Effects of Increased Temperature on Photosynthesis of C3 and C4 Plants

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Abstract

Photosynthesis is the process by which green plants synthesis their own food using sun light and carbon dioxide. High temperature influences photosynthetic function of plants by affecting the rate of chemical reactions and structural organization and conformational changes in enzymes. Photosynthetic response to temperature relies on plant species and growth conditions. C4 plants reveal high rates of photosynthesis at high temperature while C3 plants show greater photosynthesis efficiency at low temperature. In C3 plants, Rubisco activity is limited by CO_2 concentration. In C4 plants, although rubisco activation is decreased at leaf temperatures above 32°C, the high level of CO_2 in the mesophyll chloroplasts can counteract this effect until temperature approaches 40°C. Increased temperature will affect the physiological processes essential for crop growth and development of crops. If increases in temperature accompany increases in CO_2 concentration, crop yields will decrease in regions where temperatures are below or above optimum. Future research should be directed toward identifying high-temperature tolerant crop cultivars that can produce more seeds under harsh climatic conditions.

Keywords: Photosynthesis, C4, C3, Temperature

1. NTRODUCTION

Photosynthesis is the process by which the green plants, algae and many bacteria produce organic compounds and oxygen from carbon dioxide and water by using the energy from sunlight, and it is the opposite of cellular respiration, where glucose and other compounds are oxidized to produce carbon dioxide, water, and release chemical energy (Sewhag et al., 2011). Three photosynthetic pathways exist among terrestrial plants: C3, C4, and *crassulacean acid metabolism* (CAM) photosynthesis (James and Thure, 2002).

In C3 plants, which comprise most of plant species, including important food crops such as wheat, rice, soybean and potatoes, CO_2 is exclusively assimilated through the Calvin Cycle. In contrast, C4 plants, including the most productive crop species such as maize, sorghum and sugarcane, use a series of enzymes that initially combine CO_2 (HCO-3) with a three-carbon molecule (phospoenolpyruvate, PEP), producing oxaloacetate, a four-carbon compound. This reaction is catalyzed by PEP carboxylase. C3 plants have a single chloroplast type that performs all of the reactions that convert light energy into the chemical energy upon which all life depends (Robert and William, 1995).

The C4 species are plants which exhibited higher photosynthetic rates across a wide range of leaf water potentials than C3 species. However, photosynthesis of the C4 plants greatly reduced by the end of the drought period (Joy et al., 1999). The C4 plants display an effective mechanism for concentrating CO2 with Rubisco. As a consequence, Rubisco is CO2 saturated in C4 plants and the photo respiratory pathway is largely minimized (Fabio et al., 2010). C4 plants have a selective advantage under drought conditions and show higher rates of photosynthesis than C3 plants under conditions that promote high transpiration rates (James, 2001). The optimum temperature for photosynthesis is different because the tropical plants have a higher temperature optimum than the plants adapted to temperate climates (Sewhag et al., 2011). Physiological and metabolic processes decrease at temperatures higher or lower than the optimum (Sage et al., 2008). The aim of this paper is to review the effect of increased temperature on photosynthesis and the response of C3 and C4 plants.

2. LITERATURE REVIEW

2.1. C4 and C3 Plant Photosynthesis Pathway

2.1.1. C4 pathway

C4 photosynthesis occurs in the more advanced plant taxa and is especially common among monocots, such as grasses and sedges, but not very common among dicots (most trees and shrubs) (James and Thure, 2002). C4 plants show higher photosynthetic efficiencies under conditions of light saturation. They have a mechanism to reduce the opening of their stomata for minimize water loss through transpiration. Mesophyll plastids possess normal thylakoid development and photosystem II (PSII) activity, and are distributed throughout the cytoplasm. NADP-ME-type C4 species have chloroplasts that are localized to the centrifugal portion of the cells (away from the vascular centre). Some of these plants (maize, sorghum) have plastids that lack granal stacks and many of the polypeptides associated with PSII, while others (Flaveria) have bs plastids with normal PSII activity (James,

2001). C4 photosynthesis is well recognized to be inhibited by low temperatures to a greater degree than C3 photosynthesis (Berry and Raison, 1981).

The C4 pathway is a complex adaptation of the C3 pathway in a diverse collection of species, many of which grow in hot climates. The C4 pathway suppresses photorespiration at the site of Rubisco using a biochemical CO2 pump (Robert and William, 1995). C4 photosynthesis is the compartmentalization of activities into Rubisco and the C3 PCR cycle are found in the inner ring of B cells. These cells are separated from the mesophyll cells and from the air in the intercellular spaces by a lamella (Hatch, 1988). The net result is that the oxygenase activity of Rubisco is effectively suppressed and the PCR cycle operates more efficiently. C4 plants show higher rates of photosynthesis at high light intensities and high temperatures (Hatch, 1988). Maize, sugarcane, sorghum, and amaranth are examples of C4 crops, and nutgrass (Cyperus rotundus), crabgrass (Digitaria sanguinalis), and barn-yard grass (Echinochloa crusgalli) are some of the worst C4 weeds. (Robert and William, 1995). Rubisco content in C4 plants does not appear to be as responsive to changes in light availability as in C3 plants, particularly in terms of the percentage of leaf nitrogen invested in Rubisco (Rowan and Athena, 2006).

2.1.2. C3 pathway

C3 photosynthesis is the ancestral path-way for carbon fixation and occurs in all taxonomic plant groups and the first product of photosynthesis is a 3-carbon molecule. At cool temperatures, the efficiency of photosynthesis is greater in C3 photosynthesis because photorespiration is reduced and the additional ATP cost of C4 photosynthesis makes it less efficient. However, at high temperature environments C4 photosynthesis occur, where photorespiration rates are relatively high in C3 plants. As atmospheric CO2 decreases, C4 plants should become most common first in the warmest environments, than in progressively cooler environments as CO2 levels then continue to decrease (James and Thure, 2002).

In higher plants virtually all of the carbon is assimilated through the reductive pentose phosphate cycle, in the first step of calvin cycle one molecule of CO_2 reacts with a molecule of ribulose-1,5-biphosphate (RuBP) to yield two molecules of 3-phosphoglycerate, a three-carbon compound. This reaction is catalyzed by RuBP carboxylase/oxygenase, referred to as Rubisco. Photorespiration process initiates a series of physiological events in which light-dependent O_2 uptake is associated with CO_2 evolution (Fabio et al., 2010).
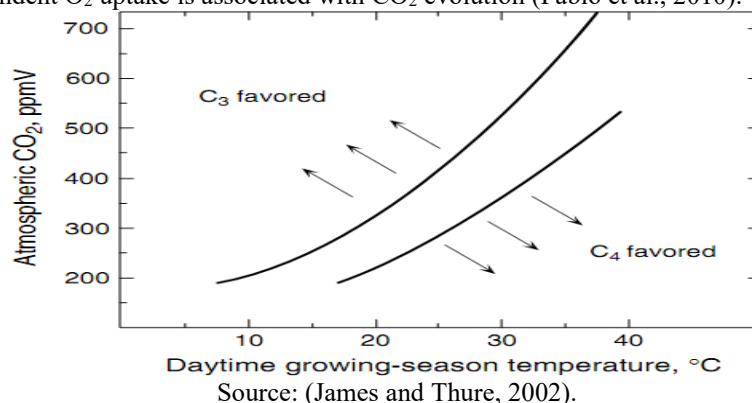

Source: (James and Thure, 2002).

Figure 1. Modeled crossover temperatures of the photosynthetic light-use efficiency (quantum yield) for C3 and C4 plants as a function of atmospheric CO2 concentrations.

The crossover-temperature is defined as the temperature (for a particular atmospheric CO2 concentration, in parts per million by volume, ppmV) at which the photosynthetic light-use efficiencies are equivalent for both the C3 and the C4 plant.

## 2.2. Photosynthetic Reactions in C3 and C4 Plants
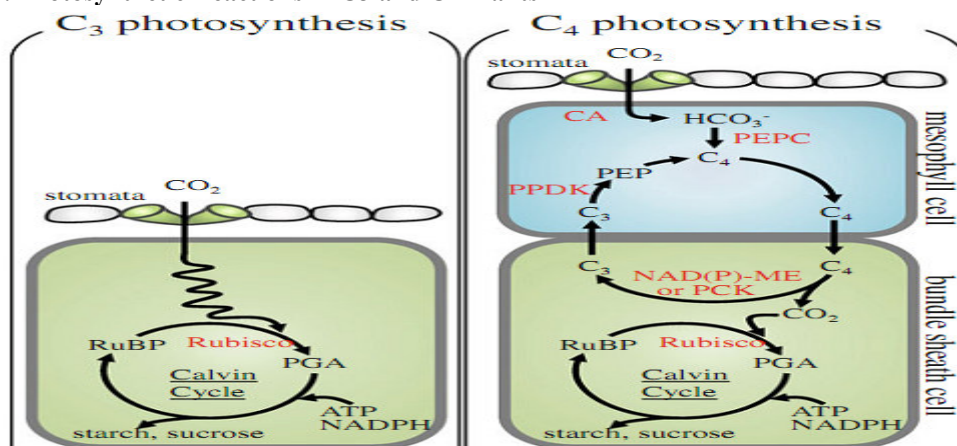
Source: Yamori et al., 2014

Figure 2. Photosynthetic reactions in C3 and C4 plants.

C3 plants convert CO2 into a 3-carbon compound (PGA) with Rubisco. On the other hand, C4 plants convert CO2 into a 4-carbon intermediate (OAA) by using PEPC. CA carbonic anhydrase, PGA phosphoglyceric acid, RuBP ribulose-1,5-bisphosphate, PEP phosphoenolpyruvate, Rubisco ribulose-1,5-bisphosphate carboxylase/oxygenase, PEPC phosphoenolpyruvate carboxylase, NAD(P)-ME NAD(P)-malic enzyme, PCK phosphoenolpyruvate carboxykinase, PPDK pyruvate phosphate dikinase, NAD(P)-MDH NAD(P)-malate dehydrogenase (OAA) with substrates of phosphoenolpyruvate (PEP) by phosphoenolpyruvate carboxylase (PEPC) located in the cytosol. PEP is produced from pyruvate and ATP, catalyzed by pyruvate phosphate dikinase (PPDK) located in the chloroplast. Among C4 plants, there are three subtypes, based on the C4 acid decarboxylation enzyme: NADP-malic enzyme (NADP-ME) type, NAD-malic enzyme (NAD-ME) type, and phosphoenol-pyruvate carboxykinase (PCK) type. Malate (or aspartate) is transported to the vascular bundle sheath cells and is finally decarboxylated, producing CO2 and pyruvate. CO2 is then fixed by Rubisco in the chloroplasts of the bundle sheath cells, which have a normal Calvin cycle, as in C3 plants (Yamori et al., 2014).

2.3. Crop Yield Response to Temperature

The effects of increased temperature exhibit a larger impact on grain yield than on vegetative growth. These effects are evident in an increased rate of senescence which reduces the ability of the crop to efficiently fill the grain or fruit. Temperature effects interact with the soil water status which would suggest that variation in precipitation coupled with warm temperatures would increase the negative effects on grain production (Hatfield and Prueger, 2015).
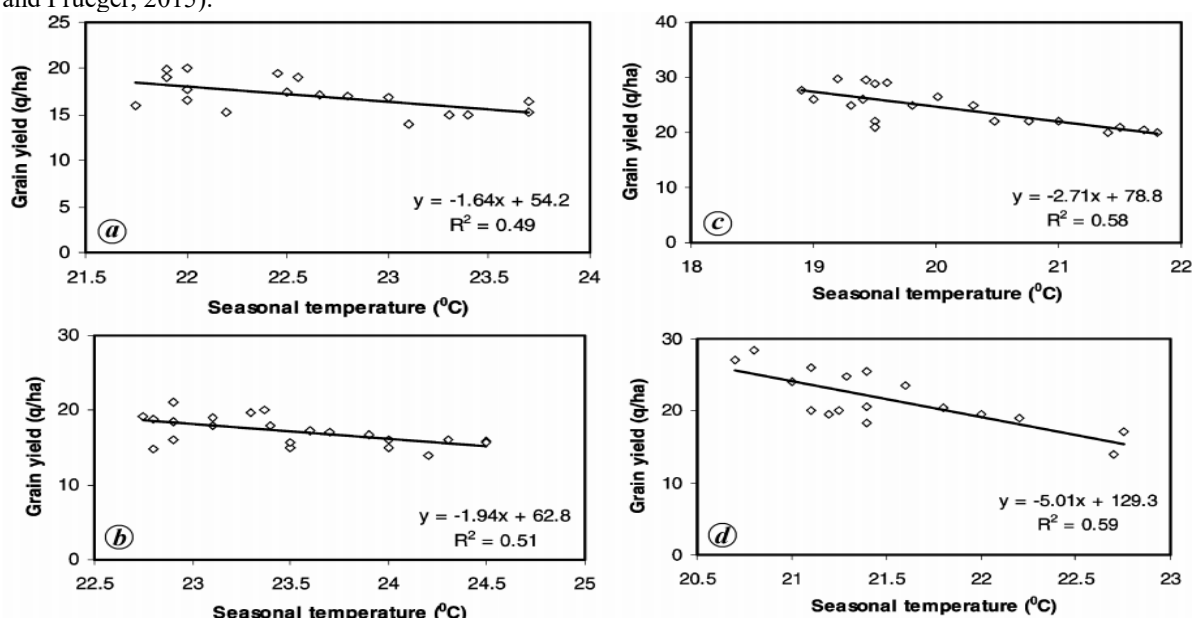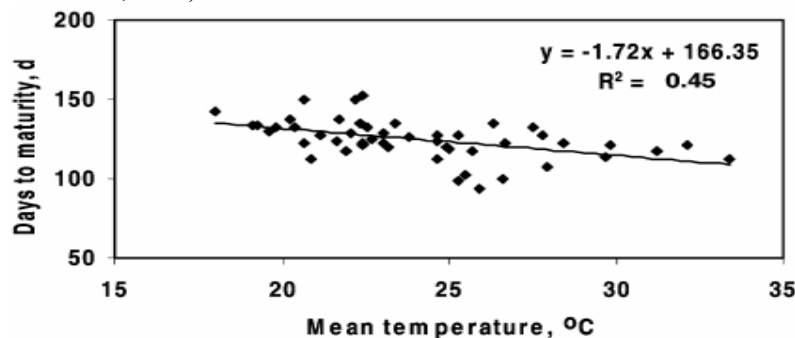

Source: Naveen et al., 2008.

Figure 3. Effect of seasonal temperature change on yield of barley in (a) Uttar Pradesh, (b) Rajasthan, (c) Punjab and (d) Haryana.

Elevated temperatures may either increase or decrease the vegetative biomass production of crops. Vegetative biomass of warm-climate species or cultivars of forages, sugarcane, soybean, and peanut may increase slightly with temperature increases, whereas vegetative biomass of cool-climate cultivars tends to decrease with increasing temperature (Allen and Prasad, 2004).

Rates of root growth and mortality increase with temperature if other factors do not limit photosynthesis and respiration. The way in which soil temperature, soil water, soil nutrients and sunlight interact to control root respiration, root growth and root mortality is very poorly understood in large, perennial plants (Pregitzer et al., 2000).The growth of shoots, roots, and inflorescences increased with increasing root temperature. With roots at 30° C growth continued throughout the experiment; with roots at 20° growth practically stopped; with roots at 11° C very little growth occurred. The distribution of dry matter between the various plant parts differed between the different root temperatures; vines with roots at 30° C had the highest shoot/root ratio (Woodham and Alexander, 1966).

Source: Naveen et al., 2008.

Figure 4. Duration of mustard crop growth as related to seasonal mean temperature.

Rising seasonal temperature and varies depending upon the locations. Optimum yield of mustard is expected when the average seasonal (winter) temperature stands between 17°C and 22°C, and the days to maturity are affected by increase in temperature as shown in Figure 4. The forced maturity (rate of hastening of maturity is 1.72 days per degree rise in temperature) might reduce the yield significantly.

2.4. Photosynthesis at Day and Night Temperature
The mean daily temperature is the arithmetic average of maximum temperature and minimum temperature which occur usually daytime and night time respectively. Both have their own significance in the growth and development of plants during their life cycle. Day temperatures in their optimum limits help the photosynthesis process in the presence of sunlight while higher night temperatures support respiration process which is the reverse process of the photosynthesis. Dry matter accumulation takes place when Photosynthesis is more than respiration which sustains the plant's growth and development vice versa retards the development process (Rasul et al., 2009).

2.5. Effect of Temperature on Reproductive Growth
Plant Reproduction is highly vulnerable to temperature and have significant consequences on the reproductive phase with serious implication in agricultural crops. Pollen tube growth is affected by temperature (Hedhly et al. 2003). Fruit decreased at higher temperature due to poor pollen viability; reduce pollen production and poor pollen tube growth, all of which lead to poor fertilization of flowers (Prasad et al., 2003). Reproductive growth leading to seed yield is often depressed by the same increase in temperature that enhances vegetative growth and development (Thomas et al., 2003).
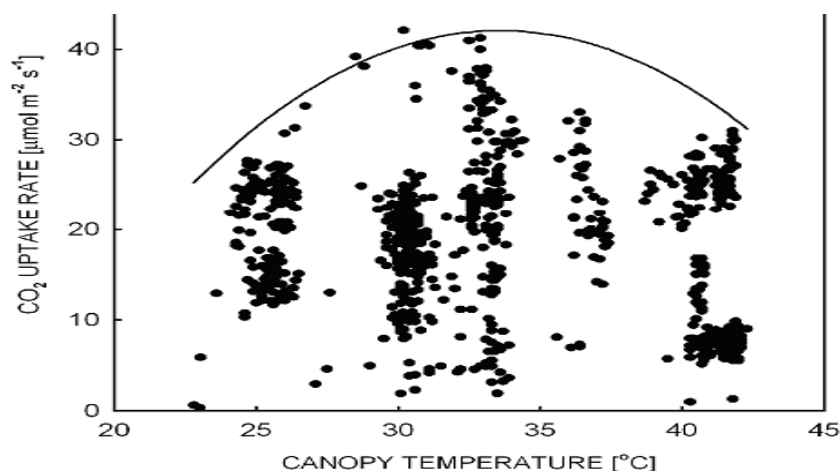
2.6. Photosynthetic Response to Temperature
Photosynthesis is strongly affected by temperature. In most plants, changes in photosynthetic rate in response to temperature are reversible over a considerable range (commonly 10° to 35°C), but below or above these range cause irreversible injury to the photosynthetic system. Extreme temperatures can drastically inhibit photosynthesis by disrupting the integrity of the system. Stomata control the resistance to the diffusive transfer of water vapor and CO_2 between the leaf and the ambient air and hence affect the CO_2 concentration in the intercellular spaces of photosynthesizing leaves (Berry and Bjorkman, 1980). The photosynthetic performance at high temperatures evidently result in decreased performance at low temperatures and vice versa, both in terms of tolerance and capacity. Increases in the level of enzymes of photosynthetic carbon metabolism are apparently important determinants of photosynthetic capacity at low temperatures, and the stability of proteins and appropriate adjustments in membrane lipids may contribute to low temperature tolerance. Changes in the physical properties of chloroplast membrane lipids leading to an increased heat stability of these membranes

evidently are a key factor in acclimation to high temperature (Berry and Bjorkman, 1980).
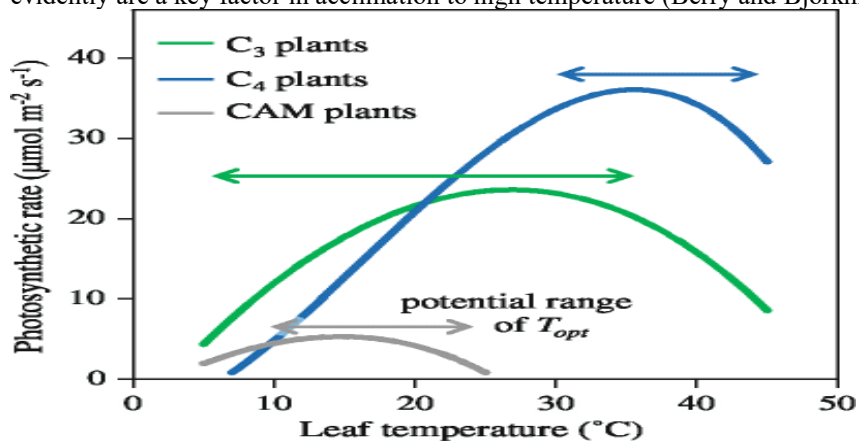

Source: Yamori et al., 2014

Figure 5. Typical temperature responses of photosynthesis in C3, C4, and CAM plants.

Source: Ben-Asher et al., 2008.

Figure 6. Temperature dependence of the net photosynthetic rate (PN) for Zea mays L. var. rugosa.

The canopy temperature increased from 22 °C to the optimal value of about 32 °C, PN gradually rose to about 42 μmol m-2 s-1. Temperatures above the optimal for PN were associated with its reduction. The highest PN was about 40 μmol m-2 s-1 and it was measured when the temperature was 30-32°C (Ben-Asher et al., 2008).
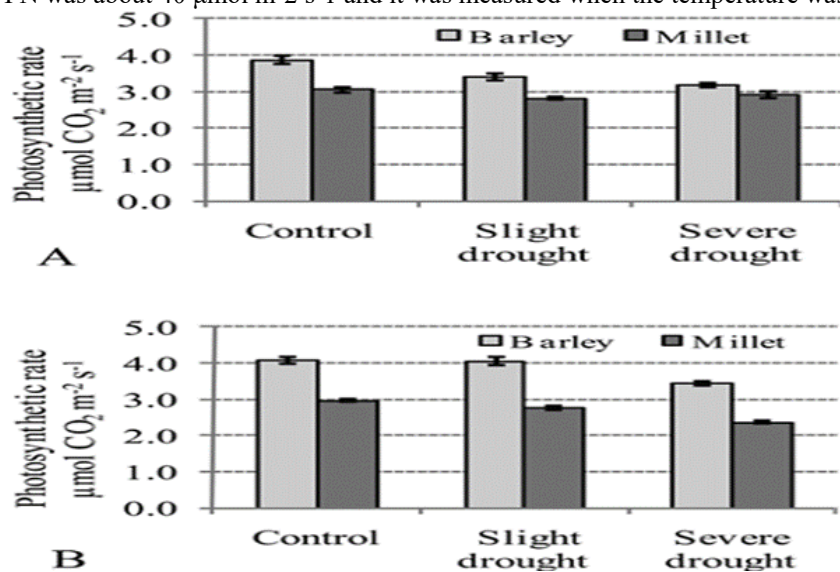
A – Photosynthesis after drought treatment, **B** photosynthesis after the period of recovery.

Source: Vitkauskaite and Enskaityte, 2011

Figure 7. Photosynthetic rate of slight and severe drought-treated barley and millet plants.

Higher photosynthetic rate was observed in the untreated barley plants compared to the millet plants. However, the CO_2 assimilation of barley was much more seriously affected by the water deficit (Fig. 7 A). On the other hand, the photosynthesis of barley was more able to recover after drought. When the plants were re-watered after slight water deficit, the photosynthetic rate of the barley plants recovered completely, whereas it remained diminished in the millet plants. Moreover, CO_2 assimilation sharply decreased during the re-watering period in the millet plants exposed to severe drought and did not change in the barley plants (Fig. 7 B).

3. SUMMARY AND CONCLUSION

Photosynthesis can be affected by temperature. High temperature influences photosynthetic function of plants by affecting the rate of chemical reactions and structural organization and conformational changes in enzymes. Photosynthetic response to temperature are dependent on species and growth conditions and has optimum temperature differing between species and growth condition. C4 plants show high rates of photosynthesis at high temperature when compare with C3 plants which show greater photosynthesis efficiency at cool temperature. In C3 plants, Rubisco activity is limited by CO_2 concentration. As temperature increases, the affinity of the enzyme for CO_2 and the solubility of CO_2 decreases. Together with Rubisco deactivation as temperature increases, photosynthesis declines at leaf temperatures greater than 32°C in C3 plants. In C4 plants, although rubisco activation is decreased at leaf temperatures above 32°C, the high level of CO_2 in the mesophyll chloroplasts can counteract this effect until temperature approaches 40°C. Increased temperature will affect the physiological processes necessary for crop growth and development of crops. If increases in temperature accompany increases in CO_2 concentration, seed yields will decrease in regions where temperatures are below or above optimum. Future research should be directed toward identifying high-temperature tolerant cultivars that can produce more seeds under harsh climatic conditions.

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