Chapter

Photosynthetic Response and Adaptation of Plants in Perspective of Global Climate Change

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Abstract

The intense agricultural and human being activities, especially after the industrialization era, have increased the CO_2 concentration, which led to changes in the global climate. Climate change and its consequences, that is, elevated CO_2, water stress, and extreme temperatures, have induced many biotic and abiotic stresses and have caused alterations in plant physiology, leading to a reduced photosynthetic capacity of plants. Photosynthesis is the most crucial biochemical process in plants that determines the final dry matter production and productivity of plants. The efficiency and status of the photosynthetic apparatus can be measured by the measurement of chlorophyll fluorescence. Measurements of chlorophyll fluorescence are easy, non-destructive, and quick, and it reflects changes in the general bioenergy status of a plant. Studies have indicated that abiotic stresses emerging from climate changes cause changes in the biological processes of plants and damage the internal structure of photosynthesis and control of the cellular process. Chlorophyll fluorescence, meanwhile, is an effective parameter and an indicator of photosynthetic status and its mechanisms under stressful conditions. Therefore, the photosynthetic changes and adaptation and the role of chlorophyll fluorescence in determining its status under climate change are discussed in this chapter.

Keywords: abiotic stress, chlorophyll fluorescence, drought, elevated CO_2, extreme temperatures, leaf physiology

1. Introduction

Food production is required to be increased by ~70% to feed the global population of 9 billion by 2050 [1], since the food demand, especially in developing countries, will be immensely enhanced. During the last 160,000 years, the concentration of atmospheric carbon dioxide has been varying between 170 and 300 μmol mol^{-1}. But with the beginning of the industrial revolution in Western Europe (between 1750 and 1800), the concentration of CO_2 increased from 280 to 385 μmol mol^{-1} [2]. According to predictions, with the rapid increase in world population, consumption of fossil

fuels, industrial development, and deforestation, the concentration of carbon dioxide, which is ~400 μmol mol^{-1}, will reach 700 micromoles by the end of this century [3].

Climate change and global warming have been one of the most controversial issues in the recent decade. Intense agricultural and industrial activities since the industrial revolution have hastened the process of global warming. The chemistry of the climate has been changed by agricultural and human being activities and consequently, many abiotic and biotic stresses have emerged and negatively affected plants' physiology and biochemistry. Crops resistant to environmental stresses should be the focus of agricultural plant development under the increased global temperatures and climate changes.

Due to continuously increasing the greenhouse gases, such as CO_2, in the atmosphere, climate change is happening rapidly. Climate change by increasing temperatures and reducing precipitations imposes abiotic stress exposure in many areas. Abiotic stresses, such as drought, salinity, cold, heat, UV radiation, and heavy metals, are the major limitations in agricultural products and adversely influence plant growth. It is estimated that abiotic stresses reduce crop yield by approximately 50% [4]. Drought, salinity, and extreme temperatures are among the most dreadful abiotic stresses in modern agriculture.

One of the most vital processes of plants that are affected by global climate change is photosynthesis. Photosynthesis is a vital biochemical process in plants that supplies the carbon and energy required for the biosynthesis of organic compounds and controls plant growth and development [5]. Photosynthesis is particularly sensitive to environmental constraints [6]. The environmental stresses adversely affect the photosynthetic capacity of plants. The increasing global population and climate change over the coming decades require enhanced photosynthetic efficiency to ensure food security. Thus, an understanding of the photosynthetic response and optimization under future climate uncertainties will be required for an improvement in crop production to meet future food requirements.

Chlorophyll fluorescence is one of the effective, non-destructive, and quick methods for evaluating the photochemical status of the plant photosynthetic system. Chlorophyll fluorescence is a useful parameter for the measurement of environmental

Plant species	**Environmental conditions**	**Parameters**	**Reference**
Potato (*Solanum tuberosum*)	Elevated CO_2	g_m, T_r, g_s ↓ A_n, C_i, R_D ↑	[10, 11]
Tomato (*Solanum lycopersicum* L.)	Elevated CO_2	A_n, V_{cmax}, J_{max}, f_v/f_m, ETR, $NADP^+$/NADPH ↑ NPQ, RL ↓	[12]
Fagus sylvatica	Elevated CO_2	A_n, R_D ↑ g_s, V_{cmax} ↓	[13]
Yucca (*Y. brevifolia and Y. schidigera*)	Elevated CO_2	A_n, f_v/f_m, Φ_{PSII} ↑ g_s ↓	[14]
Cotton (*Gossypium hirsutum* L.)	Elevated CO_2	F_o', F_m', Φ_{CO2}, ↑ *fv'/fm'*, qP, ETR, Φ_{PSII}, Φ_{PSII}/ Φ_{CO2}, ETR/A_n, ↓	[15]
Grape (*Vitis vinifera* L.)	Elevated CO_2	qP, Φ_{PSII}, ETR↑ f_v/f_m, NPQ ↓	[16]
Oak (*Picea abies*) and (*Quercus petraea*)	Elevated CO_2	A_n, g_s, T_r, WUE ↑	[17]

Plant species	Environmental conditions	Parameters	Reference
Pea (*Pisum sativum* L.)	High temperatures	A_n, g_s ↓	[18]
Wheat (*Triticum aestivum*)	High temperatures	WUE ↓	[19]
Barley (*Hordeum vulgare* L.)	High temperatures	f_v/f_m, Φ_{PSII} ↓	[20]
Tomato (*S. lycopersicum* L.)	High temperatures	ETR ↓	[21]
Alfalfa (*Medicago sativa*)	High temperatures	Chl ↓ F_o, F_m ↑	[22]
Tomato (*S. lycopersicum* L.)	High temperatures	A_n, Vc_{max}, J_{max}, f_v/f_m, ETR, $NADP^+$/NADPH ↓ NPQ ↑	[12]
Lentil (*Lens culinaris*)	Low temperatures	*fv'/fm'*, fq'/F_m' ↓	[23]
Salvia leriifolia Benth, *Visia faba*	Low temperatures	*fv'/fm'* ↓	[24–26]
Faba bean (*Vicia faba* L.)	Low temperatures	g_m, A_n, T_r, g_s, C_i, C_i:C_a ↓	[27]
Chickpea (*Cicer arietinum* L.)	Low temperatures	*fv'/fm'*, fq'/F_m' ↓	[28, 29]
Barley (*H. vulgare* L.)	Low temperatures	Φ_{PSII}, ETR ↓ NPQ ↑	[30]
Oats (*Avena sativa*)	Low temperatures	f_v/f_m ↓	[31]
Barley (*H. vulgare* L.)	Drought	Chl, F_o, f_v/f_o, f_v/f_m, ETR ↓	[32]
Maize (*Zea mays* L.)	Drought	Rubisco ↓	[33]
Black-eyed pea (*Vigna unguiculata*)	Drought	A_n, *fv'/fm'* ↓	[34]
Barley (*H. vulgare* L.)	Drought	NPQ ↑	[35]
Castor bean (Ricinus communis)	Drought	A_n, C_i ↓	[36]
Wheat (T. aestivum)	Drought	g_m, A_n, T_r, g_s ↓	[37]
Oak (P. abies) and (Q. petraea)	Drought	A_n, g_s, T_r, WUE, V_C, J ↓	[17]
Sweet corn (Z. mays L.)	Drought	f_v/f_m ↓	[38]

Increase (↑), decrease (↓).

Table 1.
Effect of climate changes induced stresses on photosynthetic and chlorophyll fluorescence parameters.

stress effects on photosynthetic apparatus and an effective indicator of photosynthesis limiting factors. The photochemical efficiency of photosystem II (PSII) is strongly influenced by the climate change consequences such as elevated CO_2, extreme temperatures, and water stress, and a reduction in leaf relative water content and the accumulation of carbohydrates in leaves decreases the quantum efficiency of PSII [7].

More food must be produced by global agriculture to sustain a growing human population in the twenty-first century [8]. Producing more food, however, is threatened by the climate change constraints that limit plant productivity [9]. Under natural conditions, plants are exposed to many adverse environmental stresses that disrupt the photosynthetic apparatus, causing a decrease in plant productivity and overall yield. In the present chapter, the impacts of changing climatic conditions on photosynthesis, with an emphasis on the main consequences of climate change, that is, elevated CO_2, extreme temperatures, and drought are discussed (**Table 1**).

2. Climate change consequences and photosynthetic response

2.1 Elevated CO_2

Carbon dioxide, like other important factors, such as light, water, and nutrients, is one of the determinant factors in plant production. Carbon dioxide is the key substrate for photosynthesis and the source of carbon for plants; however, high, or low CO_2 concentration diversely affects plant growth and productivity [39]. Carbon dioxide stimulates photosynthesis, inhibits photorespiration, and increases the efficiency of water and nitrogen use, which leads to more biomass production and changes in plant composition. Increasing CO_2 concentration by preventing photorespiration in C_3 plants increases the efficiency of photosynthesis because, in the current CO_2 concentration the carboxylation capacity of Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) does not reach the saturation limit (Drake et al., 1997). The increase in growth and yield of crop species due to doubling the CO_2 concentration was primarily due to the faster photosynthetic rate and secondarily due to less photorespiration [40].

Photosynthesis of C_3 plants is not completely saturated at the current CO_2 concentration. Increasing CO_2 concentration stimulates the rate of photosynthesis and has a positive effect on the growth and performance of plants [41]. Idso and Idso [42] believe that by doubling the current CO_2 concentration, biomass production, and yield of plants will increase by one-third or more if other factors are not limiting. However, plant species differ in response to CO_2 concentration. Faster-growing species are more stimulated and produce more biomass than slow-growing species. Also, plants growing in better nutritional conditions respond more to increased CO_2 concentration than those that are exposed to nutritional stress [43]. Apart from the indirect effects of atmospheric elevated CO_2 concentration, CO_2 concentration directly affects C_3 plants if other factors are not limiting [44]. In research on potatoes in an open-growth chamber, it was found that the photosynthesis of plants grown under elevated CO_2 concentration (720 ppm) was 10 to 40% higher than those grown under ambient CO_2 concentration (400 ppm) [45]. In addition, leaf starch and sucrose content were higher in plants grown under CO_2 concentration conditions, especially in young leaves. This shows that the response of plants to the CO_2 concentration also depends on leaf age.

In general, increasing CO_2 concentration as a substrate for photosynthesis increases leaf area, biomass, and CO_2 fixation. The main reason for the increase in photosynthesis and subsequent increase in growth is the competitive effect of the Rubisco enzyme, which increases the carboxylation of this enzyme [46]. The results of the experiments showed that the rate of photosynthesis was significantly increased under elevated CO_2 concentration in two potato cultivars [10, 11, 47]. Chen and Setter [48]

reported that cell division in physiological sinks is an important factor in increasing the photosynthesis of C_3 plants under CO_2 concentration. Increasing CO_2 concentration to 720 μmol mol^{-1} increased cotton canopy photosynthesis by 40% [49]. Also, the increased CO_2 concentration delayed the aging of sugarcane leaves [50]. Elevated CO_2 concentration also increased wheat production [51].

Potato plant leaves showed an 80–100% increase in photosynthetic rate when exposed to elevated CO_2 concentration [52]. However, long-term growth under elevated CO_2 concentration conditions led to plant acclimation to this environment and a relative decrease in photosynthesis [53]. Sicher and Bunce [54] reported that this acclimation is reversible by shifting plants to lower CO_2 concentration. Sicher and Bunce [55] stated that the acclimation response to higher CO_2 concentration is mainly due to a decrease in Rubisco activity than a decrease in the amount of this enzyme. In contrast, Schapendonk [56] found that photosynthetic acclimation, under elevated CO_2 concentration, was accompanied by a decrease in Rubisco and concluded that the acclimation is a complex mechanism resulting from the negative feedback of source-sink disequilibrium induced by high CO_2 concentration. In a study on two model tree species—coniferous Norway spruce and broadleaved sessile oak, A_n was increased in oak saplings under elevated CO_2 concentration (700 μmol CO_2 mol^{-1}), whereas in Norway spruce, Amax remained unchanged or slightly declined; indicating a down-regulation of photosynthesis. Such acclimation was associated with the acclimation of both J and V_C.

Transpiration rate and g_s were decreased with increasing CO_2 concentration, while WUE was increased [57]. Therefore, the beneficial effects of increased CO_2 concentration on yield may be due to changes in either A_n or WUE or both; on the other hand, the reduction of g_s can increase the temperature of the leaf, which further increases the speed of the developmental stages and shortens the grain filling period [58]. The increase in growth due to elevated CO_2 concentration has been attributed to the improvement of plant water relations or the increase of cell expansion [59]. An increase in C_i due to an increase in CO_2 concentration can trigger partial stomatal closure, although the process of how stomata respond to CO_2 signals remained uncertain [60].

An increase in CO_2 concentration accelerates aging in plants. One of the reasons for this is the effect of CO_2 on reducing g_s and increasing leaf temperature. Another reason is the increase in the demand for underground parts for nitrogen and the reduction of N supply to aerial organs [61]. Nitrogen redistribution from chlorophyll-binding proteins has been proposed as the main factor in chlorophyll degradation [62]. Chlorophyll is known as the first electron donor in the process of electron transfer and the photosynthesis apparatus and plays a fundamental role in absorbing light energy in the photosynthesis apparatus [63]. The results of various studies show that elevated CO_2 concentration causes a decrease [64, 65], an increase [66], or no change [52] in the chlorophyll content of potato leaves. Bindi [66] reported that the chlorophyll content of potato leaves under conditions of increased CO_2 concentration was on average 9.3% lower than that of plants under normal conditions.

Reducing g_s, oxidative stress, and decreasing the activity of Rubisco affect photosynthesis under environmental stresses [67]. In addition, PSI and PSII, ETR, and Chl biosynthesis are negatively influenced by abiotic stresses [68, 69]. The quantum efficiency of PSII is considered a quantitative indicator of electron transfer through PSII, which is related to the photochemical efficiency of PSII [69]. Non-photochemical quenching indicates how much excess energy is released as heat by the plant relative to linear electron transport. Under unfavorable conditions, *that is,* environmental stresses, more energy is required to be dissipated since *qP* is disrupted. Therefore, NPQ

is strongly enhanced when physiological sinks are few and leaf physiology and biochemistry are adversely affected by environmental stresses [70]. Working on tomato and grape plants showed that elevated CO_2 concentration decreased NPQ of leaves, while *qP* was enhanced, indicating that higher CO_2 concentration probably stimulates the photosynthetic efficiency and improves the photochemistry of leaves [12, 16].

There are different reports on the effect of elevated CO_2 concentration on chlorophyll fluorescence. Hao [71] stated that the increase in CO_2 concentration increased the rate of photosynthesis and J_{max} with an increase in f_v/f_m, the efficiency of photoreceptors, and the transfer energy of PSII reaction centers (RC). Also, *qP* was reduced under those conditions. On the other hand, Pérez [72] and Ge [73] reported reduced leaf Chl content and factors related to chlorophyll fluorescence, including the photochemical efficiency of PSII and the ETR due to an increase in CO_2 concentration. Taub [74] also reported that in most of the species in their study, the efficiency of photosystem II (f_v/f_m) was significantly higher in plants grown under elevated CO_2 concentration. They stated that this higher efficiency was due to both higher F_m and lower F_o fluorescence. The results of a study showed that elevated CO_2 concentration (800 mmol mol^{-1}) improved leaf A_n, Vc_{max}, J_{max}, and f_v/f_m of tomato (*Solanum lycopersicum* L.) plants at a 24 h recovery [12]. Furthermore, the elevated CO_2 concentration also increased the absorption flux, trapped energy flux, ETR, energy dissipation per PSII cross-section, the concentration of $NADP^+$ and ratio of $NADP^+$/NADPH, and decreased photoinhibition, damage to PSs and ROS accumulation.

2.2 Extreme temperatures

Plants are exposed to frequent low and high-temperature stresses during their life [75]. Global warming induces temperature stress on plants and limits productivity and biomass production. Climate change is likely to increase extreme temperatures beyond the optimum temperatures for the growth of plants. Temperature above or below the optimal threshold disrupts plant cellular homeostasis, which further slows down plant growth, development, and metabolism [76]. The ideal temperature for plant growth and development is in the range of 10 to 35°C. Rising temperature to a specific point enhances plants to generate excess energy; however, heat stress adversely affects plant growth and diminishes the photosynthetic rate [77]. Elevated temperature increases respiration levels in plants. Raising the temperature from 15 to 40°C elevated the respiration rate and disturbed the morphological features of crop species [78].

Heat tolerance is directly related to the ability of plants to maintain the CO_2 assimilation rate. Stomatal conductance and transpiration rate are closely related to leaf temperature [79]. Stomatal conductance, substomatal CO_2 concentration, and leaf water status are affected by the temperature above the optimum levels for plant growth [80]. The concentration of substomatal CO_2 is altered at high temperatures upon stomatal closure and inhibits net photosynthesis [81]. Moreover, high temperatures directly affect the vapor pressure deficit that alters the plant's hydraulic conductance and water supply of the leaves [82]. Studies indicated that the net CO_2 assimilation rate in soybean decreased with an increase in temperature mainly due to the reduction in gs and C_i and lower biomass accumulation [83]. A reduction in photosynthetic ET diminished ATP production and A_n under high temperatures [84]. A significant decrease in the photosynthetic electron transport chain, ATP production, and NADPH under high temperatures led to a decrease in photosynthesis [85].

The negative effect of heat stress on photosynthesis might be due to the reduced Rubisco content and activity [86]. The reduced Rubisco thermal stability decreases its activation under higher temperatures [87]. Rubisco is activated by the RA at an optimum temperature. The catalytic activity of Rubisco is stimulated by an increase in temperature, but the RA fluctuates in response to high temperature [87]. While Rubisco is stable even at 50°C, the activity of RA is decreased at temperatures beyond the optimum [88]. The first step in photosynthetic and photorespiration pathways is catalyzed by Rubisco. The carboxylation efficiency of Rubisco is decreased at high temperatures because of the temperature sensitivity of the RA protein. An elevation in temperature leads to the deactivation of the Rubisco enzyme by the generation of inhibitory compounds such as xylulose-1,5-bisphosphate. Also, the RA breakdown at high temperatures causes the Rubisco disruption [89]. The RA is the main enzyme in the CO_2 fixation process in plants, but at higher temperatures, it is not sufficiently able to keep the balance of the inactivation [90].

Chlorophyll pigments are important for light harvesting; however, temperature stress negatively affects their biosynthesis in plastids [91]. High temperatures degrade the chlorophyll molecule due to different enzymatic impairments; the first enzyme in pyrrole biosynthesis (5-aminolevulinate dehydratase (ALAD)) is negatively affected by high temperature [92]. The decreased chlorophyll biosynthesis in celery leaves at high-temperature stress was likely due to the mRNA down-regulation of 15 genes involved in chlorophyll biosynthesis [93].

Plant productivity is restricted by temperature stress in different ways [94]. The photosynthetic apparatus is the first site of inhibition and is highly sensitive to heat stress. High-temperature alter the reduction-oxidation capacity of PSII acceptors and reduce the photosynthetic electron transport (ET) efficiency of both photosystems [76]. The important components of photosynthetic apparatus are the PSI and PSII, CO_2 reduction pathways, photosynthetic pigments, and ETR and any impairment inhibits overall photosynthesis [92].

High temperatures increase the permeability of membranes, damage PSII subunits, and the manganese complex, and limit ET. The increased permeability of thylakoid membranes leads to peroxidation of membranes, membrane protein changes, the opening of ionic channels, redistribution of specific lipids in thylakoid membranes, and the formation of single-layered membranes [76, 92]. The oxygen-evolving complex of plants grown at high temperatures is partially damaged. Kalaji [6] found that low and high temperatures decreased the reduced PSII electron acceptors pool (mainly Q_A) in barley seedlings. The Φ_{PSII} and the qP were decreased at high temperatures in oak leaves [95].

Kalaji [7] believed that the PI_{ABS} is the most sensitive indicator of various stressors including extreme temperatures. Damage to thylakoid membranes and a decrease in the PSII activity can be the reason for decreased fluorescence in response to high-temperature stress [89]. PSII thermostability is often calculated with the use of fluorescence methods by determining the relationships between F_o and leaf temperature. The fast fluorescence kinetics (JIP-test parameters) can also use to determine the effects of critical temperatures, which are often affected by a much lower temperature than the F_o [7, 96].

One of the crucial factors in predicting future global warming is the response of photosynthesis to temperature. Plant CO_2 assimilation is impaired under environmental stress conditions, such as temperature, while light absorption remains unaffected. Excessive light energy absorption leads to the production of ROS and the photosynthetic machinery, mainly PSII, which is highly sensitive to photodamage, is severely

damaged. Although plants have various mechanisms to protect the PSII, photoinhibition occurs when the photodamage rate is exceeded the PSII repairment rate, leading to reduced photosynthetic efficiency [97].

High night temperature stress is increasing due to climate change, and it suppresses the net CO_2 assimilation rate in both C_3 and C_4 plants. The ratio of reduced plastoquinone (Q_B) to (Q_A) and the ratio of Q_A to RC is reduced under high night temperatures. Furthermore, f_v/f_m was decreased, and F_o was increased under high night temperatures [98]. High night temperature reduces qP, Φ_{PSII}, and ETR, increases NPQ, and inhibits the donation of electrons by the oxygen-evolving complex (OEC). Pan [12] observed that high temperature reduced tomato (*S. lycopersicum* L.) leaves photosynthesis by reducing the energy fluxes limitations, ET, and redox homeostasis. They observed that Vc_{max}, J_{max}, and f_v/f_m were diminished by high temperature (42°C for 24 h).

The saturation of fatty acids and membrane fluidity is induced by low temperatures, and it affects the efficiency of photosynthetic ET. Previous studies on various plant species elucidated that the leaf photosynthetic activity is affected by short-term or long-term high and low temperatures [7]. Plants by stimulating thermal energy dissipation and increasing the hydrophobic protein PsbS content, which participates in the thermal energy dissipation, try to reduce the generation of ROS and adapt to low temperatures [99]. Low temperatures inhibit sucrose synthesis, reduce photosynthetic ET, increase photoinhibition, and disturb the photophosphorylation process. Rapacz [100] found that mild frosts initially disturbed the energy transfer to the primary quinone electron acceptor of PSII, Q_A in wheat plants; however, lower temperatures, that is, freezing, may cease energy flow between the PSII RC, Chl, and Q_A, which these primary injuries could only be partially repaired. Consequently, further freezing hinders the ET between the PSII RCs and Q_A and the secondary damage may lead to PSII deactivation. They concluded that both primary and secondary freezing damages resulted in a decreased PI_{ABS}. Strauss [101] also observed that the PI_{ABS} was decreased at low temperatures in soybean plants. Working on faba bean (*Vicia faba* L.) landraces revealed that gas exchange variables are promising criteria for screening freezing-tolerant landraces at early growth stages [27]. The physiological, biochemical, and molecular modifications of chickpea (*Cicer arietinum* L.) seedlings were studied under freezing stress, and it was found that f_v'/f_m' and t Φ_{PSII} of the cold-tolerant genotype recovered faster compared to the cold-sensitive genotype [28, 29]. They found that f_v'/f_m' and Φ_{PSII} were significantly lower in freezing compared with higher temperatures. In a study on lentil (*Lens culinaris* Medik.) genotypes under freezing stress, Nabati [23] found that F_m', f_v'/f_m', and Φ_{PSII} were decreased at freezing temperatures. They concluded that the freezing-tolerant genotypes showed a high potential to restore PSII performance and survival rate.

2.3 Drought stress

Global climate change and lower availability of underground water induce a water crisis worldwide. The constant rise in the atmospheric global temperature induces frequent droughts around the world, which further impacts the biological systems [102]. Plants may experience different forms of abiotic stresses, such as drought during their life, which adversely affect plant growth, survival, and productivity [103]. Drought is a serious problem in arid and semiarid environments with precipitation deficiency [104].

Plant photosynthesis, growth, and yield are impaired by drought stress [105]. Photosynthesis is highly sensitive to drought stress and is the first-line process that is altered by drought stress. Lower photoassimilate production reduces leaf growth and

crop yield [37]. Impaired photosynthesis under water deficit relates to either stomatal or non-stomatal limitations. Plants enhance their tolerance levels to survive under such a harsh environment by adopting different strategies, such as stomata closure and osmotic adjustment [106]. Closure of stomata as the primary response of leaves to drought conditions prevents water loss and decreases Tr and increases WUE of plants [92]. The primary response of plants to drought stress is closing the stomata. CO_2 and water exchange in plants are regulated by stomatal openings. Although stomatal closure limits water loss, CO_2 absorption and transportation of non-structural carbon (NSC) are also hindered by stomatal closure, leading to carbon starvation which further affects further processes [107].

Nonstomatal limitations of photosynthesis might be due to lower synthesis and supply of Rubisco and/or other metabolic responses [108]. The proteins D_1 and D_2 can also be damaged by drought stress [109]. Since the PSII is quite resistant to water stress, the photochemical reactions may only be influenced by severe water stress [110]. Lauriano [111] found that changes in the values of chlorophyll fluorescence parameters in peanut leaves were more pronounced under severe drought. Decreased leaf CO_2 transport rate under prolonged and severe water stress reduces CO_2 concentration in chloroplasts, thus weakening photosynthesis. The decrease in the cells CO_2 concentration reduces the activity of sucrose phosphate synthase, nitrate reductase, and capacity for ribulose bisphosphate (RuBP) regeneration, and deactivates Rubisco [49]. The chloroplast thylakoid membrane is degraded under water stress and adversely affects photosynthetic pigment and reduces the photosynthetic rate [112].

Water stress induces oxidative stress. Under water stress, a reduction in chloroplastic CO_2 concentration due to the stomatal closure leads to the impairment of the Calvin cycle and reduces the production of $NADP^+$, leading to excessive electron transport chain (ETC) reduction and directing the electrons to O_2 via Mehler reaction to form singlet O_2, and consequently, ROS [113]. Under drought conditions, triplet chlorophyll stages ($^3Chl^*$) may be overproduced if too much energy is delivered to antenna complexes. This promotes singleton oxygen ($^1O_2$) production, which is a highly reactive form of oxygen that can photo-oxidase chlorophyll (mainly P680) and cause peroxidation of membrane lipids [111]. Partial closure of the stomatal reduces CO_2 assimilation and might lead to an imbalance between PSII photochemical activity and NADPH demand, which in turn, the generation of ROS can be stimulated and lead to higher sensitivity to photodestruction. Under stressful conditions such as low water availability and high irradiance and temperature, photosynthetic efficiency decreases due to a probable high chronic photoinhibition [7].

Studies of the alterations in the chlorophyll fluorescence kinetics provide an in-depth understanding of the structure and functions of the photosynthetic apparatus, particularly PSII [114]. Drought can change the kinetics of chlorophyll fluorescence by affecting PSII. The photochemical efficiency of PSII is strongly influenced by the relative water content of the leaf. The reduction of photosynthesis and the accumulation of carbohydrates in the leaf decrease the quantum efficiency of PSII [7]. One of the consequences of drought is stomatal closure which reduces the heat exchange of leaves. High temperature affects PSII, photosynthetic ET, and ATP synthesis [7]. A decrease in f_v/f_m and yield are indicators of photoinhibition in plants under stressful conditions, indicating lower efficiency of photosynthetic conversion of PAR photon energy [108]. The f_v/f_m is decreased at advanced stages of stress. The f_v/f_m is directly related to chlorophyll activity in the PSs RC. Working on maize plants, Karvar [38] found that deficit irrigation decreased the f_v/f_m. A decrease in leaf Chl content was the likely reason for the diminished f_v/f_m. Carotenoids are non-enzymatic antioxidants

that prevent Chl photooxidation under stressful conditions [103]. The stability of carotene and xanthophyll cycle pigments significantly contributed to the protection mechanism of PSII RCs. Furthermore, the cyclic electrons flow around PSI significantly contributed to the dissipation of excess energy in some plant species under water stress [111].

The PSII Φ_{PSII} and ETR_{PSII} are also important parameters to measure drought stress effects on leaves, which provide estimation for both stomatal and non-stomatal effects of drought stress. However, the relative fluorescence decreases ratio (Rfd) proposed by Lichtenthaler [115] as a more sensitive parameter correlated with photosynthetic assimilation than the PSII Φ_{PSII} or ETR_{PSII}. In sunflower plants, it was observed that water potential (Ψ), g_s, A_n, Φ_{PSII}, f_v/f_m, and daily accumulation of total non-structural carbohydrates (TNC) was decreased under drought, but NPQ, malondialdehyde concentration (MDA), and soluble carbohydrates content was increased [116]. The PI_{ABS} was also positively correlated with the water availability for plants. Van Heerden [104] found that a higher water supply increased PI_{ABS} in *Augea capensis* and *Zygophyllum prismatocarpum*.

3. Conclusions

Increasing greenhouse gases emission have led to global warming and climate change worldwide. The global climate change consequences, *that is,* elevated CO_2 concentration, water stress, and extreme temperatures, are serious problems affecting the photosynthetic efficiency and adaptation of plants and adversely affecting agricultural yields. Studies suggest that most plants will be more stressed and less productive in the future in response to climate change. Climate change reduces photosynthetic capacity directly by damaging photosynthetic structures and processes. The changes and modifications of the photosynthetic machinery under different stressful conditions can be evaluated by the chlorophyll fluorescence analysis. Analyses of chlorophyll fluorescence seem to be a promising tool for breeding crops with improved tolerance under stressful conditions. Therefore, the application of chlorophyll fluorescence can be useful to identify which part of the photosynthetic apparatus is affected by the stress and it might help identify good-performing genes by chlorophyll fluorescence to be used in breeding programs.

Abbreviations

A_n	net assimilation rate
Chl	chlorophyll
C_i	sub-stomatal CO_2 concentration
ETR	electron transport rate
ETR/A_n	photorespiration
F_m	maximal fluorescence
F_o	minimal fluorescence
fq'/F_m'	light-adapted operational efficiency of photosystem II
F_v'	light-adapted variable fluorescence
fv'/fm'	light-adapted maximum efficiency of photosystem II
g_m	mesophyll conductance
g_s	stomatal conductance

J	electron transport
J_{max}	maximum ribulose-1,5-bisphosphate (RuBP) regeneration rate
NPQ	non-photochemical quenching
OEC	oxygen-evolving complex
PI_{ABS}	performance index
PSI	photosystems I
PSII	photosystems II
qP	photochemical quenching
RA	Rubisco activase
R_D	dark respiration
R_L	photorespiration rate
ROS	reactive oxygen species
T_r	transpiration rate
V_C	Rubisco carboxylation rate
Vc_{max}	mximum carboxylation rate
WUE	water use efficiency
Φ_{CO2}	quantum yield of CO_2 assimilation
Φ_{PSII}	effective quantum yield

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