

THE IMPACT OF CARBON DIOXIDE (CO₂) ENRICHMENT ON RICE (*ORYZA SATIVA* L.) PRODUCTION: A REVIEW

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Abstract

Rice (*Oryza sativa* L.) is one of the world's most important crops and the primary source of calories for more than three billion people worldwide, especially in Asia. Currently, atmospheric carbon dioxide (CO₂) concentration is 416 μmol mol⁻¹ and increasing rapidly due to industrialization, which is the main cause of global warming. Current climate change and rising CO₂ concentration in the atmosphere have varying global impacts on crop performance. As CO₂ is one of the limiting factors in photosynthesis, adding this gas can increase carboxylation activity, hence increasing productivity and yield. Elevated CO₂ (eCO₂) significantly impacted C₃ crops' productivity by increasing photosynthesis, biomass, and grain yield. Plants cultivated under eCO₂ conditions demonstrated better development and photosynthesis, lower transpiration, improved water efficiency, decreased inorganic nutrition concentration, increased plant hormone, and compact stomatal density than the plants grown under ambient CO₂ (aCO₂) conditions. This review discusses the effects of eCO₂ on rice plant photosynthesis and growth. The review also describes that eCO₂ increased yield components of rice plants. Finally, the current review emphasizes the grain quality of rice that was negatively affected by eCO₂. The review paper aims to describe rice production under CO₂ increases under climate changes in the future. The synthesis of all this information is helpful to the researchers, advisors of rice farmers, and policymakers to provide a favourable plan by using eCO₂ to increase rice plant growth and yield and maintain grain quality through enriching free-air CO₂ enrichment (FACE) system for the rice plant to produce enough, and high-quality food for the increasing population of the world.

Key words: Atmospheric CO₂, CO₂ enrichment, Elevated CO₂, *Oryza sativa* L., Rice growth, Rice production.

Introduction

Rice is a semi-aquatic annual grass plant. According to Muthayya *et al.*, (2014), *Oryza sativa* is the most common rice type that has become the staple food for nearly 3.5 billion people worldwide. Rice has been a staple food for humans for centuries. It is one of the world's most important crops and the primary source of nutrition for a large number of populations in Asian countries (Wang *et al.*, 2011). Furthermore, rice is consumed by more than half of the world's population, and 90% of rice is produced and consumed in Asian countries (Jing *et al.*, 2016), where more than 60% of the world's population lives (Khush, 2005).

The population of rice-producing and consuming nations has lately increased significantly; thus, it is an urge to increase food production to fulfill half of the world's food demand. Hence, there is a need to increase rice production by 40% by 2030 due to the increasing population in several nations and the decrease in the staple food supply, leading people in the developing world to suffer from malnutrition (Khush, 2005). Moreover, it was projected that the world population will reach 8.5 billion by 2030 and 9.7 billion by 2050 (UN, 2019). Hence, the demand for rice grain will continue to rise in the coming years due to the increase in the growing population and reduction in cropland (Wang *et al.*, 2011). Currently, the worldwide production of milled rice is about 495.78 million tonnes (Shahbandeh, 2021). While in estimation, the net demand for rice will increase to 525 million tons by 2050 due to population growth in some Asian countries (Abdullah & Adhana, 2006).

Global warming is a controversial modern climatic phenomenon that has been caused by the significant increase of CO₂ levels in the atmosphere (Wang *et al.*, 2011). Various environmental factors affect crop production, especially rice production, such as air temperature, atmospheric CO₂, light, water, and soil nutrients (Patindol *et al.*, 2015). Among the factors mentioned above, the most critical factors eCO₂ levels in the atmosphere are higher now than at any time in the past (Long *et al.*, 2004), which is about 416 μmol mol⁻¹ (Tans & Keeling, 2021). Crop physiological and yield performance have changed as well as positively impacted by eCO₂ concentration. For example, CO₂ has increased photosynthesis and crop water use efficiency in rice (Hasegawa *et al.*, 2013). Thus, rice is one of the plants that responds positively to the current climate changes, significantly increasing atmospheric CO₂ and temperature.

Many studies have been conducted to evaluate the effects of eCO₂ on crop performance other than rice on yield and grain quality. In rice, eCO₂ was shown to significantly increase the growth of rice seedlings by 9% (Abzar *et al.*, 2017). Furthermore, eCO₂ enhances photosynthesis, thus increasing rice yield (Hesagawa *et al.*, 2013). The biomass and grain were increased; however, nitrogen (N) concentration in rice grain was decreased in eCO₂ condition (Lieferring *et al.*, 2004). Jia *et al.*, (2015) also stated that eCO₂ stimulates the mineral uptake through roots and upward transport of minerals in rice plants. Other studies demonstrated that eCO₂ concentration and temperature have strongly affected rice yield and the emission of methane (CH₄) and nitrous

oxide (N_2O) in rice fields (Wang *et al.*, 2018). Whereas some of the researchers reported that traditional flooded rice grown under eCO_2 tends to increase the spikelet number per panicle from 24% to 27%, the degeneration of spikelet number per panicle was reported to be 60% to 69% (Liu *et al.*, 2017). In addition, Cheng *et al.*, (2009) reported that eCO_2 significantly increased grain weight in brown rice. Nonetheless, a negative correlation between eCO_2 and rice quality was also observed, where eCO_2 , in combination with heat stress, increased the rice chalkiness and amylose content while reducing protein and grain mineral nutrients (Chaturvedi *et al.*, 2017).

Currently, a significant improvement in the global yield and quality of rice to produce sufficient food for the world population is a dire need. Therefore, there is an urgent concern to increase rice production to meet the global population demand. On the other hand, the world's significant determinants in changing food production are to fulfil the expected demands of increasing CO_2 in the atmosphere, which causes global warming (Long & Ort 2010). Rice CO_2 enrichment will not only improve rice production by increasing growth and yield, but it also can avoid the negative impacts of increasing temperature due to increase water use efficiency. One of the options to benefit from global warming significantly increasing CO_2 levels in the atmosphere is to evaluate the effects of eCO_2 on rice plants by designing several experiments and research to improve rice plant performance, growth and yield.

On the other hand, nutritional value and yield are the two most essential priorities in rice production (Wang *et al.*, 2018), which can produce more rice for the world's increasing population through increasing CO_2 concentration in the atmosphere. Recent research on the effects of eCO_2 on rice plants focused on growth and yield and grain quality separately. Many studies have reported that the development and yield were affected positively by eCO_2 , but the qualities of rice grains were negatively affected. This review addresses the impact of CO_2 enrichment on the growth, yield, and quality of rice altogether in order to provide some insight and suggestions regarding previous research on eCO_2 , specifically in rice. Moreover, this review is anticipated to facilitate further research work to improve crop production, especially in rice using CO_2 enrichment under climate changes in the future, and at the same time enhance or maintain the quality of rice grain.

Increasing atmospheric CO_2 concentration: The concentration of greenhouse gases such as CO_2 , nitrous oxide (NO_2), and methane (CH_4) has rapidly increased recently, affecting the crops' physiology, development, and structural characteristics. Before the industrial revolution, the concentration of CO_2 was around $270 \mu\text{mol mol}^{-1}$ and constant for at least 1000 years (Leakey *et al.*, 2009). Nevertheless, after the industrial revolution, the CO_2 concentration rose to $387 \mu\text{mol mol}^{-1}$ in 2009 and climate changes have been correlated with the rise in atmospheric CO_2 concentration (Leakey *et al.*, 2009). This concentration increases to $416 \mu\text{mol mol}^{-1}$ in an updated record in Aug (2021) (Tans & Keeling, 2021).

Increasing atmospheric CO_2 is one of the crucial factors that cause climate change. The concentration of CO_2 in the atmosphere is expected to increase from $370 \mu\text{mol mol}^{-1}$ to $540\text{-}970 \mu\text{mol mol}^{-1}$ at the end of the current century (Liu *et al.*, 2017). In another estimation, the concentration of CO_2 in the atmosphere is expected to increase to $550 \mu\text{mol mol}^{-1}$ at the end of this century (Leakey *et al.*, 2009). Due to deforestation, industrial and economic development, especially in industrialized nations, the concentration of CO_2 in the atmosphere is projected to increase in the next several decades (Feng *et al.*, 2014). eCO_2 of specific concentrations can positively influence plant growth and performance due to an increase in carboxylation rate of photosynthesis that leads to greater production of carbohydrates which is translated into greater yield. The stimulation of CO_2 to increase the rate of photosynthesis, particularly in rice, seems to be an important effort to improve rice yield production in order to cater to the increasing global food demand.

Carbon dioxide supply for photosynthesis: The light-independent reaction of photosynthesis is where the CO_2 is required for sugar production. Hence, CO_2 is the raw material in the photosynthesis process that has a significant effect on the growth and production of the plant (Zhang *et al.*, 2012). During photosynthesis, CO_2 diffuses through the leaf's interior to reach the chloroplast, where it is incorporated into carbohydrates, and water vapor and oxygen diffuse out through the stomata (Narawatthana, 2013). Moreover, CO_2 concentrations are also important in regulating the opening of stomata, the pores through which plants exchange gasses, with the external environment (Taub, 2010). Open stomata allow CO_2 to diffuse into leaves for photosynthesis, and at the same time, provide a pathway for water to diffuse out of leaves (Taub, 2010).

The light-independent reaction of photosynthesis consists of three main phases: carboxylation, reduction, and regeneration. In a light-independent response, the chloroplast stroma uses a large portion of the energy and reduces energy produced through photosynthetic electron transport (Dusenge *et al.*, 2019). The Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) enzyme fixes CO_2 to ribulose-1,5-bisphosphate (RuBP), resulting in a 3-phosphoglycerate (PGA) molecule (Dusenge *et al.*, 2019). This PGA is converted to 1,3-bisphosphoglycerate, which requires energy from ATP before being reduced to glyceraldehyde 3-phosphate (G3P), which requires NADPH (Dusenge *et al.*, 2019). The rest of the G3P is used to produce glucose, sucrose, and other carbon-based compounds, while some are used to regenerate RuBP (a process that also consumes ATP) (Dusenge *et al.*, 2019). CO_2 enrichment in the plants stimulates and increases the rate of carboxylation reaction and reduces oxygenation, hence producing more sugar, leading to an increase in plant growth rate.

Effects of elevated CO_2 on photosynthesis: The first process that enhances plant growth is by increasing the photosynthesis rates, contributing to the morphological changes in plants, such as changes in root to shoot proportion and increasing leaf area and tiller development

(Costa *et al.*, 2003). eCO₂ affected plants due to changes in physiological processes, biomass production, and the yield of major crops (Costa *et al.*, 2003).

Most plants use the C₃ mechanism of photosynthesis, also called the cycle of photosynthetic carbon reduction (PCR). C₃ plants have a single type of chloroplast that conducts all the reactions that transform the sun's energy into chemical energy used to fix CO₂ and synthesize carbon compounds (Furbank & Taylor, 1995). Photosynthesis response to eCO₂ in C₃ plants is photosynthetic carbon uptake which eCO₂ improves despite photosynthetic capability modification (Leakey *et al.*, 2009). In the C₃ crop, eCO₂ induced photosynthesis to increase, resulting in Rubisco's two-properties transition. First, the CO₂ enzyme's K_m (Michaelis constant), which measures the kinetics of the Rubisco, is the relative presence of CO₂ concentration; thus, eCO₂ improves carboxylation level. Second, CO₂ prevented the oxygenation reaction, glycolate production, and CO₂ released in the photo respiratory phase (Long & Ort 2010).

Responses of rice photosynthesis to elevated CO₂:

The high concentration of CO₂ demonstrated a favorable impact on the rice plant, which increased the photosynthetic intensity (Abzar *et al.*, 2017). Rice plants show more response to eCO₂ by developing several tillers in eCO₂ (700 μ mol mol⁻¹) than the control (350 μ mol mol⁻¹) in response to higher photosynthetic rates (Seneweera & Conroy 1997). The positive reactions of the rice plant to eCO₂ are due to the rice plant being one of the sources and sink plants that can increase photosynthesis and grow faster, especially at the early stage of growth, through producing more tillers. eCO₂ significantly increased leaf net photosynthetic rate A (max) at the panicle initiation stage (Wang *et al.*, 2020). The high net photosynthesis rate under eCO₂ conditions is most likely due to an increase in the carboxylation rate in photosynthesis.

eCO₂ increases photosynthesis, thus increasing development and crop yield (Hasegawa *et al.*, 2013). In addition, eCO₂ also enhanced the photosynthesis process, thus increasing rice plant tillers (Maity *et al.*, 2019). On the other hand, Leakey *et al.*, (2009) suggested that eCO₂ stimulates photosynthetic carbon build-up, and net primary development has ended down-regulation of rubisco activity, and CO₂ has even reduced dark respiration. Thus, eCO₂ increased the overall net photosynthesis per unit leaf area during the heading stage of rice plant growth (Sakai *et al.*, 2001).

In addition, considering the photosynthetic rate adjustment, carbon enhancement in CO₂-grown plants is projected to be 19-56% higher by the middle of this century (Leakey *et al.*, 2009). The rate of assimilation in the FACE plant leaves remained lower than that of the ambient leaves when exposed to the same CO₂ concentration, and this showed that there was photosynthetic eCO₂ acclimatization (Khush, 2005). Interaction effects between eCO₂ and rising temperatures will be advantageous for rice leaf photosynthesis but not growth or development due to overriding environmental factors such as increasing temperature (Wang *et al.*, 2020).

Methods of CO₂ enrichment: Research on evaluating the effects of eCO₂ on rice has been carried out since 1970 as Yoshida (1973) conducted the first research to assess the impacts of eCO₂ enrichment at different stages of rice plant panicle development on yield by using an open-top chamber (OTC) experiment. Later, many other researchers have designed various experiments and performed multiple settings for CO₂ enrichment, including greenhouses and chambers. Okada *et al.*, (2001) described the FACE system in which plants treated with high CO₂ concentrations (200 μmol mol⁻¹ above ambient) in a ring structure. Then the method described by Okada *et al.*, (2001) was used by many other researchers to evaluate the effects of eCO₂ on rice (Kim *et al.*, 2003, Xu *et al.*, 2006, Zhang *et al.*, 2008, Guo *et al.*, 2015, and Wang *et al.*, 2020). However, some researchers used OTC to study the CO₂ enrichment in rice (Wang *et al.*, 2015, and Lamichaney *et al.*, 2019). Nevertheless, it was implied that plants grown in chambers might not experience the effects of increasing CO₂ the same way as plants growing in a natural condition (Taub, 2010). For this reason, techniques of FACE have been developed that allow agricultural ecosystems to be fumigated with eCO₂ in the field (Taub, 2010).

OTC is designed to simulate climate change scenarios in rice by automatically controlling the CO₂ inside a chamber (Wang *et al.*, 2018). The chambers were constructed with different shapes of stainless-steel structures of different sizes, and a polycarbonate plate was used to cover the chamber. The top of the chambers has an opening for gas exchange, and an auto-induction control system is installed to control the CO₂ concentration inside the chamber. OTC is equipped with a CO₂ gas cylinder containing a pressure regulator valve, a flow meter, and CO₂ distribution tubes (Wang *et al.*, 2018, Satapathy *et al.*, 2015).

On the other hand, in the FACE system, the plants are exposed to eCO₂ in an open field condition. In this system, the plants are grown within an area where the above canopy is surrounded by rings or tubes that release the air containing CO₂ (Kim *et al.*, 2003) or pure CO₂ gas to generate a zone with high CO₂ concentration than the surrounding atmosphere (Okada *et al.*, 2001). A FACE system using a pure CO₂ injection on rice has been described in detail by Okada *et al.*, (2001).

Other than FACE and OTC systems, smart chambers and controlled greenhouses were also used for CO₂ enrichment in plants. For example, an ornamental plant, *Impatiens hawkeri* was grown in a smart chamber equipped with a computer system that automatically controls the temperature, relative humidity, photosynthesis active radiation (PAR), and CO₂ (Zhang *et al.*, 2012). For other crops, Hogy *et al.*, (2009) and Broberg *et al.*, (2019) treated wheat in FACE to study the effects of eCO₂ on wheat yield and quality. Soybean was also grown in an enclosed top chamber by Li *et al.*, (2013) as well kidney beans were treated with eCO₂ in a controlled environment (Prasad *et al.*, 2002). Among the above CO₂ enrichment systems, while each of the systems has its characteristics, FACE systems are the most commonly used in the recent two decades by researchers worldwide, and this method seems to be more applicable in the open area such as rice fields.

Effects of elevated CO₂ on rice plant growth: Plants respond in numerous ways to eCO₂ conditions. The differential response is limited to structural carbon accumulation and extends to the metabolism of small molecules. In regulating plant growth and stomatal movement, some of the reactions of plants may function as signaling molecules (Levine *et al.*, 2008). eCO₂ affects the productivity of C₃ plants, including rice, by increasing photosynthesis, biomass, and grain yield (Hasegawa *et al.*, 2013). eCO₂ also showed positive effects on the wheat plant where HD-2285 wheat variety grown under eCO₂ (600 ± 50 μmol mol⁻¹) in an OTC system demonstrated significantly greater photosynthetic rate, plant height, leaf area, and plant dry mass at all stages of growth than those grown under aCO₂, (350 ± 50 μmol mol⁻¹) (Pal *et al.*, 2005).

Effects of elevated CO₂ on rice seed germination: eCO₂ (800 μmol mol⁻¹) has been shown to significantly increase the growth and germination rate of the rice seedling grown in a glasshouse, which increased from 83% to 92% (Abzar *et al.*, 2017). Furthermore, high CO₂ (200 μmol mol⁻¹ above ambient) concentration increased rice seed germination rates and early seedling growth in the FACE system (Hasegawa *et al.*, 2013). Conversely, a study by Lamichaney *et al.*, (2019) on IR36 rice variety that was treated with different concentrations of eCO₂ (510 μmol mol⁻¹, 610 μmol mol⁻¹, and 710 μmol mol⁻¹) and aCO₂ of 410 μmol mol⁻¹ has reported that the exposure of rice plants to eCO₂ up to 610 μmol mol⁻¹ did not affect the germination of freshly harvested seed grown in OTC. Nevertheless, eCO₂ of 720 μmol mol⁻¹ reduced the germination of freshly harvested seeds, as well as eCO₂ at 610 and 720 μmol mol⁻¹ that showed reduced seed vigour (Lamichaney *et al.*, 2019). It was implied that the physiological makeup of the seeds or embryo might have been altered by high CO₂ concentration, thus, increases the number of abnormal and dead seedlings observed. Moreover, the reduction in the seed sugar content was reported in all eCO₂ seeds, and it was implied that the poor germination in high CO₂ treated seeds may have also been due to reduced metabolic activity due to reduced sugar content. Based on the above findings, it was shown that the eCO₂ concentration exposed to the plants has different effects on the parameters mentioned above in the FACE and OTC systems.

Effects of elevated CO₂ on plant height of rice: An increase in the concentration of atmospheric CO₂ (550 μmol mol⁻¹) has specific favourable impacts on Pusa basmati 1509 rice variety growth using the OTC system (Maity *et al.*, 2019). For example, eCO₂ dramatically increased rice plant height from 76.9 cm to 81.7 cm in an ambient condition (Maity *et al.*, 2019). Likewise, the plant height of Pusa 44 rice variety in the eCO₂ (550 ± 20 μmol mol⁻¹) treatment was 81.7 cm as compared to the plant height in the ambient condition, which was 76.9 cm with a recommended dose of N manure in the FACE system (Raj *et al.*, 2019). An increase in plant height may have been due to the fast growth of the rice plant under eCO₂ conditions, which is the result of an increase in cell division and elongation as Raj *et al.*, (2019) reported a

similar rise in rice plant height treated with eCO₂ and different levels of N treatments.

Effects of elevated CO₂ on the biomass of rice: The dry mass of the rice plant was enhanced in eCO₂ and high temperatures (Maity *et al.*, 2019). Jia *et al.*, (2015) also reported that eCO₂ (200 μmol mol⁻¹ above ambient) significantly increased the biomass of stem and panicle of Wuxiangjing 14 rice varieties grown in a FACE facility by 21.9% and 24.0%, respectively. Furthermore, shoot dry weight in Nipponbare rice variety was significantly increased by 10% under high CO₂ (700 μmol mol⁻¹) conditions (Sakai *et al.*, 2001). In an OTC, the eCO₂ enhanced the above-ground and root biomass compared to the ambient condition (Satapathy *et al.*, 2015). Moreover, eCO₂ significantly increased root and shoot biomass (Raj *et al.*, 2019). Greater rice plant biomass was the product of higher rice plant development under eCO₂ treatment (Raj *et al.*, 2019). However, shoot length, root length, total seedling length, dry weight of seedling, and root to shoot ratio showed no significant effects under eCO₂ conditions (Lamichaney *et al.*, 2019). Xu *et al.*, (2006) reported similar results that the above-ground biomass shows no major impact on N treated by eCO₂ (200 μmol mol⁻¹ above ambient) during the growing season of rice plants system. While the dry mass partitioning was altered between the root and shoot dry mass by eCO₂, which opposed the sheaths and blades, the roots partitioning dry mass was high under eCO₂ (Costa *et al.*, 2003). Sakai *et al.*, (2001) had published similar findings when eCO₂ (200 μmol mol⁻¹ above ambient) did not significantly impact the leaf area under OTC. It was also implied that eCO₂ had affected root biomass responses two times the above-ground biomass (Liebering *et al.*, 2004). These favourable eCO₂ effects on the total biomass have reduced the period of flowering in the crop growth phase (Kim *et al.*, 2003).

eCO₂ using the FACE system in Japan demonstrated that tiller numbers and dry root biomass of the Akita Komachi rice variety were greater in all growth phases, particularly during the middle to late phases under eCO₂ (200 μmol mol⁻¹ above ambient) treatment conditions. Moreover, the average tiller number per unit area of land was higher than the aCO₂ (Inubushi *et al.*, 2003). Similarly, an increase in the number of tillers of a short-duration rice variety BG-300 under eCO₂ (570 μmol mol⁻¹) than that of the aCO₂ (370 μmol mol⁻¹) treatment using OTC system was reported by Costa *et al.*, (2003) in Sri Lanka. Furthermore, the number of tillers at panicle initiation of rice was increased by eCO₂; however, the growth phases of the plant were decreased by eCO₂ than control (Kim *et al.*, 2003). Seneweera *et al.*, (2011) discovered that eCO₂ (700 μmol mol⁻¹) increased the number of tillers of Jarrah rice variety by 50%. An increase in the tiller number of rice plants has described that the rice plant potential to respond positively to the eCO₂, which increases the photosynthesis process resulting in fast cell division.

The leaf area index (LAI) of rice under eCO₂ was significantly different during the vegetative growth phases after panicle initiation (Kim *et al.*, 2003). Costa *et al.*, (2003) observed that under eCO₂ conditions (570 μmol

mol⁻¹), the LAI was significantly higher than the ambient (370 μmol mol⁻¹) condition due to high CO₂ increased carboxylation in photosynthesis and cell elongation.

Effects of elevated CO₂ on yield components of rice:

Crop yields have been documented to be significantly improved by eCO₂ treatment in previous studies (Kim *et al.*, 2003, Costa *et al.*, 2003, Cheng *et al.*, 2009, Raj *et al.*, 2019, and Lv *et al.*, 2020). The two most critical goals in rice development are improved grain yield and quality, and these two goals have been achieved by using the FACE system (Yang *et al.*, 2007). Besides, Wang *et al.*, (2015) reported that eCO₂ improved rice yield in a CO₂ concentration of 60 μmol mol⁻¹ higher than the ambient condition. Lv *et al.*, (2020) also reported that eCO₂ (200 μmol mol⁻¹ above ambient) in the FACE system increased rice yields by 13.5%, 22.6%, and 32.8% for japonica, indica, and hybrid cultivars, respectively.

Increases in rice production have also been directed by the number of panicles that contribute to many productive spikelets per unit area (Kim *et al.*, 2003). Panicle density and spikelet density were generally higher under the eCO₂ condition (Lv *et al.*, 2020). The number and filled spikelets per panicle were increased by 16% (Wang *et al.*, 2015). Cheng *et al.*, (2009) also recorded that the number of filled spikelets per panicle of IR72 rice variety was positively influenced by eCO₂ and high temperatures at night in a controlled environment chamber. Nevertheless, eCO₂ did not significantly increase the single grain weight (Lv *et al.*, 2020). In another analysis, the number of spikelets per panicle was recorded to decrease the spikelet density by night temperature, an essential factor in rice yield influenced by CO₂ and high-temperature interaction (Wang *et al.*, 2018). The number of spikelets per panicle was enhanced from 24% to 27% in the conventional flooded rice grown under eCO₂, and the degeneration of the number of spikelets per panicle was 60-69% (Li *et al.*, 2008).

Rice grain production and biomass were substantially higher under eCO₂ conditions (Raj *et al.*, 2019). Besides, the yield of fertile grains of the rice plant per land area in the eCO₂ (200 μmol mol⁻¹ above the ambient condition) was considerably improved relative to the ambient condition by 14% using FACE (Lieffering *et al.*, 2004). Moreover, OTC significantly decreased the number of grains per panicle as well as grain yield in contrast to the ambient condition (Satapathy *et al.*, 2015). However, Li *et al.*, (2008) recorded that under eCO₂ conditions, 1000 grain weight increased from 2% to 9%.

Costa *et al.*, (2003) have reported a substantial increase in yield of 25.5% in eCO₂ with the recommended nitrogen rate relative to the ambient condition. In another analysis, rice production was stated to have increased dramatically by 20%, but there were no significant grain size and yield (Wang *et al.*, 2015). Hybrid rice demonstrated substantially improved plant development under eCO₂ of 600-699 μmol mol⁻¹ (Wang *et al.*, 2015). It was speculated that the rise in grain yield of high CO₂ was attributed to an increased number of productive tillers (Seneweera & Conroy 1997).

Rice yield interaction with eCO₂ and temperature response were different in terms of eCO₂ concentration

level and fumigation method used in the experiment (Wang *et al.*, 2015). Stimulating yield components in eCO₂ in plant species is also considered smaller than expected (Leakey *et al.*, 2009). While generally, the increase in C₃ crops photosynthesis resulting from the FACE system is more significant than the biomass or yield (Leakey *et al.*, 2009). Hence, it was demonstrated that increases in the rice yield under eCO₂ conditions were most likely due to high photosynthetic capacity, fast growth, increase in tillers and panicle number, and filled grain per panicle.

Effects of elevated CO₂ on the quality of rice:

Rice is mainly consumed after milling. Therefore, the consistency of rice grain is defined by the appearances and properties that control the cooking characteristics and the rice grain's nutritional value (Seneweera & Conroy 1997). Rice grain quality has also been reported to be impacted by eCO₂ alone or by combination with heat stress by growing chalkiness, altering amylose content, and reducing protein and grain mineral nutrients in an OTC experiment (Chaturvedi *et al.*, 2017). ECO₂ slightly increased the amylose to amylopectin ratio by 10.1% (Jing *et al.*, 2016). The critical features in rice quality production are directly linked to the market value and impact the benefit for both the manufacturer and the processor of rice (Yang *et al.*, 2007).

ECO₂ not only increased the yields by 27%, but it decreased grain content, such as protein concentration, by 27%, which was due to a decrease in grain N (Seneweera & Conroy 1997). It was also reported that CO₂ treatments (ambient 350 μmol mol⁻¹ and elevated 700 μmol mol⁻¹) and phosphorus (P) fertilizer, according to chemical properties, has negatively influenced the consistency of the rice grain (Seneweera & Conroy 1997). Moreover, the hardness of rice grains has been decreased by eCO₂ conditions (Yang *et al.*, 2007). Furthermore, the leaf nitrogen content of rice treated with eCO₂ was lower than that of the control (Peipei *et al.*, 2020).

A chemical study found that the amylose and minerals of cooked rice grain collected from eCO₂ plants were higher, and the concentration of zinc (Zn) and iron (Fe) was lower, as compared to ambient conditions (Seneweera & Conroy 1997). Likewise, Jai *et al.*, (2015) reported that eCO₂ significantly increased the contents of Ca, Mg, Fe, Zn, and Mn in the panicle by 61.2, 28.9, 87.0, 36.7, and 66.0%, respectively, and in the stem by 13.2, 21.3, 47.2, 91.8, and 25.2%, respectively. The content of these minerals in the leaf, however, was not significantly affected. Moreover, there were no increases in grain macronutrients under eCO₂, but the decline in grain protein content was substantial (Seneweera, 2011). Furthermore, the results revealed that eCO₂ reduced nitrogen concentration but only for the early growth stage (Kim *et al.*, 2003). It has been proposed that proper control in applying macro and microelements is the secret to preserving grain consistency under eCO₂ conditions (Seneweera, 2011).

Low N in the plant was the first cause of grain protein reduction under eCO₂ conditions (Seneweera, 2011). ECO₂ did not influence crop hull thickness or seed-specific gravity but significantly decreased the

concentration of total nitrogen and protein (Chen *et al.*, 2015). Other findings showed that the milling effect was not interchangeable for both FACE and ambient rice plants, slightly relative to the ambient condition of grain from FACE treatments (Yang *et al.*, 2007). Greater knowledge of CO₂ impacts on food quality, such as mineral nutrients, would greatly benefit food stability and human health (Jia *et al.*, 2015).

From all the information mentioned above regarding rice seed quality treated by eCO₂, it can be concluded that eCO₂ has negatively affected rice grain quality, especially for N and protein. However, for other macro and micronutrients and milling characteristics, it was unchanged or reduced.

Future direction and challenges in applying elevated CO₂ to plants: Due to the current climate change in the world caused by rising CO₂ concentration and temperature, and increasing population globally, especially in Asian developing countries, the use of CO₂ in crop production, especially in rice, is a promising alternative to face global warming in the future. In previous research, rice plants showed positive responses to eCO₂ treatment, however negative responses to increasing temperature. Thus, studies on CO₂ enrichment for rice production using FACE systems will help improve rice growth, development, and yield and improve water uses efficiency, which is beneficial when water is limited. The concept of CO₂ enrichment in rice can be applied commercially in developing countries by government agencies, private companies, and research centers, but it may not be efficiently utilized or adopted by conventional farmers in many developing countries such as Malaysia. This limitation is due to the high cost of providing and installing the eCO₂ facilities and equipment such as the FACE system, OTC, innovative greenhouse, CO₂ sources, expertise, and technical staff. Given that the cost to set up the facilities is very high, it would be more beneficial for conventional farmers if these agencies could provide some assistance in terms of facilities or equipment and CO₂ resources for a lower price, thus affordable for the regular farmers to adopt this technology in their field.

Rice serves as the primary staple food for more than half of the world's increasing population, especially in Asian countries; hence, many studies focusing on CO₂ enrichment on this crop within this region should be conducted to prepare for the rise in CO₂ concentration in the upcoming years. Although the increase of CO₂ showed a positive response to rice plant growth and grain yield in many studies, the grain quality was negatively affected. Furthermore, it is recommended that further research be carried out to determine the optimum concentration of CO₂ and the amount of macro and microelements required to enhance grain quality and growth, and yield. This will facilitate in determining the correct number of resources to be used with low production costs while improving rice production and quality under typical rice field cultivation.

Conclusions

Since ancient times, rice has been the staple food for individuals in different nations. Global warming is a controversial modern climatic phenomenon that is the primary cause for the significant increase of carbon dioxide (CO₂) levels in the atmosphere. Currently, CO₂ levels in the atmosphere are higher than at any time in the past. The changes in the current climate and rising atmospheric CO₂ concentration have different impacts on crop performance globally. The most important response of plants to higher CO₂ levels in the atmosphere is increased growth and yield. Elevated CO₂ (eCO₂) has been shown to increase rice plant net photosynthesis and water use efficiency.

Furthermore, eCO₂ increased rice seedling germination, vigour, and speed of germination. Likewise, eCO₂ increased the number of tillers, biomass, plant dry mass, plant height, leaf area, shoot dry weight. eCO₂ affected rice plant growth and increased rice grain yield and yield components such as the number of panicles, the number and fertile spikelets, filled spikelets, and 1000 grain weight. However, eCO₂ has negatively affected rice grain quality by increasing the rice chalkiness, reducing the amylose content, and reducing protein and grain mineral nutrients. Grain N and protein concentration, rice grains' hardness, Zn concentration, and Fe decreased by eCO₂; however, increased the amylose to amylopectin ratio under eCO₂.

On the other hand, an increase in atmospheric CO₂ has led to increased atmospheric temperature and further negatively affected rice plant growth and production. In conclusion, eCO₂ of a particular concentration, such as 200 $\mu\text{mol mol}^{-1}$ above the ambient condition, has positively affected rice plant growth and yield and decreased grain N and protein concentration. Due to this, it is recommended that treating rice plants with different concentrations of eCO₂ supplemented with varying doses of macro and micronutrients could possibly help to improve rice plant growth, productivity, yield, and ultimately the grain quality. Moreover, it was suggested that the application of eCO₂ at an optimum concentration with a moderate increase in temperature could be beneficial for rice plants to improve their growth, yield, and grain quality in future climate changes. This strategy may help reduce the negative effects of high temperature, and the plants will be more tolerant to drought due to an increase in water use efficiency under eCO₂.

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