We are IntechOpen, the world's leading publisher of Open Access books
Built by scientists, for scientists

6,900
Open access books available

186,000
International authors and editors

200M
Downloads

Our authors are among the

154
Countries delivered to

TOP 1%
most cited scientists

12.2%
Contributors from top 500 universities

CLARIVATE ANALYTICS

BOOK CITATION INDEX

INDEXED

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com

Photosynthesis and Quantum Yield of Oil Palm Seedlings to Elevated Carbon Dioxide

H.Z.E. Jaafar and Mohd Hafiz Ibrahim
Universiti Putra Malaysia (UPM)
Malaysia

1. Introduction

Photosynthesis is a metabolic process through which green plants synthesize organic compounds from inorganic raw materials in the presence of sunlight. This process can be regarded as a procedure of converting radiant energy of the sun into chemical energy of plant tissues in the form of organic molecules. Photosynthesis increases the total free energy available to organism and provides energy to the world, directly or indirectly, necessary for sustaining all forms of life on earth. Farming is basically a system of exploiting solar energy to synthesize organic matter through photosynthesis. The yield of crop plants ultimately depends on the size and efficiency of their photosynthetic system (Anderson, 2000). The most important factors of biomass production of any crop are the amount of radiation intercepted by the crop and the effectiveness of using the radiation in dry matter production. All organisms on earth need energy for growth and maintenance. As a result, higher plants, algae and certain types of bacteria capture this energy directly from the sunlight and utilise it for the biosynthesis of essential food materials for dry matter increase. The plant photosynthetic apparatus contain the necessary pigments in leaf able to absorb light and channel the energy of the excited pigment molecules into a series of photochemical and enzymatic reactions. Light energy is absorbed by protein-bound chlorophylls that are located in light-harvesting complexes and the energy migration to photosynthetic reaction centres results in electron excitation and transfer to other components of the electron transfer chain (Hall and Rao, 1999).

Carbon dioxide is a trace gas in the atmosphere, presently accounting for about 0.037%, or 370 parts per million (ppm), of air. The partial pressure of ambient CO_2 (Ca) varies with atmospheric pressure and is approximately 36 pascals (Pa) at sea level. The current atmospheric concentration of CO_2 is almost twice the concentration that has prevailed during most of the last 160,00 years, as measured from air bubbles trapped in glacial ice in Antarctica. For the last 200 years, CO_2 concentrations during the recent geological past have been low, fluctuating between 180 and 260 ppm. These low concentrations were typical of times extending back to the Cretaceous, when Earth was much warmer and the CO_2 concentration may have been as high as 1200 to 2800 ppm (Ehleringer et al., 1991). However, with the rapid increases in world population and economic activity, a doubling of the present atmospheric [CO_2], assuming a mean annual increase rate of 1.5 ppm, which was observed over the past decade 1984–1993 (Stoskoptf, 1981), could be expected before the end

of the 21st century (Baker and Ort, 1992). Rising atmospheric [CO_2] could benefit many economically important crops, especially the C3; however, gains may or may not be realized in long-term growth because of the interaction of various environmental factors that complicate the issue (Farquhar and Sharkley, 1982). The current CO_2 concentration of the atmosphere is increasing by about 1 ppm each year, primarily because of the burning of fossil fuels. Since 1958, when systematic measurements of CO_2 began at Mauna Loa, Hawaii, atmospheric CO_2 concentrations have increased by more than 17% (Keeling et al. 1995), and by 2020 the atmospheric CO_2 concentration could reach up to 600 ppm.

With the increase in [CO_2], many crops may be affected either positively or negatively. Oil palm is an industrial perennial plant widely cultivated in Southeast Asia where it plays a major role in the economics of the regional income. Claimed to be the most productive oil bearing plant as compared to coconut, olive, rapeseed and soybean, the crop has contributed about 8.2% of Malaysian gross domestic products (GDP) and the second largest economic contributor after exported goods and petroleum. In 2009, large area of about 4.6 million ha had been cultivated with oil palm. As the concentration of CO_2 is expected to increase to 600 ppm by 2020, the productivity of oil palm could also be increased. However, the research on oil palm acclimation to increased CO_2 issue is still lacking especially in the leaf gas exchange aspects.

Net photosynthesis and quantum yield are good indicators of plant acclimation to elevated CO_2. The notion of photosynthetic efficiency in the literature involves some different terms including photosynthetic rate, quantum yield of carbon assimilation and photochemical efficiency of PSII, which is often expressed as a ratio of variable to maximal fluorescence (Xu and Shen, 2000). These terms are different but they linked to each other. Both photosynthetic rate and quantum yield are related to characteristics of the leaf, cell, and chloroplast itself and the environmental conditions. Photosynthetic rate is often expressed as number of molecules of CO_2 fixed or O_2 evolved per unit leaf area per unit time while quantum yield is expressed as number of molecules of CO_2 fixed or O_2 evolved per photon absorbed. The efficiency of photosynthesis of the whole plant is crucial to agriculture, forestry, ecology, etc. when it comes to analyzing productivity for food and fuels and many other product users. The quality and quantity of photosynthetic incident light (or photosynthetic active radiation, PAR), temperature and water availability, mineral nutrients availability and utilization, photorespiratory losses, presence of pollutants in the atmosphere and in the soil (heavy metals), etc., are some of the factors that affect plant productivity. How these factors interact with the changing environment is now the subject of much practical and basic research.

This chapter focuses on the photosynthetic responses, particularly net photosynthesis and apparent quantum yield, of oil palm to enhanced growth [CO_2]. The leaf gas exchange and apparent quantum yield response of oil palm seedling to elevated [CO_2] will be discussed. The net photosynthesis and apparent quantum yield data are directly collected from LICOR 6400 using light response curve analysis. As the photosynthetic mechanism of a plant species is the major determinant of how it will respond to rising atmospheric [CO_2], understanding the mechanisms of photosynthesis acclimation to rising [CO_2] could potentially be translated into a basic framework for improving the efficiency of crop production in a future climate-changed world.

2. Factors limiting photosynthetic rates

A number of external environmental factors can influence the rate of photosynthesis, leading to up-regulation or down-regulation of photosynthetic capacity. These factors might

be low or high temperature, deficiency or over supply of water or nutrient, low CO_2 or high O_2 concentration, and low light intensity. In the meantime, many plant internal factors including developmental hormones and respiration, etc. may also have a significant effect on net photosynthetic rate. The main limitation site of net photosynthetic rate in C3 plants, however, is often in the reaction centre catalyzed by the enzyme ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco). Therefore, reducing or eliminating its oxygenase function or photorespiration or increasing the affinity of the enzyme for CO_2 is a long-term goal to increase productivity of the plant (Xu and Shen, 2000).

3. Quantum yield

The quantum yield of a process in which molecules give up their excitation energy (known as "decay") is the fraction of excited molecules that decay via that pathway (Wells et al., 1982; Taiz and Zieger, 1991). The quantum yield of a process, such as photochemistry, has been defined (Clayton 1971; 1980) mathematically as the yield of photochemical products divided by total number of quanta absorbed. For a particular process, the value of quantum yield can range between 0 (when the process does not involve any decay of the excited state) and 1.0 (when the process involves deactivation of the excited state). Taiz and Zieger (1991) explained that all possible processes would ultimately contribute to a sum 1.0 of the quantum yields. Basically, in functional chloroplast that is kept in dim light, the quantum yield of photochemistry is approximately 0.95, the quantum yield of fluorescence is 0.05 or lower, and the quantum yields of other processes are negligible. The vast majority of excited chlorophyll molecules, therefore, lead to photochemistry.

The reciprocal of the quantum yield is called the quantum requirement. For a high yielding crop, it is not only a high photosynthetic rate in strong light is important but a high quantum yield in weak light is also crucial. Therefore, Ort and Baker (1988) believed that the improvement of future crop production should aim at increasing their quantum yield. It is well known that in photosynthesis of the Calvin-Benson cycle, the assimilation of one molecule of CO_2 into carbohydrate requires 2NADPH and 3ATP. The production of 2NADPH is the result of transporting four electrons from $2H_2O$ to 2NADP along an electron transport chain. Because the chain includes two photosystems in series, two photons are needed for one electron transport. Thus, at least eight photons are required for the production of 2NADPH. Therefore, the maximal or theoretical quantum yield for photosynthetic carbon assimilation is 0.125 mole CO_2/mole photons. In field studies Xu (1988) found that the apparent quantum yield of photosynthetic carbon assimilation often displayed a significant midday decline in many C3 plants such as soybean and wheat but not in C4 plants such as maize and sorghum. It was deduced that photoinhibition may be a cause of the midday decline of the photosynthetic efficiency (Xu et al. 1990). The molecular mechanism of photoinhibition, however, is still not fully understood. For more than a decade photoinhibition has been considered almost synonymous with photodamage to the photosynthetic apparatus (Nigoyi, 1999). In addition to photoinhibition, enhanced photorespiration is another cause of the midday decline in the photosynthetic efficiency of C3 plants (Guo et al., 1994). For a long time photorespiration has been considered a wasteful process. Many efforts have been made to eliminate or reduce photorespiration but no success has yet been reported. Extensive screening programs involving several species (wheat, barley, oats, soybean, potato, tall fescue) failed to identify genotypes with low CO2 compensation point (Hay and Walker, 1989). Attempts to select C3 plants with low rates of

photorespiration and high rates of net photosynthesis also have had little success (Xu and Shen, 2000).

3.1 Factors affecting quantum yield
3.1.1 External factors
Emerson and Lewis (1943) showed that the values of quantum yield were related to the quality of light. A high quantum yield was measured at red light around 680 nm. The quantum yields of sun and shade leaves grown under different light intensities were similar, although there was a significant difference in light saturated photosynthetic rate between them (Oquist and Hallgren, 1982). At 21% O_2 and a temperature range of 15–35°C the quantum yield decreased gradually with temperature increase in C3 plants but not in C4 plants (Ku and Edwards, 1978; Xu and Shen, 2000). Water deficiency and excessive water or flooding could lead to a decline in quantum yield (Mohanty and Boyer, 1976). After several rainy days, the photosynthetic quantum efficiency became lower in spinach leaves (Li et al. 1991). The reason may be that the reduction of NADP is severely hindered in swollen chloroplasts under hypotonic conditions (Ye et al., 1995). Decreasing O_2 concentration or increasing CO_2 concentration in air could increase quantum yield in C3 plants but not in C4 plants (Monson et al., 1982). This may be due to decreased excitation energy transport from antenna pigments to PSII reaction centers and enhanced excitation energy dissipation as heat under phosphate deficiency conditions (Jacob, 1995; Xu and Shen, 2000).

3.1.2 Internal factors
Among all internal factors, photorespiration has the most significant effect on quantum yield. The effects of air temperature and CO_2 or O_2 concentration on quantum yield mentioned earlier, in fact, are related to the changes in photorespiratory rate caused by these factors. In normal air and at 20–25°C, the quantum yields of C3 and C4 plants were similar. However, when the air temperature was over 30°C, the quantum yield in C4 plants was slightly higher than that in C3 plants (Ehleringer and Pearcy, 1983). When photorespiration was inhibited by high CO_2 and/or low O_2, C4 plants had about 30% lower quantum yields than C3 plants because they used two additional ATP molecules in the C4 pathway for fixation of one molecule of CO_2 to form carbohydrate (Osmond et al. 1980; Xu and Shen, 2000).

4. C$_3$ species response to elevated CO$_2$

The present atmospheric [CO_2] limits the photosynthetic capability, growth, and yield of many agricultural crop plants, among which the C3 species show the greatest potential for response to rising [CO_2] (Xu et al., 1984). Current atmospheric CO_2 and O_2 levels and C3 Rubisco specificity factors translate into photorespiratory losses of 25% or more for C3 species (Farquhar and Sharkey, 1982). The projection that a rise in atmospheric [CO_2] will reduce the deleterious effect of O_2 on C3 photosynthesis but that it has a negligible effect on C4 photosynthesis is indeed supported by experimental growth data. Exposure of C3 plants to elevated [CO_2] generally results in stimulated photosynthesis and enhanced growth and yield (Sharkawy et al., 1990).

A compilation of the existing data available from the literature for C3 agricultural crops, including agronomic, horticultural, and forest tree species, shows an average enhancement

in net CO_2 exchange rates up to 63% and growth up to 58% with a doubling of the present atmospheric [CO_2] (Brinkman and Frey, 1978). Long-term exposure to elevated [CO_2] leads to a variety of acclimation effects, which include changes in the photosynthetic biochemistry and stomatal physiology and alterations in the morphology, anatomy, branching, tillering, biomass, and timing of developmental events as well as life cycle completion (Evan and Dunstone, 1970). A greater number of mesophyll cells and chloroplasts have been reported for plants grown under elevated [CO_2] (Poskuta and Nelson, 1986). In terms of dark respiration, the exposure of plants to elevated [CO_2] usually results in lowering the dark respiration rate, which can be explained by both direct and indirect effects (Pettigrew and Meredith, 1994). The mechanism for the direct effect appears to be an inhibition of the enzymes in the mitochondrial electron transport system, and for the indirect (acclimation) effect of elevated [CO_2] on dark respiration may be related to changes in tissue composition (Yin et al., 1956; Xu and Shen, 2000).

Many C3 species grown for long periods at elevated [CO_2] show a down-regulation of leaf photosynthesis (Zelith, 1982); and carbohydrate source-sink balance is believed to have a major role in the regulation of photosynthesis through the feedback inhibition (Wells et al., 1986). Source-sink imbalances may occur during exposure to elevated [CO_2] when photosynthetic rate exceeds the export capacity or the capacity of sinks to use photosynthates for growth resulting in an accumulation of carbohydrates in photosynthetically active source leaves (Dong, 1991). Although growth is enhanced under elevated [CO_2] the extent to which starch and soluble sugars accumulate depends largely on the species differences. In many plants, the increase in starch also seems to be greater than that of soluble sugars. More frequently observed is the correlation between starch accumulation and inhibition of leaf photosynthesis (Wells et al., 1986) implying that high starch content may be responsible for down regulation of photosynthesis under elevated [CO_2]. For many plant species, the long exposure to elevated [CO_2] has also resulted in a down-regulation of Rubisco (Mohanty and Boyer, 1976). Zhang et al. (1992) observed the down-regulation in cotton, cucumber, parsley, pea, radish, soybean, spinach, tobacco and wheat exposed to elevated [CO_2] due to increased leaf acid invertase activities, an indication of starch accumulation in the leaf; conversely, an up-regulation of photosynthesis in bean, plantain and sunflower was also detected suggesting variations in responses by species differences to elevated [CO_2].

Levels of soluble sugars in plant cells have been shown to influence the regulation of expression of several genes coding for key photosynthetic enzymes (Osmond et al., 1980; Xu and Shen, 2000). The buildup in carbohydrates may signal the repression but does not directly inhibit the expression of Rubisco and other proteins that are required for photosynthesis (Oquist et al., 1982). Although the signal transduction pathway for regulation of the sugar-sensing genes may involve phosphorylation of hexoses, derived from sucrose hydrolysis by acid invertase via hexokinase (Guo et al., 1996), unknown gaps still exist between hexose metabolism and repression of gene expression at elevated growth [CO_2] (Hong and Xu, 1998; Xu and Shen, 2000).

5. Photosynthetic and quantum yield up-regulation under elevated CO_2

Carbon dioxide is the substrate that through the light and dark reactions of photosynthesis, are combined into dry mass (Pinkard et al., 2010). Thus [CO_2] can be a major factor limiting photosynthesis (Hall and Rao, 1992). Stomata regulate the diffusion of CO_2 into leaves;

stomata can respond sensitively to [CO_2] as part of a proportionate response to the CO_2 requirement for photosynthesis; increasing concentrations are, therefore, associated with a closing response and vice-versa (Pinkard et al., 2010). Hence, elevated [CO_2] is anticipated to increase or up-regulate photosynthesis, decrease stomatal conductance and increase intrinsic water-use efficiency i.e. the ratio of leaf photosynthesis to stomatal conductance (Long et al., 2004). Many factors other than [CO_2] determine photosynthetic rate, and the law of limiting factors (von Liebig, 1840) will ultimately determine photosynthetic responses to [CO_2] where more than one limiting factors may be involved. Sala and Hoch (2009) suggested that elevated CO_2 would improve carbon balance in light-limited as well as high-light environments through the CO_2 enhancement of quantum yield. The present CO_2:O_2 ratio of the air constrains photosynthesis by 30-40% because of O_2 inhibition of carboxylation and associated photorespiration (Booth and Jayanovic, 2005). As CO_2 concentration increases, quantum yield is increased because the ratio of carboxylation to oxygenation by Rubisco increases and photorespiration decreases (Pinkard et al., 2010). Several studies have shown that CO_2 enrichment enhances photosynthesis and growth under limiting irradiance condition, and in some cases the relative enhancement was greater at low rather than at high irradiances (Gifford et al., 1981). In C3 plants, elevated [CO_2] increases the quantum yield of photosynthesis by reducing photorespiration caused by the oxygenase activity of Rubisco. Maximum, single-leaf quantum yield was increased from 0·065 to 0·080 (Long and Drake, 1992).

Up-regulation of photosynthesis refers to a significant increase in the light-saturated rate of photosynthesis (A_{sat}), the rate of photosynthesis under ambient light (A), and/or diurnal photosynthesis (A). Elevated [CO_2] up-regulates photosynthesis by increasing the carboxylation rate (Vc) of ribulose bisphosphate carboxylase (Rubisco) and competitively inhibiting the oxygenation of ribulose bisphosphate (RuBP), thereby reducing photorespiration (Luo and Reynold, 1999). Elevated [CO_2] is also associated with the expression of several other changes that affect photosynthesis. The common observation of reduced stomatal conductance, gs, will tend to dampen the extent to which any up-regulation is expressed at a leaf-scale, but may conserve water such that stand-scale responses are positive (Ainsworth and Rogers, 2007).

Photosynthetic acclimation refers to longer-term adaptive changes in the photosynthetic responses to external stimuli that reduce the net level of the initial response; acclimation is also referred to as down-regulation (Pinkard et al., 2010). Acclimation is commonly observed and arises from the plant's need to balance all resources that are allocated for photosynthetic processes, including the external [CO_2] (Gunderson and Wullschleger, 1994). For elevated [CO_2], acclimation is mechanistically linked to decreased maximum apparent carboxylation velocity (Vc_{max}) and reduced investment in Rubisco (Rogers and Humphries, 2000). It is also associated with reduction in N content. These changes are linked to a decrease in control of A_{max} by Vc_{max} but an increase in the regeneration of RuBP, J_{max} (Long and Drake, 1992). There is also an increase in starch and sugar content.

In the short term, rising [CO_2] increases photosynthesis in many of the woody species as have been studied by Ainsworth and Long (2005). These species have the potential to yield significantly with increases in the rates of biomass accumulation. The allocation of dry mass to the above-ground parts in forest free air carbon dioxide enrichment (FACE) experiment was also found to increase by 28% on the average; this includes a greater allocation to woody components. In general, larger responses in growth, biomass production and leaf

area index to elevated [CO_2] have been observed in trees than other functional types (Ainsworth and Long, 2005). Nevertheless, there is often a poor correlation between photosynthetic capacity measured as A_{max} and total biomass production under elevated [CO_2] enrichment (Oren et al., 2001).

6. Environmental factors determining the response of photosynthesis to elevated [CO_2]

6.1 Nitrogen supply

At elevated [CO_2] condition, when plant photosynthesis becomes RubP limited, Rubisco will be in excess of requirements (Ainsworth and Rogers, 2007). The excess capacity for carboxylation could be reduced through a reduction in the activation state of Rubisco (Cen and Sage, 2005). Alternatively, because less Rubisco is required by these plants at elevated [CO_2], redistribution of the excess N invested in Rubisco could further increase N use efficiency at elevated [CO_2] without negatively impacting potential C acquisition (Parry et al., 2003; Ainsworth and Rogers, 2007). However, there is only benefit in reducing the amount of N invested in Rubisco at elevated [CO_2] when the resources invested in it can be usefully deployed elsewhere (Parry et al. 2003). Ainsworth and Long (2005) reported that the stimulation in A_{sat} at elevated [CO_2] was 23% lower in plants grown with a low N supply. Meanwhile, under elevated [CO_2] the Vc_{max} was decreased at both high and low N, with greater reduction of 85% in low N condition. This result is in agreement with summaries of earlier studies conducted in controlled environments and field enclosures by Ainsworth and Rogers (2007), Drake et al. (1997), Moore et al. (1999) and Stitt and Krapp (1999), and is consistent with current understanding of the mechanism underlying acclimation under elevated [CO_2]. When plants are N limited, sink development is restricted, C supply is in excess of demand, and the sugar feedback mechanism as outlined earlier can operate to reduce Rubisco content and increase N use efficiency. As N supply increases, the limitation imposed by sink capacity decreases and the sugar linked signal for down-regulating Rubisco content is reduced (Ainsworth and Rogers, 2007; Drake et al. 1997; Rogers et al. 1998; Long et al., 2004).

6.2 Sink strength

Defined here as the capacity to utilize photosynthate, sink strength can be a major constraint on carbon acquisition (Ainsworth and Rogers, 2007). A reduced or insufficient sink capacity may be the result of many potentially limiting processes e.g. N supply (Rogers et al., 1998), genetic constraints (Ainsworth et al., 2004), temperature (Ainsworth et al., 2003b) or developmental changes (Bernacchi et al., 2005; Rogers and Ainsworth, 2006). However, the net result is the same, i.e. the appearance of a carbohydrate-derived signal that can lead to the subsequent down-regulation (acclimation) of photosynthetic machinery, principally Rubisco (Stitt and Krapp, 1999; Long et al., 2004). Davey et al. (2006) showed that poplar grown at elevated [CO_2] had a large sink capacity. Poplar was able to export >90% of its photosynthate during the day; it also had a large capacity for the temporary storage of overflow photosynthate as starch (Ainsworth and Rogers, 2007; Stitt and Quick 1989; Davey et al., 2006). These two traits enabled poplar to maintain high photosynthetic rates at elevated [CO_2] and avoid a major source–sink imbalance that could lead to a reduction in the potential for C acquisition (Ainsworth and Rogers, 2007). In contrast, *L. perenne* can

become extremely sink limited at elevated [CO_2] (Rogers and Ainsworth, 2006). As reported, large accumulations of carbohydrate which build up in grasses over several days and weeks are common (Fischer et al., 1997; Isopp et al., 2000; Rogers & Ainsworth 2006). The most likely explanation for the sink limitation observed in *L. perenne* is an insufficient N supply (Fischer et al., 1997; Rogers et al., 1998).

The excess of C and shortage of N may explain why grasses reduced their Rubisco content at elevated [CO_2] despite the negative impact on potential carbon gain (Rogers et al., 1998). Therefore, a reduction in carboxylation capacity would be expected. However, legumes can trade photosynthate for reduced forms of N with their bacterial symbionts (Rogers et al., 2006b). The benefit of an increase in N use efficiency resulting from the reduction of Rubisco content and the sugar-derived signal required for a reduction in carboxylation capacity would not be expected (Ainsworth & Rogers, 2007). It follows that acclimation in legumes is likely to occur through reduction in Rubisco activity rather than through a loss of Rubisco protein content. This occurs in order to maintain the balance between the supply and demand for the products of the light reactions (Ainsworth & Rogers, 2007). Alternatively, other nutrient limitations may also impact N-fixation and sink capacity at elevated [CO_2] (Almeida et al., 2000; Hungate et al., 2004).

7. Oil palm responses to elevated CO_2

An experiment was carried out using three levels of [CO_2] (400, control; 800 and 1200 μmol mol^{-1} CO_2) to demonstrate the responses of oil palm seedlings on photosynthesis and quantum yield to elevated [CO_2]. Photosynthetic light response curves of oil palm were measured at growth CO_2 concentrations on with an open flow infrared gas analyzer with an attached red LED light source (LI-6400, Li-Cor, Inc., Lincoln, NE). Measurements began with approximately 5 minutes of saturating light (1500 μmol m^{-2}s^{-1}) followed by nine incremental reductions until the irradiance was 0 μmol m^{-2}s^{-1}. Decreasing light was used rather than increasing light to reduce the equilibrium time required for stomatal opening and photosynthetic induction (Kubiske & Pregitzer, 1996). Preliminary trials indicated that photosynthetic rates reached steady state within 2 minutes following each incremental decrease in light. Measurements were made on fully expanded leaves. Gas exchange measurements were restricted to the hours between 0800 and 1200 hours on sunny days to minimize diurnal effects on photosynthesis. Leaf temperatures averaged 28.89 ± 0.89°C within each measurement period. The differences in light response curves due to CO_2 concentration were examined by calculating and statistically comparing light-saturated photosynthesis (A_{sat}), dark respiration (Rd), light compensation point (Γ) (where A = Rd), and apparent quantum yield (φ). Apparent quantum yield (φ) and Rd were estimated from the measured data. Values of φ were calculated as the slope of photosynthesis (A) versus the incident irradiance. Light compensation points (Γ) were estimated by extrapolating between measured data. The shape of the average light response curve in each CO_2 concentration and canopy position was modeled by fitting data to a non-rectangular hyperbola (Leverenz, 1987; Leverenz, 1995) by means of a nonlinear least squares curve-fitting program (JMP, SAS Institute, Inc., Cary, NC)

Photosynthetic light response curves of oil palm are shown in Figure 1. Light-saturated net photosynthesis (A_{sat}) was greater in elevated treatment than in ambient CO_2. The elevated [CO_2] exposure of oil palm seedling resulted in higher rates of A_{sat} (P < 0.001; Figure 2a). The enhancement of A_{sat} by [CO_2] enrichment was significantly greater for 1200 μmol mol^{-1} CO_2

followed by 800 μmol mol^{-1} and 400 μmol mol^{-1} CO_2. During the experiment, elevated CO_2 had caused the A_{sat} of oil palm to increase by 52 to 78% compared to the ambient. Apparent quantum yield, calculated from the initial slope of the light response curves, was slightly lower in ambient treatment compared to the elevated CO_2 treatments (800 and 1200 μmol mol^{-1} CO_2; Figure 2b). During measurements, the elevated treatment exhibited a higher quantum yield than the ambient leaves (P < 0.05). Quantum yield was enhanced by 2 fold and 3 fold respectively in the 800 and 1200 μmol mol^{-1} CO_2 treatments compared to 400 μmol mol^{-1} CO_2 one.
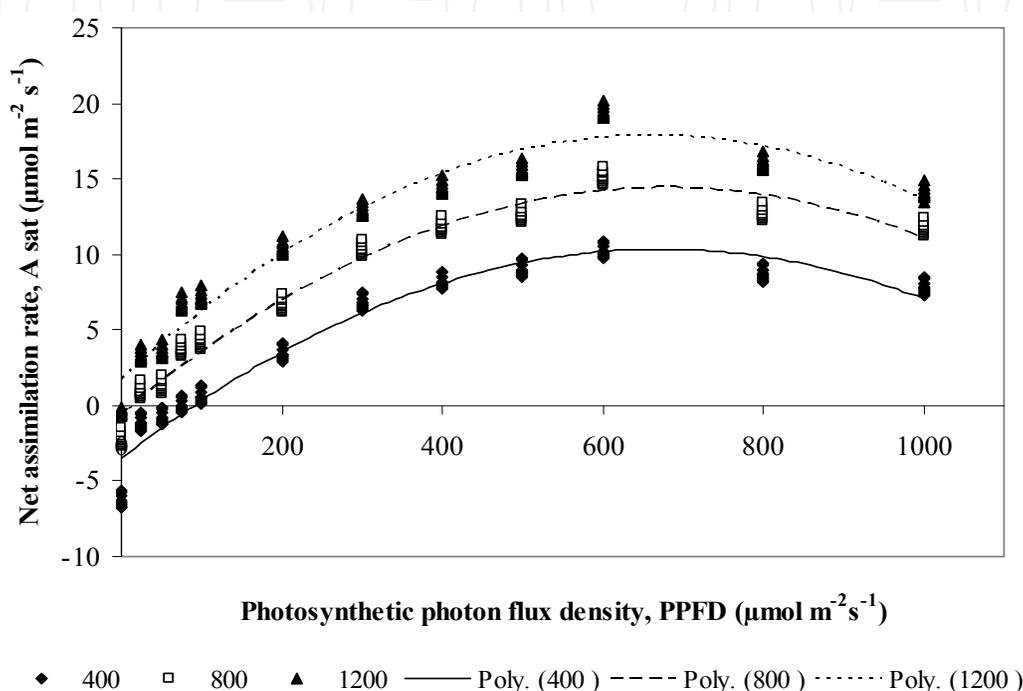
Fig. 1. Light response curve as affected by different CO_2 levels in oil palm seedlings

Elevated CO_2 leaves had a lower light compensation point (Γ) and dark respiration rate (R_d) than the ambient leaves (Figure 2c; 2d). Estimated from the photosynthetic light response curves, it was also demonstrated a significant effect of elevated CO_2 on Γ or Rd (P≤0.01). Using the light response curves, the light compensation point for ambient CO_2 was recorded at 78.21 followed by 66.21 for 400 and 800 μmol mol^{-1} CO_2 respectively and 30.24 for 1200 μmol mol^{-1} CO_2 treatment. It was also observed that the dark respiration was reduced by 1.72 to 3.21 μmol m^{-2}s^{-1} compared to ambient levels that recorded 5.71 μmol m^{-2}s^{-1}.

Many studies have suggested that the enriched CO_2 leaves respond to atmospheric CO_2 enrichment to a greater extent than the ambient- CO_2 leaves as a result of increased quantum yields (Hanstein & Felle, 2002). A small increase in quantum yield may increase daily carbon gain under low light conditions (Kiirats et al., 2002). In our study, elevated CO_2 increased apparent quantum yields in the 800 and 1200 μmol mol^{-1} CO_2 treatments. Light response curve analysis of oil palm seedling had showed that CO_2 enriched seedlings had reduced their dark respiration rate by 43 to 70% through enhancement of their A_{sat} and apparent quantum yield (φ) by 52 to 78% and 15 to 62%, respectively. The enhancement of Γ and φ signify direct inhibition of the activity of key respiratory enzymes under elevated CO_2 (Drake et al., 1997). This result has been supported by Henson and Haniff (2005) who reported productivity or dry matter production of plants would increase if respiration could

be minimized without affecting gross assimilation, or if gross assimilation could be increased without increasing respiration. This shows that increase in CO_2 would enhance gross assimilation and reduce respiration by compensating respiration rate with high carbon gain. Usually, compensation irradiance is reduced while quantum efficiency is increased in plant under elevated CO_2 (Vavin et al., 1995). The same result was also observed by Kubiske and Preigitzer (1996) with red oak seedlings grown at elevated CO_2 in shaded open top chamber.
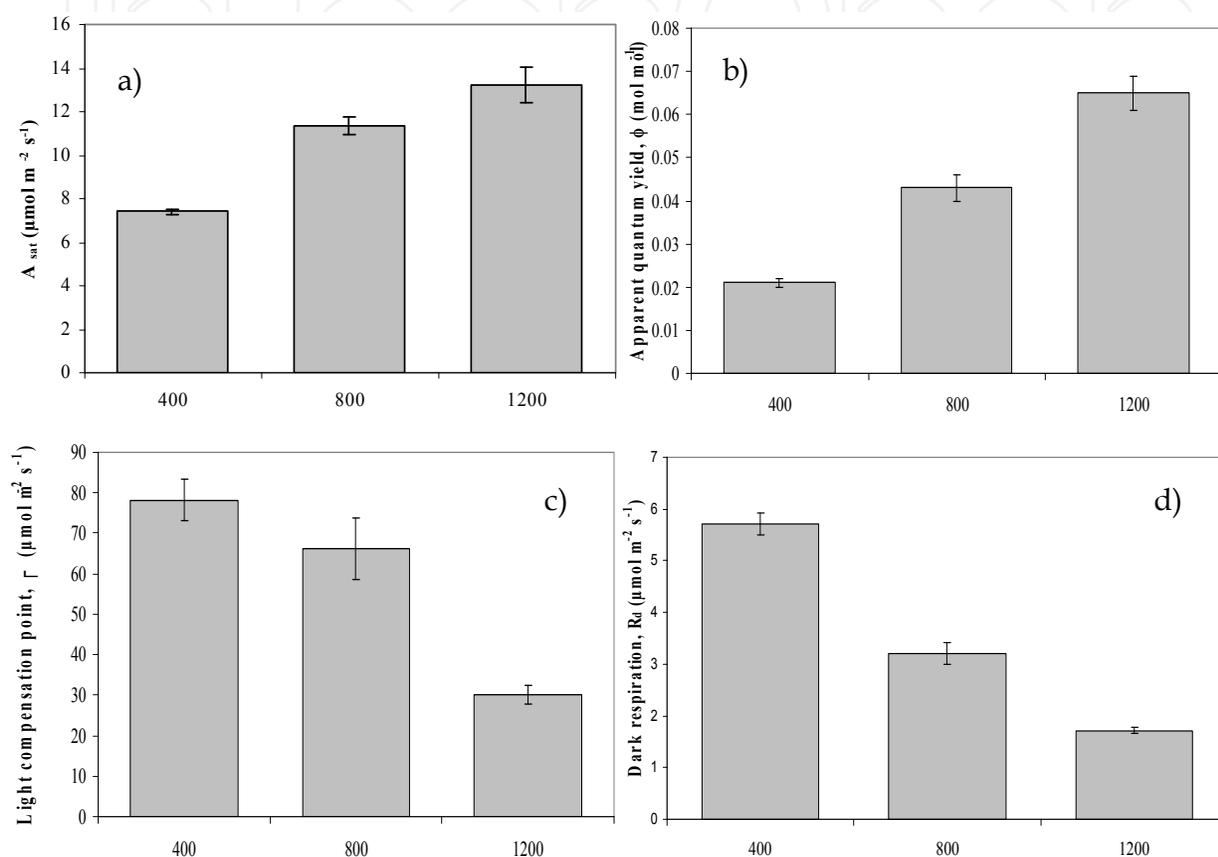
Fig. 2. The maximum net assimilation rate Asat (a), apparent quantum yield (b), Light compensation point (c) and dark respiration rate (d) as affected by different CO2 levels in oil palm seedlings

In oil palm, it was found that enrichment with high levels of [CO_2] have enhanced the leaf gas exchange of oil palm seedlings. As CO_2 levels increased from 400 to 800 and 1200 μmol mol^{-1} CO_2 the net photosynthesis (Figure 3) and water use efficiency (Figure 4) were also improved. Net photosynthesis (A) and water use efficiency (WUE) were been enhanced by respective 211 to 278% and 158 to 224% when enriched with [CO_2] (800 and 1200 μmol mol^{-1} CO_2). As CO_2 levels increased, it was observed that the intercellular CO_2 (Ci) increased higher in oil palm seedling treated with high levels of [CO_2] (Figure 5). The Ci for 1200 μmol mol^{-1} CO_2 recorded the highest (361.11 μmol mol^{-1} CO_2) value followed by that of 800 μmol mol^{-1} CO_2 (311.11 μmol mol^{-1} CO_2) with the lowest at 400 μmol mol^{-1} CO_2 that recorded 289.12 μmol mol^{-1}. Up-regulation of A may as represented by increases in leaf intercellular CO_2 concentration (C_i) that could also be related to increase in the thickness of the leaves (high SLA) achieved under elevated [CO_2] that contains high photosynthetic protein

especially Rubisco (Ramachandra & Das, 1986). The latter might also up–regulate several enzymes related to carbon metabolism which simultaneously increase the C_i (Anderson et al., 2001). This data imply that high A under elevated CO_2 could be due to more efficient net assimilation resulting from extra carbon fixation as exhibited by high C_i per unit area which is related to increased thickness of mesophyll layer, mainly due to increased palisade layer (Lawson et al., 2002). Up-regulation of A may as represented by increases in leaf intercellular CO_2 concentration (C_i) may also be related to increase in the thickness of the leaves under elevated CO_2 that contain high photosynthetic protein especially Rubisco (Ramachandra and Das, 1986). The latter might up–regulate several enzyme related to carbon metabolism that simultaneously increase the C_i (Anderson et al., 2001). This data implied that high A under elevated CO_2 could be due to more efficient net assimilation due to extra carbon fixation exhibited by high C_i per unit area which is related to increased thickness of mesophyll layer, mainly due to increased palisade layer (Lawson et al., 2002).
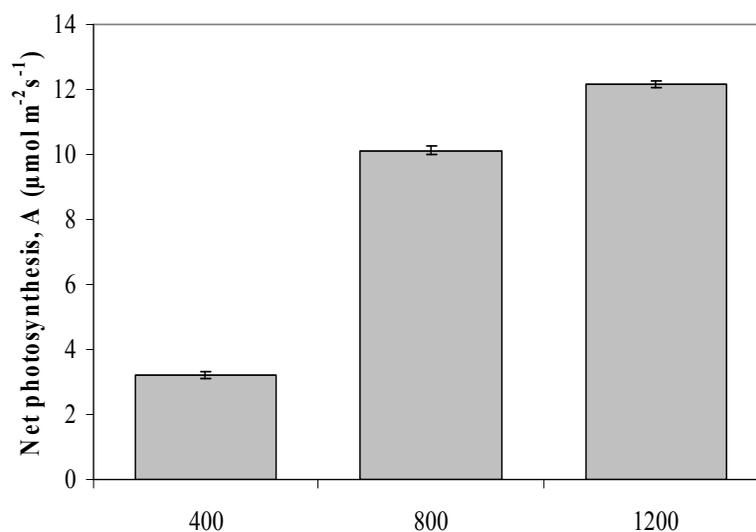
Fig. 3. Net photosynthesis as affected by CO2 levels in oil palm seedlings
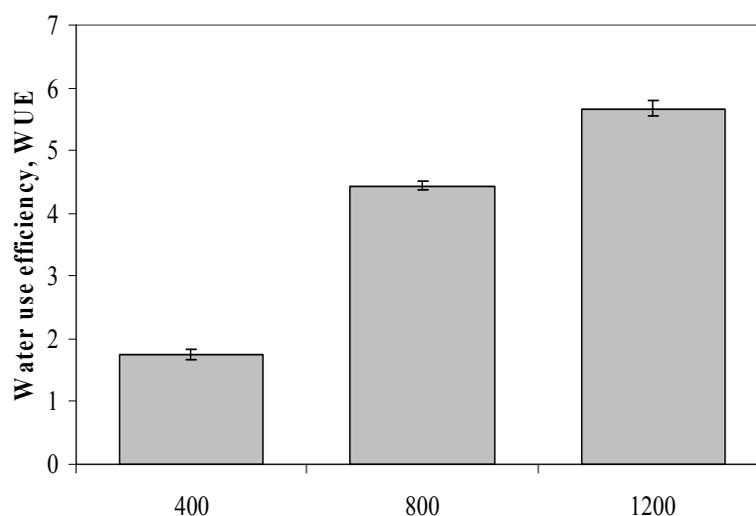
Fig. 4. Water use efficiency as affected by CO_2 levels in oil palm seedlings
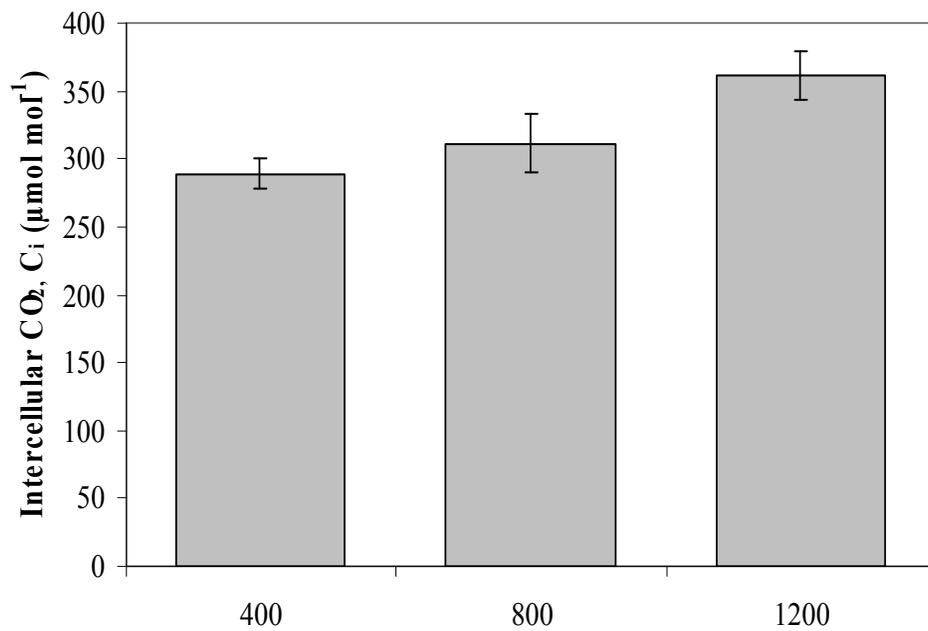
Fig. 5. Intercelluar CO_2 as affected by CO_2 levels in oil palm seedlings
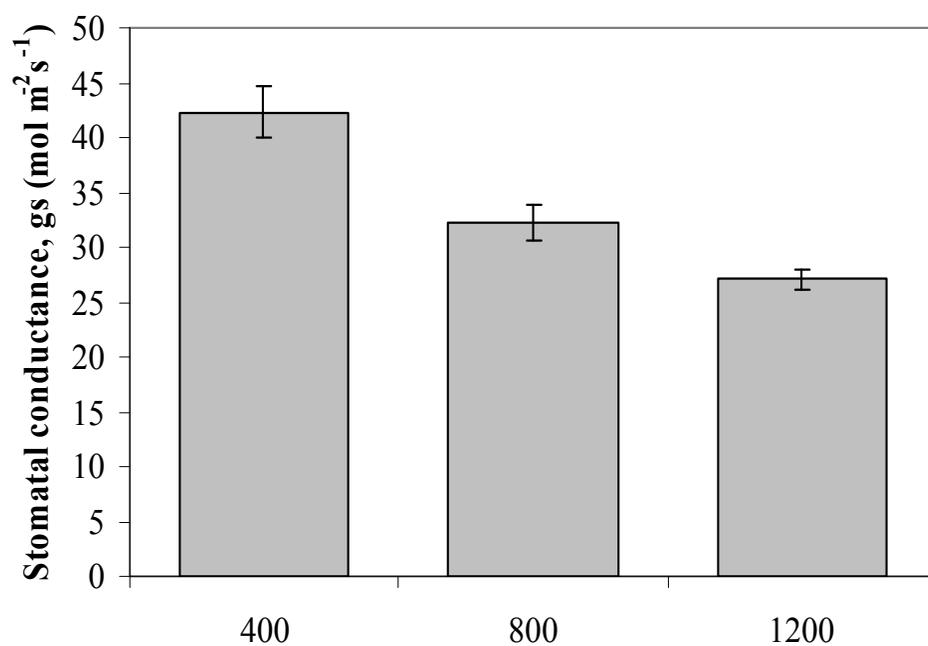

Fig. 6. Stomatal conductance, gs as affected by CO_2 levels in oil palm seedlings

Statistically, higher A was observed over the controlled plants as the levels of enrichment increased. Similar result was obtained by Downtown (1990) and Van and Megonigal (2001). Theoretically, exposure to higher [CO_2] would increase A by increasing the availability of the substrate (CO_2; Downtown, 1990). In the present study, the increase in A might be

justified by reduced light compensation point (Γ) and dark respiration rate (R_d), with the plant enriched with high CO_2 having enhanced apparent quantum yield and net assimilation rates (Kubiske & Preigitzer, 1996).

Despite increases in A and WUE, stomatal conductance of oil palm seedlings enriched with high levels of CO_2 decreased as levels of CO_2 increases (Figure 6). In 400 µmol mol^{-1} CO_2, stomatal conductance recorded a value at 42.3 mmol m^{-2} s^{-1}; with increasing [CO_2] to 800 and 1200 µmol mol^{-1} the stomatal conductance documented lower values (27.1 to 32.3 mmol m^{-2} s^{-1}). Further enhancing the plants to 800 and 1200 µmol mol^{-1} had shown to reduce stomatal conductance (g_s) of the CO_2-enriched seedlings versus the ambient CO_2-treated plants with lowest g_s. The decreased g_s simultaneously reduced the transpiration rate (E) of plant under elevated CO_2. This phenomenon is usually reported in plant treated with high than ambient CO_2 (Rashke, 1986; Lodge et al., 2001; Lawson et al., 2002). It was believed that reduced g_s might contribute to plant acclimation to high intercellular CO_2 (C_i) (Morrison & Jarvis, 1980).

It was also found that nitrogen levels were influenced by CO_2 levels applied to the oil palm seedlings. From Figure 7 it is observed that the nitrogen levels were highest in leaves followed by stems and lowest in the roots. As [CO_2] levels increased from 400 to 1200 µmol mol^{-1} CO_2 the nitrogen content decreased highly in 1200 followed by 800 and lowest in 400 µmol mol^{-1} CO_2. This implies that plant enriched with high levels of [CO_2] have high dilution of nitrogen content in the plant tissues. Nitrogen content was influenced by the application of CO_2 levels to the seedlings. As the levels of CO_2 increased from 400 to 1200 µmol mol^{-1} CO_2, nitrogen content were found to be reduced. The decrease in nitrogen content with increasing CO_2 levels has been reported by Porteus et al. (2009). Several researchers attributed this phenomenon to decreasing uptake of nitrogen as transpiration rate (E) was decreased due to reduction in stomata conductance (g_s) under elevated CO_2 level (Conroy and Hawking, 1993).
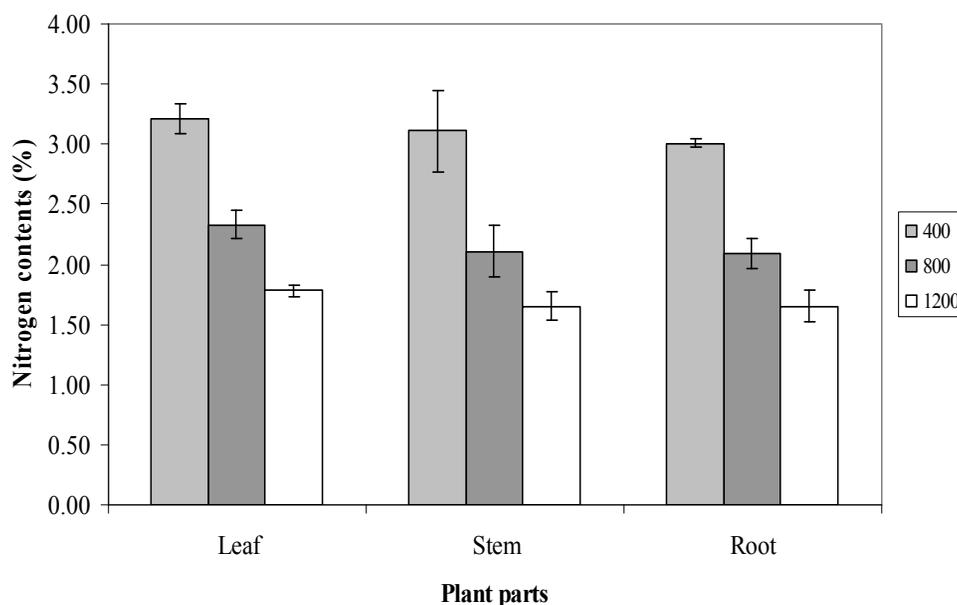

Fig. 7. Nitrogen levels as affected by CO_2 levels in different part of oil palm seedlings

8. Conclusion

The results demonstrated by the oil palm seedlings indicated a positive response of oil palm seedling to elevated CO_2 enrichment in term of enhanced photosynthesis rate and quantum yield as compared with ambient CO2 condition. The positive impact of oil palm seedlings to CO2 enrichment was shown by enhancement of the leaf gas exchange characteristics of oil palm. The positive responses have been shown to cause increases in net photosynthesis, Asat, apparent quantum yield and reduction of dark respiration rate and light compensation point. The findings suggest that in the next 22nd century, it would be expected that oil palm to benefit from changes in the climate as long as temperature does not increase beyond the palm optimum level. Further research in the future needs to be conducted to confirm these effects especially involving many environmental conditions under elevated [CO_2]. Producing crops under climate change conditions, then, would be a growing challenge in the new agriculture of the world.

9. Acknowledgment

10. References

Ainsworth E.A., Rogers A., Blum H., Nösberger J. & Long S.P. (2003b) Variation in acclimation of photosynthesis in Trifolium repens after eight years of exposure to free air CO2 enrichment (FACE). *Journal of Experimental Botany* Vol 54, pp. 2769–2774

Ainsworth, E.A. & Long, S.P. (2005).What havewe learned from15 years of free-air CO2 enrichment (FACE)? Ameta-analytic reviewof the responses of photosynthesis canopy properties and plant production to rising CO2. *New Phytologist* Vol165, pp 351–372.

Ainsworth, E.A. & Rogers, A., 2007. The response of photosynthesis and stomatal conductance to rising [CO2]: mechanisms and environmental interactions. *Plant, Cell & Environment* Vol 30, pp 258–270.

Almeida J.P.F., Hartwig U.A., Frehner M., Nösberger J. & Löscher A. (2000) Evidence that P deficiency induces N feedback regulation of symbiotic N2 fixation in white clover (Trifolium repens L.). *Journal of Experimental Botany* Vol 51, pp. 1289–1297.

Anderson J.M. (2000). "Strategies of Photosynthetic Adaptations and Acclimation." In Probing Photosynthesis: Mechanisms, Regulation and Adaptation. M. Yunus, U. Pathre, P. Mohanty, eds. London

Baker, N.R. & Ort, D.R. (1992). Light and crop photosynthesis performance. In: NR Baker, H Thomas, eds. Crop Photosynthesis: Spatial and Temporal Determinants. Amsterdam: Elsevier Science Publishers, 1992, pp 289–312.

Bernacchi C.J., Portis A.R.,Nakano H., von Caemmerer S. & Long S.P. (2002) Temperature response of mesophyll conductance. Implications for the determination of rubisco

enzyme kinetics and for limitations to photosynthesis in vivo. *Plant Physiology* Vol 130, pp 1992–1998.

Booth, T.H.& Jovanovic, T. (2005). Tree Species Selection and Climate Change in Australia. Australian Greenhouse Office, Canberra.

Brinkman, M.A. & Frey, K.J.(1978). Flag leaf physiological analysis of oat isolines that differ in grain yield from their recurrent parents. *Crop Science* Vol 18, pp.69–73

Cen Y.P. & Sage R.F. (2005) The regulation of rubisco activity in response to variation in temperature and atmospheric CO2 partial pressure in sweet potato. *Plant Physiology* Vol 139 pp 979–990

Clayton, R.K. (1971) Light and living matter: A guide to the study of photobiology. New York, USA: McGraw-Hill.

Clayton, R.K. (1980) Photosynthesis: Physical mechanism and chemical patterns. Cambridge, England: Cambridge University Press

Conroy, J. and Hocking, P. (1993). Nitrogen nutritions of C_3 plants at elevated carbon dioxide concentration. *Plant physiology* Vol 89: 570 – 576.

Davey P.A., Olcer H., Zakhleniuk O., Bernacchi C.J., Calfapietra C., Long S.P. & Raines C.A. (2006) Can fast-growing plantation trees escape biochemical down-regulation of photosynthesis when grown throughout their complete production cycle in the open air under elevated carbon dioxide? *Plant, Cell & Environment* Vol 29, pp. 1235–1244.

Dong, S.T. (1991). Studies on the relationship between canopy apparent photosynthesis and grain yield in high-yielding winter wheat. *Acta Agronomy Singapore* Vol 17, pp 461–469

Downton, W.J.S., Grant, W.J.R. and Chacko, E.K. (1990). Effect of elevated carbon dioxide on the photosynthesis and early growth of mangosteen (*Garcinia mangostana L*). *Scientia Horticulturae* Vol 44, pp 215 – 225

Drake B.G., Gonzalez-Meler M.A. & Long S.P. (1997) More efficient plants: a consequence of rising atmospheric CO2? *Annual Review of Plant Physiology and Plant Molecular Biology* Vol 48, pp. 609–639.

Drake, B.G., Gonzalez, M.M.A., and Long, S.P. (1997). More efficient plants : a consequence of rising atmospheric CO_2. *Annual Review Plant Physiology Plant Molecular Biology* Vol 48 pp 609 – 639

Ehleringer, J. & Pearcy, R.W.(1983). Variation in quantum yield for CO2 uptake among C3 and C4 plants. *Plant Physiology* Vol 73, pp. 555–559

Ehleringer, J. R.; Sage, R. F.; Flanagan, L. B. & Pearcy, R. W. (1991). Climate change and the evolution of C4 photosynthesis. *Trends in Ecology Evolution*. Vol 6, pp. 95–99

Emerson, R. & Lewis, C.M. (1943). The dependence of the quantum yield of chlorella photosynthesis on wave length of light. *American Journal of Botany* Vol 30, pp.165–178

Evans, L.T.& Dunstone, R.L.(1970). Some physiological aspects of evolution in wheat. *Australian Journal Biological Science* Vol 23 pp.725–741

Farquhar, G.D. & Sharkey, T.D. (1982). Stomatal conductance and photosynthesis. *Annual Review Plant Physiology* Vol33, pp. 317–345

Gifford, R.M.& Evans, L.T. (1981). Photosynthesis, carbon partitioning, and yield. *Annual Review of Plant Physiology* Vol 32, pp 485–509

Gunderson, C.A. & Wullschleger, S.D. (1994). Photosynthetic acclimation in trees to

Guo, L.W.; Xu,D.O.; & Shen, Y.K.(1996). Photoinhibition of photosynthesis without net loss of D1 protein in wheat leaves under field conditions. *Acta Botany Singapore* Vol 38, pp. 196–202

Guo, L.W; Xu, D.Q & Shen, Y.K. (1994). The causes of midday decline of photosynthetic efficiency in cotton leaves under field conditions. *Acta Phytophysiol Singapore* Vol 20, pp.360–366

Hall, D.O. & Rao, K.K. (1999). Photosynthesis. Cambridge: Cambridge University Press

Hanstein S.M. & Felle H.H. (2002) CO_2-triggered chloride release from guard cells in intact fava bean leaves. Kinetics of the onse of stomatal closure. *Plant Physiology* Vol 130, pp. 940–950.

Hay, R.K.M & Walker, A.K.(1989). An Introduction to the Physiology of Crop Yield. New York: Longman Scientific & Technical copublished in the United States with John Wiley & Sons, pp 31–86.

Henson,I.E. and Haniff, M.H., (2006). Carbon dioxide enrichment in oil palm canopies and its possible influence on photosynthesis. *Oil Palm Bulletin*. Vol 51, pp 1–10

Hong, S.S.& Xu, D.Q. (1998).Light-induced increase in initial chlorophyll fluorescence Fo level and its possible mechanism in soybean leaves. In: G Garab, ed. Photosynthesis: Mechanisms and Effects. Vol III. Dordrecht, The Netherlands: Kluwer Academic Publishers, 1998, pp 2179–2182.

Hungate B.A., Stiling P.D., Dijkstra P., Johnson D.W., Ketterer M.E., Hymus G.J., Hinkle C.R. & Drake B.G. (2004) CO_2 elicits long-term decline in nitrogen fixation. *Science* Vol 304, pp. 1291.

Jacob, J.(1995). Phosphate deficency increases the rate constant of thermal dissipation of excitation energy by photosystem II in intact leaves of sunflower and maize. *Australian Journal of Plant Physiology* Vol 22, pp. 417–424

K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G.& Katul, G.G. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. *Nature* Vol 411, pp 469–472.

Keeling, C. D.; Whorf, T. P. Wahlen, M. & Van der Plicht, J. (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* Vol 375, pp. 666–670.

Kiirats O.,Lea P.F., Franceschi V.R. & Edwards G.E. (2002) Bundle sheath diffusive resistance to CO_2 and effectiveness of C4 photosynthesis and refixation of photorespired CO_2 inaC4 cycle mutant and wild-type Amaranthus edulis. *Plant Physiology* Vol 130,pp. 964–976.

Ku, S.B; & Edwards, G.E. (1978). Oxygen inhibition of photosynthesis. III. Temperature dependence of quantum yield and relation to O_2/CO_2 solubility ratio. *Planta* Vol 140 pp.1–6.

Kubiske, M.E. and Pregitzer, K.S. (1996). Effects of elevated CO_2 and light availability on the photosynthetic response of trees of contrasting shade tolerance. *Tree Physiology* Vol 16, pp 351-358.

Lawson, T., Carigon, J., Black, C.R., Colls, J.J., Landon, G. and Wayers, J.D.B. (2002). Impact of elevated CO_2 and O_3 on gas exchange parameters and epidermal characteristics of potato (*Solanum tuberosum* L.). *Journal of Experimental Botany*. Vol 53, No 369, pp 737-746

Li, D.Y.; Ye, J.Y.& Shen, Y.K.(1991). Effect of rainy weather on the photosynthetic efficiency in spinach. *Plant Physiology Community Singapore* Vol 27, pp.413–415

Lodge, R.J., Dijkstra, P., Drake, B.G. and Morrison, J.I.L. (2001). Stomatal acclimation to increased level of carbon dioxide in a Florida scrub oak species *Quercus myritifolia*. *Plant Cell. Environment* Vol 14, pp 729 – 739

Long S.P., Ainsworth E.A., Rogers A. & Ort D.R. (2004) Rising atmospheric carbon dioxide: plants FACE the future. *Annual Review of Plant Biology* Vol 55, pp 591–628.

Long, S.P. & Drake, B.G. (1992). Photosynthetic CO2 assimilation and rising atmospheric CO2 concentration. In: Baker, N.R., Thomas, H. (Eds.), Topics in Photosynthesis Research. Elsevier, pp. 69–104.

Long, S.P. &Drake, B.G. (1992). Photosynthetic CO2 assimilation and rising atmospheric CO2 concentration. In: Baker, N.R., Thomas, H. (Eds.), Topics in Photosynthesis Research. Elsevier, pp. 69–104.

Long, S.P., Ainsworth, E.A., Rogers, A.& Ort, D.R., (2004). Rising atmospheric carbon dioxide: Plants face the future. *Annual Review of Plant Biology* Vol 55, pp 591– 628

Luo, Y. & Reynolds, J. (1999). Validity of extrapolating field CO2 experiments to predict carbon sequestration in natural ecosystems. *Ecology* Vol 80, pp 1568–1583

Mohanty, P. & Boyer, J.S. (1976). Chloroplast response to low leaf water potentials. IV. Quantum yield is reduced. *Plant Physiology* Vol 57, pp 704–709

Mohanty,P. & Boyer, J.S. (1976). Chloroplast response to low leaf water potentials. IV. Quantum yield is reduced. *Plant Physiology* vol 57 pp.704–709

Monson, R.K; Littlejohn, J.L.& Williams, G.J. (1982). The quantum yield for CO2 uptake in C3 and C4 grasses. *Photosynthesis Research* Vol 3, pp.153–159

Moore B.D., Cheng S.H., Sims D. & Seemann J.R. (1999) The biochemical and molecular basis for photosynthetic acclimation to elevated atmospheric CO2. *Plant, Cell & Environment* Vol 22, pp 567–582.

Morison, J.I.L. (1987). Intercellular carbon dioxide concentration and stomatal responses to carbon dioxide. In *Stomatal Function*, ed. Zeiger, E., Farquhar, G.D. and Cowan, I.R., pp. 229 - 251. Stanford, California: Stanford University Press.

Niyogi, K.K. (1999). Photoprotection revisited: genetic and molecular approaches. Annual Revision Plant Physiology Plant Molecular Biology Vol 50, pp .333–359

Oquist, G.; Brunes, L. & Hallgren, G.E. (1982). Photosynthetic efficiency of Betula pendula acclimated to different quantum flux densities. *Plant Cell Environment* Vol 5, pp 9– 15

Oquist,G.; Brunes, L.& Hallgren, G.(1982). Photosynthetic efficiency during ontogenesis of leaves of Betula pendula.*Plant Cell Environment* Vol 5, pp. 17–21

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schafer,K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G.& Katul, G.G. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. *Nature* Vol 411, pp 469–472.

Ort, D.R. & Baker, N.R. (1988). Consideration of photosynthetic efficiency at low light as a major determinant of crop photosynthetic performance. *Plant Physiology Biochemistry* Vol 26, pp.555–565.

Osmond, C.B.; Bjorkman, O & Anderson, D.J. (1980). Physiological Processes in Plant Ecology. Berlin: Springer-Verlag, pp. 291–377

Parry M.A.J., Andralojc P.J., Mitchell R.A.C., Madgwick P.J. & Keys A.J. (2003) Manipulation of Rubisco: the amount, activity, function and regulation. *Journal of Experimental Botany* Vol 54 pp 1321–1333.

Pettigrew, W.T.; & Meredith, B.R. (1994). Leaf gas exchange parameters vary among cotton genotypes. *Crop Science* Vol 34, pp700–705

Pinkard, E.A.; Beadle, C.L.; Mendham, D.S; Carter, J.& Glen, M. 2010. Determining photosynthetic responses of forest species to elevated [CO2]: Alternatives to FACE. *Forest ecology and Management* Vol 260, pp 1251 – 1261

Porteaus,F., Hill, J., Ball, A.S., Pinter, P.J., Kimbal, B.A., Wall, G.W. and Ademsen, F.J. and Morris, C.F.(2009). Effects of free air carbon dioxide enrichment (FACE) on the chemical composition and nutritive value of wheat grain straw. *Animal Feed Science Technology* Vol 149, pp 322 – 332.

Poskuta, J.W. & Nelson, C.J.(1986). Role of photosynthesis and photorespiration and of leaf area in determining yield of tall fescue genotypes. *Photosynthetica* Vol 20, pp.94–101

Ramachandra, A.R. and Das, V.S.R. (1986). Correlation between biomass production and net photosynthetic rates and kinetic properties of RuBP carcoxylase in certain C_3 plants. *Biomass* Vol 10, pp 157 – 164

Raschke, K. (1986). The influence of carbon dioxide content of the ambient air on stomatal conductance and the carbon dioxide concentration in leaves. In Enoch, H.Z. and Kimball, B.A. [eds] *Carbon dioxide enrichment of greenhouse crops*, Volume 2, ed. pp. 87 -102, Boca Raton: CRC Press.

Rogers, A. and Ainsworth, E.A. (2006) The response of foliar carbohydrates to elevated carbon dioxide concentration. In Managed Ecosystems and CO2. Case Studies, Processes and Perspectives (eds J. Nösberger, S.P. Long, R.J. Norby,M. Stitt, G.R. Hendrey & H. Blum), pp. 293–308. Springer-Verlag, Heidelberg, Germany.

Rogers A., Fischer B.U., Bryant J., Frehner M., Blum H., Raines C.A. & Long S.P. (1998) Acclimation of photosynthesis to elevated CO2 under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free air CO2 enrichment. *Plant Physiology* Vol 118, pp 683–689

Rogers A.,Allen D.J.,Davey P.A., et al. (2004) Leaf photosynthesis and carbohydrate dynamics of soybeans grown throughout their life-cycle under Free-Air Carbon dioxide enrichment. *Plant,Cell & Environment* Vol 27,pp 449–458

Rogers, A.& Humphries, S.W. (2000). Amechanistic evaluation of photosynthetic acclimation at elevated CO2. *Global Change Biology* Vol 6, pp. 1005–1011.

Rogers A.,Gibon Y., Stitt M.,Morgan P.B.,Bernacchi C.J.,OrtD.R. & Long S.P. (2006b) Increased C availability at elevated carbon dioxide concentration improves N assimilation in a legume.*Plant, Cell & Environment* Vol 29, pp. 1651–1658

Sala, A.& Hoch, G. (2009). Height-related growth declines in ponderosa pine are not due to carbon limitation. *Plant, Cell and Environment* Vol32, pp 22–30

Schimel, D. (2006). Rising CO2 levels not as good for crops as thought. *Science* Vol 312,

Sharkawy, M.A.; Cock, J.H.; Lynam, J.K; Hernandez, A.P.& Cadavid, L.L.F. (1990). Relationships between biomass, root yield and single-leaf photosynthesis in field-grown cassava. *Field Crop Research* Vol 25, pp. 183–201

Stitt M. & Krapp A. (1999) The interaction between elevatedbcarbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant, Cell & Environment* Vol 22, pp 583–621.

Stitt M. & Quick P. (1989) Photosynthetic carbon partitioning: its regulation and possibilities for manipulation. *Physiologia Plantarum* Vol 77, pp 663–641

Stoskopf, N.C.(1981).Understanding Crop Production. Reston, VA: Reston Publishing Company, pp 1–12.

Taiz, L. & Zieger, E. (1991). *Plant Physiology*. The Benjamin/Cummings Publishing Company, Inc., ISBN 0-8053-0153-4, California, USA

Van, C.D. and Megonigal, J.P. (2002). Productivity of Acer rubrum and taxodium distichum seedlings to elevated carbon dioxide and flooding. *Environmental pollution* Vol 116, pp 31 – 36

Vivin, .P, Gross, P., Aussenac, G. and Guehl, J.M., (1995). Whole plant CO_2 exchange, carbon partitioning and growth in *Quercus robur* seedlings exposed to elevated CO_2. *Plant Physiology Biochemistry* Vol 33, pp 201 – 211

Von Liebig, J. (1840). Die organische Chemie in Ihrer Anwendung auf Agricultur und Physiologie. Friedrich Vieweg und Sohn Braunschweig, Germany

Wells, R., Schulze, L.L., Ashley, D.D., Boerma, H.R. & Brown, R.H. (1982). Cultivar differences in canopy apparent photosynthesis and their relationship to seed yield in soybeans. *Crop Science*, Vol 22, pp. 886–890

Wells, R; Meredith, W.R & Williford, J.F. (1986). Canopy photosynthesis and its relationship to plant productivity in near-isogenic cotton lines differing in leaf morphology. *Plant Physiology* Vol 82, pp. 635–640

Xu, D.O. & Shen, Y.K. (2000). Photosynthetic efficiency and crop yield. In handbook of plant and crop physiology Revised and updated. pp 821 – 830.

Xu, D.Q. (1988). Photosynthetic efficiency. *Plant Physiology Community Singapore* Vol 24, pp.1–6

Xu, D.Q; Xu, B.J &.Shen, G.Y.(1990). Diurnal variation of photosynthetic efficiency in C3 plants. *Acta Phytophysiology Singapore* Vol 16, pp 1–5

Xu,D.Y.; Li, D.Y.; Shen,Y.G & Liang, G.A. (1984). On midday depression of photosynthesis of wheat leaf under field conditions. *Acta Phytophysiol Singapore* vol 10 pp.269–276.

Ye, J.Y.; Li, D.Y & Shen, Y.G. (1995). Effect of hypotonic swelling on photosynthesis in spinach intact chloroplasts. *Acta Phytophysiol Singapore* Vol 21, pp.73–79.

Yin, H.C.; Shen, Y.C.; Chen, Y; Yu, C.H. & Li, P.C. 1956. Accumulation and distribution of dry matter in rice after fllowering. *Acta Botany Singapore* Vol 5, pp 177–184

Zelitch, I. (1982). The close relationship between net photosynthesis and crop yield. *Bioscience* Vol 32 pp796–802

Zhang, S.Y.; Lu, G.Y. ;Wu, H.; Shen, Z.X.; Zhong, H.M.; Shen,Y.G.; Xu, D.Y.; Ding, H,G. &, Hu, W.X. (1992). Photosynthesis of major C3 plants on Qinghai plateau. Acta Botany Singapore Vol 34, pp 176–184
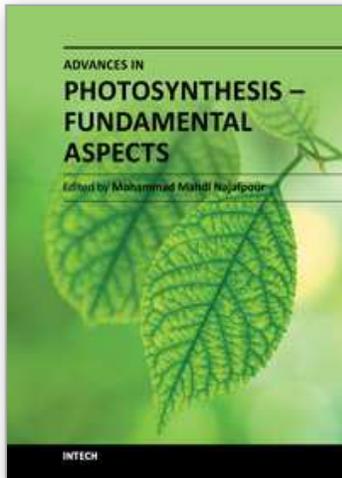
Advances in Photosynthesis - Fundamental Aspects

Edited by Dr Mohammad Najafpour

Photosynthesis is one of the most important reactions on Earth. It is a scientific field that is the topic of many research groups. This book is aimed at providing the fundamental aspects of photosynthesis, and the results collected from different research groups. There are three sections in this book: light and photosynthesis, the path of carbon in photosynthesis, and special topics in photosynthesis. In each section important topics in the subject are discussed and (or) reviewed by experts in each book chapter.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

H.Z.E. Jaafar and Mohd Hafiz Ibrahim (2012). Photosynthesis and Quantum Yield of Oil Palm Seedlings to Elevated Carbon Dioxide, Advances in Photosynthesis - Fundamental Aspects, Dr Mohammad Najafpour (Ed.), ISBN: 978-953-307-928-8, InTech, Available from: http://www.intechopen.com/books/advances-in-photosynthesis-fundamental-aspects/photosynthesis-and-quantum-yield-responses-of-oil-palm-to-elevated-carbon-dioxide

INTECH
open science | open minds