

REVIEW

Photosynthesis under stressful environments: An overviewM. ASHRAF^{*,+} and P.J.C. HARRIS^{**}*Department of Botany, University of Agriculture, Faisalabad, Pakistan***Centre for Agroecology and Food Security, Coventry University, United Kingdom*****Abstract**

Stressful environments such as salinity, drought, and high temperature (heat) cause alterations in a wide range of physiological, biochemical, and molecular processes in plants. Photosynthesis, the most fundamental and intricate physiological process in all green plants, is also severely affected in all its phases by such stresses. Since the mechanism of photosynthesis involves various components, including photosynthetic pigments and photosystems, the electron transport system, and CO₂ reduction pathways, any damage at any level caused by a stress may reduce the overall photosynthetic capacity of a green plant. Details of the stress-induced damage and adverse effects on different types of pigments, photosystems, components of electron transport system, alterations in the activities of enzymes involved in the mechanism of photosynthesis, and changes in various gas exchange characteristics, particularly of agricultural plants, are considered in this review. In addition, we discussed also progress made during the last two decades in producing transgenic lines of different C₃ crops with enhanced photosynthetic performance, which was reached by either the overexpression of C₃ enzymes or transcription factors or the incorporation of genes encoding C₄ enzymes into C₃ plants. We also discussed critically a current, worldwide effort to identify signaling components, such as transcription factors and protein kinases, particularly mitogen-activated protein kinases (MAPKs) involved in stress adaptation in agricultural plants.

Additional key words: drought; fluorescence; gas exchange; heat; photosynthesis; photosynthetic pigments; salinity, salinity stress.

Introduction

Although the plant growth is controlled by a multitude of physiological, biochemical, and molecular processes, photosynthesis is a key phenomenon, which contributes substantially to the plant growth and development. The chemical energy expended in a number of metabolic processes is, in fact, derived from the process of photosynthesis, which is capable of converting light energy into a usable chemical form of energy. This key process occurs in all green plants, whether lower or higher, occurring in oceans or on land as well as in photosynthetic bacteria (Taiz and Zeiger 2010, Pan *et al.* 2012). However, stressful environments, including drought, salinity, and unfavourable temperatures, considerably

hamper the process of photosynthesis in most plants by altering the ultrastructure of the organelles and concentration of various pigments and metabolites including enzymes involved in this process as well as stomatal regulation.

In the process of photosynthesis (Fig. 1), two key events occur mandatorily; light reactions, in which light energy is converted into ATP and NADPH and oxygen is released, and dark reactions, in which CO₂ is fixed into carbohydrates by utilizing the products of light reactions, ATP and NADPH (Lawlor 2001, Taiz and Zeiger 2010, Dulai *et al.* 2011). There are two main pathways of CO₂ fixation, C₃ and C₄. Plants have been categorized into C₃,

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Abbreviations: ABA – abscisic acid; ALA – 5-aminolevulinic acid; Car – carotenoids; Chl – chlorophyll; F_i – the fluorescence at transient inflection level; F_o – the minimal fluorescence; F_m – the maximal fluorescence; F_p – the fluorescence at peak level; F_v – the variable fluorescence; g_s – stomatal conductance; LHC – light harvesting complex; MAPKs – mitogen-activated protein kinases; NADPH – reduced form of nicotinamide adenine dinucleotide phosphate; NADP-ME – NADP-malic enzyme; OEC – oxygen evolving complex; q_N or NPQ – nonphotochemical quenching; Pchl_{id} – protochlorophyllide; PEPC – phosphoenolpyruvate carboxylase; P_N – net photosynthetic rate; PPK – phosphopyruvate dikinase; PSII – photosystem II; q_p – photochemical quenching; RWC – relative water content; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; RUBP – ribulose-1,5-bisphosphate; WUE – water-use efficiency.

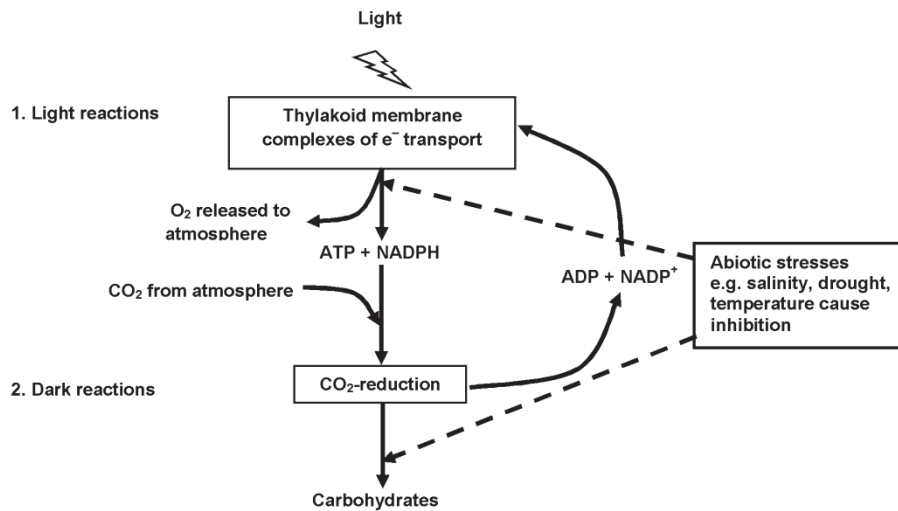


Fig. 1. Light and dark reactions of photosynthesis.

C_4 , or C_3 - C_4 intermediate plants depending on the spatial distribution of these two pathways within leaf tissues or as crassulacean acid metabolism (CAM) plants with a temporal distribution (Doubnerová and Ryšlavá 2011, Freschi and Mercier 2012). Plants possessing the different types of photosynthetic mechanisms are adapted to specific climatic zones. For example, C_3 plants, representing over 95% of the Earth plant species, thrive well in cool and wet climates, with usually low light intensity. In contrast, C_4 plants occur in hot and dry climatic conditions with usually high light intensity. Generally, C_4 and CAM plants are the best adapted to arid environments, because they have higher water-use efficiency (WUE) than that of C_3 plants. C_4 plants have higher photosynthetic efficiency than C_3 plants, namely in arid, hot, and under high-light conditions, because they possess an additional carbon fixation pathway and characteristic anatomy to limit photorespiration. Furthermore, CAM plants can effectively save metabolic energy and water during harsh environmental conditions by closing their stomata during the day (Taiz and Zeiger 2010).

Different growth and development related processes depend on the interplay of intracellular organelles. The chloroplast is the key site for photosynthesis, in which both light and dark reactions of photosynthesis take place. However, this organelle is highly sensitive to different stressful environments such as salinity, drought, extremes of temperature, flooding, varying light intensity, and UV radiation, and it plays a premier role in the modulation of stress responses (Biswal *et al.* 2008, Saravanavel *et al.* 2011). All these stresses reduce the photosynthetic rate by stress-induced stomatal or nonstomatal limitations (Saibo *et al.* 2009, Rahnama *et al.* 2010). For example, drought stress, particularly at its mild intensity, can inhibit leaf photosynthesis and stomatal conductance in most green plants (Medrano *et al.* 2002). A number of reports showed that stomata usually close during the initial stages of drought stress resulting in increased WUE (net CO_2 assimilation rate/transpiration). Stomata closure is known

to have a more inhibitory effect on transpiration of water than that on CO_2 diffusion into the leaf tissues (Chaves *et al.* 2009, Sikuku *et al.* 2010). However, in contrast, under severe drought stress, dehydration of mesophyll cells takes place causing a marked inhibition of basic metabolic processes of photosynthesis as well as a reduction of plant WUE (Damayanthi *et al.* 2010, Anjum *et al.* 2011). Drought stress also reduces the efficiency of mesophyll cells to utilize the available CO_2 (Karaba *et al.* 2007, Dias and Bruggemann 2010a,b).

The regulation of leaf stomatal conductance (g_s) is a key phenomenon in plants as it is vital for both a prevention of desiccation and CO_2 acquisition (Dodd 2003, Medici *et al.* 2007). Stomata closure in response to drought and salinity stress generally occurs due to decreased leaf turgor and atmospheric vapor pressure along with root-generated chemical signals (Chaves *et al.* 2009). Thus, the decrease in photosynthetic rate under stressful conditions (salinity, drought, and temperature) is normally attributed to a suppression in the mesophyll conductance and the stomata closure at moderate and severe stress (Flexas *et al.* 2004, Chaves *et al.* 2009). The effects of salinity and drought on photosynthesis are attributed directly to the stomatal limitations for diffusion of gases, which ultimately alters photosynthesis and the mesophyll metabolism (Parida *et al.* 2005, Chaves *et al.* 2009). However, of various physiological processes, the accumulation of a plant hormone, abscisic acid (ABA), shows a vitally important role in the plant growth and metabolism under stress conditions. ABA is usually known as a stress hormone due to its high accumulation under stress environments (Kempa *et al.* 2008, Melcher *et al.* 2009). One of the immediate responses to water stress is stomata closure, which is caused mainly due to the action of ABA. High ABA level has been reported to cause an increase in cytosolic Ca^{2+} and activation of plasma membrane-localized anion channels (Hamilton *et al.* 2000, Kohler and Blatt 2002). This, in turn, causes potassium efflux, guard cell depolarization, loss of guard cell volume

and turgor, high H₂O₂ production, and finally the stomata closure (Zhang *et al.* 2006, Wang *et al.* 2012).

Similar effects of salinity-induced, osmotic stress on photosynthetic machinery and metabolism can be expected. However, salt-induced, ionic effects on organelle ultrastructure and photosynthetic metabolic processes are additional and important (Lawlor 2009, Sade *et al.* 2010). Long ago, it was reported that cellular membranes are highly sensitive to stresses (Ashraf and Ali 2008, Tayefi-Nasrabadi *et al.* 2011). High concentrations of injurious ions, such as Na⁺ and Cl⁻, which accumulate in the chloroplasts under salinity stress, are known to damage thylakoid membranes (Wu and Zou 2009, Omoto *et al.* 2010). Electron transport and photophosphorylation of isolated thylakoid membranes were reported to be swiftly and irrevocably inactivated by high concentrations of inorganic salts (Veiga and Silva 2007, Mittal *et al.* 2012).

As other stresses, photosynthesis is highly sensitive to

Stress-induced changes

Effects on photosynthetic pigments

Salt stress: Different stressful environments have been reported to reduce the contents of photosynthetic pigments. For example, salt stress can break down chlorophyll (Chl), the effect ascribed to increased level of the toxic cation, Na⁺ (Pinheiro *et al.* 2008, Li *et al.* 2010, Yang *et al.* 2011). Reduction in photosynthetic pigments, such as Chl *a* and *b* has been reported in some earlier studies on different crops, *e.g.*, sunflower, *Heliantus annuus* (Ashraf and Sultana 2000, Akram and Ashraf 2011), alfalfa, *Medicago sativa* (Winicov and Seemann 1990), wheat, *Triticum aestivum* (Arfan *et al.* 2007, Perveen *et al.* 2010), and castor bean, *Ricinus communis* (Pinheiro *et al.* 2008). The salt-induced alterations in a leaf Chl content could be due to impaired biosynthesis or accelerated pigment degradation. However, during the process of Chl degradation, Chl *b* may be converted into Chl *a*, thus resulting in the increased content of Chl *a* (Fang *et al.* 1998, Eckardt 2009). A series of experiments with sunflower callus and plants (Santos and Caldeira 1999, Santos *et al.* 2001, Santos 2004, Akram and Ashraf 2011) have shown that the important precursors of Chl, *i.e.*, glutamate and 5-aminolaevulinic acid (ALA), decreased in salt-stressed calli and leaves, which indicates that salt stress affects more markedly Chl biosynthesis than Chl breakdown.

Although salt stress reduces the Chl content, the extent of the reduction depends on salt tolerance of plant species. For example, it is generally known that in salt-tolerant species, Chl content increases, whereas it decreases in salt-sensitive species under saline regimes (Hamada and El-Enany 1994, Khan *et al.* 2009, Akram and Ashraf 2011). In view of this, an accumulation of Chl has been proposed as one of the potential biochemical indicators of salt tolerance in different crops, *e.g.*, in

a high temperature (Wang *et al.* 2010, Centritto *et al.* 2011). Heat stress causes membrane disruption, particularly of thylakoid membranes, thereby inhibiting the activities of membrane-associated electron carriers and enzymes (Ristic *et al.* 2008, Rexroth *et al.* 2011), which ultimately results in a reduced rate of photosynthesis.

In this review, the role of three major abiotic stresses, such as drought, salinity, and high temperature (heat), was emphasized in various aspects of photosynthesis, mainly of agricultural plants. In this review, we described to what extent the different components of photosynthesis, including gas-exchange characteristics, photosynthetic pigments, photosystems, components of electron transport system, and activities of different enzymes involved in carbon metabolism are affected by such stresses. Furthermore, the progress in improving photosynthetic capacity of C₃ plants by producing transgenic lines was discussed in this review.

wheat (Abdel Samad 1993, Sairam *et al.* 2002, Raza *et al.* 2006, Arfan *et al.* 2007), pea (Hernandez *et al.* 1995, Noreen *et al.* 2010), melon (*Cucumis melo*) (Romero *et al.* 1997), sunflower (Ashraf and Sultana 2000, Akram and Ashraf 2011), alfalfa (Winicov and Seemann 1990, Monirifari and Barghi 2009), and proso millet (*Panicum miliaceum*) (Sabir *et al.* 2009). Since the crops listed here belong to either dicots or monocots, it means that Chl accumulation is not an indicator of salt tolerance of a specific group of plants. Although the above-cited studies suggest that Chl accumulation could be used as biochemical marker for salt tolerance in different crops, in some other studies, Chl accumulation under saline stress is not always associated with salt tolerance. For example, Juan *et al.* (2005) found a weak relationship between leaf Na⁺ and photosynthetic pigments in tomato cultivars differing in salinity tolerance. They concluded that Chl *a* and *b* are not good indicators for salt tolerance in tomato. Therefore using Chl accumulation as an indicator of salt tolerance depends on the nature of the plant species or cultivar.

Carotenoids (Car) are necessary for photoprotection of photosynthesis and they play an important role as a precursor in signaling during the plant development under abiotic/biotic stress. They have a significant potential to enhance nutritional quality and plant yield. Nowadays, enhanced Car contents in plants are of considerable attention for breeding as well as genetic engineering in different plants (Li *et al.* 2008). Recently, working with sugar cane, Gomathi and Rakkiyapan (2011) found that imposition of salt stress (7–8 dS m⁻¹) at various plant growth stages caused a marked reduction in Chl and Car contents, but salt-tolerant varieties exhibited higher membrane stability and pigment contents. In another study, Ziaf *et al.* (2009) found significantly higher Chl

and Car contents at 60 mM NaCl and they suggested that relative water (RWC) and Car contents could be used as reliable selection criteria for salt tolerance in hot pepper. In wheat, Car accumulation was less sensitive under high-temperature stress (37°C for 24 h and 50°C for 1 h) as compared to that of Chl. A considerable reduction (about 52%) in Chl/Car ratio was reported in wheat plants under high-temperature stress (Yildiz and Terzi 2008). Car are also present in the plant cellular membranes. They protect the membranes from light-dependent oxidative damage. The role of Car in scavenging reactive oxygen species (ROS) has been well studied (Davison *et al.* 2002, Verma and Mishra 2005). Plants more tolerant to high light and high temperature could be attributed to having reduced lipid peroxidation, necrosis, as well as lower production of another stress indicator, anthocyanins (Davison *et al.* 2002). Growth improvement in plants under stressful environment has been widely reported to be due to the significant role of zeaxanthin in alleviating oxidative damage of membranes (Davison *et al.* 2002, Verma and Mishra 2005, Isaksson and Andersson 2008).

Drought stress: As salinity stress, drought stress causes not only a substantial damage to photosynthetic pigments, but it also leads to deterioration of thylakoid membranes (Huseynova *et al.* 2009, Anjum *et al.* 2011, Kannan and Kulandaivelu 2011). Thus, a reduction in photosynthetic capacity in plants exposed to drought stress is expected. The decrease in Chl content is a commonly observed phenomenon under drought stress (Bijanazadeh and Emam 2010, Mafakheri *et al.* 2010, Din *et al.* 2011). In contrast, Kulshretha *et al.* (1987) found no significant effect of drought stress on Chl content in wheat. There are also some reports, which show an enhanced accumulation of Chl under drought stress (Estill *et al.* 1991, Hamada and Al-Hakimi 2001, Pirzad *et al.* 2011). Ashraf and Karim (1991) reported an increase in some cultivars of blackgram (*Vigna mungo*) and a decrease in others under water-deficit conditions (3 and 6 cycles of drought as wilting and rewatering) and suggested that it may be due to variation in Chl synthesis among the cultivars mediated by the variation in the activities of specific enzymes involved in the biosynthesis of Chl. However, studies on chlorophyllase and peroxidase revealed that the decrease may be attributed to accelerated breakdown of Chl rather than its slow synthesis (Harpaz-Saad *et al.* 2007, Kaewsuksaeng 2011).

It is generally known that under drought stress the reduction of Chl *b* is greater than that of Chl *a*, thus, transforming the ratio in favor of Chl *a* (Jaleel *et al.* 2009, Jain *et al.* 2010). For example, in wheat, there were reported a slight rise in Chl *a/b* ratio in drought tolerant cultivars and a significant decrease in the susceptible ones under water deficit conditions (PEG-6000 at -0.6 MPa) (Ashraf *et al.* 1994). These differences could be due to a shift in an occurrence of photosynthetic systems towards a lower ratio of photosystem (PS) II to PSI (Estill *et al.*

1991). On the other hand, Ashraf and Mehmood (1990) found a decrease in Chl *a/b* ratio in three out of four *Brassica* species under water-deficit conditions.

Temperature stress: A number of reports indicate that plants exposed to high-temperature stress show reduced Chl biosynthesis (Efeoglu and Terzioglu 2009, Balouchi 2010, Reda and Mandoura 2011). The impaired Chl biosynthesis is the first of the processes occurring in plastids affected by the high temperature (Dutta *et al.* 2009, Li *et al.* 2010). Lesser accumulation of Chl in high-temperature-stressed plants may be attributed to impaired Chl synthesis or its accelerated degradation or a combination of both. The inhibition of Chl biosynthesis under high-temperature regimes results from a destruction of numerous enzymes involved in the mechanism of Chl biosynthesis (Dutta *et al.* 2009, Reda and Mandoura 2011). For example, the activity of 5-aminolevulinic dehydratase (ALAD), the first enzyme of pyrrole biosynthetic pathway, decreased in cucumber and wheat under high-temperature regimes (Tewari and Tripathy 1998, 1999; Mohanty *et al.* 2006).

Tewari and Tripathy (1998) found that Chl synthesis under the low temperature (7°C)- and high temperature (42°C)-stressed cucumber (cv. Poinsette) seedlings was affected by 90 and 60%, respectively. The suppression in Chl biosynthesis was found to be partially due to the inhibition in 5-aminolevulinic acid (ALA) biosynthesis under both low- (78%) and high-temperature (70%) regimes. Furthermore, biosynthesis of protochlorophyllide (Pchl) in low- and high-temperature-stressed seedlings was impaired by 90 and 70%, respectively. In hexaploid wheat (cv. HD2329) seedlings, Pchl synthesis, porphobilinogen deaminase, and Pchl oxidoreductase were affected similarly to that of cucumber, which suggests that temperature stress has generally a similar effect on enzymes involved in Chl biosynthesis in both wheat and cucumber.

PSII has been long believed to be a prominent heat sensitive component of photosynthesis (Schrader *et al.* 2004), but it can perform normal functioning up to 45°C (Gombos *et al.* 1994). However, there are some reports showing that moderately high temperature (35–45°C) can induce the cyclic transport of electrons and thylakoid membranes become leaky (Sharkey 2005). Similarly, permeability of the thylakoid membranes is one of the most heat-sensitive components of the photosynthetic apparatus (Havaux *et al.* 1996), which could be counteracted by zeaxanthin. An increased stability of thylakoid membranes was observed at mild heat treatment of potato (35°C for 2 h), which indicated that de-epoxidized xanthophylls maintained thylakoids and thylakoid membranes against heat-induced disorganization (Havaux *et al.* 1996, Brugnoli *et al.* 1998). The deactivation of Rubisco at mild heat stress could be attributed to the deleterious effects of heat on chloroplast reactions (Sharkey 2005, Velikova *et al.* 2012).

Photosynthesis is sensitive to changes in temperature, but a reversible decline has been observed under mild temperature stress, while a permanent impairment was found after an exposure to severe heat stress. At high temperatures, PSII and stroma become oxidized and a significant reduction takes place in PSI. In addition, evidence supports the existence of considerable cyclic electron flow at high temperature, which suggests that maintenance of an energy gradient across the thylakoid membrane as well as adenosine triphosphate homeostasis might be involved in the prevention of irreversible impairment under high-temperature regimes (Sharkey and Zhang 2010).

Altogether, different stressful environments, including salinity, drought, and heat cause generally a considerable reduction in contents of important photosynthetic pigments, particularly Chl. This reduction may occur due to stress-induced impairment in pigment biosynthetic pathways or in pigment degradation. However, the extent of these phenomena depends on the species, variety, duration of plant exposure, and tolerance of the stress. Reduction in photosynthetic pigments, whether through the impairment in pigment biosynthesis or destruction of pigments, may lead to the impairment in electron transport and hence reduced photosynthetic capacity in most plants.

Effects on photosystems: Photosynthetic pigments present in the photosystems are believed to be damaged by stress factors resulting in a reduced light-absorbing efficiency of both photosystems (PSI and PSII) and hence a reduced photosynthetic capacity (Geißler *et al.* 2009, Zhang *et al.* 2011). Light energy absorbed by Chl is transformed into Chl fluorescence (Maxwell and Johnson 2000). Despite the fact that the extent of Chl fluorescence does not comprise more than 1–2% of total light absorbed by the Chl, its measurement is convenient and noninvasive. It gives a valuable insight into exploitation of the excitation energy by PSII, and indirectly by the other protein complexes of the thylakoid membranes (Walker 1987, Roháček 2002), particularly in plants exposed to stressful conditions.

Xanthophylls are Car located in light-harvesting antenna complexes (LHC) of almost all photosynthetic organisms; they play an important role in light harvesting, photoprotection, and assemblage of LHC (Latowski *et al.* 2004, Misra *et al.* 2006). Zeaxanthin (one of xanthophylls) is formed from violaxanthin by violaxanthin de-epoxidase; it plays a key role in minimizing the overexcitation in higher plants (Kuczyńska *et al.* 2012). In the xanthophyll cycle (Fig. 2), the interconversion of two Car, violaxanthin and zeaxanthin, takes place and it has a substantial role in photoprotection of plants. Due to its considerable importance, it is a promising target for genetic engineering to enhance stress tolerance in plants. The overexpression of the *chyB* gene, which is responsible for encoding β -carotene hydroxylase (one of

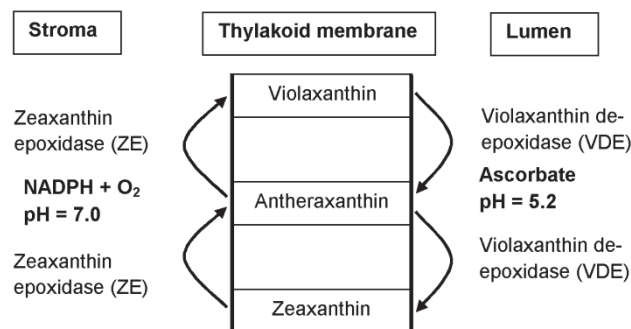


Fig. 2. The xanthophyll cycle in higher plants (modified from Hieber *et al.* 2004 with permission).

enzymes in zeaxanthin biosynthetic pathway), induced two-fold enhancement in the pool size of the xanthophyll cycle in *Arabidopsis thaliana* (Davison *et al.* 2002).

The dissipation of excess light energy as heat within LHC protects photosynthetic apparatus against the oxidative damage. The xanthophyll cycle, particularly the de-epoxidation of violaxanthin to zeaxanthin through antheraxanthin, was reported to play an important role in energy dissipation at high light intensity (Demmig-Adams and Adams 1992, Misra *et al.* 2006). The dissipation of excitation energy is determined as nonphotochemical quenching (NPQ) of Chl fluorescence during photosynthetic electron transport, which significantly correlates with contents of zeaxanthin and antheraxanthin produced during the xanthophyll cycle (Niyogi *et al.* 1997).

Although the photochemical efficiency of PSII was similar in both cabbage and kidney bean seedlings, the de-epoxidation state of violaxanthin increased six-fold in kidney bean, while no significant change was observed in cabbage under saline treatments. Similarly, NPQ increased in kidney bean, but decreased in cabbage. This showed that pigments involved in the xanthophyll cycle influenced NPQ in both cabbage and kidney. Thus, the increase in the de-epoxidation state of violaxanthin in salt-stressed kidney plants may be a signal to shield the pigment-protein complexes from salt-induced photodamage (Misra *et al.* 2006).

During NPQ, the LHC of PSII undergo conformational changes, thereby generating a modification in pigment interactions causing the development of energy traps. Thus, NPQ plays a key role in the protection of PSII from photodamage. NPQ is considered as an indicator of excess excitation energy (Joshi *et al.* 1995, Ruban *et al.* 2002, Parida *et al.* 2007). Overall, the fast fluorescence transients following OJIP curve indicate the size of plastoquinone pool within a leaf tissue. However, the curve undergoes changes in response to different stressful environments, such as drought, temperature, salinity, heavy metals, light intensity, *etc.* (Haldimann and Strasser 1999, Popovic *et al.* 2003, Jafarinia and Shariati 2012).

It was widely reported that the suppression in photosynthetic rate can occur due to a number of biotic and abiotic factors, which can substantially alter fluorescence emission kinetic characteristics of plants (Baker and Rosenqvist 2004, Baker 2008). Moreover, the fluorescence induction parameters, such as F_o , F_i , F_m , F_v , F_p , and in particular their ratios, are commonly used to determine a number of metabolic disorders in the leaves of many species subjected to a variety of stresses (Baker and Rosenqvist 2004, Baker 2008, Bączek-Kwinta *et al.* 2011). The F_v/F_m ratio is an important parameter, which determines the maximum quantum efficiency of PSII. It provides a measure of the rate of linear electron transport, hence, an indication of overall photosynthetic capacity (Jamil *et al.* 2007, Tang *et al.* 2007, Balouchi 2010). In healthy leaves, F_v/F_m value is usually close to 0.8 in most plant species, therefore a lower value indicates that a proportion of PSII reaction centers is damaged or inactivated, a phenomenon, termed as photoinhibition, commonly observed in plants under stress (Baker and Rosenqvist 2004, Zlatev 2009, Vaz and Sharma 2011).

Salt-stress-induced inhibition in plant is often ascribed to the reduced photosynthetic performance (Wu *et al.* 2010, Akram and Ashraf 2011, da Silva *et al.* 2011), but the underlying mechanisms are still not fully elucidated. However, since PSII is known to play a major role in photosynthetic response to environmental adversity (Han *et al.* 2010, Liu and Shi 2010, Xu *et al.* 2010), the salt-induced effect on PSII has been studied thoroughly with a number of contradictory reports appearing in the literature. For example, some studies have shown a significant inhibitory effect of salinity on PSII activity (Everard *et al.* 1994, Akram and Ashraf 2011, Saleem *et al.* 2011), whereas other reports found no significant effect on the structure and function of PSII (Al-Taweel *et al.* 2007, Abdeshahian *et al.* 2010). Recently, Mehta *et al.* (2010) have reported that the donor side of the PSII was damaged more than the acceptor side due to salt stress (0.1–0.5 M NaCl) in wheat (*Triticum aestivum*). Furthermore, the salt-induced damage to PSII was reversible, because 100% recovery of the acceptor side and about 85% of the donor side has been reported (Mehta *et al.* 2010).

Similarly to others, drought stress is known to alter the Chl *a* fluorescence kinetics and hence to damage the PSII reaction center (Zhang *et al.* 2011). A number of studies conducted *in vivo* have shown that drought stress causes considerable damage to the oxygen evolving center (OEC) coupled with PSII (Skotnica *et al.* 2000, Kawakami *et al.* 2009) as well as degradation of D1 polypeptide leading to the inactivation of the PSII reaction center (He *et al.* 1995, Liu *et al.* 2006, Zlatev 2009). The changes lead to the generation of reactive oxygen species (ROS), which ultimately cause the photoinhibition and oxidative damage (Ashraf 2009, Gill and Tuteja 2010, Anjum *et al.* 2011). Plants have evolved a variety of protective mechanisms against the ROS-

induced damage to cellular components, such as the dissipation of excess excitation energy and the synthesis of protective pigments, such as Car and anthocyanins (Efeoglu *et al.* 2009, Huang *et al.* 2010).

Chl *a* fluorescence is considered as one of the important indicators of drought tolerance in different species and cultivars/genotypes, *e.g.*, durum wheat cultivars (Havaux *et al.* 1988, Flagella *et al.* 1996, Araus *et al.* 1998), bread wheat cultivars (Havaux *et al.* 1988), and tobacco cultivars (Van Rensburg *et al.* 1996). All these reports suggest that drought-resistant and drought-sensitive cultivars can be easily screened at the level of PSII (Guoth *et al.* 2009, da Graça *et al.* 2010).

A number of earlier studies have shown that drought stress adversely affected the functionality of both PSII and PSI, particularly PSII. This led to decreased electron transport through these two systems (Liu *et al.* 2006, Zlatev 2009). The amounts of PSII proteins, such as D1, D2, and LHCII as well as mRNA corresponding to genes of *psbA*, *psbD*, and *cab*, also declined markedly due to water deficit; this was ascribed to decreased rates of transcription and translation as well as fast deterioration of proteins and mRNAs (Duan *et al.* 2006, Liu *et al.* 2009).

Phosphorylation of proteins is known as a key molecular mechanism that plays a vital role in an adaptation of living organisms to unfavorable growth conditions. In chloroplasts, an exceptional, redox-regulated, protein phosphorylation has been found (Wang and Portis 2007, Dutta *et al.* 2009); it can phosphorylate about 20 thylakoid membrane proteins. Most prominent of these phosphoproteins are those of the LHCII as well as of PSII reaction center such as D1, D2, CP43, and a 9-kD (PsbH) polypeptide. Phosphorylation of PSII proteins has been reported to regulate the stability, degradation, and turnover of the reaction center proteins (Lundin *et al.* 2007, Fristedt *et al.* 2009). However, dephosphorylation of these proteins can also take place under stressful environments and it is catalyzed by phosphatases (Vener *et al.* 1999, Liu *et al.* 2009). Phosphorylation and dephosphorylation of PSII are the main regulatory factors and they play a major role in PSII repair. Liu *et al.* (2009) have shown that water stress caused the rapid dephosphorylation of PSII proteins, coupled with the phosphorylation of LHCII b4 and CP29, in barley (*Hordeum vulgare*). The accelerated dephosphorylation is brought about by both intrinsic and extrinsic membrane protein phosphatases. However, the authors also reported that the reduction in dephosphorylation exacerbated stress-induced damages and inhibited the recovery of the photosystems, when the stress was relieved by rewatering. Furthermore, they also found that the thylakoid structure remained almost intact under water stress except that CP29 migrated slightly from granal thylakoid to stroma thylakoid, whereas the rest of PSII proteins remained unaffected and intact. However, drought stress activated chloroplast proteins and caused the release of TLP40, a potential inhibitor of the membrane phosphatases. It was

suggested that phosphorylation of CP29 may cause uncoupling LHCII from the PSII complex and splitting up the LHCII trimer and thus causing its degradation. In contrast, dephosphorylation of PSII proteins may play a role in the repair process of PSII proteins and signal transduction in response to stress (Liu *et al.* 2009, Los *et al.* 2010).

Photosynthesis is sensitive to heat stress and PSII has been reported to be highly sensitive (Fig. 3) (Allakhverdiev *et al.* 2007, Yan *et al.* 2011). It has been also reported that plants exposed to heat stress for even a short time experience the inhibition of the OEC and the reaction center of PSII (Wang *et al.* 2010, Hamdani *et al.* 2011), although the former is more sensitive to heat than the latter. Smith and Low (1989) reported that the PSII core complex undergoes denaturation at about 60 °C, whereas the denaturation of LHCII proteins occurs at about 74°C (Smith *et al.* 1989). The major reason considered for heat-induced inactivation of OEC was the release of 33 kDa extrinsic protein from the complex (Zhang *et al.* 2011). The heat-induced deterioration of PSII leads to considerable perturbation in electron transport mediated by PSII. From a number of studies, it is evident that changes occurring in the ultrastructure of thylakoid membranes above 40°C cause dissociation of the LHCII Chl *a/b*-proteins from the PSII core complex (Tang *et al.* 2007, Iwai *et al.* 2010). These proteins normally take part in membrane stacking (Várkonyi *et al.* 2009). However, heat-induced alteration in these proteins leads to destacking of the appressed membranes of the granum (Fristedt *et al.* 2009, Lemeille and Rochaix 2010), which is mediated by the separation of non-bilayer-forming lipids. Dobrikova *et al.* (2002) found that the electric dipole moments of the thylakoids and the membranes enriched with PSII were significantly temperature dependent. They also found that the reduction in the electric dipole moments of thylakoids and PSII-enriched membranes correlated well with heat-induced nonfunctionality in the PSII photochemical activity and restructuring of the macroassemblies in thylakoid membranes.

As in the case of drought stress, phosphorylation and dephosphorylation of thylakoid proteins has been suggested to play a critical role in responses of plants to elevated temperature (Krishnan and Pueppke 1987, Conde *et al.* 2011). For example, Rokka *et al.* (2000) have shown that rapid dephosphorylation of PSII core proteins took place in isolated spinach (*Spinacia oleracea*) thylakoids at high temperatures. They also found that an increase in temperature from 22°C to 42°C caused a more than 10-fold increase in the dephosphorylation rates of D1 and D2 and of CP43 (Chl *a* binding protein). In contrast, the dephosphorylation rates of LHC and the 9-kD protein of the PSII (PsbH) were accelerated only 2- to 3-fold. This rapid dephosphorylation is catalyzed by a PSII-specific membrane protein phosphatase, the activity of which is regulated by the temperature.

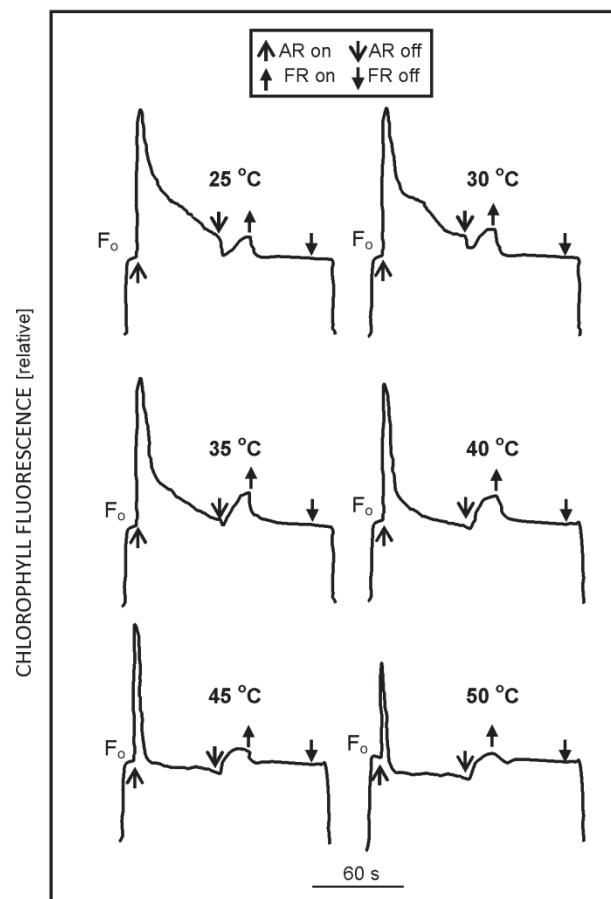


Fig 3. Effects of varying temperatures on Chl fluorescence induction in maize. Arrows indicate switching on (↑) or off (↓) of actinic or FR irradiation (reproduced from Jin *et al.* 2002 with permission).

Thus, the activation of the membrane protein phosphatase was considered to initiate a fast repair of photodamaged PSII and to act as an early signal for other responses to heat stress in chloroplasts. It is evident that drought, salinity, and high-temperature stress adversely affect the functionality of both photosystems and reduce electron transport through them. This results in a low production of ATP and NADPH, the two main products of the light reactions (electron transport), which are essential for CO₂ fixation in the dark reactions of the photosynthesis. Thus, stress-induced impairment of the photosystems ultimately limits the CO₂ reduction process.

Effects on gas-exchange characteristics: CO₂-exchange characteristics have been regarded an important indicator of the growth of plants, because of their direct link to net productivity (Ashraf 2004, Piao *et al.* 2008). However, the effect of any stress on photosynthesis could be caused by stomatal, nonstomatal or both factors (Athar and Ashraf 2005, Saibo *et al.* 2009), nevertheless, the extent of stress-induced stomatal or nonstomatal regulation depends on the species. It is known that salinity stress,

similarly to other abiotic stresses, can significantly affect both stomatal and nonstomatal regulation of photosynthesis (Ashraf 2004, Saibo *et al.* 2009). Muranaka *et al.* (2002) observed that under salt (NaCl) stress, the rate of photosynthesis in wheat plants decreased in two stages. In the first stage, photosynthetic reduction was slow without any discernible photochemical changes. However, in the second stage, photosynthetic decline was prompt and coupled with a degeneration in the energy conversion efficiency in PSII. They suggested that the salt-induced osmotic effect may induce a gradual decline in photosynthesis due to stomata closure under saline regimes. However, an uptake and accumulation of excessive amounts of Na⁺ may directly affect the electron transport and cause a marked reduction in photosynthetic capacity. A reduced activity of the Hill reaction was also observed in salt-stressed chloroplasts (El-Shintinawy 2000, Zeid 2009). Salt stress imposed at the reproductive stage was reported to decrease the net CO₂ assimilation rate and stomatal conductance of intact leaves in various wheat genotypes (Shahbaz and Ashraf 2007, Perveen *et al.* 2010). The inhibitory effect of salt-induced osmotic stress (water deficit) on the rate of photosynthesis was related to decreased production of ATP due to the impaired electron transport (Moud and Maghsoudi 2008, Curtiss *et al.* 2011).

Down-regulation of various gas-exchange characteristics to a varying extent has been observed in different plant species exposed to saline stress in a number of studies (Raza *et al.* 2007, Ali *et al.* 2008, Ashraf and Akram 2011, Noreen *et al.* 2012). The salinity-induced osmotic effect on plants causes a substantial accumulation of abscisic acid (ABA), particularly in the guard cells of stomata, which consequently leads to a partial stomata closure thereby lowering the stomatal conductance as well as substomatal CO₂ concentration (Zhao *et al.* 2009b).

The association of the growth and yield with gas-exchange characteristics in several species is summarized in Table 1. It is evident that photosynthetic capacity has a positive association with a biomass production or a seed yield in plants under saline stress, including the crops, *Triticum aestivum* (James *et al.* 2002), *Oryza sativa* (Moradi and Ismail 2007), *Phaseolus vulgaris* (Seemann and Critchley 1985), *Zea mays* (Crosbie and Pearce 1982), *Vigna mungo* (Chandra Babu *et al.* 1985), *Gossypium hirsutum* (Pettigrew and Meredith 1994), *Gossypium barbadense* (Cornish *et al.* 1991), *Spinacia oleracea* (Robinson *et al.* 1983), *Asparagus officinalis* (Faville *et al.* 1999), the grass species, *Panicum hemitomon*, *Spartina patens*, and *Spartina alterniflora* (Hester *et al.* 2001), and six *Brassica* diploid and amphiploid species (Ashraf 2001). In contrast, there are other studies (Table 1), which show no or little association of photosynthetic capacity with the growth in various plant species, *e.g.*, *Hordeum vulgare* (Rawson *et al.*

1988), *Triticum aestivum* (Hawkins and Lewis 1993, Ashraf and O'Leary 1996), *Hibiscus cannabinus* (Curtis and Läubli 1986), *Olea europea* (Loreto *et al.* 2003), *Trifolium repens* (Rogers and Noble 1992), and castor bean (*Ricinus communis*) (Pinheiro *et al.* 2008). In view of all these reports, it is evident that photosynthetic capacity cannot be used as a general indicator for salt tolerance.

Drought stress is also known to depress gas-exchange characteristics to a varying extent thereby affecting overall photosynthetic capacity of most plants. For example, Lawlor and Cornic (2002) reported that the leaf net CO₂ assimilation rate (P_N) of higher plants decreased substantially as the leaf water potential and relative water content (RWC) decreased. However, there are contrasting opinions, whether drought impairs photosynthesis primarily through stomatal or nonstomatal (metabolic) limitations (Saibo *et al.* 2009, Dias and Brüggemann 2010, Mafakheri *et al.* 2010). The control of water loss through stomatal regulation has been recognized as an early plant response to drought (Jia and Zhang 2008, Harb *et al.* 2010). As drought continues, the stomata closure occurs for longer periods during the day. This, in turn, leads to the reduced carbon assimilation rate and water loss, resulting in maintenance of the carbon assimilation at the cost of low water availability (Brock and Galen 2005, Sausen and Rosa 2010, Pan *et al.* 2011). Stomatal limitation was generally considered to be the major factor of reduced photosynthesis under water deficit conditions (Galmes *et al.* 2007, Bousba *et al.* 2009). This has been ascribed to a decline in both P_N and substomatal CO₂ concentration (C_i) that consequently inhibit overall photosynthesis.

Several researchers have proposed the use of stomatal conductance (g_s) as an indicator to assess the difference between stomatal and nonstomatal limitations to photosynthesis under water-limited environments (Xu and Zhou 2008, Yu *et al.* 2008). For example, Flexas *et al.* (2002) showed that P_N and C_i had a strong correlation with g_s in both field-grown and potted grape wine plants. Such a strong relationship led to the proposal that the down-regulation of photosynthesis depends more on the availability of CO₂ in the chloroplast than on leaf water content or water potential (Flexas *et al.* 2002, Saibo *et al.* 2009, Galmes *et al.* 2011). However, a relationship of g_s with leaf water potential or RWC was not observed, *i.e.*, reduced photosynthesis caused by water-deficit conditions occurred at different leaf water levels in different species, even though at similar g_s (Athar and Ashraf 2005, Peri *et al.* 2009). Thus, it is likely that either water deficit has no effect on photosynthesis until a threshold is reached, beyond which it is impaired or a consistent suppression in metabolism is caused (Lawlor 2002, Athar and Ashraf 2005, Lawlor and Tezara 2009). It has also been shown that leaves that survive drought often show

Table 1. Association of growth and yield of different plant species with gas-exchange characteristics under stress conditions. A – photosynthetic capacity; g_s – stomatal conductance; + positive association, – negative association, ns – insignificant.

Stress	Plant species	Relationship of growth or yield with gas-exchange characteristics	Reference		
Salinity	Wheat (<i>Triticum aestivum</i> L.)	A ; biomass and yield	+	James <i>et al.</i> 2002	
	Common bean (<i>Phaseolus vulgaris</i> L.)	A ; biomass and yield	+	Seemann and Critchley 1985	
	Cotton (<i>Gossypium hirsutum</i> L.)	A ; biomass and yield	+	Pettigrew and Meredith 1994	
	Cotton (<i>Gossypium barbadense</i> L.)	A ; biomass and yield	+	Cornish <i>et al.</i> 1991	
	Spinach (<i>Spinacia oleracea</i> L.)	A ; biomass and yield	+	Robinson <i>et al.</i> 1983	
	Asparagus (<i>Asparagus officinalis</i> L.)	A ; biomass and yield	+	Faville <i>et al.</i> 1999	
	Grasses (<i>Panicum hemitomon</i> , <i>Spartina patense</i> and <i>Spartina alterniflora</i>)	A ; biomass and yield	+	Hester <i>et al.</i> 2001	
	Six <i>Brassica</i> species	A ; biomass and yield	+	Ashraf 2001	
	Barley (<i>Hordeum vulgare</i> L.)	A ; growth	–	Rawson <i>et al.</i> 1988	
	Wheat (<i>Triticum aestivum</i> L.)	A ; growth	–	Hawkins and Lewis 1993, Ashraf and O'Leary 1996	
	Kenaf (<i>Hibiscus cannabinus</i> L.)	A ; growth	–	Curtis and Lauchli 1986	
	Olive (<i>Olea europea</i> L.)	A ; growth	–	Loreto <i>et al.</i> 2003	
	White clover (<i>Trifolium repens</i> L.)	A ; growth	–	Rogers and Noble 1992	
	Caster bean (<i>Ricinus communis</i> L.)	A ; growth	–	Pinheiro <i>et al.</i> 2008	
	Drought	Wheat (<i>Triticum aestivum</i> L.)	A and g_s ; yield	+	Fischer <i>et al.</i> 1998
		Maize (<i>Zea mays</i> L.)	A ; growth	+	Ashraf <i>et al.</i> 2007
		Rice (<i>Oryza sativa</i> L.)	A ; growth	+	Garg <i>et al.</i> 2002
		Cotton (<i>Gossypium hirsutum</i> L.)	A ; yield	+	Yan <i>et al.</i> 2004
		Tobacco (<i>Nicotiana tabacum</i> L.)	A ; growth	+	Shou <i>et al.</i> 2004
Cotton (<i>Gossypium barbadense</i> L.)		A ; yield	+	Levi <i>et al.</i> 2009	
Blackgram [<i>Vigna mungo</i> (L.) Hepper]		A ; yield	+	Chandra Babu <i>et al.</i> 1985	
Cotton (<i>Gossypium hirsutum</i> L.)		A ; seed yield	+	Pettigrew and Meredith 1994	
Sunflower (<i>Helianthus annuus</i> L.)		A ; seed yield	+	Kiani <i>et al.</i> 2007	
Wheat (<i>Triticum aestivum</i> L.)		A and g_s ; yield	ns	Hura <i>et al.</i> 2006	
Grasses (<i>Cynodon dactylon</i> and <i>Cenchrus ciliaris</i>)		A and g_s ; growth	ns	Akram <i>et al.</i> 2007	
Cotton (<i>Gossypium hirsutum</i> L.)		A ; yield	–	Levi <i>et al.</i> 2009	
Tomato (<i>Lycopersicon esculentum</i> L.)		A ; growth	+	Camejo <i>et al.</i> 2005	
Tomato (<i>Lycopersicon esculentum</i> L.)		A ; growth	+	Singh <i>et al.</i> 2005	
Melon (<i>Cucumis melo</i>)		A ; growth	+	Kitroongruang <i>et al.</i> 1992	
Creeping bentgrass (<i>Agrostis palustris</i> Huds.)		A ; growth	+	Xu and Huang 2001	
Potato (<i>Solanum tuberosum</i> L.)		A ; growth	–	Thornton <i>et al.</i> 1996	

higher rates of photosynthesis (Ludlow and Ng 1974, Akram *et al.* 2007, Bayramov *et al.* 2010) and of Rubisco content per unit leaf area (David *et al.* 1998, Kumar and Singh 2009).

In several studies, attempts have been made to identify morpho-physiological and molecular processes involved in controlling the yield under water-deficit conditions. Attempts have also been made to show the relationship between gas-exchange parameters, particularly P_N , and drought tolerance of crop species or cultivars (Table 1). For example, a positive association of P_N with drought tolerance has been reported in different crops, *e.g.*, semi-dwarf spring wheat (Fischer *et al.* 1998), maize (Ashraf *et al.* 2007), transgenic lines of rice (Garg *et al.* 2002), and transgenic cotton lines (Yan *et al.* 2004).

Fig. 4 shows how different abiotic stresses affect the MAPK-activated defense responses in plants. Shou *et al.* (2004) expressed constitutively a tobacco mitogen-

activated protein kinase kinase kinase (MAPKKK or NPK1) in maize. It was reported that the NPK1 expression considerably improved drought tolerance in transgenic maize, which was associated with the enhanced rate of photosynthesis, suggesting the effective role of NPK1 in protecting the photosynthetic machinery from the drought-induced injurious effects. In another study (Yu *et al.* 2008), a mutant, *enhanced drought tolerance1*, of *Arabidopsis* with improved drought tolerance was developed. The mutant showed significantly reduced leaf stomata density, but enhanced photosynthetic capacity. In addition, the positive correlation between the rate of photosynthesis and the crop yield has been reported earlier in several studies (Pettigrew and Meredith 1994, Fischer *et al.* 1998, Ashraf *et al.* 2007, Makino 2011). However, such a positive relationship of photosynthetic capacity to drought tolerance is not a general rule and in other studies the reverse results were obtained. For

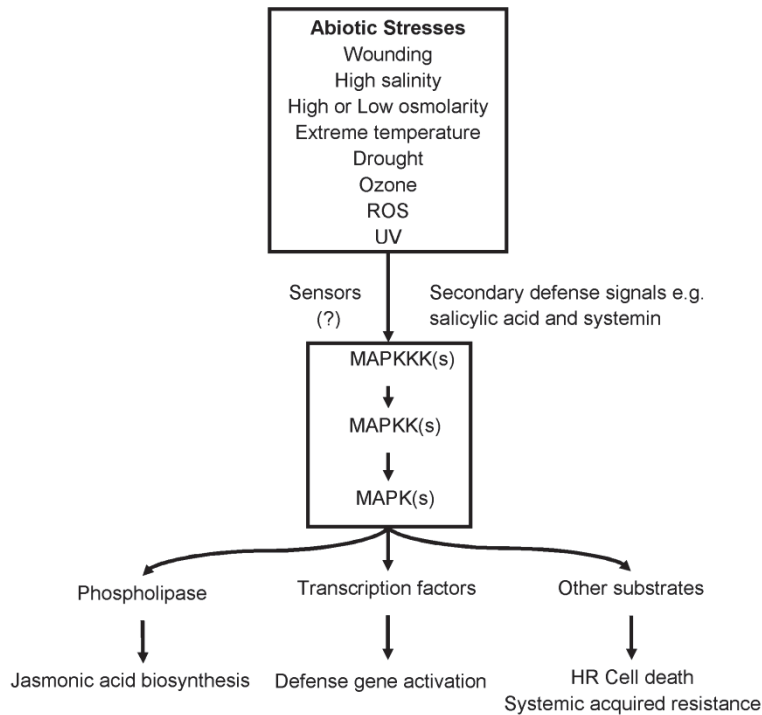


Fig 4. Effect of abiotic stresses on MAPK activated defense responses of plants (redrawn from Zhang and Klessig 2001 with permission).

example, Hura *et al.* (2006) did not find a significant relationship between P_N and g_s and the drought tolerance of some winter triticale (\times *Triticosecale*) genotypes (Table 1). Similarly, Akram *et al.* (2007) did not find a significant relationship between the photosynthetic capacity and drought tolerance of some genetically diverse populations of two grasses, *Cynodon dactylon* (L.) Pers. and *Cenchrus ciliaris* L. Recently, Levi *et al.* (2009) have developed near-isogenic lines of two species of cotton (*Gossypium hirsutum*, GH, and *G. barbadense*, GB) using marker-assisted selection. It is interesting to note that the GB near-isogenic lines showed a positive association with P_N contrary to the GH near-isogenic lines, even if in the latter case, the parent line and the near-isogenic lines showed almost similar values of P_N . All the reports, showing the positive, null, or negative association of photosynthetic capacity with drought tolerance in different plant species, can be explained in the view of Guo *et al.* (2002) by the fact that also other factors such as assimilate partitioning and utilization may affect the crop yield.

In view of a number of reports, it is evident now that CO_2 uptake and photosynthetic yield decline considerably or even cease, when temperature exceeds an optimum (Aniszewski *et al.* 2001, Islam 2011, Xie *et al.* 2011). High temperature can damage the ultrastructure of the thylakoid membrane, thereby modulating its biochemical properties (Berry and Björkman 1980, Wang *et al.* 2010). Substantially high temperature has been reported to inactivate the OEC of PSII (Zhang *et al.* 2001, Toth *et al.* 2011). For example, a 15-min treatment (at 38°C) to

leaves previously grown at 23°C caused a marked inactivation of PSII in potato (Havaux 1996). The heat-induced damage to the OEC may occur due to the release of Mn ions from the complex (Nash *et al.* 1985).

Photosynthetic capacity (rate of photosynthesis) has also been considered as one of the potential indicators of heat-stress tolerance in different plant species, because the gas-exchange characteristic showed a positive association with the drought tolerance in different species or cultivars within the species in several studies, *e.g.*, tomato (Camejo *et al.* 2005, Singh *et al.* 2005) and melon (Kitroongruang *et al.* 1992).

Although the above reports (Table 1) suggest that photosynthetic rate could be used as a potential indicator of heat tolerance, there are other studies reporting little or no association of this physiological trait with heat tolerance, *e.g.*, in potato (*Solanum tuberosum*) (Thornton *et al.* 1996) and creeping bentgrass (*Agrostis palustris*) (Xu and Huang 2001), no positive association of P_N was observed with heat tolerance of cultivars within each species.

From these reports, it is amply clear that genetic differences in photosynthetic capacity exist at intraspecific and interspecific levels. Since a varying association of photosynthetic capacity with the degree of stress tolerance exists in different species, the use of the photosynthetic capacity as a selection criterion will be plausible and effective only in those species, where a positive association between the photosynthetic capacity and the growth exists under stress conditions.

Effects on activities of key photosynthetic enzymes:

One of the most prominent effects of various stresses is the stomata closure, which leads to a lower concentration of intercellular CO₂, which in turn causes deactivation of Rubisco as well as other enzymes such as sucrose-phosphate synthase (SPS) and nitrate reductase (Chaves *et al.* 2009, Mumm *et al.* 2011). Stress-induced increase and decrease in the activities of enzymes involved in photosynthesis are summarized in Table 2. Increased levels of Na⁺ and Cl⁻ (above 250 mM) in the leaf tissue may substantially perturb the metabolic processes of photosynthesis (Tavakkoli *et al.* 2009, Biswal *et al.* 2011). Furthermore, the salt-induced, osmotic effect can adversely affect the activities of a number of stroma enzymes involved in CO₂ reduction (Kaiser and Heber 1981, Xue *et al.* 2008).

Flowers *et al.* (1977) reported that Rubisco activity is inhibited *in vitro* by high levels of salt, while Aragao *et al.* (2005) suggested that Rubisco can also be affected by salt *in vivo* (Table 2). The increase in the amount of Rubisco can be beneficial for the survival of plants under harsh environmental conditions, because a positive relationship of leaf Rubisco contents with P_N has been reported in most C₃ plants (Taub 2010, Makino 2011). However, in contrast, such a relationship between leaf Rubisco and P_N was not found in a glycophytic species, *Vigna unguiculata*, where Rubisco activity decreased in a salt-tolerant cultivar Vita 3, whereas it increased markedly in a salt-sensitive cultivar Vita 5 (Aragao *et al.* 2005). Thus, in view of such contrasting reports, further

research is needed to affirm whether the association between these two traits is positive or negative. In another study with two species of rice, Ghosh *et al.* (2001) found that not only Rubisco is affected, but also the enzymes involved in regeneration of the Rubisco substrate, ribulose-1,5-bisphosphate (RuBP) are regulated by salt stress and they can play a key role in the regulation of the Calvin cycle (Table 2). Fructose-1,6-bisphosphatase has been considered as one of the potential enzymes that can cause the decline of photosynthetic activity under stressful conditions, because it is involved in the regeneration of RuBP. Earlier, Seemann and Sharkey (1982) observed that salt stress caused a substantial reduction in the RuBP pool size in *Phaseolus vulgaris*, which was primarily ascribed to the salt-induced effect on the RuBP regeneration potential (Table 2). Similar findings have been also reported in *Phaseolus vulgaris* by Caemmerer and Farquhar (1984) and in sunflower (*Helianthus annuus*) (Gimenez *et al.* 1992).

Ghosh *et al.* (2001) reported that the activity of fructose-1,6-bisphosphatase was positively associated with the different salt tolerance of the two rice species, because it was inhibited in the salt-sensitive species (*Oryza sativa*), but it remained unaffected in the wild, salt-tolerant species (*Porteresia coarctata*) under saline regimes (Table 2). Similarly, in another study with potato, a transgenic line expressing the chloroplastic fructose-1,6-bisphosphatase at less than 15% compared with the wild-type plants showed considerably reduced P_N and growth; it shows that the enzyme has a key role

Table 2. Stress-induced increase/decrease in the activities of enzymes involved in photosynthesis. Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; FBP – fructose-1,6-bisphosphatase; PEPC – phosphoenolpyruvate carboxylase; NADP-ME – NADP malic enzyme; PPK – pyruvate orthophosphate dikinase.

Stress	Plant species	Enzyme	Enzyme activity	Reference
Salt	Blackeyed pea (<i>Vigna unguiculata</i> L.)	Rubisco	Decreased	Aragao <i>et al.</i> 2005
	Common bean (<i>Phaseolus vulgaris</i> L.)	FBP	Decreased	Seemann and Sharkey 1982
	Sunflower (<i>Helianthus annuus</i> L.)	FBP	Decreased	Giménez <i>et al.</i> 1992
	Common bean (<i>Phaseolus vulgaris</i> L.)	FBP	Decreased	Caemmerer and Farquhar 1984
	Potato (<i>Solanum tuberosum</i> L.)	FBP	Increased	Kossman <i>et al.</i> 1994
	Rice (<i>Oryza sativa</i> L.)	FBP	Increased	Ghosh <i>et al.</i> 2001
	Wheat (<i>Triticum aestivum</i> L.) and maize (<i>Zea mays</i> L.)	PEPC	Decreased	Abdel-Latif 2008
Drought	Subterranean clover (<i>Medicago sativa</i> L.)	Rubisco	Not affected	Medrano <i>et al.</i> 1997
	Setaria (<i>Setaria sphacelota</i>)	Rubisco	Decreased	Marques and Arrabica 1995
	Tobacco (<i>Nicotiana tabacum</i> L.)	Rubisco	Not affected	Gunasekera and Berkowitz 1993
	Maize (<i>Zea mays</i> L.)	PEPC	Increased	Jeanneau <i>et al.</i> 2002
	Sugar cane (<i>Saccharum officinarum</i> L.)	PEPC, NADP-ME, FBPase, PPK	Decreased	Du <i>et al.</i> 1998
Heat	Maize (<i>Zea mays</i> L.)	Rubisco activase	Decreased	Crafts-Brandner and Salvucci 2002, Salvucci and Crafts-Brandner 2004
	Cotton (<i>Gossypium hirsutum</i> L.) and Tobacco (<i>Nicotiana tabacum</i> L.)	Rubisco	Decreased	Crafts-Brandner and Salvucci 2000
	Pea (<i>Pisum sativum</i> L.) and <i>Amaranthus hypochondriacus</i>	PEPC	Decreased	Chinthapalli <i>et al.</i> 2003
	Wheat (<i>Triticum aestivum</i> L.)	Rubisco, PEPC	Decreased	Xu <i>et al.</i> 2003

in the regulation of the Calvin cycle (Kossman *et al.* 1994). Abdel-Latif (2008) observed that although the activities of phosphoenolpyruvate carboxylase (PEPC) isolated from wheat (C_3 plant) and that from maize (C_4 plant) were inhibited under saline regimes, the enzyme from wheat was less sensitive to salt than that from maize (Table 2).

Similarly as the salt stress, drought stress can also adversely affect levels and activities of different enzymes involved in the mechanism of photosynthesis, thereby impairing the synthesis of carbohydrates as well as WUE of plants, which in turn adversely affects the overall plant yield (Kumar and Singh 2009, Gill *et al.* 2011). An appraisal of Rubisco content and activity has been considered as one of the useful indicators for breeding programmes aiming to enhance WUE as well as the yield (Hirel *et al.* 2007). For example, in subterranean clover (*Trifolium subterraneum*), water deficit conditions reduced the initial and total Rubisco activity, but it did not decrease the overall amount of Rubisco protein per unit of leaf area (Medrano *et al.* 1997). In another study, Marques and Arrabica (1995) found that Rubisco activity in *Setaria sphacelota* declined slightly under moderate drought, but substantially under severe drought. The decline in the rate of Rubisco-catalyzed reaction was reported to be due to alteration in CO_2 availability at the chloroplast level or the availability of the substrate, RUBP, or the deactivation of Rubisco. The main reason for the inhibition of photosynthesis under both mild and severe drought was suggested to be a low supply of CO_2 to Rubisco, as the substomatal CO_2 is generally known to be reduced by stress conditions. However, in order to assess the extent of the decline in photosynthesis due to reduced Rubisco activity under drought conditions, Gunasekera and Berkowitz (1993) used transgenic tobacco plants transformed with antisense Rubisco. They showed that a 68% decrease in Rubisco activity did not hamper P_N under water-limited regimes, suggesting that drought stress may affect any of the steps involved in the regeneration of RuBP rather than Rubisco itself. Using the transgenic approach, Jeanneau *et al.* (2002) developed a maize line with enhanced expression of C_4 -PEPC. This transgenic line showed a 30% increase in WUE and a 20% increase in dry biomass under moderate water-deficit conditions. These results suggest that drought-tolerant crop cultivars can be developed by engineering the genes of endogenous enzymes involved in the mechanism of photosynthesis. In another study concerning nonstomatal limitations of photosynthesis, Du *et al.* (1998) reported that the activities of the various C_4 photosynthesis enzymes, such as PEPcase, NADP-malic enzyme (NADP-ME), Rubisco, and fructose-1,6-bisphosphatase, decreased 2 to 4 times under drought conditions, whereas the activity of phosphopyruvate dikinase (PPDK) declined 9.1 times in C_4 plant, sugar cane. This suggests that PPDK is potentially the limiting enzyme to photosynthesis under water-deficit conditions.

High temperature has been reported to reduce the solubility of CO_2 relative to O_2 within the leaf tissue resulting in reduced availability of CO_2 as a substrate for CO_2 concentrating mechanisms (Salvucci and Crafts-Brandner 2004, Li *et al.* 2007). This in turn significantly affects the activities of key photosynthetic enzymes. At temperatures above the thermal optimum, Rubisco activase, the key regulatory enzyme of Rubisco, is reported to dissociate in both C_3 and C_4 species, causing a reduction in the photosynthetic capacity (Raines 2011, Sage and Zhu 2011). C_3 plants require a stabilization of Rubisco activase to acclimate themselves to high temperatures (Kurek *et al.* 2007, Kumar *et al.* 2009). Crafts-Brandner and Salvucci (2000) reported that Rubisco activity was markedly inhibited in both cotton and tobacco, when leaf temperatures exceeded $35^\circ C$. They suggested that the decrease in Rubisco activation could happen, when the rate of enhanced Rubisco activation was insufficient to overcome the accelerated rate of Rubisco deactivation at higher temperatures. Furthermore, they also observed that in the absence of activase, the rate of deactivation of isolated Rubisco increased substantially with rising temperature. The activase capability to maintain or enhance Rubisco activation *in vitro* was also reported to decline with temperature. A mechanism of an acclimation to elevated temperatures has also been found in C_4 maize, wherein the acclimation to high temperature was associated with manifestation of a larger subunit of Rubisco and limited recovery of the Rubisco activation state (Crafts-Brandner and Salvucci 2002). C_4 plants are generally more tolerant to elevated temperatures than C_3 plants. However, photosynthesis in C_4 plants is also perturbed by high temperatures. For example, as well as high-temperature-induced impairment in Rubisco activase functioning and the activation state in C_4 plants, the inhibition occurs also in electron transport, PEP carboxylation, and PEP regeneration at elevated temperatures (Raines 2006, Kelly *et al.* 2006). Chinthapalli *et al.* (2003) showed that the PEPCase from the C_4 plant (*Amaranthus hypochondriacus*) was less sensitive to supraoptimal temperature, but more sensitive to suboptimal temperature than the enzyme from the C_3 species (*Pisum sativum*). This shows that the key photosynthetic enzymes in C_3 and C_4 plants are unlikely sensitive to temperature. Furthermore, various enzymes differ in their response to temperature stress. For example, in wheat (*Triticum aestivum*), heat stress imposed for 12 days caused a sharp decline in Rubisco activity, whereas the activity of PEPC increased first, but later decreased, which caused a marked increase in PEPC/Rubisco ratio (Xu *et al.* 2003).

From the preceding discussion, it is evident that the activities of enzymes involved in C_3 and C_4 photosynthetic pathways are altered to a varying extent under stressful environments. However, it depends on the type of species, stomatal and nonstomatal factors, as well as their interaction, how far the changes in the activities of

these enzymes affect photosynthetic capacity. Furthermore, a number of enzymes of both CO₂ concentrating mechanisms are regulated by light (Taiz and Zeiger 2010, Doubnerová and Ryšlavá 2011), so the light intensity and its duration in addition to the intensity of additional stress play also a significant role in the regulation of these

Improvement in photosynthetic capacity under stress by engineering photosynthesis-related genes or transcription factors

Two approaches are currently used to improve the photosynthetic capacity in different plant species. Firstly, an effort is devoted to developing transgenic C₃ plants with over-expression of Rubisco genes or other enzymes of the C₃ pathway. Secondly, attempts are underway to transfer the genes of a key C₄ photosynthetic pathway to C₃ plants (Table 3). Considerable progress has been made during the last two decades in engineering the photosynthetic genes using advanced protocols of the recombinant DNA technology. Using the first strategy, Feng *et al.* (2007) produced a transgenic line of japonica rice by overexpressing *OsSbp* cDNA from an indica rice cultivar. This transgenic line showed beside an enhanced activity of the C₃ enzyme sedoheptulose-1,7-bisphosphatase (SBPase, EC 3.1.3.37), which is involved in the regeneration of RuBP, also the enhanced photosynthetic capacity as well as the increased tolerance to salt stress. They suggested that the enhanced rate of photosynthesis under salt stress might have been due to the enhanced supply of RuBP to Rubisco by the activation of SBPase. In another study, Tanaka *et al.* (2005) assessed the role of the overexpression of chloroplastic glutamine synthetase (a key enzyme of photorespiratory pathway involved in the utilization of NH₃ released as a result of conversion of two molecules of glycine into serine in mitochondrion), in salt tolerance of rice (Table 3). They showed that the overexpression of glutamine synthetase significantly reduced the tissue Na⁺ content under saline regimes, suggesting the putative role of this enzyme in salt tolerance of rice. The enhanced salt tolerance in this transgenic rice was suggested to be associated with increased re-assimilation of NH₃ in the photorespiratory process. Similarly to this study, Kozaki and Takeba (1996) showed enhanced protection from photoinhibition of transgenic tobacco plants overexpressing glutamine synthetase.

Karaba *et al.* (2007) found a significant improvement in WUE and in biomass production due to improved photosynthetic assimilation and decreased transpiration rate in transgenic rice plants under salt- and drought-stress conditions by overexpressing *Arabidopsis* HARDY (*HRD*) gene (Table 3). The expression of the pea *ABR17* (ABA-responsive17) cDNA, a member of pathogenesis-related proteins (PR10), in *Arabidopsis thaliana* showed the improved rate of germination under salt, cold temperature, or both conditions. Furthermore, the transgenic *Arabidopsis* plants showed the enhanced tolerance to

enzymes. It has also been observed that under most stresses the balance between different enzymes is also perturbed. However, an optimal balance of different enzymes is necessary for the normal functioning of the photosynthetic pathways.

freezing temperature, suggesting the potential utility of the *ABR17* gene to engineer multiple stress tolerance due to *ABR17*-mediated increased photosynthesis (Srivastava *et al.* 2004).

Water deficits and heat stress or both together adversely affected photosynthesis of transgenic *Arabidopsis thaliana* plants constitutively expressing *ABP9*, a bZIP transcription factor (Zhang *et al.* 2008) by regulating photosynthetic carbon- and light-use efficiencies together with a leaf ABA content, pigment composition, and an expression of stress- and light harvesting-responsive genes. P_N and g_s of the transgenic plants were less reduced by a single stress, although P_N and the electron transport rate declined more under well watered conditions in the transgenic plants in comparison with those under water-deficit conditions. The results revealed that *ABP9* transgenic plants were less susceptible to the stress than the wild type plants. In addition, the increased ABA contents in both transgenic and wild type plants in response to water stress and/or heat stresses suggest that declines in P_N and g_s might have been due to ABA-induced stomata closure.

Recently, Patra *et al.* (2010) have shown that expression of *PcINO1* and *McIMTI* genes in chloroplasts as well as in cytosol caused higher accumulation of total inositol compared with nontransgenic plants under saline regimes. The transgenic plants showed higher photosynthetic activity and the growth, while lesser oxidative damage was found as compared with the wild type plants under saline conditions.

Transfer of C₄ genes/traits to C₃ plants: Several attempts have been made during the past three decades to improve capacity of C₃ plants by transferring C₄ traits to C₃ plants. Initially, classical hybridization of C₄ plants with those of C₃ was done, but most of the resultant C₃-C₄ hybrids were infertile (Brown and Bouton 1993). However, with the advent of recombinant DNA technology, it is possible now to transfer and express substantially the enzymes of C₄ pathways in appropriate places within the leaves of C₃ plants (Miyao 2003, Begonia and Begonia 2007, Kajala *et al.* 2012). For example, Häusler *et al.* (2002) reported that the first cDNAs of the C₄-PEPC sequences for cloning were derived from maize (Izui *et al.* 1986) and *Flaveria trinervia* (Poetsch *et al.* 1991). Later on, a tobacco

Table 3. Improving photosynthetic efficiency of C₃ plants through engineering photosynthesis-related genes or transcription factors from C₃ or C₄ plants.

Gene engineered	C ₃ transgenic host	Source organism	Trait improved	Reference
<i>OsSbp</i> cDNA	Rice (<i>Oryza sativa</i> L. ssp. japonica), cv. Zhonghual 1	Rice (<i>Oryza sativa</i> L. ssp. Indica), cv. 9311 -C ₄	The transgenic cultivar showed enhanced activity of the C ₃ enzyme sedoheptulose-1,7-bisphosphatase (SBPase) and enhanced photosynthetic capacity as well as increased tolerance to salt stress. SBPase maintained the activation of Rubisco by providing more regeneration of the acceptor molecule ribulose-1,5-bisphosphate in the soluble stroma and by preventing the sequestration of Rubisco activase to the thylakoid membrane from the soluble stroma	Feng <i>et al.</i> 2007
Chloroplastic glutamine synthetase (<i>GS2</i>)	Rice (<i>Oryza sativa</i> L.) cvs. G39-2, G39-4, G241-12 and G241-15	Rice (<i>Oryza sativa</i> L.) -C ₃	Enhanced salt tolerance in transgenic plants due to re-assimilation of NH ₃ in the photorespiration and reduction in the accumulation of Na ⁺	Tanaka <i>et al.</i> 2005
<i>Brassica oleracea</i> var. Acephala (Water stress responsive <i>BoRS1</i> gene)	(<i>Nicotiana tabacum</i> var. Petit Havana SR1)	<i>Brassica oleracea</i> var. Acephala -C ₃	Transgenic plants exhibited better growth, dry matter accumulation higher levels of leaf chlorophyll content and enhanced water stress tolerance than those of the untransformed control plants.	Tang <i>et al.</i> 2005
Transcription factor yeast activator protein 1 (<i>YAP1</i>)	<i>Arabidopsis thaliana</i> (Ecotype, Columbia).	Yeast (<i>Saccharomyces cerevisiae</i>)	Transgenic plants maintained high photosynthetic efficiency and low amounts of H ₂ O ₂ under salt stress, suggesting that ROS production was reduced under saline regimes	Zhao <i>et al.</i> 2009a
Ectoine biosynthetic gene (<i>ectABC</i>)	Tobacco (<i>Nicotiana tabacum</i> cv. Petit Havana)	<i>Halomonas elongata</i>	Considerable protection of rubisco proteins, and improved rate of photosynthesis under salt stress	Moghaieb <i>et al.</i> 2006
L-Δ ¹ -pyrroline-5-carboxylate reductase (<i>P5CR</i> gene)	Soybean (<i>Glycine max</i> L.)	<i>Arabidopsis thaliana</i> L. -C ₃	Oxygen evolving complex (OEC) dissociation was bypassed by proline feeding electrons into photosystem-II (PSII), and NADPH level was maintained, which indirectly ameliorated the inhibition and/or the effect of uncoupling of the OEC under drought and heat stress	De Ronde <i>et al.</i> 2004
Chloroplastic Fe superoxide dismutase (FeSOD)	Tobacco (<i>Nicotiana tabacum</i> L.)	<i>Arabidopsis thaliana</i> L. -C ₃	Overproduction of FeSOD did not confer tolerance to H ₂ O ₂ , singlet oxygen, chilling-induced photoinhibition and salt stress at the whole plant level	Van Camp <i>et al.</i> 1996

Table 3 continues on the next page.

Table 3 (continued)

Gene engineered	C ₃ transgenic host	Source organism	Trait improved	Reference
ω -3 fatty acid desaturase (<i>FAD7</i>)	Rice (<i>Oryza sativa</i> L.)	<i>Arabidopsis thaliana</i> L. -C ₃	Increased growth rate (shoot and root mass), chlorophyll contents, and maximum photochemical efficiency of photosystem II in the transgenic plants compared with those of wild-type rice under temperature stress	Sohn and Back 2007
Heat shock protein (<i>HSP21</i>)	Tomato (<i>Lycopersicon esculentum</i> L.) cv. TF36	Tomato (<i>Lycopersicon esculentum</i> L.) -C ₃	The protein protected PSII from temperature-dependent oxidative stress, improved fruit reddening, conversion of chloroplasts to chromoplasts and carotenoid contents under heat stress in the transgenic plants	Neta-Sharir <i>et al.</i> 2005
<i>Nicotiana</i> protein kinase (<i>NPK1</i>)	Maize (<i>Zea mays</i> L.)	Tobacco (<i>Nicotiana tabacum</i> L.) -C ₃	NPK1 expression enhanced drought tolerance in transgenic maize by maintaining high photosynthetic rate	Shou <i>et al.</i> 2004
Stable protein 1 (<i>SP1</i>)	<i>Arabidopsis thaliana</i> L.	Aspen (<i>Populus tremula</i>) -C ₃	Transgenic plants exhibited better growth, chlorophyll contents, chlorophyll fluorescence, and proline and malondialdehyde (MDA) contents under heat stress	Zhu <i>et al.</i> 2008
Apoplast invertase (<i>Apo-Inv</i>)	Tobacco (<i>Nicotiana tabacum</i> L.)	Yeast (<i>Saccharomyces cerevisiae</i>)	Transgenic <i>Apo-Inv</i> tobacco plants maintained constant photosynthetic activities under salt stress	Fukushima <i>et al.</i> 2001
Glyphosate herbicide (<i>cp4-epsps</i> gene)	Soybean (<i>Glycine max</i> L. Merr.) cv. BRS 245RR	Soybean (<i>Glycine max</i> L. Merr.)	A comparative analysis of the fluorescence ratios of the cultivars revealed that nontransgenic plants had higher chlorophyll content than that of transgenic ones under water stress	Caires <i>et al.</i> 2010

transgenic line was developed overexpressing maize PEPC gene under the control of its own promoter (Hudspeth *et al.* 1992) or by using the constitutively expressing *Cauliflower mosaic virus* (CaMV) 35S promoter (Benfey and Chua 1990, Kogami *et al.* 1994). However, in all these transgenic lines, although the activity of C₄-PEPC increased two-fold compared with that in nontransformed plants, the transgenic and nontransformed lines did not differ significantly in the net CO₂ assimilation rate. In another study, Ku *et al.* (1999) transferred the complete maize PEPC gene to rice plants; the activity of PEPC in the transgenic rice increased about 110-fold compared with the nontransgenic plants and three-fold the maize activity. The incorporation of the intact maize C₄-*Pdk* gene into rice was also reported to be effective in overproducing PPDK about 40-fold over that of wild-type rice plants (Fukayama *et al.* 2001). Similarly, the introduction of the maize C₄-specific NADP-ME cDNA to rice plants enhanced the activity of NADP-ME to 30- or 70-fold in rice leaves compared with the non-transgenic rice (Takeuchi *et al.* 2000, Tsuchida *et al.* 2001). Although Matsuoka *et al.* (2001) have reported that a number of C₃ plants over-expressing C₄ PEPC have shown enhanced photosynthetic capacity, the success is not so significant, when the PEPC gene is transferred to a phylogenetically distant plant species. For example, the intact, maize C₄-specific PEPC gene was transferred to tobacco plants, but it was not fully expressed in the tobacco leaves (Hudspeth *et al.* 1992). This was ascribed to incorrect transcription initiation. In addition, incorrect splicing may take place, when genes from monocots are transferred to dicots (Goodall and Filipowicz 1991, Ruan *et al.* 2012). Furthermore, the conversion of C₃ to C₄ plant requires a rearrangement or *de novo* formation of anatomical structures within the leaves to localize the photosynthetic enzymes in appropriate leaf tissues. Such promising anatomical changes, parallel to C₄ leaf anatomy, have not been achieved so far. Therefore, the manipulation of genes responsible for the development of C₄ specific structures in C₃ plants is essential rather than only engineering the genes of key C₄ enzymes. Thus, this is one of the major causes of the little success in achieving the desired goal in terms of developing C₃ transgenic lines with C₄ trait. In addition, although photosynthesis-related genes have been transferred from C₄ to C₃ plants and their photosynthetic capacity has been examined under nonstress conditions, no attempts have been reported to test the effectiveness of this approach under stressful conditions.

Role of transcription factors in regulation of genes involved in photosynthesis: Transcription factors are found in all organisms, because they are essential for the regulation of the gene expression. Different types of transcription factors exist and an organism with a larger genome usually contains more transcription factors than one with a smaller genome. Elucidation of the mechanism

of the gene expression for a particular trait is a major focus of molecular biologists to find out how different types of transcription factors are involved in the gene expression. Recently, Saibo *et al.* (2009) have described the role of a number of transcription factors involved directly or indirectly in the regulation of genes involved in photosynthesis. For example, a transcription factor LONG HYPOCOTYL 5 (HY5), a bZIP-type, was reported to be mainly involved in the regulation of *CAB* gene expression by light, although it may also exhibit a significant role in abiotic stress tolerance (Maxwell *et al.* 2003, Saibo *et al.* 2009). This transcription factor, despite controlling the expression of *Chl a/b* binding protein 2 (*CAB2*) (Maxwell *et al.* 2003), regulates the expression of the gene for the Rubisco small subunit (*RbcS1A*) (Chattopadhyay *et al.* 1998, Lee *et al.* 2007). There is another transcription factor, *OsMYB4*, the over-expression of which has been reported to be involved in high accumulation of glycine betaine, which in turn increases stress tolerance in *Arabidopsis thaliana* (Mattana *et al.* 2005), because glycine betaine can stabilize Rubisco structure under high-saline regimes (Sakamoto and Murata 2002, Yang *et al.* 2005, Khafagy *et al.* 2009). Thus, the overexpression of this transcription factor has an indirect effect on the regulation of photosynthetic genes under stressful environments. In maize, the expression of photosynthetic genes has been reported to be partly controlled by two factors *DOF1* and *DOF2*. From the expression studies, it was evident that *DOF1* is an activator of transcription, whereas *DOF2* is a repressor (Yanagisawa and Sheen 1998). However, *DOF1* was found to enhance the expression of the maize C₄-PEPC gene.

Saibo *et al.* (2009) have reported that enhanced expression of CAM-specific genes in plants under drought or saline conditions is mediated through transcriptional regulation, in which both *cis*-acting DNA sequences and *trans*-acting factors play a vital role. Schaeffer *et al.* (1995) showed enhanced transcription of the *Ppchl* gene encoding a CAM-specific isozyme of PEPCase and *Gap1* encoding NAD-dependent glyceraldehyde-3-phosphate dehydrogenase under salt stress. Since several of the sequences of the promoters of both genes resemble consensus binding sites for the MYB class of transcription factors, it was suggested that the salt-induced up-regulation of these specific photosynthesis-related genes may be mediated by MYB-type transcription factors (Schaeffer *et al.* 1995).

Role of mitogen-activated protein kinases (MAPKs) in photosynthesis: MAPKs respond to a variety of extracellular stimuli including mitogens, proinflammatory cytokines, osmotic stress, and heat shock (Fig. 4), and they pass on information from sensors to cellular processes in all eukaryotes (Nakagami *et al.* 2005, Diédhiou *et al.* 2008, Inagaki *et al.* 2008). They are known to regulate a multitude of cellular processes, such

as mitosis, differentiation, gene expression, and cell death or survival (Zhang and Klessig 2001). MAP kinases are widespread in eukaryotes. They are effectively involved in the signal transduction of various metabolic processes. MAPK cascades comprise minimally three protein kinases, a MAP kinase kinase kinase (MAPKKK), a MAP kinase kinase (MAPKK), and a MAP kinase (MAPK), which function in concert. Activation of each MAPK occurs when it undergoes phosphorylation. Following the activation, MAPKs move from the cytoplasm into the nucleus, wherein they phosphorylate many transcription factors leading to alterations in the gene expression (Whitmarsh and Davis 2000, Janknecht 2003, Zhang *et al.* 2011). There is strong evidence now that MAP kinases are involved in the mechanisms of tolerance to a variety of biotic and abiotic stresses in plants (Huang *et al.* 2011, Zhang *et al.* 2011). For example, increased expression of genes encoding a MAP kinase module is strong evidence of the involvement of this enzyme cascade in plants exposed to cold, salt, or drought stress (Mizoguchi *et al.* 1996, Dai *et al.* 2007, Kant *et al.* 2007). In *Arabidopsis*, the MAPK kinase 2 (MKK2) has been reported to be activated by both cold and salt stress (Teige *et al.* 2004). Similarly, MAPKs have been reported to be activated by osmotic stresses in *Medicago sativa* and tobacco (Jonak *et al.* 2002) and by salt stress in rice (Diédhiou *et al.* 2008). Shou *et al.* (2004) have shown that the tobacco MAPKKK (NPK1) expressed constitutively in maize resulted in a maize transgenic line with enhanced drought tolerance trait measured in terms of kernel mass and P_N . The enhanced drought tolerance of the transgenic line of maize was shown to be strongly associated with a markedly high rate of photosynthesis, suggesting the active role of NPK1 in the mechanism of protection of photosynthesis machinery from water stress damage.

From the above, it is evident that development of transgenic lines of C_3 plants overexpressing C_4 photo-

synthetic enzymes is a meaningful approach to improve photosynthetic capacity of C_3 plants and to bring it to the level of C_4 plants. However, the extent, to which C_4 enzymes transferred to C_3 plants play a role in effectively fixing CO_2 , depends on a number of factors including the localization of introduced C_4 enzymes within the leaf tissues and coordination of C_4 enzymes with already CO_2 fixing pathways or other allied pathways operative in C_3 plants. It has been observed that although overexpression of a single C_4 enzyme can modulate the photosynthetic metabolism in C_3 plants, in most cases, it does not have significant effects on photosynthesis. Furthermore, little success of attaining photosynthetic capacity in C_3 plants equivalent to that of C_4 plants by transferring C_4 genes to C_3 plants could have been due to non-transformation of C_3 leaf anatomical structure to that of C_4 leaf. This may be the main reason of a low effectiveness of the attempts to bring C_3 photosynthetic capacity at par with that of C_4 through genetic engineering. Thus, alternatively, efforts should be made to improve the efficiency of CO_2 concentrating processes in C_3 plants by enhancing the activities of key enzymes through genetic manipulation. However, transgenic C_3 plants overexpressing multiple C_4 enzymes are now in the focus of most scientists to improve photosynthetic capacity in C_3 plants (Miyao 2003, Begonia and Begonia 2007, Kajala *et al.* 2012).

Little information is available in the literature on the components involved in either the perception or signaling involved in a stress response. This necessitates a comprehensive elucidation of the signal transduction pathways induced by different stresses so that appropriate programmes can be devised to improve plant tolerance to a variety of abiotic stresses including the functioning of the photosynthetic system. Thus, identification of signaling components involved in the stress adaptation in plants is a meaningful approach to identify transcriptional activators of adaptive mechanisms to stressful environments that are promising for improvement of crop tolerance.

Conclusion and future prospects

It is now evident that stresses lead to the considerable reduction in photosynthetic performance mediated through stress-induced stomatal or nonstomatal limitations (Athar and Ashraf 2005, Rahnama *et al.* 2010, Taiz and Zeiger 2010). However, it is not easy to discriminate between the effects of these limitations on overall photosynthetic capacity of a plant. Certainly, it depends on the species to what extent the process of photosynthesis under stress conditions is controlled by stomatal or nonstomatal factors. Nevertheless, knowledge of the proportion of the stomatal and nonstomatal factors controlling the process of photosynthesis is vital for appointing the future research on photosynthesis.

Salinity, drought, or high temperatures modulate gas exchange characteristics, such as P_N , g_s , E , and C_i . Although genetic differences in photosynthetic capacity

exist at intraspecific and interspecific levels, P_N is considered as one of the potential, physiological, selection criteria for stress tolerance (Ashraf 2004). Since an unreliable association of the photosynthetic capacity with the degree of stress tolerance exists in many species, use of the photosynthetic capacity as a physiological marker will be realistic only in those species for which a positive relationship between the photosynthetic performance and the growth under stress conditions has been confirmed.

Improvement in the photosynthetic performance of C_3 plants to bring it at par with that of C_4 plants has been an important goal of plant biologists. This could be achieved either by overexpressing the key C_3 enzymes or by transferring the C_4 enzymes to C_3 plants. The production of transgenic lines overexpressing C_3 or C_4 enzymes has had limited success in enhancing photosynthetic perform-

ance in most transformed lines. It is not clear yet up to what extent C_4 enzymes transferred to C_3 plants take part in effective assimilation of CO_2 in C_3 engineered plants. It depends undoubtedly on a multitude of factors including the partitioning of introduced C_4 enzymes within the leaf tissues and the interlinking of C_4 enzymes with photosynthesis-related pathways functioning in C_3 plants. In most of the studies on generations of transgenic lines made for enhanced photosynthetic performance that were published so far, a single C_4 enzyme gene has been transferred, but in most cases this did not result in a major success in terms of enhanced photosynthetic capacity in transgenic C_3 lines. Thus, a generation of transgenic C_3 plants overexpressing multiple C_4 enzymes is one of the premier themes of future research.

The elucidation of stress-induced signal transduction pathways is vital to enhance plant tolerance to different stresses. Undoubtedly, by integrating the advances in molecular genetics and cell biology, our knowledge of the signaling pathways has increased greatly over recent years, although it is still far from a full understanding to perception and signaling of environmental cues in plants. There is little information on the components involved in either the perception or signaling involved in stress responses. One of several promising advances made recently in stress biology, knowledge of long- and short-distance signaling is contemplated as of vital importance for understanding up- or down-regulation of photosynthesis under various stresses, because signaling pathways involved in plant stress responses are interconnected at several points (Chaves *et al.* 2009). This

calls for ample understanding of the signal transduction pathways induced by different stresses to improve plant tolerance to various, stressful conditions. Efforts get currently underway in different laboratories all over the world to identify signaling components, such as transcription factors and protein kinases, particularly MAPKs, involved in stress adaptation in plants. Thus, understanding the prospective association between the stress-induced protein kinase pathways and the genetic and epigenetic regulation of the gene expression in plants remains the important area of the future research.

Photosynthetic response to different types of stresses is quite intricate, because it entails the interaction of several restrictions occurring at different locations of the cell or the leaf, and at different phases of the plant growth and development. Furthermore, the duration and intensity of the stress can also significantly affect the photosynthetic capacity. Thus, the complete elucidation of factors involved in the regulation of photosynthetic capacity under stressful environments would help devise appropriate strategies to grow plants successfully in stress-prone areas.

It is evident that stressful factors depending on their intensity and duration can differently down- or up-regulate the genes involved in the mechanism of photosynthesis in plants. Thus it could be useful to know expression patterns of such genes for understanding plant photosynthetic or other metabolic responses to various stresses and to develop transgenic lines of different crops with enhanced photosynthetic capacity under stressful conditions.

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