for keeping global warming levels below 1.5°C to circumvent the upcoming issues in the area of climate change.

Various strategies are framed worldwide for lowering the levels of atmospheric CO<sub>2</sub>, such as geological and oceanic confiscation, energy use reduction, low or no carbon fuel development, carbon sequestration through engineering approaches and other forestry/agro-forestry practices (Dhyani et al. 2020). Carbon sequestration is the process of taking out carbon from various sources and depositing it in long or short-lived reservoirs (Nogia et al. 2016). Of various methods, carbon sequestration in terrestrial biomass is a meaningful and cost-effective approach for reducing the ill effects of climate change.

Over the past 40 years, dedicated efforts have been taken up by the international scientific community for the study of direct responses of terrestrial ecosystems to CO<sub>2</sub> enrichment. Since the end of 1980, a sizable number of original research, synthesis, and review papers have been published in the area of elevated CO<sub>2</sub> effects on plants, interacting organisms' and ecosystems (Leuzinger & Hattenschwiler 2013). Experiments on the responses of grasses to elevated CO<sub>2</sub> found momentum at the beginning of the 1990s. Among terrestrial plants, grasses (Poaceae) are one of the most ecologically adapted angiosperm groups and are distributed in all possible habitats (Tzvelev 1989). Poaceae is the fifth most species-rich angiosperm family with approximately 11000 species (Clayton et al. 2015). The world's savannas and grasslands are dominated by C<sub>3</sub> and C<sub>4</sub> grasses. These ecosystems extend to more than 20% of the Earth's terrestrial surface and contribute to 30% of global net primary productivity (Mishra & Young 2020). Savannas and grasslands have a much influential role in carbon and nutrient cycles. Grasslands, constituted by a multitude of species have an immense potential for carbon storage (O'Mara 2012). The underground biomass of grasslands also serves as a sink for carbon storage (Frank et al. 2004). Many of these grasses

are with an extensive root system, which helps them in the transfer and storage of carbon into the soil annually, by shedding widespread roots (Anderson et al. 2008, Fissore et al. 2009, Odiwe et al. 2016). Further, it influences the global land-atmosphere energy balance (Mishra & Young 2020). Unlike grasslands, owing to the growth or life cycle patterns, many grass species are less studied as sinks of carbon storage. Annual grasses are short-lived, and thus need to be managed each year and with perennial grasses, there are defoliation-related management issues. Further, perennial grasses require quite different ecological conditions; hence climatic limitations may hinder the cultivation of these plants (Scordia & Cosentino 2019). Thus researches on elevated CO<sub>2</sub> responses of individual grass species become limited. Even then, individual performances of selected grass species under controlled conditions, with elevated CO<sub>2</sub> were reported. A broad synthesis of elevated CO<sub>2</sub> responses in grass species has not been attempted yet. Strengthening the knowledge base on the responses of grasses to elevated CO<sub>2</sub> will improve our ability for the selection of ideal species and conditions for effective CO<sub>2</sub> mitigation efforts.

The present review consolidated the physiological and growth responses of grass species (C<sub>3</sub> and C<sub>4</sub>) maintained under different growth systems to elevated levels of CO<sub>2</sub>. The specific objective of this synthesis was to provide estimates of the significance and reasons for CO<sub>2</sub> enrichment effects on photosynthetic rate (Pn), intercellular CO<sub>2</sub> concentration (Ci), stomatal conductance (g<sub>s</sub>), transpiration rate (E), water use efficiency (WUE), total nonstructural carbohydrate

(TNC), biomass responses and nitrogen concentration (N) in grasses. Since these responses are the basic direct plant responses towards a changed environment as enrichment in CO<sub>2</sub>, this consolidation will urge a selection of the best grasses for carbon mitigation efforts.

## CARBON DIOXIDE ELEVATION AND ASSOCIATED CLIMATIC FACTORS

Studies on the effect of varying concentrations of CO<sub>2</sub> on the growth/development/physiology and biochemistry of 24 grass species were considered in this synthesis. The authors set well-established micro-environmental systems to maintain a near-natural condition for the growth of grasses at CO<sub>2</sub> enrichment (Table 1). Growth responses of grasses at elevated CO<sub>2</sub> are linked with other climatic factors too. Cold temperatures and nutrient-poor soil down-regulate growth stimulation, however, at low light and water-stressed conditions growth enhancement was evident (Poorter & P´erez-Soba 2002). Besides, at increased levels of ozone concentration, plants show a much stronger response, since CO<sub>2</sub> elevation ameliorates ozone toxicity in plants due to reduced stomatal conductance (Turcsanyi et al. 2000). Some of the scrutinized CO<sub>2</sub> elevation experiments maintained grasses under different conditions such as water stress, varying nutrient supply, drought stress, temperature stress including warming temperatures and low/high light. These interaction effects will play an important role in formulating adaptive strategies in the future. Temperature is an important determinant of plant responses at elevated CO<sub>2</sub>, since an

Table 1: Experimental models & designs used for CO<sub>2</sub> enrichment experiment on grasses.

Sl. No.	Experimental model	Volume/other dimensions	Design	Microclimatic environment	Author
1.	Controlled environmental chamber	-	Aluminum panel Foamed polyurethane insulation	350ppm aCO <sub>2</sub> 675ppm eCO <sub>2</sub> 14h photoperiod Temperature : light/dark- 29/20°C RH: light/dark -70/100	Riechers and Strain (1988)
2.	Closed top chamber	3.165m <sup>3</sup>	Cylindrical	337 ± 32 ppm aCO <sub>2</sub> 658 ± 81 ppm eCO <sub>2</sub>	Kirkham et al. (1992)
3.	Growth cabinet	-	-	340 ± 15 ppm aCO <sub>2</sub> 680 ± 15 ppm eCO <sub>2</sub>	Ryle et al. (1992)
4.	Large OTC	63.578m <sup>3</sup>	Cylindrical UV-resistant polyethylene film and aluminum frame	350 ppm aCO <sub>2</sub> 700 ppm eCO <sub>2</sub> Intermittent nutrient supply	Knapp et al. (1993)
5.	OTC	1.286m <sup>3</sup>	Cylindrical PVC sheet	340 ppm aCO <sub>2</sub> 680 ppm eCO <sub>2</sub>	Baxter et al. (1994 a, 1994b)
6.	OTC	0.331m <sup>3</sup>	Cylindrical	Ambient Ambient +350 ppm eCO <sub>2</sub> Sandstone soil, no nutrient or water supply	Jackson et al. (1995)

Table cont....

Sl. No.	Experimental model	Volume/other dimensions	Design	Microclimatic environment	Author
7.	FACE	18m diameter	FACE ring	340 ppm aCO <sub>2</sub> 600 ppm eCO <sub>2</sub> 2 nutrient regimes-low & high	Jongen et al. (1995)
8.	OTC	63.578m <sup>3</sup>	Cylindrical 1.5mm thick UV-resistant polyethylene Aluminum frame with frustrum*	350 ppm aCO <sub>2</sub> 700 ppm eCO <sub>2</sub>	Bremer et al. (1996)
9.	Expt.1: glass dome Expt.2: growth chamber Expt.3: a glass house	-	Naturally lit glass dome Growth chamber lit by metal halide & incandescent bulbs Naturally lit glass house	700 ppm eCO <sub>2</sub> Expt 1: RH exceeding 90% Temperature : 30°C/25°C for 15/9 h day/night Low light (9.2 mol m <sup>-2</sup> d <sup>-1</sup> irradiance)/high light (24.9 mol m <sup>-2</sup> d <sup>-1</sup> irradiance)treatment Expt 2: PPFD 750 Expt 3: RH 60 % Irradiance midday peak 1350 μmol m <sup>-2</sup> S <sup>-1</sup>	Ghannoum et al. (1997)
10.	OTC	1.3m between parallel sides 1.95m <sup>2</sup> soil area	Hexagonal 3mm polycarbonate sheet	365-380ppm aCO <sub>2</sub> 716-720ppm eCO <sub>2</sub> (1995) 751-756ppm eCO <sub>2</sub> (1996) A cooling system to decrease the temperature	Oijen et al. (1999)
11.	OTC	1.13m <sup>3</sup>	Cylindrical UV-stabilized plastic sheet Lightweight steel frame	360 ppm aCO <sub>2</sub> 700 ppm eCO <sub>2</sub> Half of the chambers- moderate nutrient supply Half of the chambers-low nutrient supply	Davey et al. (1999)
12.	OTC	61.70m <sup>3</sup>	Hexagonal Galvanized steel frame Clear Lexan panels with Lexan frustrum	360 ± 20 aCO <sub>2</sub> 720 ± 20 eCO <sub>2</sub> The outlet fan equilibrated the pressure inside & outside the chambers	Morgan et al. (2001)
13.	Growth chamber	-	-	350ppm aCO <sub>2</sub> 700ppm eCO <sub>2</sub> Day/night temperature - 24°C/16°C RH- 70% PPFD- 600-1200μmolm <sup>-2</sup> S <sup>-1</sup>	Goverde et al. (2002)
14.	OTC	6.18m <sup>3</sup>	Cylindrical	370ppm aCO <sub>2</sub> 720ppm eCO <sub>2</sub> PPFD- 1500 μmolm <sup>-2</sup> s <sup>-1</sup>	De Souza et al. (2008)
15.	OTC	-	-	370-380ppm aCO <sub>2</sub> 600 ± 50 ppm eCO <sub>2</sub>	Bhatt et al. (2010)
16.	Environmental growth chamber	-	-	400 ± 10 ppm aCO <sub>2</sub> 800 ± 10 ppm eCO <sub>2</sub> Average Day/Night temperature- 21°C/18°C PAR-650μmolm <sup>-2</sup> s <sup>-1</sup> RH-60% 14h photoperiod Fertilized with Hoagland's solution	Burgess and Huang (2014)
17.	CO <sub>2</sub> growth chambers	2m <sup>3</sup>	Closed topped PVC frame Polyester sheeting	400ppm aCO <sub>2</sub> 800ppm eCO <sub>2</sub> Draught/non-draught treatment	Nackley et al. (2014)

Table cont....

Sl. No.	Experimental model	Volume/other dimensions	Design	Microclimatic environment	Author
18.	Environmental growth chamber	-	-	400 ± 20ppm aCO <sub>2</sub> 800 ± 20ppm eCO <sub>2</sub> 5 temperature treatments (15/12,20/17,25/22,30/27,35/32-day/night) RH-70 % PAR-660 μmol m <sup>-2</sup> s <sup>-1</sup> 12h photoperiod	Song et al. (2014)
19.	Glass dome	700m <sup>3</sup>	Semi-open design with adjustable window	385ppm aCO <sub>2</sub> 700 ppm eCO <sub>2</sub> PAR-1200 μmol m <sup>-2</sup> s <sup>-1</sup>	Klem et al. (2017)
20.	OTC inside a glass house	1.53m <sup>3</sup>	-	345.43 ± 38.59ppm aCO <sub>2</sub> & room temperature 345.55 ± 38.47 aCO <sub>2</sub> & room temperature + 3°C 714.63 ± 89.40 eCO <sub>2</sub> & room temperature 724.56 ± 88.85 eCO <sub>2</sub> & room temperature + 3°C	Faria et al. (2018)
21.	Growth chamber	152.102m <sup>3</sup>	-	400 ppm aCO <sub>2</sub> 950 ppm eCO <sub>2</sub> Temperature day/night 25/22°C RH 70% - 80%	Tom Dery et al. (2018)
22.	OTC	3.378m <sup>3</sup>	Hexahedron	390 ppm aCO <sub>2</sub> 550 ppm eCO <sub>2</sub> 5 precipitation patterns	Wang et al. (2019)

Note: OTC = Open top chamber; FACE = Free air CO<sub>2</sub> enrichment; \* = portion between two parallel planes create artificial microclimate; aCO<sub>2</sub> = ambient CO<sub>2</sub>; eCO<sub>2</sub> = elevated CO<sub>2</sub>; RH = Relative humidity; PPFD = Photosynthetic photon flux density; PAR = photosynthetically active radiation

increase in CO<sub>2</sub> causes warming. Due to a consequence of elevated CO<sub>2</sub>, maximum biomass enrichment happens in tall grass prairie in dry years with high temperatures and abundant solar radiation (Knapp et al. 1993). In *Poa pratensis* elevated CO<sub>2</sub> alleviated the adverse effect of severely high temperatures (Song et al. 2014). The authors attributed this alleviation effect to the accumulation of soluble sugars and total non-structural carbohydrates. A study on the combined effect of CO<sub>2</sub> elevation and higher temperature on Brazilian Cerrado biome grasses shows that the species are tolerant to high temperatures and could even benefit from temperature rise. Nackley et al. (2014) reported drought tolerance of *Arundo donax* at elevated CO<sub>2</sub>. Here elevated CO<sub>2</sub>-induced decline in transpiration rate is ascribed to increased water use efficiency and thereby drought tolerance. Soil nutrient profiles and elevated CO<sub>2</sub> responses are also attempted by previous authors. Open-top chamber study on UK grassland species reveals stimulation of photosynthesis under low nutrient supply (Davey et al. 1999). This is the most important stimulation in carbon acquisition.

During the period of evaluation, a gradual increase in experimental CO<sub>2</sub> supply from 600 to 950 ppm has been noticed. This was in concurrence with the increase in CO<sub>2</sub>

levels in the ambient atmosphere from a global perspective. The duration of CO<sub>2</sub> treatment studies under experimental conditions was from 40 days to 3 years. The most measured response factors were net photosynthetic rate (Pn) and biomass. Authors also evaluated the effect of elevated CO<sub>2</sub> on intercellular CO<sub>2</sub> concentration (Ci), stomatal conductance (gs), transpiration rate (E), water use efficiency (WUE), total nonstructural carbohydrates (TNC) and total nitrogen concentration (N) on various grass species.

### ELEVATED CARBON DIOXIDE AND PHOTOSYNTHETIC RESPONSES IN C<sub>3</sub>/C<sub>4</sub> PATHWAYS

Photosynthetic responses of plants are considered as an important measure of carbon capture efficiency in CO<sub>2</sub> sequestration studies. Augmentation in CO<sub>2</sub> levels leads to increased photosynthetic rate (Ziska et al. 1999, Aranda et al. 2020). This review also signifies a positive response in the photosynthetic rate of 86.36% of grasses (Table 2). However, species like *Andropogon gerardii* (Kirkham et al. 1992) and *Pascopyrum smithii* (Davey et al. 1999) lack a significant response in photosynthetic rate under elevated levels of CO<sub>2</sub>. *Arundo donax* exhibits a negative

Table 2: Changes in the photosynthetic rate at elevated CO<sub>2</sub>.

Sl. No.	Plant species	Duration of CO <sub>2</sub> treatment	Pn	Reference
1.	<i>Andropogon gerardii</i> (C <sub>4</sub> )	40 days	+ 8.75% (NS)	Kirkham et al. (1992)
2.	<i>Poa pratensis</i> (C <sub>3</sub> )	40 days	+ 141%	Kirkham et al. (1992)
3.	<i>Lolium perenne</i> (C <sub>3</sub> )	49 days	+ 50%	Ryle et al. (1992)
4.	<i>Andropogon gerardii</i> (C <sub>4</sub> )	2 growing seasons one with water stress	+	Knapp et al. (1993)
5.	<i>Agrostis capillaris</i> (C <sub>3</sub> )	79 days	+	Baxter et al. (1994 a, 1994b)
6.	<i>Avena barbata</i> (C <sub>3</sub> )	One growing season	+ 20%	Jackson et al. (1995)
7.	<i>Panicum laxum</i> (C <sub>3</sub> )	1.5 months with low light/high light	+18% in low light NS	Ghannoum et al. (1997)
8.	<i>Panicum antidotale</i> (C <sub>4</sub> )	1.5 months with low light/high light	+10% in high light (NS)	Ghannoum et al. (1997)
9.	<i>Triticum aestivum</i> (C <sub>4</sub> )	2 growing seasons	+ 30%	Oijen et al. (1999)
10.	<i>Agrostis capillaris</i> (C <sub>3</sub> )	2 years with nutrient supply (low & moderate)	+38% at low +12% at moderate	Davey et al. (1999)
11.	<i>Pascopyrum smithii</i> (C <sub>3</sub> )	2 years with nutrient supply (low & moderate)	NS	Davey et al. (1999)
12.	<i>Bouteloua gracilis</i> (C <sub>4</sub> )	7 months	+	Morgan et al. (2001)
13.	<i>Pascopyrum smithii</i> (C <sub>3</sub> )	7 months	+	Morgan et al. (2001)
14.	<i>Saccharum officinarum</i> (C <sub>4</sub> )	50 weeks	+ 30%	De Souza et al. (2008)
15.	<i>Panicum maximum</i> (C <sub>4</sub> )	2 growing seasons	+ 53%	Bhatt et al. (2010)
16.	<i>Agrostis stolonifera</i> (C <sub>3</sub> )	84 days	+ 21%	Burgess and Huang (2014)
17.	<i>Arundo donax</i> (C <sub>3</sub> )	78 days (28 days drought stress)	- NS	Nickley et al. (2014)
18.	<i>Poa pratensis</i> (C <sub>3</sub> )	2 weeks (temperature treatment)	+	Song et al. (2014)
19.	<i>Calomagrostis arundinacea</i> (C <sub>3</sub> )	3 years	+	Klem et al. (2017)
20.	<i>Urochloa brizantha</i> (C <sub>4</sub> )	75 days with temperature treatment	+	Faria et al. (2018)
21.	<i>Megathyrsus maximus</i> (C <sub>4</sub> )	75 days with temperature treatment	+	Faria et al. (2018)
22.	<i>Stipa baicalensis</i> (C <sub>3</sub> )	3 months	+93.4%-158%	Wang et al. (2019)

Note: Pn = photosynthetic rate; + = increase; - = decrease; NS = not significant

photosynthetic response (Nickley et al. 2014). Feedback inhibition is associated with an excess of unutilized N and carbon resources, consequent to the lack of carbohydrate sinks attributed to the down-regulation of photosynthesis during CO<sub>2</sub> enrichment in *Arundo donax* in its specific experimental conditions (Paul & Foyer 2001). A comparative evaluation of the CO<sub>2</sub> elevation experiment conducted in *Poa pratensis* and *Andropogon gerardii* (Kirkham et al. 1992) reveals a rise in the photosynthetic rate in *Poa pratensis* (C<sub>3</sub>) owing to the domination of carboxylation activity of Rubisco enzyme under high CO<sub>2</sub> environment. Yet there is

no significant change in the assimilation rate of *A. gerardii* (C<sub>4</sub>). In C<sub>3</sub> at CO<sub>2</sub> limited environment, Rubisco catalyzes the oxygenation of Ribulose-1, 5-bisphosphate (RubP), a reaction that is competitively inhibited by CO<sub>2</sub> (Drake et al., 1997). Kranz anatomy eliminates this phenomenon in C<sub>4</sub>. Thus CO<sub>2</sub> elevation is not much beneficial to C<sub>4</sub>. CO<sub>2</sub> enrichment treatment eliminates energy-losing photorespiration under a doubled CO<sub>2</sub> environment in C<sub>3</sub> plants and growth is stimulated to a range of 40-45%, whereas in C<sub>4</sub> plants, growth only to a range of 10-20% (Ghannoum et al. 2000). Thus CO<sub>2</sub> elevation is more advantageous to C<sub>3</sub>

plants than C<sub>4</sub> (Waggoner 1984). This advantage is apparent in the photosynthetic rate of 84.62% of C<sub>3</sub> grasses scrutinized.

Contrary to the C<sub>3</sub> advantage, the positive photosynthetic response is also shown by 88.88% of C<sub>4</sub> grasses reviewed in the present study. Arid environments with temperature ascending and limited nutrients favor C<sub>4</sub> plants and eventually exhibit positive responses at CO<sub>2</sub> elevation (Ghannoum et al. 2000, Sage & Kubein 2003). Even though CO<sub>2</sub> concentrating mechanism makes C<sub>4</sub> plants insensitive to elevated CO<sub>2</sub>, superior photosynthetic nitrogen use efficiency (Sage & Kubein 2003) is more advantageous to them at elevated CO<sub>2</sub> than C<sub>3</sub> plants. Rubisco accounts for about 30% of leaf nitrogen content in C<sub>3</sub> plants, while only 4 - 21% in C<sub>4</sub> species (Sage et al. 1987, Evans & Von Caemmerer 2000). Carbohydrate dilution of nitrogen content (Wong 1990, Kuehny et al. 1991, Gifford et al. 2000) at elevated CO<sub>2</sub> decreases nitrogen use efficiency of C<sub>3</sub> plants, thus C<sub>3</sub> leaves need to invest more nitrogen on Rubisco. Such nitrogen requirements down-regulate C<sub>3</sub> plants at elevated CO<sub>2</sub> environments (Lara & Andreo 2011). In the case, of C<sub>3</sub> plants like *Panicum laxum* and *Arundo donax*, reduction in assimilation are attributed to decreased Rubisco activity (Ghannoum et al. 1997). Photosynthetic acclimatization and down-regulation reported for long-term exposure of plants to elevated CO<sub>2</sub> are attributed to this decline in Rubisco activity (Fredeen et al. 1995, Sicher & Bunce 1997). Enhanced cellular carbohydrate levels may down-regulate

genes transcribing Rubisco and other photosynthetic proteins (Stitt 1991, Krapp et al. 1991). Another observation states that an increased requisite of ATP (required for RuBP regeneration) for increased carbon fixation before CO<sub>2</sub> elevation results in a decline in the Rubisco activation state. Such reduction was also observed in previous studies (Sage et al. 1988, Cen & Sage 2005). Besides augmented levels of CO<sub>2</sub>, nutrient conditions and other factors of a microenvironmental condition such as temperature, light intensity, and treatment duration also influence the response of grasses. Nevertheless, most of the grasses (86.36%) assessed here respond almost identically in various microclimatic conditions.

### ELEVATED CARBON DIOXIDE - INTERCELLULAR CO<sub>2</sub> CONCENTRATIONS AND STOMATAL CONDUCTANCE

Stomatal responses occur due to the intensity of intercellular CO<sub>2</sub> concentration (C<sub>i</sub>), preceded by mesophyll CO<sub>2</sub> demands (Mott 1988). With the rise in atmospheric CO<sub>2</sub>, intercellular CO<sub>2</sub> concentration raises (Kirkham et al. 1992). C<sub>3</sub> plants have a higher C<sub>i</sub> than C<sub>4</sub> plants. C<sub>4</sub> plants maintain a lower C<sub>i</sub> due to its CO<sub>2</sub> concentrating mechanism with a special arrangement of bundle sheath cells and mesophyll cells (kranz anatomy). Few studies on C<sub>3</sub> and C<sub>4</sub> grasses measured C<sub>i</sub> and an increase is evident in both cases, while stomatal conductance decreased in these grasses, with the exception of *Panicum maximum*, *Urochloa brizantha*, and

Table 3: Changes in intercellular CO<sub>2</sub> concentration and stomatal conductance at elevated CO<sub>2</sub>.

Sl. No.	Plant species	Duration of CO <sub>2</sub> treatment	C <sub>i</sub>	g <sub>s</sub>	Reference
1.	<i>Andropogon gerardii</i> (C <sub>4</sub> )	40 days	+180%		Kirkham et al. (1992)
2.	<i>Poa pratensis</i> (C <sub>3</sub> )	40 days	+67.79%		Kirkham et al. (1992)
3.	<i>Andropogon gerardii</i> (C <sub>4</sub> )	2 growing seasons one with water stress		-52%	Knapp et al. (1993)
4.	<i>Andropogon gerardii</i> (C <sub>4</sub> )	6 months		-54.4%	Bremer et al. (1996)
5.	<i>Sorghastrum nutans</i> (C <sub>4</sub> )	6 months		-39.6%	Bremer et al. (1996)
6.	<i>Panicum laxum</i> (C <sub>3</sub> )	1.5 months with low light/high light		-50%	Ghannoum et al. (1997)
7.	<i>Panicum antidotale</i> (C <sub>4</sub> )	1.5 months with low light/high light		- 50%	Ghannoum et al. (1997)
8.	<i>Saccharum officinarum</i> (C <sub>4</sub> )	50 weeks		-37%	De Souza et al. (2008)
9.	<i>Panicum maximum</i> (C <sub>4</sub> )	2 growing seasons	+	+	Bhatt et al. (2010)
10.	<i>Agrostis stolonifera</i> (C <sub>3</sub> )	84 days		-40%	Burgess and Huang (2014)
11.	<i>Arundo donax</i> (C <sub>3</sub> )	78days(28days drought stress)	+	-	Nickley et al (2014)
12.	<i>Calomagrostis arundinacea</i> (C <sub>3</sub> )	3years		-	Klem et al. (2017)
13.	<i>Urochloa brizantha</i> (C <sub>4</sub> )	75 days with temperature treatment		+	Faria et al. (2018)
14.	<i>Megathyrus maximus</i> (C <sub>4</sub> )	75 days with temperature treatment		+	Faria et al. (2018)
15.	<i>Cenchrus pedicellatus</i> (C <sub>4</sub> )	68days(wet&dry treatment)		-40%	Tom Dery et al. (2018)
16.	<i>Stipa baicalensis</i> (C <sub>3</sub> )	3 months	+72.3 - 129.6		Wang et al. (2019)

Note: C<sub>i</sub> = intercellular CO<sub>2</sub> concentration; g<sub>s</sub> = stomatal conductance; + = increase; - = decrease

*Megathyrsus maximus* (Table 3). The grasses undergone experimentation so far showed a decreased range of stomatal conductance, between 35-55%. Previous reviews on plant CO<sub>2</sub> responses support this view (Curtis & Wang 1998, Wand et al. 1999, Ainsworth et al. 2002, Ainsworth & Rogers 2007, Aranda et al. 2020). The positive response of *Panicum maximum* is attributed to the lack of stomatal functioning effect at higher CO<sub>2</sub> concentrations (600 ± 50) (Bhatt et al. 2010). Elevated temperature treatment in combination with elevated CO<sub>2</sub> explains positive stomatal conductance rates of *Urochloa brizantha* and *Megathyrsus maximus* (Faria et al. 2018). A feedback mechanism works to decrease stomatal conductance under elevated CO<sub>2</sub> in most plants. It has been implicit that guard cells sense the concentration of CO<sub>2</sub> in the intercellular spaces, and as the mesophyll requirement for CO<sub>2</sub> increases, Ci decreases, causing stomatal opening and increasing Ci (Mott 1988). Depolarization of the guard cell membrane is the main requirement for stomatal closure (Assmann 1999). At elevated CO<sub>2</sub>, depolarization happens to a larger extent, which leads to the reduced stomatal aperture (Ainsworth & Rogers 2007). Reduced stomatal conductance shown by plants at long-term elevated CO<sub>2</sub> exposure is ascribed to the changes in stomatal aperture or stomatal index or stomatal density (Pritchard & Rogers 2007). A putative 3-keto acyl-coenzyme A synthase encoded by HIC (high carbon dioxide) gene is a negative regulator of stomatal development (Gray et al. 2000) and is also reported to be related to stomatal closure.

## ELEVATED CARBON DIOXIDE - TRANSPIRATION RATE AND WATER USE EFFICIENCY

The transpiration rate was noted to decline for individual grasses scrutinized (Table 4). Yet *Panicum maximum* responds positively to elevated levels of CO<sub>2</sub> and is attributed to increased chamber temperature (Bhatt et al. 2010). Declining transpiration is a stress protection method that limits water loss and minimizes damage linked with desiccation. Plants and ecosystems under drought condition experience greater WUE (Water Use Efficiency) (Field et al. 1997; Arp et al. 1998). Increased WUE is also said to be a result of morphological adjustments rather than stomatal (Norby & O'Neill 1991) under elevated CO<sub>2</sub>. Studies indicate that crop plants grown at higher CO<sub>2</sub> environments have larger and highly branched root systems, which increases the capacity for resource acquirement but at lesser efficiency (Pritchard & Rogers 2000). Day et al. (1996) observed higher root production towards nutrient-available surfaces and water-available depths in a sandy nutrient-poor Oak-palmetto system. Upon review of the literature on root growth under elevated CO<sub>2</sub>, Wullschleger et al. (2002) found that elevated CO<sub>2</sub> increases root growth and it leads to enhanced water uptake and improved water balance, thus helping to evade water deficits. Yet when soil moisture is sufficient to meet transpirational loss of water, the CO<sub>2</sub> effect on root volume is seemingly extraneous, thus this mechanism could be

Table 4: Changes in transpiration rate and water use efficiency at elevated CO<sub>2</sub>.

Sl. No.	Plant species	Duration of CO <sub>2</sub> treatment	E	WUE	Reference
1.	<i>Andropogon gerardii</i> (C <sub>4</sub> )	40 days	- 54%	+ 41.6%	Kirkham et al. (1992)
2.	<i>Poa pratensis</i> (C <sub>3</sub> )	40 days	-7%	+158%	Kirkham et al. (1992)
3.	<i>Lolium perenne</i> (C <sub>3</sub> )	49 days			Ryle et al. (1992)
4.	<i>Andropogon gerardii</i> (C <sub>4</sub> )	6 months	-18%		Bremer et al. (1996)
5.	<i>Sorghastrum nutans</i> (C <sub>4</sub> )	6 months	-22%		Bremer et al. (1996)
6.	<i>Saccharum officinarum</i> (C <sub>4</sub> )	50 weeks		+62%	De Souza et al. (2008)
7.	<i>Panicum maximum</i> (C <sub>4</sub> )	2 growing seasons	+	+	Bhatt et al. (2010)
8.	<i>Agrostis stolonifera</i> (C <sub>3</sub> )	84 days	-40%	+30%	Burgess and Huang (2014)
9.	<i>Arundo donax</i> (C <sub>3</sub> )	78days(28days drought stress)	-100%	+	Nickley et al. (2014)
10.	<i>Calomagrostis arundinacea</i> (C <sub>3</sub> )	3years	-	+	Klem et al. (2017)
11.	<i>Urochloa brizantha</i> (C <sub>4</sub> )	75 days with temperature treatment		+	Faria et al. (2018)
12.	<i>Megathyrsus maximus</i> (C <sub>4</sub> )	75 days with temperature treatment		+	Faria et al. (2018)
13.	<i>Stipa baicalensis</i> (C <sub>3</sub> )	3 months		+87.2%	Wang et al. (2019)

Note: E = transpiration rate; WUE = water use efficiency; + = increase; - = decrease

detected only under specific conditions (Wullschleger et al. 2002). Since the rise in atmospheric CO<sub>2</sub> usually upholds WUE, there will be a tendency for plants to tolerate draught in the future (Beerling et al. 1996).

### ELEVATED CARBON DIOXIDE AND TOTAL NON-STRUCTURAL CARBOHYDRATES

The principal non-structural carbohydrates present in leaves are total soluble sugars and starch. Evaluation of literature on individual grasses explains a significant increase in non-structural carbohydrates (Table 5) in CO<sub>2</sub>-rich environments. Growth and development of grasses thrive with an accumulation of non-structural carbohydrates; which are also related to environmental stress tolerance (Moraes et al. 2013). Elevated CO<sub>2</sub> exposure creates a considerable increase in soluble sugar and starch content (Teng et al. 2006). Previous investigations revealed that augmented levels of soluble sugars and starch contents in leaves are due to increased assimilation rates (Delucia et al. 1985, Long & Drake 1992, Moore et al. 1997, Teng et al. 2006). Elevated CO<sub>2</sub>-based increases in sugar levels may also be due to an indirect effect of declined nitrogen concentrations leading to lowered respiration rates (Oijen et al. 1999). Storage of non-structural carbohydrates such as starch and fructans is common among some grasses (Morvan-Bertrand et al. 2001, Xue et al. 2009). Temperate climate grasses usually store carbohydrates as fructans (Halford et al. 2011). Fructans are formed from imported sucrose and the site of synthesis is the vacuolar lumen (Pollock et al. 2003). A limited number of grasses use starch as a carbohydrate storage pool and is

synthesized in plastids or amyloplasts (Slewinski 2012). The storage of carbohydrate polymers increases the sequestration capability of grasses. Drought stress tolerance of non-structural carbohydrates is hypothesized by previous authors (Moraes et al. 2013). Low hydraulic conductance of grass stems due to the accumulation of soluble sugars facilitates easy conductance of water from the soil to plant parts (Fu et al. 2011). Along with carbon sequestration capability, this adaptation for draught tolerance will also be advantageous for grasses in facing future environmental challenges.

### ELEVATED CARBON DIOXIDE AND BIOMASS RESPONSES

Growth and biomass responses of plants to elevated levels of CO<sub>2</sub> are widely studied. Literature reveals that the biomass has increased to varying levels at elevated CO<sub>2</sub> environments (Table 6). Even though C<sub>4</sub> grasses have no additional benefit at elevated CO<sub>2</sub> owing to internal CO<sub>2</sub> concentrating mechanisms, increased photosynthetic rates or increased biomass are reported in C<sub>4</sub> grasses. These increases are resulting in faster development of inflorescence, changes in partitioning, delayed leaf senescence, or enhanced water potential at CO<sub>2</sub> elevation (Carter & Petersen 1983, Potvin & Strain 1985, Knapp et al. 1993). Other studies state that the increase in growth and biomass at CO<sub>2</sub> ascent is attributed to an enhancement in leaf area (Poorter & Remkes, 1990). Roumet & Roy (1996) also stated a positive correlation of plant growth to specific leaf area (leaf surface area per unit of leaf weight) and leaf area ratio (leaf area per unit

Table 5: Changes in total non-structural carbohydrates at elevated CO<sub>2</sub>.

Sl. No.	Plant species	Duration of CO <sub>2</sub> treatment	TNC	Reference
1.	<i>Agrostis capillaris</i> (C <sub>3</sub> )	79 days	+	Baxter et al. (1994 a, 1994b)
2.	<i>Festuca vivipara</i> (C <sub>3</sub> )	189 days	+	Baxter et al. (1994 a, 1994b)
3.	<i>Lolium perenne</i> -Root (C <sub>3</sub> )	One growing season	+46.9%	Jongen et al. (1995)
4.	<i>Panicum laxum</i> (C <sub>3</sub> )	1.5 months with low light/high light	NS	Ghannoum et al. (1997)
5.	<i>Panicum antidotale</i> (C <sub>4</sub> )	1.5 months with low light/high light	NS	Ghannoum et al. (1997)
6.	<i>Triticum aestivum</i> (C <sub>4</sub> )	2 growing seasons	+	Oijen et al. (1999)
7.	<i>Agrostis stolonifera</i> (C <sub>3</sub> )	65 days	+	Goverde et al. (2002)
8.	<i>Anthoxanthum odoratum</i> (C <sub>3</sub> )	65 days	+	Goverde et al. (2002)
9.	<i>Festuca rubra</i> (C <sub>3</sub> )	65 days	+	Goverde et al. (2002)
10.	<i>Poa pratensis</i> (C <sub>3</sub> )	65 days	+	Goverde et al. (2002)
11.	<i>Poa pratensis</i> (C <sub>3</sub> )	2 weeks (temperature treatment)	+38% at 25 - 35°C	Song et al. (2014)
12.	<i>Urochloa brizantha</i> (C <sub>4</sub> )	75 days with temperature treatment	+	Faria et al. (2018)
13.	<i>Megathyrus maximus</i> (C <sub>4</sub> )	75 days with temperature treatment	+	Faria et al. (2018)

Note: TNC = total non-structural carbohydrates; + = increase; NS = not significant



of total plant dry weight) in 11 closely related types of grass.

Changes in moisture relationships have a key role in grassland productivity (Owensby et al. 1993). Previous investigations revealed that elevated CO<sub>2</sub> significantly stimulated plant growth even at water-limited conditions (Gifford & Morison 1985, King & Greer 1986, Samarakoon & Gifford 1995, Owensby et al. 1996). According to Pritchard et al. (1999), stimulation of cell wall-related genes at elevated CO<sub>2</sub> uphold enhanced cell production and cell elongation. This view is a possible explanation for biomass increase at elevated CO<sub>2</sub>. Temperature is yet another factor, which defines growth at elevated CO<sub>2</sub>. Growth and storage of

carbohydrates are limiting at low temperatures, however, an increase in temperature creates a positive response towards growth at elevated CO<sub>2</sub>. This view is supported by Oliveira et al. (2013), where the accumulation of biomass and enhanced grain yield in wheat is noticed under elevated CO<sub>2</sub>, combined with high-temperature treatment. The same authors imply that the combination of high temperature and elevated CO<sub>2</sub> will lessen the awful effects of terminal drought. Fisher et al. (1994) estimated the carbon sequestration potential of deep-rooted grasses in South American savannas and reported a sequestration of 100-507 Mt carbon per year. Through this study, the authors 'demonstrated the importance of grass biomass as a major sink of atmospheric carbon.

Table 6: Changes in plant biomass at elevated CO<sub>2</sub>.

Sl. No.	Plant species	Duration of CO <sub>2</sub> treatment	Biomass	Reference
1.	<i>Bouteloua gracilis</i> (C <sub>4</sub> )	7 weeks	+35%	Riechers and Strain (1988)
2.	<i>Lolium perenne</i> (C <sub>3</sub> )	49 days	+	Ryle et al. (1992)
3.	<i>Andropogon gerardii</i> (C <sub>4</sub> )	2 growing seasons one with water stress	+41%	Knapp et al. (1993)
4.	<i>Agrostis capillaries</i> (C <sub>3</sub> )	79 days	+	Baxter et al. (1994 a, 1994b)
5.	<i>Poa alpinia</i> (C <sub>3</sub> )	105 days	+	Baxter et al. (1994 a, 1994b)
6.	<i>Festuca vivipara</i> (C <sub>3</sub> )	189 days	-48%	Baxter et al. (1994 a, 1994b)
7.	<i>Lolium perenne</i> -Root (C <sub>3</sub> )	One growing season	+48%	Jongen et al. (1995)
8.	<i>Panicum laxum</i> (C <sub>3</sub> )	1.5 months with low light/high light	+1.41 fold in low light +1.71 fold in the highlight	Ghannoum et al. (1997)
9.	<i>Panicum antidotale</i> (C <sub>4</sub> )	1.5 months with low light/high light	+1.28 fold in the highlight	Ghannoum et al. (1997)
10.	<i>Triticum aestivum</i> (C <sub>4</sub> )	2 growing seasons	+	Oijen et al. (1999)
11.	<i>Agrostis capillaries</i> (C <sub>3</sub> )	2 years with nutrient supply(low & moderate)	-23% at low -16% at moderate	Davey et al. (1999)
12.	<i>Lolium perenne</i> (C <sub>3</sub> )	2 years with nutrient supply(low & moderate)	-29% at low -17% at moderate	Davey et al. (1999)
13.	<i>Bouteloua gracilis</i> (C <sub>4</sub> )	7 months	+	Morgan et al. (2001)
14.	<i>Pascopyrum smithii</i> (C <sub>3</sub> )	7 months	+	Morgan et al. (2001)
15.	<i>Agrostis stolonifera</i> (C <sub>3</sub> )	65 days	NS	Goverde et al. (2002)
16.	<i>Anthoxanthum odoratum</i> (C <sub>3</sub> )	65 days	+	Goverde et al. (2002)
17.	<i>Festuca rubra</i> (C <sub>3</sub> )	65 days	+	Goverde et al. (2002)
18.	<i>Poa pratensis</i> (C <sub>3</sub> )	65 days	NS	Goverde et al. (2002)
19.	<i>Saccharum officinarum</i> (C <sub>4</sub> )	50 weeks	+40%	De Souza et al. (2008)
20.	<i>Panicum maximum</i> (C <sub>4</sub> )	2 growing seasons	+	Bhatt et al. (2010)
21.	<i>Agrostis stolonifera</i> (C <sub>3</sub> )	84 days	+35%	Burgess and Huang (2014)
22.	<i>Poa pratensis</i> (C <sub>3</sub> )	2 weeks (temperature treatment)	+	Song et al. (2014)
23.	<i>Urochloa brizantha</i> (C <sub>4</sub> )	75 days with temperature treatment	+54.5%	Faria et al. (2018)
24.	<i>Megathyrsus maximus</i> (C <sub>4</sub> )	75 days with temperature treatment	+56.7%	Faria et al. (2018)
25.	<i>Stipa baicalensis</i> (C <sub>3</sub> )	3 months	+	Wang et al. (2019)

Note: + = increase; - = decrease; NS = not significant

## ELEVATED CARBON DIOXIDE AND NITROGEN CONCENTRATION IN PLANT PARTS

CO<sub>2</sub> elevation brings about a negative response on N concentration among most of the grasses considered (Table 7). A reduction in total leaf nitrogen content has been reported in previous studies (Davey et al. 1999). Cotrufo et al. (1998) reviewed experiments regarding elevated CO<sub>2</sub> effects on nitrogen concentration of plants including grasses and found a statistically significant decline in N concentration in plants grown under elevated CO<sub>2</sub> than control. Due to increased assimilation at elevated CO<sub>2</sub>, up to 30% of leaf nitrogen is transported to Rubisco (Evans 1989). At elevated CO<sub>2</sub>, a major portion of leaf nitrogen is reallocated to other photosynthetic and non-photosynthetic processes (Sage 1994). A contradictory opinion by Coleman et al. (1993) is that the CO<sub>2</sub>-induced reduction in N concentration is not due to physiological changes, but is size dependent and results from enhanced plant growth. The actual mechanism responsible for the reduction of N under elevated CO<sub>2</sub> is not yet established; however, there are substantial hypotheses explaining this phenomenon (Taub & Wang 2008). The same authors opined increased carbohydrate levels and decreased N uptake as key mechanisms affecting plant N concentration at elevated CO<sub>2</sub>. Observations by McDonald et al. (2002) also testify to these hypotheses. The same study states that the plants with high WUE possess morphological,

allocational, and physiological root traits, thus there is a low transpiration-mediated N supply, compared with the rate of carbon accumulation. There are further reports on the inhibition of N uptake and transport under CO<sub>2</sub> elevation due to reduced transpiration rates (Correia et al. 2005, Jauregui et al. 2016). A recent report (Padhan et al. 2020) illustrates the genetic mechanisms behind N reduction under elevated CO<sub>2</sub>. Their CO<sub>2</sub> elevation experiment on bread wheat had shown the down-regulation of ammonia assimilating genes and up-regulation of reactive oxygen species at CO<sub>2</sub> enrichment.

## FUTURE STEPS

The carbon mitigation potential of terrestrial plants has been proven effective and profitable. Grasses possess more special adaptations and characteristics than other plant groups. Their fast growth even under unfavorable environmental conditions such as limited water and nutrient supply, higher temperature, higher CO<sub>2</sub> environments, etc. attribute to more consideration in CO<sub>2</sub> mitigation programs. Approximately 11000 species of grasses are reported worldwide (Clayton et al. 2015), but the carbon sequestration potential of a major share of them is still unexplored. Extensive experimentations on the CO<sub>2</sub> mitigation potential of remaining grass species over the world's savannas and grasslands is an upcoming need to improve our ability for selecting ideal species for CO<sub>2</sub> mitigation efforts. Effective utilization of grasses for

Table 7: Changes in nitrogen concentration at elevated CO<sub>2</sub>.

Sl. No.	Plant species	Duration of CO <sub>2</sub> treatment	N	Reference
1.	<i>Lolium perenne</i> (C <sub>3</sub> )	49 days	-	Ryle et al. (1992)
2.	<i>Agrostis capillaris</i> (C <sub>3</sub> )	79 days	NS	Baxter et al. (1994 a, 1994b)
3.	<i>Poa alpinia</i> (C <sub>3</sub> )	105 days	NS	Baxter et al. (1994 a, 1994b)
4.	<i>Festuca vivipara</i> (C <sub>3</sub> )	189 days	-	Baxter et al. (1994 a, 1994b)
5.	<i>Avena barbata</i> (C <sub>3</sub> )	One growing season	-25%	Jackson et al. 1995
6.	<i>Lolium perenne</i> -Root (C <sub>3</sub> )	One growing season	-	Jongen et al. (1995)
7.	<i>Panicum laxum</i> (C <sub>3</sub> )	1.5 months with low light/high light	NS	Ghannoum et al. (1997)
8.	<i>Panicum antidotale</i> (C <sub>4</sub> )	1.5 months with low light/high light	NS	Ghannoum et al. (1997)
9.	<i>Triticum aestivum</i> (C <sub>4</sub> )	2 growing seasons	-	Oijen et al. (1999)
10.	<i>Bouteloua gracilis</i> (C <sub>4</sub> )	7 months	-	Morgan et al. (2001)
11.	<i>Pascopyrum smithii</i> (C <sub>3</sub> )	7 months	-	Morgan et al. (2001)
12.	<i>Agrostis stolonifera</i> (C <sub>3</sub> )	65 days	-	Goverde et al. (2002)
13.	<i>Anthoxanthum odoratum</i> (C <sub>3</sub> )	65 days	-	Goverde et al. (2002)
14.	<i>Festuca rubra</i> (C <sub>3</sub> )	65 days	-	Goverde et al. (2002)
15.	<i>Poa pratensis</i> (C <sub>3</sub> )	65 days	-	Goverde et al. (2002)
16.	<i>Stipa baicalensis</i> (C <sub>3</sub> )	3 months	-9.7%	Wang et al. (2019)

Note: - = decrease; NS = not significant

agro-forestry practices is yet another option for effective and profitable mitigation of atmospheric carbon dioxide and soil stabilization.

## CONCLUSION

This review aimed to consolidate experimental findings on the physiological and growth responses of grass species at elevated CO<sub>2</sub> and to establish the significance and reasons for their responses. Positive responses of photosynthetic rate and total biomass at elevated CO<sub>2</sub> signify the potency of grass species to cope with CO<sub>2</sub>-enriched environments. Gas exchange parameters such as C<sub>i</sub> and g<sub>s</sub> showed contradictory responses. Augmented levels of C<sub>i</sub> could be considered an admirable response as it can further enhance the photosynthetic rate. As well, the stomatal conductance declined at elevated levels of CO<sub>2</sub> due to the feedback mechanism. This decline is also connected with parameters of water relations such as transpiration and WUE. The transpiration rate decreased and WUE increased at CO<sub>2</sub> elevation. Thus in effect, the decline in stomatal conductance is a positive response, as the grasses can survive in environments with enriched CO<sub>2</sub> and associated drought. TNC and plant biomass are yet other factors, which reflect carbon capture and storage. Increased TNC affects plant N concentration at elevated CO<sub>2</sub>. A C<sub>3</sub>-C<sub>4</sub> controversy exists in each of these plant responses discussed. C<sub>3</sub> plants benefit more at elevated CO<sub>2</sub> since it eliminates photorespiration. However, at longer periods of carbon dioxide ascend, C<sub>4</sub> grasses could nurture well due to their high water use and nitrogen use efficiency. After all, each grass species stores plentiful carbon in soil annually through the shedding of its fine-spread roots. This review ascertains that, despite the treatment condition, treatment duration, or photosynthetic pathway (C<sub>3</sub>/C<sub>4</sub>), the grasses subjected to experimentation could respond identically to elevated CO<sub>2</sub>. In CO<sub>2</sub>-enriched environments, grasses have the potential to mitigate atmospheric carbon dioxide and store photosynthates in their biomass and this ensures their effective utilization for carbon mitigation strategies.

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