

Rubisco and abiotic stresses in plants: Current assessment

Abdulkali Shehu ABDULBAKI^{1,2,*}, Hameed ALSAMADANY¹, Yahya ALZHRANI¹, Bolaji Umar OLAYINKA³

¹Department of Biological, Faculty of Science, King Abdulaziz University, Jeddah, Saudi Arabia.

²Department of Plant Science and Biotechnology, Faculty of Life Sciences, Federal University Dutsinma, Katsina State, Nigeria.

³Department of Plant Biology, Faculty of Life Sciences, University of Ilorin, Ilorin, Nigeria

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Abstract: Abiotic stresses are serious environmental factors militating against the production of many crops around the world. The consequence of this, is the difficulty of meeting the demands of the increasing world population. Aside from other negative effects, reduction in photosynthesis is an important feature of abiotic stresses. Abiotic stresses limit photosynthesis in a number of ways. The reduction in ribulose 1, 5-bisphosphate carboxylase/oxygenase (Rubisco) content and activity is one of the paramount ways through which abiotic stresses affect photosynthesis. Rubisco is the CO₂ fixing enzyme of photosynthesis and also catalyses the photo-respiratory carbon oxidation. The enzyme has low turnover and also copes with competitive inhibition by O₂. Hence, manipulating the enzyme in order to boost photosynthesis has been the target of scientists, especially in stressed environments. Based on recent studies, the mechanism of the harmful effects of abiotic stresses on Rubisco is examined in this review. In addition, the prevalent ways through which Rubisco can be made to thrive well despite the various abiotic stresses are evaluated. This review paper also outlines practicable approaches to promote existing ways of enhancing Rubisco tolerance to abiotic stresses in order to produce more crops with higher stress resilience.

Key words: Abiotic stress, Rubisco, photosynthesis, crop production

1. Introduction

Abiotic stresses are stresses caused by nonliving factors. Compared to biotic stress, they are relatively more common and pose greater damage to crop yield (Minhas et al., 2017). They disrupt the growth and development of plants and ultimately lead to decreased yield and productivity. Abiotic stresses are particularly harmful to the process of photosynthesis. Photosynthesis is tampered with during abiotic stresses through a number of ways like closure of stomata and decline in the Ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) level and activity (Hassan et al., 2015; Niinemets et al. 2017). Studying Rubisco in relation to abiotic stresses is therefore important in the focus of research in the field of plant science.

Rubisco (EC 4.1.1.39) is an enzyme that is required in the first major step of carbon fixation in the photosynthesis of C₃ plants. In other words, it is the primary acceptor of CO₂ during photosynthesis. Rubisco, RuBPCase, and RuBPCo are the popular abbreviations used to represent it. It is a very important enzyme in the photosynthesis of C₃ plants and considered the most abundant enzyme on earth (Raven, 2013). The enzyme requires many chaperones for its biosynthesis in plants and is composed

of 8 large (RbcL) and 8 small subunits (RbcS) (Lin et al., 2020). The RbcL and RbcS genes could be modified to improve photosynthesis efficiency (Chen et al., 2015a). The chloroplasts are composed of essential proteins like Rubisco-binding protein (RBP, or chaperonin 60-Cpn60) and Rubisco activase (Rca) with a chaperone nature, which assist in preserving the amount and activity of Rubisco. The transport of these particles from chloroplasts to vacuoles has been recorded (Buet et al. 2019). Rca plays the role of removing sugar phosphate inhibitors in the active sites of both carbamylated and decarbamylated Rubisco (Bacu et al., 2020).

Rubisco is largely a poor catalyst and can only fix about 2–10 CO₂ per min (Ogbaga et al., 2019). The low turnout of Rubisco is because of the complication it undergoes in concentrating on carboxylation or oxygenation depending on the molecular concentration of CO₂ or O₂. Rubisco is composed of more than 50% of soluble leaf protein which justifies its significance in plants. While it is located in the stroma of all chloroplasts in C₃ plants, its presence in C₄ plants is limited to the bundle sheath cells.

Due to its importance, many researchers have studied Rubisco (level and activity) in relation to abiotic stresses in many plants. Some of these researches are captured in

* Correspondence: abdulbakias@gmail.com

Table 1. This review focused on the latest studies on the topic and outlined the available ways in rescuing Rubisco from the various abiotic stresses. Suggestions for future research on the topic were proposed since Rubisco is an excellent target for enhancing the photosynthesis of plants under challenges of abiotic stresses.

2. Drought stress and Rubisco

Drought as expressed by prolonged water deficit is one of the abiotic stresses limiting plant growth and productivity. Photosynthesis, the main process driving plant growth, requires that Rubisco activity is at its maximum potential. In general, water stress has been shown to limit photosynthesis on account of the inhibition of CO₂ metabolism and diminution of leaf proteins such as Rubisco (Carmo-Silva et al., 2012; Lyu et al., 2016; Simova-Stoilova et al., 2020; Wang H et al., 2020).

In crop plants grown under prolonged water deficit, Rubisco activity may be impaired depending on how different plant species respond differently to factors such as alteration in water status of the cell, low CO₂ concentration, high temperature, stomata limitation and mode of CO₂ fixation. The foregoing factors have been variously established to limit Rubisco activity under drought stress. For instance, Khedr et al. (2011) while using a xero-halophyte described the ionic imbalance in cells occasioned by the diminished cellular water content, as the primary causative factor in the fall of not in Rubisco. However, while working on a Mediterranean species, Galmés et al. (2011) believed that stomatal limitation is better correlated with Rubisco reduction than relative water content.

The impact of species and genotypic difference on Rubisco activity during drought was also vivid in the experiments on different coffee species (Semedo et al., 2021) and in wheat varieties under drought stress (Hassan et al., 2015; Nagy et al., 2013). Furthermore, as stated by Gomes et al. (2020), despite that a certain landrace of cowpea is drought sensitive, its Rubisco level was rather constant under drought stress suggesting that its susceptibility to drought is therefore unrelated to Rubisco. Accordingly, Lima Neto et al. (2017) demonstrated that the diminution in Rubisco content in *Ricinus communis* is different from that of *Jatropha curcas* despite being put under the same during drought scheme. Based on the understanding of this relationship between Rubisco activity and species difference, Chakhchar et al. (2019) considered Rubisco activity as one of the yardsticks in determining tolerance to drought in Argan tree.

Aside the species difference, the severity and duration of drought are other factors related to a drought-induced reduction in Rubisco activity (Arquero et al., 2006; Flexas et al., 2006). Bota and Flexas (2004) concluded the arguments on whether Rubisco activity in C₃ plants is

reduced in progressive drought stress or not by stating that considerable reduction in the activity of the enzyme only occurs when the drought is severe.

In comparing C₃, C₄ and CAM plants with regards to Rubisco activity and drought stress, current results by Shameer et al. (2018) and Gonçalves et al. (2020) have established the similarity in C₃ and CAM plants with respect to carboxylase activity of Rubisco. C₄ plants, on the other hand, differ. Thus, while the enhancement of Rubisco in rice, a C₃ plant, did not translate to increased photosynthetic activity, the opposite was true for maize, a C₄ plant (Doron et al., 2020; Suzuki and Makino, 2012). It is however worthy of noting that C₄ plants largely adopt Phosphoenolpyruvate carboxylase (PEPC) for carbon fixation. PEPC has been observed to have a higher ability of CO₂ fixation than Rubisco under drought stress (Jia et al., 2015; Kong et al., 2010).

The relegation of photosynthetic activities during drought was proportional to the down-regulation of Rubisco subunits, rbcL and rbcS as seen in wheat (Demirevska et al., 2009) and in winter rapeseed (Chen et al., 2015a). If these subunits were enhanced, ameliorating the activities of Rubisco and photosynthesis would be achieved. This was demonstrated by Zhao et al. (2017) using 2, 4-epibrassinolide (EBR) applied exogenously to wheat plants under the combined stresses of heat and drought. In drought-stressed Maize, alpha lipoic acid (ALA) application had similar ameliorative results (Sezgin et al., 2019). As shown in cotton, decapitalised Potassium fertilizer is also one of the agents that have proven positive in the enhancement of Rubisco activity despite water-deficient conditions (Zahoor et al., 2017). These agents could have enhanced CO₂ assimilation or reduced stomatal closure and hence were able to compensate for the drop in Rubisco activity and photosynthesis caused by drought. In *Camellia oleifera*, Mi et al. (2018) had asserted the effectiveness of these subunits as a marker in selecting drought-tolerant tea oil cultivars.

Furthermore, through externally applied cytokinin, the suppression of Rubisco was reversed in drought-stressed rice. The feat was achieved as a result of the proper management of Rubisco regulatory enzymes; Rca and Rubisco accumulation factor 1 (Raf1) ensured by the synthetic cytokinin (Gujjar et al., 2020). Rca belonging to the AAA+ family, acts as a catalytic chaperone in regulating the activity of Rubisco by facilitating the dissociation of inhibitory sugar phosphates from the active site of Rubisco in an ATP-dependent manner (Perdomo et al., 2017). On the other hand, Raf1 is an essential molecular chaperone, which aids the gathering of the Rubisco subunits (Vitlin et al., 2018). In the study of Hassan et al. (2020), it was discovered that drought stress was against high Rubisco levels in wheat and that Polyamines (PA) alleviation of the stress was achieved through mechanisms including the

Table 1. A list of plants and their abiotic stresses against which Rubisco (level and activity) was reported.

Plant	Abiotic Stress	Reference
Alfalfa	Drought	Wang H et al. (2020)
Arabidopsis	Drought	Wijewardene et al. (2020)
	Salinity	Wijewardene et al. (2020)
	Heat	Wijewardene et al. (2020)
<i>Argania spinosa</i>	Drought	Chakhchar et al. (2019)
<i>Azalea sp</i>	Heat	Wang et al. (2020)
Barley	Drought	Aliakbari et al. (2021)
	Salinity	Aliakbari et al. (2021)
<i>Brassica rapa</i>	Drought	Mi et al. (2018)
<i>Chenopodium quinoa</i>	Salinity	Delatorre-Herrera et al. (2021)
Chickpea	Heat	Pipaliya and Gajera (2020)
	Cold	Poormazaheri et al. (2021)
Coffea spp	Drought	Dubberstein et al. (2020), Semedo et al. (2021)
	Heat	Dubberstein et al. (2020)
Cotton	Heat	Carmo-Silva et al. (2012)
	Drought	Carmo-Silva et al. (2012), Zahoor et al. (2017)
Cowpea	Drought	Gomes et al. (2020)
Cucumber	Heat	Nada et al. (2021)
<i>Glycine max</i>	Heat	Kuzmina and Wulfraaat (2020)
Grapevine	Cold	Hendrickson et al. (2004)
<i>Haloxylon salicornicum</i>	Salinity	Panda et al. (2020)
<i>Hordeum vulgare</i>	Cold	Jurczyk et al. (2019)
<i>Jatropha curcas</i>	Drought	Lima Neto et al. (2017)
	Salinity	Pompelli et al. (2021)
<i>Kandelia obovata</i>	Cold	Fei et al. (2021)
Maize	Drought	Doron et al. (2020), Sezgin et al. (2019)
	Heat	Perdomo et al. (2017)
	Cold	Salesse-Smith et al. (2020), Turk et al. (2020)
	Cadmium	Wang et al. (2009)
<i>Miscanthus giganteus</i>	Heat	Kuzmina and Wulfraaat (2020)
	Cold	Serrano-Romero and Cousins (2020)
	Salinity	Sun et al. (2021)
<i>Morus alba</i>	Lead	Huihui et al. (2020)
	Cadmium	Huihui et al. (2020)
Mustard	Cadmium	Kaur et al. (2021), Per et al. (2016)
Olive tree	Salinity	Moula et al., 2020
	Potassium	Arquero et al. (2006)
<i>Phaseolus vulgaris</i>	Salinity	ElSayed et al. (2021)
<i>Pyrus ussuriensis</i>	Drought	Lyu et al. (2016)
Rice	Drought	Gujjar et al. (2020), Ohno et al. (2018)
	Arsenate	Mishra and Singh (2021)
	Heat	Qu et al. (2021), Scafaro et al. (2016)

Table 1. (Continued).

	Salinity	Reddy et al. (2017)
<i>Ricinus communis</i>	Drought	Lima Neto et al. (2017)
<i>Saussurea involucrata</i>	Cold	Mu et al. (2021)
<i>Sonneratia apetala</i>	Cold	Shen et al. (2021)
<i>Sorghum bicolor</i>	Lead	Rathika et al. (2020)
	Nickel	Rathika et al. (2020)
Soybean	Salinity	Lu et al. (2009)
Tobacco	Cadmium	Zhang et al. (2020)
	Zinc	Zhang et al. (2020)
Tomato	Heat	Parrotta et al. (2020), Wang et al. (2015)
	Cold	Zhang L et al. (2020)
	Cold	Zhou et al. (2020)
<i>Vigna radiata</i>	Salinity	Hussain et al. (2021)
Watermelon	Salinity	Li et al. (2017)
Wheat	Heat	Alsamman et al. (2021), Degen et al. (2021) Kumar et al. (2019)
	Drought	Alsamman et al. (2021), Demirevska et al. (2009), Hassan et al. (2020)
	Salinity	Bacu et al. (2020), Talaat (2021)
	Cadmium	Moussa and El-Gamal (2010)

elevation of Rubisco levels. These findings point to the fact that the manipulation of Rca, giving its closeness to Rubisco is, therefore, a sure way in enhancing photosynthesis. Unfortunately, bioengineering in that direction has not recorded resounding success owing to the complexities required in the metabolism and biogenesis of Rubisco (Bracher et al. 2017).

3. Salt stress and Rubisco

Salinity or salt stress affects Rubisco activity negatively. In fact, according to Lu et al. (2009), there are no biochemical limitations to photosynthesis that is as much as salt-stress induced fall in Rubisco activity. In addition, Sun et al. (2021) while working with *C₄ Miscanthus sinensis* plant depicted that the reduction in photosynthesis caused by salt stress was partly associated with the diminution in Rubisco activity. Hence, in a study analysing the photosynthetic differences between two contrasting ecotypes of Quinoa under severe salt stress, it was discovered that the ruggedness of the tolerant ecotype against the stress is partly from its ability to maintain Rubisco activities and other nondiffusional mechanisms of photosynthesis (Delatorre-Herrera et al., 2021).

Salt stress, especially when high, impacts on the level and activity of Rubisco adversely through degradation and modulation of its biosynthesis (Li et al., 2017; Reddy et al., 2017; Xu et al., 2018). The reduction in Rubisco in plants under salt stress could also result from the inhibition generated by the instability in the folding configuration

of native proteins (Hasanuzzaman et al., 2020). Since salt-stressed plants often exhibit relatively low water, they are known with a metabolic impairment which is another factor related to the diminution of Rubisco (Pompelli et al., 2021).

Based on the discovery through proteomic analysis of a xero-halophyte, *Haloxylon salicornicum*, that salt stress induced up-regulation of Rubisco proteins, ameliorating the Rubisco activity during salt stress using tolerant organisms is, therefore, possible (Panda et al., 2020). Accordingly, in the two most important crops affected by salt stress (i.e. rice and tomato), the use of Halotolerant bacteria thus aided in combating the salt challenge via various means including ensuring the carboxylation efficiency of Rubisco and photosynthesis (Taj and Challabathula, 2021).

The overexpression of Rca genes has also assisted in the acquisition of tolerance against salinity in transgenic plants (Wijewardene et al., 2020). Aliakbari et al. (2021) in their experiment on the Barley plant using meta-analysis observed that the RcaA gene is responsive to not only drought stress but to both salt and drought stress. The adequate manipulation of the gene was, therefore, important to counter the commonly natural condition of combined salt and drought stress. During the salinity stress of the young wheat plant, the rate of photosynthesis was observed to be directly proportional to the amount of Rubisco genes. This lends credence to the hypothesis that the observed resistance to salinity stress noticed in the plant is connected to the heightened level of Rubisco in response to the stress (Bacu et al., 2020).

Furthermore, in boosting the Rubisco activity during salt stress to enhance photosynthesis, Jasmonic acid (JA) has been proven as a useful agent (Arif et al., 2020). In salt-stressed green beans, melatonin applied exogenously also affected the boosting of Rubisco activity and eventually the rate of photosynthesis (ElSayed et al., 2021). Similarly, foliar-applied salicylic acid in *Mentha pulegium* and Gibberellic acid in *Olea europaea* were efficient in mitigating reduced Rubisco activity triggered by salt salinization (Moula et al., 2020; Ghassemi-Golezani and Farhadi, 2021). In the wheat plant, when melatonin and salicylic were applied jointly, the improved tolerance against salt stress was more significant than using any of the agents singly. This induced tolerance was made via routes including the boosting of Rubisco activity and Rubisco activation state (Talaat, 2021). Mung bean showed a reduction in Rubisco activity up to 36% but both sulphur and salicylic acid effectively helped in mitigating this imbalance in Rubisco activity, especially when they are jointly applied (Hussain et al., 2021). In not with ginger seedlings, the utilization of low pH to improve the salt stress-induced reduction in Rubisco activities was achieved (Yang W et al., 2020).

4. Heat stress and Rubisco

A clear understanding of Rubisco regulation at elevated temperatures is of great significance especially as the world still contends with the challenge of the warming climate. Temperature above the optimal level of plant growth limits photosynthesis through the reduction of Rubisco content and activity (Kumar et al., 2019; Parrotta et al., 2020; Scafaro et al., 2018).

The inactivation of Rca follows the damage to the chloroplast caused by increased temperature (Li et al., 2018). Shao et al. (2021) in their experiments believed that the loss of both initial and total activity of Rubisco induced by heat stress could have resulted from rapid leaf senescence. It has also been deduced that the heat-stress response of Rubisco is connected with its constituent amino acids and the association of its RbcL and RbcS isoforms (Degen et al. 2020; Perdomo et al. 2021; Scafaro et al 2019). In other words, it could be said that, the deactivation of Rubisco under high temperature goes in line with the inadequacy of Rca or decrease in the Rubisco activation (Alsamman et al., 2021; Degen et al., 2021; Dubberstein et al., 2020; Galmés et al., 2019; Wijewardene et al., 2021).

Since increasing temperature promotes the proliferation of Rubisco inhibitors, therefore the role of Rca in reactivating Rubisco requires the removal of these inhibitors through remodelling of the active site (Bhat et al., 2017). Hence, under heat stress, improving the expression of Rubisco and Rca has the potential of inducing heat tolerance and maintenance of photosynthesis (Scafaro et al., 2016). Perdomo et al. (2017) had exemplified this

with their experiments on cereals under heat stress. Coupled with other agents, Wang et al. (2020) recently revealed that Rca does not only play an active role in heat-induced tolerance in *Rhododendron hainanense* but also in achieving heat stress acclimation memory in the plant. More recently, Qu et al. (2021) also confirm the claim in three heat-stressed rice lines as the joint overexpression of both Rubisco and Rca translated to improved CO₂ assimilation and photosynthesis. When the Rca of heat-tolerant *Larrea tridentate* (*LtRCA*) was tested to improve the thermo-tolerance of Arabidopsis, it was discovered that it greatly aided the activity of Rubisco and over heat tolerance of Arabidopsis (Wijewardene et al., 2021). Quite surprising, however, despite the overexpression of Rca in transgenic rice, there was a fall in Rubisco content and CO₂ assimilation. According to Fukayama et al. (2012), this imbalance might have resulted from posttranscriptional mechanisms.

In furtherance, since it is assumed that the manipulation of the Rubisco isoforms would be vital in regulating Rubisco under heat stress (Figure 1), Degan et al. (2020) successfully carried out the substitution of a single amino acid (methionine) with isoleucine in the Rca2 β isoform to improve the Rubisco activation and heat stability of the wheat plant. However, in C₄ plants under heat stress, it is the Rca- α isoform that showed better thermos-stability and was more related to Rubisco activation and photosynthesis (Kim et al., 2021).

Despite the advantages manipulating the Rca offer in improving the Rubisco activity and photosynthesis, the challenges of its complex structure, the requirement of expansive labour and time, and the dangerous impacts associated with the manipulation limited research in that area (Wilson et al., 2019). Experiments like those of Daki et al. (2021) and Kuzmina and Wulffraat (2020) involving the exploitation of the relatively large quantity of Rca isoforms, in addition to the introduction of superior forms of Rca via genetic engineering or breeding to induce the maintenance of Rubisco and make it more tolerant to the prevailing warming climate, are therefore more required.

Some chemical agents and priming techniques have been used in alleviating heat-induced reduction in Rubisco. For instance, chickpea showed reduction in Rubisco activity following the onset of heat stress at the flowering stage but was rescued under the influence of salicylic acid (Pipaliya and Gajera, 2020). In the same pattern, magnesium-treated wheat under heat temperature was able to maintain stable photosynthesis during grain filling through the enhancement of Rubisco activation (Shao et al., 2021). In cucumber leaves, Nada et al. (2021) also showed that thermal acclimation was effective in alleviating the reduced photosynthesis caused by heat stress.

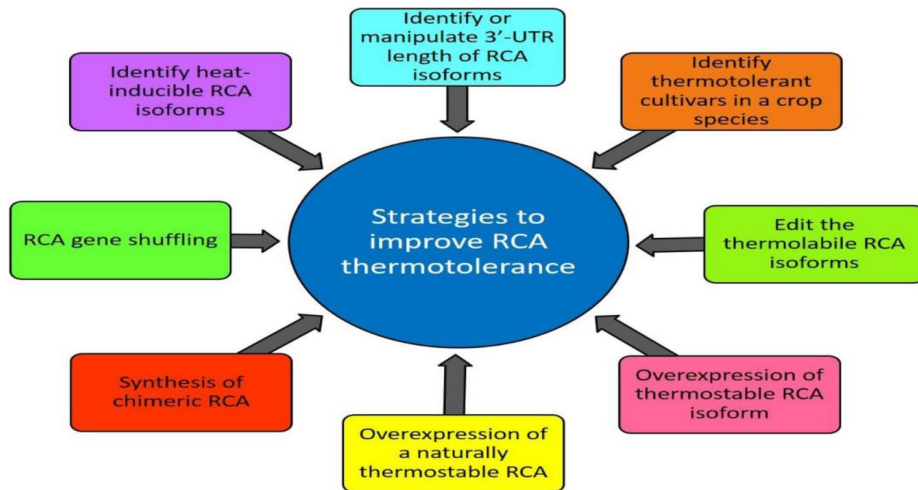


Figure 1. Probable ways of using Rca to enhance photosynthesis at high temperatures (Wijewardene et al., 2021). Rca = Rubisco activase. 3' UTR = 3' untranslated region.

Some researchers have made outstanding efforts in detecting proteins related to Rubisco activity during heat stress. The proteins identified to be of considerable influence in maintaining Rubisco activity during heat stress are SICDJ2 and TaRCA1 (Wang et al., 2015).

5. Cold stress and Rubisco

Like heat stress, cold or low-temperature stress also induces Rubisco inactivation, limits photosynthesis, and adversely affects the general crop growth and yield (Hendrickson et al., 2004; Ohno et al., 2018; Wang et al., 2021b). In fact, according to Chen et al. (2015b), the main factor in the reduction of photosynthesis in cold-stressed rice is the degradation of Rubisco. In plants generally, Hashida and Kawai-Yamada (2019) established that the fall in photosynthesis rate and disruption of the photosystem due to cold are significantly connected with the impairment of Rubisco activity and its abundance.

It is a common belief that C_4 plants like *Miscanthus giganteus* coordinate chilling-tolerance via improved activities of Rubisco and other biochemical agents (Serrano-Romero and Cousins, 2020). However, according to Iniguez et al. (2020), C_3 plants tend to adapt to cold environments better than C_4 plants because the former achieves the saturation of Rubisco better than the latter in cold temperatures.

Current findings confirmed that both the RbcS and RbcL subunits are down-regulated following cold stress. Therefore, the overexpression of the Rubisco subunits and the Rca show great efficiency in achieving stability in Rubisco activity despite chilling conditions (Salesse-Smith et al., 2018, 2020).

In addition, since experiments like Poormazaheri et al. (2021) and Fei et al. (2021) have revealed that proteins relating to the abundance and activities of Rubisco were

the most significantly enhanced proteins in cold-tolerant plants, researchers like Mu et al. (2021), therefore induced overexpression of cold-responsive factor like *SiFBA5* (Fructose-1, 6-bisphosphate aldolase from *Saussurea involucrata*) in enhancing photosynthesis and tolerance against low temperature. Zhang L et al. (2020) reported a similar enhancement in Rubisco and photosynthesis in chilled-stressed tomatoes via the overexpression of *SikRbcs2*.

Also, using proteomic analysis, it has been illustrated that the induction of chilling tolerance through prior cold-acclimation promotes the increase in the expression of proteins related to photosynthesis like Rubisco proteins (Jurczyk et al., 2019; Shen et al., 2021; Zhou et al., 2012). In the study of Inal et al. (2021) on *Chlamydomonas reinhardtii*, the external application of Putrescine was enough to counter the reduction in Rubisco proteins. The same positive boosting of Rubisco was observed in chilled maize seedlings following the application of carnitine (Turk et al., 2020).

6. Heavy metal stress and Rubisco

Heavy metals lower the activity of Rubisco level and activity in many different ways. These metals generally interfere with the oxygenation and structure of Rubisco (Amari et al., 2017; Huihui et al., 2020; Manna et al., 2021; Wang et al., 2009). Incredibly, some other heavy metals stresses like lead (Pb), Nickel (Ni), and copper (Cu) stresses have recorded an increase in the Rubisco activity (Arena et al., 2017; Rathika et al., 2020; Singh and Singh, 2020; Son et al., 2014; Yang et al., 2020). Other heavy metals like decapitalize Zinc (Zn) had little impact on the Rubisco subunits and Rca (Zhang et al., 2020).

Considering that heavy metals had been proven generally to down-regulate Rubisco, it is thus not surprising that up-regulating Rubisco using chemical agents plays a vital role in

achieving better photosynthesis under metal toxicity (Moussa and El-Gamal, 2010). For example, citric acid and vermicompost had been used to further the enhancement of Rubisco activity in both Pb and Ni-stressed Sorghum plants (Rathika et al., 2020). Salicylic acid (SA) and hydrogen sulphide (H₂S) were used to assist the modulation of the photosynthesis of the Mustard plant under Cadmium stress via routes including majorly the up-regulation of Rubisco activity (Kaur et al., 2021). Same as SA and H₂S, gibberellins (GAs), nitric oxide (NO), methyl jasmonate (MeJA) and Brassinosteroids (BRs) also help in ensuring tolerance against heavy metals through mechanisms involving the maintenance of the Rubisco activity (Arif et al., 2021; Emamverdian et al., 2020; Mishra and Singh, 2021; Per et al., 2016; Xia et al., 2009). Glutathione is another agent, that when externally applied had great results in alleviating the heavy metal stress as exemplified in Tobacco (Son et al., 2014).

7. Conclusion and future prospects

The dearth of information on the detailed mechanisms of Rubisco in higher plants has made the progression in the enhancement of Rubisco against abiotic stresses

rather slow. Studies like those of Ng et al. (2020) revolving around the sites of interaction between Rubisco and Rca are regarded as useful in solving this challenge and hence more studies in that direction are needed.

Also, at present only a few plants like *Tamarindus indica* (Ogbaga et al., 2019) have their Rubisco gene characterized and thus in the coming years, advancement in the characterisation of the Rubisco and interaction with the activase should be a point of focus, especially using 'omic' approaches.

Lastly, like Lin et al. (2020), experiments revealing the kinetic ability of the Rubisco subunits of different plants are also handy in improving the photosynthetic ability of Rubisco. It is concluded that all these suggestions will ensure actualizing resilience of Rubisco in the face of unfavourable abiotic conditions and ultimately enhance the sustainability of world agriculture.

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References

- Aliakbari M, Cohen SP, Lindlöf A, Shamloo-Dashtpajardi R (2021). Rubisco activase A (RcaA) is a central node in overlapping gene network of drought and salinity in Barley (*Hordeum vulgare* L.) and may contribute to combined stress tolerance. *Plant Physiology and Biochemistry* 161:248-58. doi:10.1016/j.plaphy.2021.02.016
- Alsamman AM, Bousba R, Baum M, Hamwiah A, Fouad N (2021). Comprehensive analysis of the gene expression profile of wheat at the crossroads of heat, drought and combined stress. *Highlights in BioScience* 4:1-14. doi:10.36462/H.BioSci.202104
- Amari T, Ghnaya T, Abdelly C (2017). Nickel, cadmium and lead phytotoxicity and potential of halophytic plants in heavy metal extraction. *South African Journal of Botany* 111:99-110. doi:10.1016/j.sajb.2017.03.011
- Arena C, Figlioli F, Sorrentino MC, Izzo LG, Capozzi F et al. (2017). Ultrastructural, protein and photosynthetic alterations induced by Pb and Cd in *Cynara cardunculus* L., and its potential for phytoremediation. *Ecotoxicology and Environmental Safety* 145:83-89. doi:10.1016/j.ecoenv.2017.07.015
- Arif MS, Yasmeen T, Abbas Z, Ali S, Rizwan M, et al. (2021). Role of exogenous and endogenous hydrogen sulfide (H₂S) on functional traits of plants under heavy metal stresses: a recent perspective. *Frontiers in Plant Science* 2021:2063. doi:10.3389/fpls.2020.545453
- Arif Y, Singh P, Siddiqui H, Bajguz A, Hayat S (2020). Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. *Plant Physiology and Biochemistry* 156:64-77. doi:10.1016/j.plaphy.2020.08.042
- Arquero O, Barranco D, Benlloch M (2006). Potassium starvation increases stomatal conductance in olive trees. *HortScience* 41:433-6. doi:10.21273/HORTSCI.41.2.433
- Bacu A, Ibro V, Nushi M, Krekaj M, Kristollari K (2020). Rubisco genes expression and pigment synthesis at early stages of development of wheat cultivar dajti under saline stress conditions. *Journal of Environmental Protection and Ecology* 21:1239-46.
- Bhat JY, Miličić G, Thieulin-Pardo G, Bracher A, Maxwell A et al. (2017). Mechanism of enzyme repair by the AAA+ chaperone Rubisco activase. *Molecular cell* 67:744-56. doi:10.1016/j.molcel.2017.07.004
- Bota J, Medrano H, Flexas J (2004). Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress?. *New phytologist* 162:671-81. doi:10.1111/j.1469-8137.2004.01056.x
- Bracher A, Whitney SM, Hartl FU, Hayer-Hartl M (2017). Biogenesis and metabolic maintenance of Rubisco. *Annual review of plant biology* 68:29-60. doi:10.1146/annurev-arplant-043015-111633
- Chakhchar A, Lamaoui M, Aissam S, Ferradous A, Wahbi S et al. (2019). Physiological and carbohydrate metabolism traits for discrimination of drought-tolerant elite ecotypes of *Argania spinosa*. *Plant Physiology Reports* 24:388-98. doi:10.1007/s40502-019-00463-x
- Carmo-Silva AE, Gore MA, Andrade-Sanchez P, French AN, Hunsaker DJ et al. (2012). Decreased CO₂ availability and inactivation of Rubisco limit photosynthesis in cotton plants under heat and drought stress in the field. *Environmental and Experimental Botany* 83:1-1. doi:10.1016/j.envexpbot.2012.04.001

- Chen Y, Wang B, Chen J, Wang X, Wang R et al. (2015a). Identification of Rubisco rbcL and rbcS in *Camellia oleifera* and their potential as molecular markers for selection of high tea oil cultivars. *Frontiers in Plant Science* 6:189. doi:10.3389/fpls.2015.00189
- Chen Y, Wang XM, Zhou L, He Y, Wang D et al. (2015b). Rubisco activase is also a multiple responder to abiotic stresses in rice. *PLoS one* 10: e0140934. doi:10.1371/journal.pone.0140934
- Daki A, Qu K, Ummareddy R (2021). Investigating plastome expression of Rubisco Activase in *Chlamydomonas reinhardtii* as a platform for directed evolution. In: Proceedings of IMSAloquium Student Investigation Showcase; Illinois, USA
- Degen GE, Orr DJ, Carmo-Silva E (2021). Heat-induced changes in the abundance of wheat Rubisco activase isoforms. *New Phytologist* 229:1298-311. doi:10.1111/nph.16937
- Degen GE, Worrall D, Carmo-Silva E (2020). An isoleucine residue acts as a thermal and regulatory switch in wheat Rubisco activase. *The Plant Journal* 103:742-51. doi:10.1111/tpj.14766
- Delatorre-Herrera J, Ruiz KB, Pinto M (2021). The Importance of Non-Diffusional Factors in Determining Photosynthesis of Two Contrasting Quinoa Ecotypes (*Chenopodium quinoa* Willd.) Subjected to Salinity Conditions. *Plants* 10:927. doi:10.3390/plants10050927
- Demirevska K, Zasheva D, Dimitrov R, Simova-Stoilova L, Stamenova M et al. (2009). Drought stress effects on Rubisco in wheat: changes in the Rubisco large subunit. *Acta Physiologiae Plantarum* 31:1129. doi:1007/s11738-009-0331-2
- Doron L, Xu L, Rachmilevitch S, Stern DB (2020). Transgenic overexpression of rubisco subunits and the assembly factor RAF1 are beneficial to recovery from drought stress in maize. *Environmental and Experimental Botany* 177:104126. doi:10.1016/j.envexpbot.2020.104126
- Dubberstein D, Lidon FC, Rodrigues AP, Semedo JN, Marques I et al. (2020). Resilient and sensitive key points of the photosynthetic machinery of *Coffea* spp. to the single and superimposed exposure to severe drought and heat stresses. *Frontiers in Plant Science* 11:1049. doi:10.3389/fpls.2020.01049
- ElSayed AI, Rafudeen MS, Gomaa AM, Hasanuzzaman M (2021). Exogenous melatonin enhances the reactive oxygen species metabolism, antioxidant defense-related gene expression, and photosynthetic capacity of *Phaseolus vulgaris* L. to confer salt stress tolerance. *Physiologia Plantarum* 1:1-13. doi:10.1111/pl.13372
- Emamverdian A, Ding Y, Mokhberdorani F (2020). The role of salicylic acid and gibberellin signaling in plant responses to abiotic stress with an emphasis on heavy metals. *Plant Signaling & Behavior* 15(7):1777372. doi:10.1080/15592324.2020.1777372
- Fei J, Wang YS, Cheng H, Sun FL, Sun CC (2021). Comparative physiological and proteomic analyses of mangrove plant *Kandelia obovata* under cold stress. *Ecotoxicology* 30:1826-40. doi:10.1007/s10646-021-02483-6
- Flexas J, Bota J, Galmes J, Medrano H, Ribas-Carbó M (2006). Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. *Physiologia Plantarum* 127:343-52. doi:10.1111/j.1399-3054.2006.00621.x
- Fukayama H, Ueguchi C, Nishikawa K, Katoh N, Ishikawa C et al. (2012). Overexpression of Rubisco activase decreases the photosynthetic CO₂ assimilation rate by reducing Rubisco content in rice leaves. *Plant and Cell Physiology* 53:976-86. doi:10.1093/pcp/pcs042
- Galmés J, Capó-Bauçà S, Niinemets Ü, Iñiguez C (2019). Potential improvement of photosynthetic CO₂ assimilation in crops by exploiting the natural variation in the temperature response of Rubisco catalytic traits. *Current Opinion in Plant Biology* 49:60-7. doi:10.1016/j.pbi.2019.05.002
- Galmés J, Ribas-Carbó M, Medrano H, Flexas J (2011). Rubisco activity in Mediterranean species is regulated by the chloroplastic CO₂ concentration under water stress. *Journal of Experimental Botany* 62:653-65. doi:10.1093/jxb/erq303
- Ghassemi-Golezani K, Farhadi N (2021). The Efficacy of Salicylic Acid Levels on Photosynthetic Activity, Growth, and Essential Oil Content and Composition of Pennyroyal Plants under Salt Stress. *Journal of Plant Growth Regulation* 1:1-3. doi:10.1007/s00344-021-10515-y
- Gonçalves AZ, Latansio S, Detmann KC, Marabesi MA, Neto AA et al. (2020). What does the RuBisCO activity tell us about a C3-CAM plant?. *Plant Physiology and Biochemistry* 147:172-80. doi:10.1016/j.plaphy.2019.12.020
- Gomes AM, Rodrigues AP, António C, Rodrigues AM, Leitão AE et al. (2020). Drought response of cowpea (*Vigna unguiculata* (L.) Walp.) landraces at leaf physiological and metabolite profile levels. *Environmental and Experimental Botany* 175:104060. doi:10.1016/j.envexpbot.2020.104060
- Gujjar RS, Banyen P, Chuekong W, Worakan P, Roytrakul S et al. (2020). Synthetic Cytokinin Improves Photosynthesis in Rice under Drought Stress by Modulating the Abundance of Proteins Related to Stomatal Conductance, Chlorophyll Contents, and Rubisco Activity. *Plants* 9:1106. doi:10.3390/plants9091106
- Hasanuzzaman M, Bhuyan MH, Zulfiqar F, Raza A, Mohsin SM et al. (2020). Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants* 8:681. doi:10.3390/antiox9080681
- Hashida SN, Kawai-Yamada M (2019). Inter-organelle NAD metabolism underpinning light responsive NADP dynamics in plants. *Frontiers in Plant Science* 10:960. doi:10.3389/fpls.2019.00960
- Hassan N, Ebeed H, Aljaarany A (2020). Exogenous application of spermine and putrescine mitigate adversities of drought stress in wheat by protecting membranes and chloroplast ultra-structure. *Physiology and Molecular Biology of Plants* 26:233-45. doi:10.1007/s12298-019-00744-7

- Hassan N, El-Bastawisy Z, Ebeed H, Alla MN (2015). Role of defense enzymes, proteins, solutes and $\Delta 1$ -pyrroline-5-carboxylate synthase in wheat tolerance to drought. *Rendiconti Lincei*. 26(3):281-91. doi:10.1007/s12210-015-0429-y
- Hendrickson L, Ball MC, Wood JT, Chow WS, Furbank RT (2004). Low temperature effects on photosynthesis and growth of grapevine. *Plant, Cell & Environment* 27:795-809. doi:10.1111/j.1365-3040.2004.01184.x
- Huihui Z, Xin L, Zisong X, Yue W, Zhiyuan T et al. (2020). Toxic effects of heavy metals Pb and Cd on mulberry (*Morus alba* L.) seedling leaves: Photosynthetic function and reactive oxygen species (ROS) metabolism responses. *Ecotoxicology and Environmental Safety* 195:110469. doi:10.1016/j.ecoenv.2020.110469
- Hussain SJ, Khan NA, Anjum NA, Masood A, Khan MI (2021). Mechanistic elucidation of salicylic acid and sulphur-induced defence systems, nitrogen metabolism, photosynthetic, and growth potential of mungbean (*Vigna radiata*) under salt stress. *Journal of Plant Growth Regulation* 40:1000-16. doi:10.1007/s00344-020-10159-4
- Inal MS, Unal D, Unal BT, Ozturk M (2022). Effect of Putrescine on Low-Temperature Acclimation in *Chlamydomonas reinhardtii*. *Phyton* 91:583. doi:10.32604/phyton.2022.018223
- Iniguez C, Capó-Bauçà S, Niinemets Ü, Stoll H, Aguiló-Nicolau P et al. (2020). Evolutionary trends in RuBisCO kinetics and their co-evolution with CO₂ concentrating mechanisms. *The Plant Journal* 101:897-918. doi:10.1111/tj.14643
- Jia S, Lv J, Jiang S, Liang T, Liu C et al. (2015). Response of wheat ear photosynthesis and photosynthate carbon distribution to water deficit. *Photosynthetica* 53:95-109. doi:10.1007/s11099-015-0087-4
- Jurczyk B, Grzesiak M, Pocięcha E, Wlazło M, Rapacz M (2019). Diverse stomatal behaviors mediating photosynthetic acclimation to low temperatures in *Hordeum vulgare*. *Frontiers in Plant Science* 9:1963. doi:10.3389/fpls.2018.01963
- Kaur H, Hussain SJ, Al-Huqail AA, Siddiqui MH, Al-Huqail AA et al. (2021). Hydrogen sulphide and salicylic acid regulate antioxidant pathway and nutrient balance in mustard plants under cadmium stress. *Plant Biology* 1:1-10. doi:10.1111/plb.13322
- Khedr AH, Serag MS, Nemat-Alla MM, Abo-Elnaga AZ, Nada RM et al. (2011). A DREB gene from the xero-halophyte *Atriplex halimus* is induced by osmotic but not ionic stress and shows distinct differences from glycophytic homologues. *Plant Cell, Tissue and Organ Culture (PCTOC)* 106:191-206. doi:10.1007/s11240-010-9906-2
- Kim SY, Slattery RA, Ort DR (2021). A role for differential Rubisco activase isoform expression in C4 bioenergy grasses at high temperature. *GCB Bioenergy* 13:211-23. doi:10.1111/gcbb.12768
- Kong L, Wang F, Feng B, Li S, Si J et al. (2010). The structural and photosynthetic characteristics of the exposed peduncle of wheat (*Triticum aestivum* L.): an important photosynthate source for grain-filling. *BMC Plant Biology* 10:1-0. doi:10.1186/1471-2229-10-141
- Kumar RR, Goswami S, Dubey K, Singh K, Singh JP et al. (2019). RuBisCo activase—a catalytic chaperone involved in modulating the RuBisCo activity and heat stress-tolerance in wheat. *Journal of Plant Biochemistry and Biotechnology* 28:63-75. doi:10.1007/s13562-018-0463-9
- Kuzmina E, Wulffraat G (2020). Protein Engineering to Increase the Thermal Tolerance of Rubisco activase in *Miscanthus giganteus* and *Glycine max*. In: *Proceedings of IMSAloquium Student Investigation Showcase*. Illinois. USA
- Li H, Chang J, Chen H, Wang Z, Gu X et al. (2017). Exogenous melatonin confers salt stress tolerance to watermelon by improving photosynthesis and redox homeostasis. *Frontiers in plant science* 8:295. doi:10.3389/fpls.2017.00295
- Lin MT, Stone WD, Chaudhari V, Hanson MR (2020). Small subunits can determine enzyme kinetics of tobacco Rubisco expressed in *Escherichia coli*. *Nature Plants* 10:1289-99. doi:10.1038/s41477-020-00761-5
- Lu KX, Cao BH, Feng XP, He Y, Jiang DA (2009). Photosynthetic response of salt-tolerant and sensitive soybean varieties. *Photosynthetica* 47:381-7. doi:10.1007/s11099-009-0059-7
- Lyu S, Du G, Liu Z, Zhao L, Lyu D (2016). Effects of biochar on photosystem function and activities of protective enzymes in *Pyrus ussuriensis* Maxim. under drought stress. *Acta Physiologiae Plantarum* 38:1-0. doi:10.1007/s11738-016-2236-1
- Manna I, Sahoo S, Bandyopadhyay M (2021). effect of engineered nickel oxide nanoparticle on reactive oxygen species–nitric oxide interplay in the roots of *Allium cepa* L. *Frontiers in Plant Science* 12. doi:10.3389/fpls.2021.586509
- Mi C, Zhao Y, Liu Z, Chen Q, Sun W et al. (2018). Cloning of RuBisCo subunits genes rbcL and rbcS from winter rapeseed (*Brassica rapa*) and their expression under drought stress. *Acta Agronomica Sinica* 44:1882-90.
- Minhas PS, Rane J, Pasala RK (2017). Abiotic stresses in agriculture: An overview. In: Minhas PS, Rane J, Pasala RK (editors). *Abiotic Stress Management for Resilient Agriculture*, Vol. 1. Springer, Singapore, pp. 3-8. doi:10.1007/978-981-10-5744-1_1
- Mishra V, Singh VP (2021). Implication of nitric oxide and hydrogen sulfide signalling in alleviating arsenate stress in rice seedlings. *Environmental Pollution* 291:117958. doi:10.1016/j.envpol.2021.117958
- Moula I, Boussadia O, Koubouris G, Hassine MB, Boussetta W et al. (2020). Ecophysiological and biochemical aspects of olive tree (*Olea europaea* L.) in response to salt stress and gibberellic acid-induced alleviation. *South African Journal of Botany* 132:38-44. doi:10.1016/j.sajb.2020.04.022
- Moussa HR, El-Gamal SM (2010). Effect of salicylic acid pretreatment on cadmium toxicity in wheat. *Biologia Plantarum* 54:315-20. doi:10.1007/s10535-010-0054-7
- Mu J, Fu Y, Liu B, Zhang Y, Wang A et al. (2021). SiFBA5, a cold-responsive factor from *Saussurea involucreta* promotes cold resilience and biomass increase in transgenic tomato plants under cold stress. *BMC Plant Biology* 1:1-0. doi:10.1186/s12870-021-02851-8

- Nada K, Nagaya Y, Hiratsuka S (2021). Short-term thermal acclimation increases ribulose 1, 5 biphosphate carboxylase/oxygenase activity and content and enhances heat stress tolerance of photosynthesis in cucumber. *Environmental Control in Biology* 59:69-75. doi:10.2525/ecb.59.69
- Navarro-León E, Paradisone V, López-Moreno FJ, Rios JJ, Esposito S et al. (2021). Effect of CAX1a TILLING mutations on photosynthesis performance in salt-stressed *Brassica rapa* plants. *Plant Science* 311:111013. doi:10.1016/j.plantsci.2021.111013
- Ng J, Mueller-Cajar O (2020). Rubisco activase remodels plant Rubisco via the large subunit N-terminus. *bioRxiv*. doi:10.1101/2020.06.14.151407
- Niinemets Ü, Berry JA, von Caemmerer S, Ort DR, Parry MA et al. (2017). Photosynthesis: ancient, essential, complex, diverse and in need of improvement in a changing world. *New Phytologist* 213:43-7. doi:10.1111/nph.14307
- Lima Neto MC, Cerqueira JV, da Cunha JR, Ribeiro RV, Silveira JA (2017). Cyclic electron flow, NPQ and photorespiration are crucial for the establishment of young plants of *Ricinus communis* and *Jatropha curcas* exposed to drought. *Plant Biology* 19:650-9. doi:10.1111/plb.12573
- Li X, Cai C, Wang Z, Fan B, Zhu C et al. (2018). Plastid translation elongation factor Tu is prone to heat-induced aggregation despite its critical role in plant heat tolerance. *Plant Physiology* 176:3027-45. doi:10.1104/pp.17.01672
- Ogbaga CC, Maishanu RA, Okolo D (2019). Characterisation of the Rubisco content and bioactive compound analysis of leaf and seed extracts of *Tamarindus indica*. In: 15th International Conference on Electronics, Computer and Computation (ICECCO). IEEE. p. 1-6. doi:10.1109/ICECCO48375.2019.9043238
- Ohno H, Banayo NP, Bueno C, Kashiwagi JI, Nakashima T et al. (2018). On-farm assessment of a new early-maturing drought-tolerant rice cultivar for dry direct seeding in rainfed lowlands. *Field Crops Research* 219:222-8. doi:10.1016/j.fcr.2018.02.005
- Panda A, Rangani J, Parida AK (2020). Comprehensive proteomic analysis revealing multifaceted regulatory network of the xero-halophyte *Haloxylon salicornicum* involved in salt tolerance. *Journal of Biotechnology* 324:143-61. doi:10.1016/j.jbiotec.2020.10.011
- Parrotta L, Aloisi I, Faleri C, Romi M, Del Duca S et al. (2020). Chronic heat stress affects the photosynthetic apparatus of *Solanum lycopersicum* L. cv Micro-Tom. *Plant Physiology and Biochemistry* 154:463-75. doi:10.1016/j.plaphy.2020.06.047
- Per TS, Khan NA, Masood A, Fatma M (2016). Methyl jasmonate alleviates cadmium-induced photosynthetic damages through increased S-assimilation and glutathione production in mustard. *Frontiers in Plant Science* 7:1933. doi:10.3389/fpls.2016.01933
- Perdomo JA, Buchner P, Carmo-Silva E (2021). The relative abundance of wheat Rubisco activase isoforms is post-transcriptionally regulated. *Photosynthesis Research* 148:47-56. doi:10.1007/s11120-021-00830-6
- Perdomo JA, Capó-Bauçà S, Carmo-Silva E, Galmés J (2017). Rubisco and rubisco activase play an important role in the biochemical limitations of photosynthesis in rice, wheat, and maize under high temperature and water deficit. *Frontiers in Plant Science* 8:490. doi:10.3389/fpls.2017.00490
- Pipaliya HR, Gajera HP (2020). Sucrose metabolism and RUBISCO activity influenced by salicylic acid at flowering stage revealed tolerance to heat stress in chickpea genotypes. *Indian Journal of Agricultural Biochemistry* 33:67-75. doi:10.5958/0974-4479.2020.00011.8
- Pompelli MF, Ferreira PP, Chaves AR, Figueiredo RC, Martins AO et al. (2021). Physiological, metabolic, and stomatal adjustments in response to salt stress in *Jatropha curcas*. *Plant Physiology and Biochemistry* 168:116-27. doi:10.1016/j.plaphy.2021.09.039
- Poormazaheri H, Maali-Amiri R, Eshaghi F (2021). Assessment of relative expression of some genes involved in cold tolerance in chickpea (*Cicer arietinum* L.). *MGJ* 16:183-92.
- Qu Y, Sakoda K, Fukayama H, Kondo E, Suzuki Y et al. (2021). Overexpression of both Rubisco and Rubisco activase rescues rice photosynthesis and biomass under heat stress. *Plant, Cell & Environment* 44:2308-2320. doi:10.1111/pce.14051
- Rathika R, Khalifa AY, Srinivasan P, Praburaman L, Kamala-Kannan S et al. (2021). Effect of citric acid and vermi-wash on growth and metal accumulation of *Sorghum bicolor* cultivated in lead and nickel contaminated soil. *Chemosphere* 243:125327. doi:10.1016/j.chemosphere.2019.125327
- Raven JA (2013). Rubisco: still the most abundant protein of Earth. *New Phytologist* 198:1-3. doi:10.1111/nph.12197
- Reddy IN, Kim BK, Yoon IS, Kim KH, Kwon TR (2017). Salt tolerance in rice: focus on mechanisms and approaches. *Rice Science* 24:123-44. doi:10.1016/j.rsci.2016.09.004
- Salesse-Smith CE, Sharwood RE, Busch FA, Kromdijk J, Bardal V et al. (2018). Overexpression of Rubisco subunits with RAF1 increases Rubisco content in maize. *Nature Plants* 4:802-10. doi:10.1038/s41477-018-0252-4
- Salesse-Smith CE, Sharwood RE, Busch FA, Stern DB (2020). Increased Rubisco content in maize mitigates chilling stress and speeds recovery. *Plant Biotechnology Journal* 18:1409-20. doi:10.1111/pbi.13306
- Scafaro AP, Atwell BJ, Muylaert S, Reusel BV, Ruiz GA et al. (2018). A thermotolerant variant of Rubisco activase from a wild relative improves growth and seed yield in rice under heat stress. *Frontiers in Plant Science* 9:1663. doi:10.3389/fpls.2018.01663
- Scafaro AP, Bautsoens N, den Boer B, Van Rie J, Gallé A (2019). A conserved sequence from heat-adapted species improves Rubisco activase thermostability in wheat. *Plant Physiology* 181:43-54. doi:10.1104/pp.19.00425
- Scafaro AP, Gallé A, Van Rie J, Carmo-Silva E, Salvucci ME et al. (2016). Heat tolerance in a wild *Oryza* species is attributed to maintenance of Rubisco activation by a thermally stable Rubisco activase ortholog. *New Phytologist* 211:899-911. doi:10.1111/nph.13963

- Semedo JN, Rodrigues AP, Lidon FC, Pais IP, Marques I et al. (2021). Intrinsic non-stomatal resilience to drought of the photosynthetic apparatus in *Coffea* spp. is strengthened by elevated air [CO₂]. *Tree Physiology* 41:708-27. doi:10.1093/treephys/tpaa158
- Serrano-Romero EA, Cousins AB (2020). Cold acclimation of mesophyll conductance, bundle-sheath conductance and leakiness in *Miscanthus × giganteus*. *New Phytologist* 226:1594-606. doi:10.1111/nph.16503
- Sezgin A, Altuntaş C, Demiralay M, Cinemre S, Terzi R (2019). Exogenous alpha lipoic acid can stimulate photosystem II activity and the gene expressions of carbon fixation and chlorophyll metabolism enzymes in maize seedlings under drought. *Journal of Plant Physiology* 232:65-73. doi:10.1016/j.jplph.2018.11.026
- Simova-Stoilova L, Pecheva D, Kirova E (2020). Drought stress response in winter wheat varieties—changes in leaf proteins and proteolytic activities. *Acta Botanica Croatica* 79:121-30. doi:10.37427/botcro-2020-018
- Singh AD, Singh GP (2020). Biopigments and Rubisco expression under Heavy metal stress in *Spirulina platensis*. *Ecology Environment and Conservation* 26: S351-S356
- Shameer S, Baghalian K, Cheung CY, Ratcliffe RG, Sweetlove LJ (2018). Computational analysis of the productivity potential of CAM. *Nature Plants* 4(3):165-71. doi:10.1038/s41477-018-0112-2
- Shao Y, Li S, Gao L, Sun C, Hu J et al. (2021). Magnesium application promotes rubisco activation and contributes to high-temperature stress alleviation in wheat during the grain filling. *Frontiers in Plant Science* 12:888. doi:10.3389/fpls.2021.675582
- Shen ZJ, Qin YY, Luo MR, Li Z, Ma DN et al. (2021). Proteome analysis reveals a systematic response of cold-acclimated seedlings of an exotic mangrove plant *Sonneratia apetala* to chilling stress. *Journal of Proteomics* 248:104349. doi:10.1016/j.jprot.2021.104349
- Son JA, Narayanankutty DP, Roh KS (2014). Influence of exogenous application of glutathione on rubisco and rubisco activase in heavy metal-stressed tobacco plant grown in vitro. *Saudi Journal of Biological Sciences* 21:89-97. doi:10.1016/j.sjbs.2013.06.002
- Sun Q, Yamada T, Han Y, Takano T (2021). Influence of salt stress on C4 photosynthesis in *Miscanthus sinensis* Anderss. *Plant Biology* 23:44-56. doi:10.1111/plb.13192
- Suzuki Y, Makino A (2012). Availability of Rubisco small subunit up-regulates the transcript levels of large subunit for stoichiometric assembly of its holoenzyme in rice. *Plant Physiology* 160:533-40. doi:10.1104/pp.112.201459
- Taj Z, Challabathula D (2021). Protection of photosynthesis by halotolerant *Staphylococcus sciuri* ET101 in tomato (*Lycopersicon esculentum*) and rice (*Oryza sativa*) plants during salinity stress: Possible interplay between carboxylation and oxygenation in stress mitigation. *Frontiers in microbiology* 11:3232. doi:10.3389/fmicb.2020.547750
- Talaat NB (2021). Co-application of Melatonin and Salicylic Acid Counteracts Salt Stress-Induced Damage in Wheat (*Triticum aestivum* L.) Photosynthetic Machinery. *Journal of Soil Science and Plant Nutrition* 21:2893-906. doi:10.1007/s42729-021-00576-z
- Turk H, Erdal S, Dumlupinar R (2020). Carnitine-induced physio-biochemical and molecular alterations in maize seedlings in response to cold stress. *Archives of Agronomy and Soil Science* 66:925-41. doi:10.1080/03650340.2019.1647336
- Vitlin Gruber A, Feiz L (2018). Rubisco assembly in the chloroplast. *Frontiers in Molecular Biosciences* 5:24. doi:10.3389/fmolb.2018.00024
- Wang G, Kong F, Zhang S, Meng X, Wang Y et al. (2015). A tomato chloroplast-targeted DnaJ protein protects Rubisco activity under heat stress. *Journal of experimental botany* 66:3027-40. doi:10.1093/jxb/erv102
- Wang H, Zhao SC, Liu RL, Zhou W, Jin JY (2009). Changes of photosynthetic activities of maize (*Zea mays* L.) seedlings in response to cadmium stress. *Photosynthetica* 47:277-83. doi:10.1007/s11099-009-0043-2
- Wang H, Zhou Q, Mao P (2020). Ultrastructural and photosynthetic responses of pod walls in alfalfa to drought stress. *International Journal of Molecular Sciences* 21:4457. doi:10.3390/ijms21124457
- Wang X, Li Z, Liu B, Zhou H, Elmongy MS et al. (2020). Combined proteome and transcriptome analysis of heat-primed azalea reveals new insights into plant heat acclimation memory. *Frontiers in Plant Science* 11:1278. doi:10.3389/fpls.2020.01278
- Wijewardene I, Mishra N, Sun L, Smith J, Zhu X et al. (2020). Improving drought-, salinity-, and heat-tolerance in transgenic plants by co-overexpressing Arabidopsis vacuolar pyrophosphatase gene AVPI and Larrea Rubisco activase gene RCA. *Plant Science* 296:110499. doi:10.1016/j.plantsci.2020.110499
- Wijewardene I, Shen G, Zhang H (2021). Enhancing crop yield by using Rubisco activase to improve photosynthesis under elevated temperatures. *Stress Biology* 1:1-20. doi:10.1007/s44154-021-00002-5
- Wilson RH, Thieulin-Pardo G, Hartl FU, Hayer-Hartl M (2019). Improved recombinant expression and purification of functional plant Rubisco. *FEBS letters* 593:611-21. doi:10.1002/1873-3468.13352
- Xia XJ, Huang LF, Zhou YH, Mao WH, Shi K et al. (2009). Brassinosteroids promote photosynthesis and growth by enhancing activation of Rubisco and expression of photosynthetic genes in *Cucumis sativus*. *Planta* 230:1185-96. doi:10.1007/s00425-009-1016-1
- Xu H, Lu Y, Tong S (2018). Effects of arbuscular mycorrhizal fungi on photosynthesis and chlorophyll fluorescence of maize seedlings under salt stress. *Emirates Journal of Food and Agriculture* 1:199-204. doi:10.9755/ejfa.2018.v30.i3.1642
- Yang R, Xia X, Wang J, Zhu L, Wang J et al. (2020). Dose and time-dependent response of single and combined artificial contamination of sulfamethazine and copper on soil enzymatic activities. *Chemosphere* 250:126161. doi:10.1016/j.chemosphere.2020.126161

- Yang W, Wang F, Liu LN, Sui N (2020). Responses of membranes and the photosynthetic apparatus to salt stress in cyanobacteria. *Frontiers in Plant Science* 11:713. DOI: doi:10.3389/fpls.2020.00713
- Zahoor R, Dong H, Abid M, Zhao W, Wang Y et al. (2017). Potassium fertilizer improves drought stress alleviation potential in cotton by enhancing photosynthesis and carbohydrate metabolism. *Environmental and Experimental Botany* 137:73-83. doi:10.1016/j.envexpbot.2017.02.002
- Zhang H, Xu Z, Guo K, Huo Y, He G et al. (2020). Toxic effects of heavy metal Cd and Zn on chlorophyll, carotenoid metabolism and photosynthetic function in tobacco leaves revealed by physiological and proteomics analysis. *Ecotoxicology and Environmental Safety* 202:110856. doi:10.1016/j.ecoenv.2020.110856
- Zhang L, Yang J, Guo X, Wang A, Zhu J (2020). Overexpression of *SikRbcs2* gene promotes chilling tolerance of tomato by improving photosynthetic enzyme activity, reducing oxidative damage, and stabilizing cell membrane structure. *Food Science & Nutrition* 8:3479-91. doi:10.1002/fsn3.1631
- Zhao G, Xu H, Zhang P, Su X, Zhao H (2017). Effects of 2, 4-epibrassinolide on photosynthesis and Rubisco activase gene expression in *Triticum aestivum* L. seedlings under a combination of drought and heat stress. *Plant Growth Regulation* 81:377-84. doi:10.1007/s10725-016-0214-7
- Zhong X, Che X, Zhang Z, Li S, Li Q et al. (2019). Slower development of PSI activity limits photosynthesis during *Euonymus japonicus* leaf development. *Plant Physiology and Biochemistry* 136:13-21. doi:10.1016/j.plaphy.2019.01.004
- Zhou J, Wang J, Shi K, Xia XJ, Zhou YH et al. (2012). Hydrogen peroxide is involved in the cold acclimation-induced chilling tolerance of tomato plants. *Plant Physiology and Biochemistry* 60:141-9. doi:10.1016/j.plaphy.2012.07.010