



Impact of Urban Ecology and Related Stresses on Photosynthetic Activities of Plants

***Corresponding Author(s): Vijay Kumar Dalal**

Assistant Prof, Guest, Department of Botany, Dayalbagh Educational Institute, Agra, Uttar Pradesh 282005, India.
Tel: +91-562-280-1545, Fax: +91-11-562-280-1226;
Email: dalalvijay@yahoo.com

Abstract

Urban plants have an important role in the maintenance and sustainability of urban ecosystem. They provide CO₂ sequestration, air pollution reduction, cooling effect through shading and evapotranspiration, prevention of water runoff and soil erosion, and aesthetic values. Urban plants are exposed to various abiotic stresses such as drought, flooding, low/high temperature/light, dust, salinity, heavy metal toxicity, nutritional deficiency, pollution, proximity to concrete/metal structures, vandalism and root obstructions with underground structures. Plant's development, growth and yield are severely affected due to these stresses.

This review explores mechanistic and molecular aspects (especially photosynthesis) of environmental perturbations i.e. dust, drought, heat, high CO₂ and toxic gas SO₂ that Urban plants are frequently subjected to, in terms of photosynthetic electron transfer and ATP synthesis, dissociation of oxygen evolving complexes, cleavage of the reaction center protein D1/D2, and any resultant alterations to photochemical reactions, fixation of CO₂ as well as assimilation of carbohydrates. Current knowledge on physiological and biochemical changes in trees/plants at the cellular level that are associated with various stresses including osmolyte production, inhibited metabolism, light and dark reactions of photosynthesis, antioxidant responses and protein aggregation are discussed.

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Introduction

When subjected to stress, plants invest their energy into combating stress rather than growth [1]. The effect of stress depends on various factors such as plants ability to tolerate/resist it, duration of stress, time of stress (developmental phase of plant) and the intensity of stress. Plants show alarm phase initially when plants see shock in the form of stress and if the stress is too severe, permanent damage may occur. Later resistance/adaptation phase sets in when adaptation processes take place in plants and then exhaustion phase begins wherein adaptive capacity of plants is overwhelmed and permanent damage to plants occur.

Continuous increase in the global temperature will lead to frequent occurrences of drought worldwide. According the World Economic Forum, global land area and number of people facing extreme droughts could go from 3% during 1976-2005 to 7%-8% in recent future, i.e. approximately doubling. Plants have also shown adaptive responses in terms of reduced water loss, osmotic adjustment and tolerance to desiccation [2].

Growth and development of plants is severely affected by these stresses. As a result the yield of urban plants is drastically reduced. One of the first responses of the plants to stress is to stop the growth so as to conserve the energy. Second and equally fast response of plants is closure of stomata. Due to



stomatal closure, the CO₂ cannot diffuse into the leaf mesophyll and thus not fixed. Concomitantly there is over-reduction of photosynthetic electron transport and leakage of electrons at various places to oxygen/nitrogen and other species to form Reactive Oxygen/Nitrogen Species. Thus the light become excess which results in the irreversible photo inhibition of reaction centers, therefore triggering the adaptation mechanisms in plants. Thus generally, under stress conditions, plants need to protect themselves from light instead of striving to gain light.

Photosystem in plants is comprised of PSI and PSII complexes and the connecting Cyt b₆/f. PSII complex is composed of around 25 subunits. PSII reaction center consists of two hydrophobic core proteins D1 and D2 which are conserved in higher plants. Core is surrounded by minor antenna complexes CP43 and CP47. LHCII trimers of major antenna complexes, composed of Lhcb1, Lhcb2 and Lhcb3 further surround these core complexes [3]. Antennae absorb the energy and transfer it to the reaction centers that is utilized to break the water molecule and remove the electron from the reaction center Chl a molecule. On the luminal side, PSII is surrounded by oxygen evolving complexes PSB16, PSB23 and PSB33 as well as other complexes PSBR, PSBK, PSBN and PSBS as shown in Fig 1.

The cyt b₆f complex is the best characterized and simplest of the multisubunit complexes that catalyses the light reaction of photosynthesis. It mediates the transfer of electrons from plastoquinone to plastocyanin, and is involved in noncyclic electron

flow from PSII to PSI [4] as well as in cyclic electron flow around PSI [5].

PSI complex consists of at least 13 different polypeptides in higher plants [6]. It uses light energy to catalyze the photo oxidation of plastocyanin, a copper protein present in the lumen of thylakoid membrane and the photo reduction of ferredoxin (Fd), an [2Fe-2S] protein present in chloroplast stroma. As with PSII, all PSI proteins are also believed to be present as one copy per P700 Reaction Center. The co-factors of PSI are bound to the PsaA, PsaB, and PsaC proteins [6]. The photochemical reaction that generates redox potential to oxidize plastocyanin and reduce Fd occurs in PSI Reaction Center.

Discussion

Urban plants, also known urban vegetation, urban green infrastructure and urban green etc. that include urban forests, parks, allotments, street trees, and green roofs [7], play an important role in providing Urban ecosystem services (UES) [8]. Urban plants provide CO₂ sequestration, air pollution reduction, cooling effect through shading and evapo-transpiration, prevention of soil water runoff and erosion, and aesthetic values. Urban plants, compared to plants present in rural or scarce-human population areas, are subjected more to stresses like drought, temperature, nutrition, dust and pollution. The effect of these stresses on photosynthetic machinery are depicted in Figure 1 and discussed in detail below:

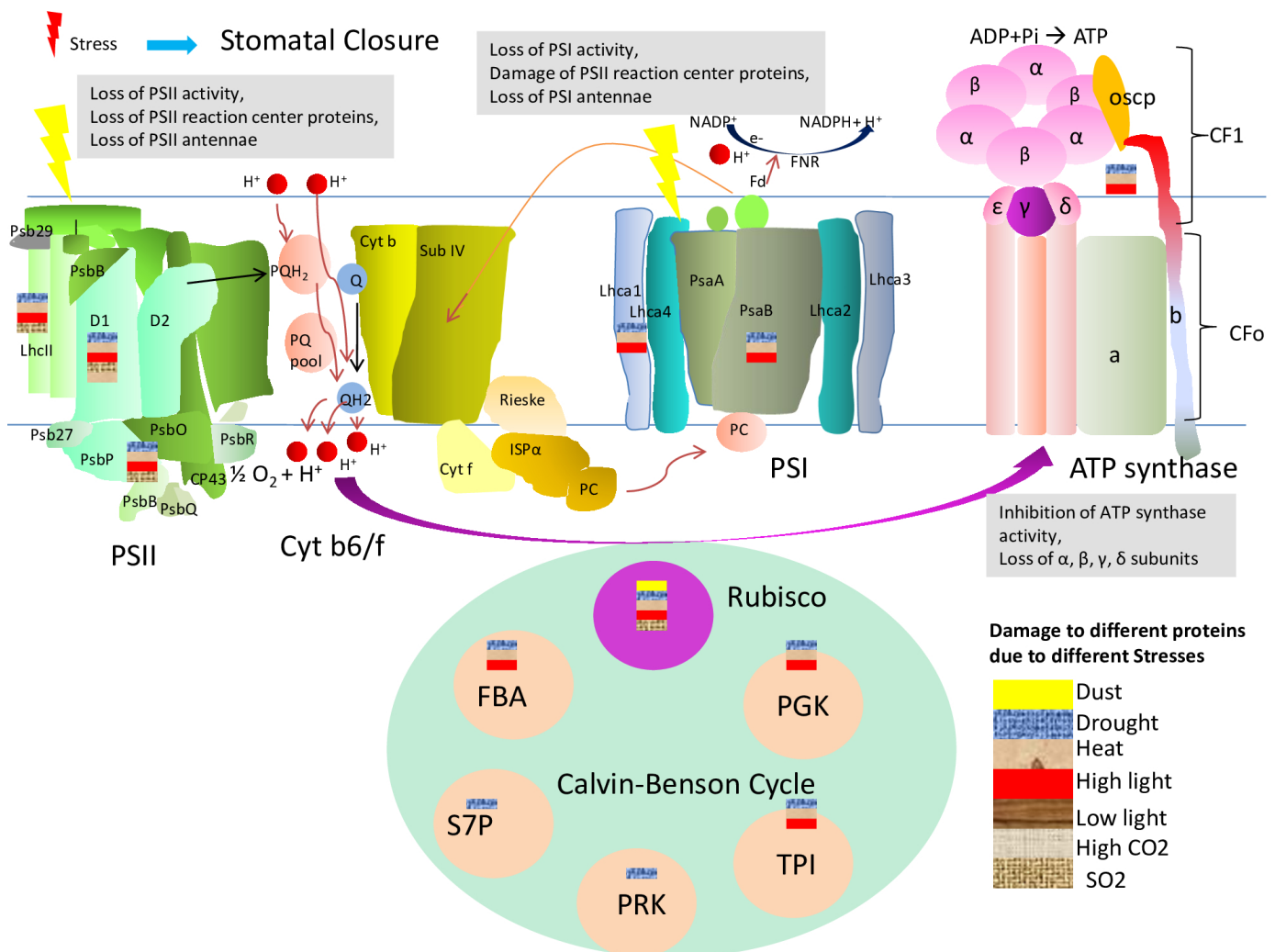


Figure 1: Schematic representation of photosynthetic electron transport chain and Calvin-Benson cycle, as affected by various stresses. Rubisco-Ribulose 1,5-bisphosphate Carboxylase/ Oxygenase, PGK: Phosphoglycerate Kinase; TPI: Triose Phosphate Isomerase; PRK: Phospho Ribulokinase; S7P: Sedoheptulose, 7 bisphatase; FBA: Fructose 1,6-Bisphosphate Aldolase.

Dust

Dust is one of the main phenomenon in some cities in developing countries to which urban plants are subjected. There are scarce investigations on evaluation of the effect of dust on plants. Compared to developed countries where the air is laden with comparatively lesser dust due to cleanliness, better infrastructure and environmental factors, in developing countries the problem of dust in urban air is enormous. Therefore many investigations in the recent years have focused on the effect of dust on plants [9–11]. Due to deposition of dust particles on the leaf surface, photosynthesis is drastically impaired, stomata are blocked interfering with gas exchange.

Solid particles, coming out of vehicular exhaust and dust, generated due to plying of vehicles, are the main sources of deposition on leaf surfaces. Plants are one of the main reservoirs that collect the dust from atmosphere. Dust, collected on leaf surfaces over a long period of time, can act as an indicator as well as scavenger of air pollution. Climatic factors such as rainfall, temperature, wind speed and relative humidity influence the quality and quantity of dust stress on plants [12]. Plants have high endurance from dust. Dust particles, deposited on the upper surface of plants, affect the light quantity and quality reaching the leaf interior, e.g. less light penetrates the leaves and some wavelengths are especially blocked and also raise the leaf temperature [13]. Deposited dust can alter the optical properties of leaf e.g. surface reflectance in the visible and near-infrared range [14]. Dust particles on the leaf surface may also lead to the blocking of stomata which interferes with gas exchange [15]. The reduction of leaf stomatal conductance influences plant biomass formation and yield. Dust can also indirectly affect plants through altering the chemical characteristics of soil [16].

In a study conducted on the plane trees (*Platanus orientalis*) in Mashhad (Iran), leaves mostly accumulated lead although several toxic elements were enriched in air and soil [17]. Moreover, stomata were not occluded and the cuticle was thinner. However other anatomical properties were unaffected. In a study performed in Northwest China on cotton trees, dust decreased the stomatal conductance and leaf temperature [18]. Trichomes develop on leaf surfaces in some plants to prevent the entry of dust particles in leaf stomata. In *Mimusops elengi*, it was observed that the trichomes were completely absent in the non-polluted region but in the polluted region, unicellular trichomes developed on the abaxial leaf surface. Additionally, the development of trichomes was maximal near stomata. Trichomes help in absorption of Particulate Matter on surface of leaves [19] and also provide plant's protection from various stresses such as UV light [20]. Most of the plants are tolerant upto a dustload of $300 \mu\text{g m}^{-3}$; on the other hand, at $1500 \mu\text{g m}^{-3}$, many plants show sensitivity e.g. *Morus alba* and *Melia azedarach* showed intermediate-tolerance, however *Celtis caucasica* and *Fraxinus rotundifolia* showed dust sensitivity [21].

Plant's sensitivity to pollutants in terms of greening can be determined by Air Pollution Tolerance Index (APTI) which is based on a combination of chlorophyll (Chl), relative water content (RWC), ascorbic acid (AsA), and leaf pH. In a study in Iran, the dust capturing efficiency and APTI values were found to be in the order of *Morus alba* L., *Celtis caucasica* Willd., *Fraxinus rotundifolia* Mill., and *Melia azedarach* L. In terms of APTI values *Mangifera indica*, *Azadirachta indica* and *Ficus religiosa* were found to be most tolerant species [22, 23] while *Ficus bengalensis* and *Alstonia scholaris* were intermediately tolerant

[23] and *Artocarpus sp.* and *Eucalyptus sp.* least tolerant [22]. Although many studies have been carried out for dust response, there is hardly any study regarding mechanistic, functional and molecular changes e.g. transcription, translation, enzyme activities and post-translational modification of proteins etc., in leaves in response to dust which provides great opportunities to work in this area.

Sulphate, nitrates and metal ions are most common stress causing pollutants that are present in dust [24]. Being soluble in aqueous solution these ions form acidic solutions and diffuse into the mesophyll of leaves, causing stress to them [25,26]. Photosynthesis was drastically impaired when leaf surfaces were dusted in a study conducted by Thomson et al. [27]. Nanos et al. [28] reported the modulation of physiological parameters in olive subjected to dust. Highly alkaline cement dust led to the clogging of stomata, destruction of Chl, obstruction of incident light and reduced leaf area of affected plants [29]. Ash from steel/coal industries and dust from cement kilns reduced photosynthesis [30] e.g. by 90% in apple trees [31] and by 73% in green beans [32] respectively. As with other stresses, dust can also make plants more susceptible to insect attack [33].

Drought

Drought which is a combination of water deficiency, low humidity and high temperature, adversely affects plant and crop production by reducing leaf size, stem and root proliferation, disturbing plant water and nutrient relations.

Drought is the major stress in urban trees [34]. Trees among the pavements along roadside, decrease photosynthesis in urban areas during drought [35]. Therefore studies should be carried out to find drought tolerance, on a variety of plants or different genotypes of a plant and suitable varieties/genotypes should be planted in drought prone cities. For example, a study on *Fraxinus* (contains ca 65 genotypes) in UK found many genotypes such as *F. excelsior* 'Aurea Pendula' drought tolerant and *F. americana* L., *F. americana* 'Autumn Purple' and *F. velutina* Torr. as drought sensitive [36].

Drought adversely affects plant and crop production by reducing leaf size, stem extension and root proliferation, disturbing plant water and nutrient relations, and inhibiting water-use efficiency.

Drought affects the growth and development of plants if imparted at an early stage. When provided at later stages, the first response of plants to drought is closure of stomata. Physiological and biochemical changes at the cellular level that are associated with drought stress include water loss from cells and resultant high osmotic potential, turgor loss, inhibited metabolism, photosynthesis, cuticle permeability, and altered membrane fluidity and composition, solute and ion concentrations, protein-protein and protein-lipid interactions, antioxidant responses, protein aggregation and reduction in enzyme catalyzed reactions [37–39] and to cell death if drought persists [40]. Osmolytes accumulate in plants to counteract the loss in protein conformation and activity [41]. Some common osmolytes viz. carbohydrates (trehalose, sucrose, glycerol, myoinositol, and sorbitol), methylamines [trimethylamine N-oxide (TMAO), betaine, and glycerophosphoryl-cholin], amino acids and their derivatives (proline, serine, taurine, glycine, arginine, and Gamma amino butyric acid (GABA)) accumulate in plants to counteract the loss in protein conformation and activity [41]. Photosynthesis [42] as well as chlorophyll biosynthesis [43] is

decreased under drought (Figure 1).

Stomata close as soon as plants perceive drought as a result of endogenous ABA synthesis. In *Arabidopsis*, ABA production is triggered by a rapid upregulation of 9-cisepoxycarotenoid dioxygenase 3 (NCED3) gene expression by drought stress in a vascular tissue-specific manner [44]. Photosynthesis may decline due to restricted diffusion of CO₂ into mesophyll and in turn to rubisco carboxylation-site and can be recovered fully if CO₂ concentration is increased [39]. Mesophyll conductance may be due to reduced levels of aquaporins that carry CO₂ to the site of carboxylation in rubisco [45]. However some studies stressed on the biochemical and physiological limitations in photosynthesis process i.e. reduced RuBP regeneration due to low ATP availability/generation [37, 46] or from damage in PSII oxygen-evolving complexes [47].

Light reaction: Electron transport is reported to be decreased in mature rice plants due to water stress [48]. D1 protein of PSII reaction center was decreased in apple, wheat and two cultivars of *Vigna radiata* [49–51]. Chlorophyll b rich, light-harvesting complexes (LHC-II/I) are highly abundant proteins in thylakoid membranes and contain approximately half of chloroplastic chlorophyll [52]. LHC-II were reduced in rice seedling in response to water-stress [42, 43]. Furthermore, water-stress damaged the reaction centers of PSII and PSI and oxygen-evolving complexes of PSII [42,47,53–55]. Closure of stomata (decreased stomatal conductance) under water-limitation leads to decreased availability of CO₂ for reduction, resulting into over-reduction of photosynthetic electron transport chain and generation of ROS (O₂⁻) at PS I [56, 57]. Under such conditions, singlet oxygen (¹O₂) formation from excited triplet state of Chl also takes place that damages the thylakoid membrane [58]. Steady-state levels of the core antenna polypeptides of PS II (CP47 and CP43) that connect LHC II and Reaction Centre PS II, decreased in drought resistant durum wheat cultivar Barakatli 95, and remained almost same in drought sensitive Garagylchyg 2 [59]. Similar results were obtained previously for other plants [47, 60, 61]. Yardonov et al [62] reported the damage to PSII reaction centers as a result of drought. As a result of damage to the PSII capacity or due to damage to the thylakoid membranes or subunits of ATP synthase, pH gradient is not sufficiently maintained across the chloroplast inner membrane, in turn ATP synthesizing capacity of chloroplasts is compromised. As a result of drought, γ -subunit of ATP synthase in tomato [63] and α and β -subunits of ATP synthase were reduced in soyabean and *Vitis* [64,65].

Dark reaction: Many enzymes of dark reaction of photosynthesis e.g. large and small subunits of rubisco, sedoheptulose-1,7-bisphosphatase, Fructose 1, 6-bisphosphate aldolase, Phosphoglycerate kinase and Triose phosphate isomerase are reduced in abundance as well as activity under drought [64,66,67]. Phosphoglycerate kinase and Triose phosphate isomerase were also reported to be reduced in maize [70] and tomato [63] cultivars upon water stress treatment. Similarly protein abundance of sedoheptulose 1, 7 bisphosphatase and carbonic anhydrase have also been reported to be increased in *Poa pratensis* [68] and *Malus domestica* [69]. The active site of rubisco is inhibited by various phosphate inhibitors, their removal is facilitated by rubiscoactivase, an enzyme that requires ATP to carry out this reaction [71]. Abundance of rubiscoactivase was also found to be decreased in drought [64, 67, 72]. Fragmentation of rubisco have also been widely reported [73,

74] e.g. in the leaf proteome of wheat [75] and in susceptible wheat lines [76].

Heat

Heat stress is also an important factor regulating growth and development in Urban trees. Heat stress usually comes in combination with drought in tropical countries. However, it may be a *per se* stress in areas where water resources are available.

Air in Urban areas has high temperature (known as Urban heat island effect), high pollution, low humidity and less speed [77, 78]. The climate which is already bad in urban areas is expected to be worse in future [79, 80] as around 68% of world population is expected to live in cities by 2050 (www.un.org). It is normally accepted that the vegetation improves the Urban air/climate by lowering air pollution and reducing the heat island effect [77,78,81]. Urban greens therefore remain the most important strategy to improve quality of life in Urban areas.

The Urban Heat Island effect happens due to i) Absorption of sunlight by air pollution and re-emission in long wavelength Infra Red heat radiations, ii) trapping of short radiation by multiple reflections among buildings and streets, and low albedo surfaces, iii) Obstruction of re-emission loss to atmosphere, of long wavelength radiations by building and other structures, iv) Contribution from anthropogenic heat, v) Increased heat storage by large surface areas in cities and quality of material used in buildings, vi) reduced evaporative areas and trees compared to rural areas, vii) energy conversion into sensible heat is more, conversely latent heat is less and viii) reduction in the wind speed and its obstruction by buildings cause lesser distribution and loss of heat to surroundings [78,82].

The Urban Heat Island effect can be mitigated with increasing trees at pavements, along roadsides and creating more parks or urban forests. The average return per dollar invested on trees was found to be \$1.37 to \$3.09 in five US cities in a study conducted by McPherson et al [83]. Trees save an enormous amount of energy through their cooling effect. Evapotranspiration from a single tree is equivalent to more than 10 air-conditioning units i.e. equal to 20–30 kW power [80, 84]. Urban forests or parks create a cooling effect known as Park Cool Island (PCI). A park of a bigger area or forest can have even higher cooling effect. A study in Göteborg (Germany) showed that a park of 156 hectares could decrease (maximally) the air temperature by 5.9 °C in summer season [85]. Even a very small park of 0.15 hectare area could decrease the average daily temperature by 1.5 °C in a study at Tel Aviv (Israel). The cooling effect reached upto 3 °C at noon [86].

Heat Stress (HS) is also an important factor regulating growth and development of trees in cities. Urban heat island effect and its consequences in plants are studied by many [80,82,87]. Thermal stress causes morphological changes e.g. cessation of plant growth, chlorosis, necrosis, wilting, decrease in photosynthetic capacity, and in turn reduced yield [88–93]. Physiological and biochemical changes in trees/plants at the cellular level that are associated with heat stress include osmolyte production, inhibited metabolism, altered light and dark reactions of photosynthesis, and antioxidant responses, loss in enzyme activities, protein aggregation [92]. Photosynthetic processes perturbed at molecular level are photosynthetic electron transfer and ATP synthesis [92,94,95], dissociation of oxygen evolving complexes and inhibition of electron transport from OEC to donor side of PSII [88,95–97] and cleavage of the reaction

center protein D1. Alterations to photochemical reactions that is a result of decreased variable to maximum fluorescence of PSII [88, 98], fixation of CO₂ as well as assimilation, transport and interconversion of carbohydrates [89,98] is also observed. Although rubisco is highly resistant to heat stress, ribulose-1,5-bisphosphate (RuBP) regeneration and rubiscoactivase are sensitive [99–101], as is the case with drought. Contrarily reduced amount of rubisco might also be responsible for heat sensitivity [98]. Similarly to drought, HS also leads to destacking and disruption of thylakoid membranes [88,102]. In pea plants, heat stress was found to reduce the protein import into the chloroplast [103]. ROS are among the most important stress indicators that are produced as a result of HS as well as other stresses and cause damage to membranes and organelles [104, 105].

High temperatures of 35–45 °C resulted in the induction of cyclic electrons transport and leakage of electrons from thylakoid membrane [89]. However under mild heat treatment, epoxidised xanthophylls could protect the thylakoid in potato [106].

In heat and drought prone cities, the plants should be chosen based on their cooling potential which is dependent on area, density as well as evapotranspiration of leaves, to mitigate the effect of stress. In a study conducted by Gillner et al. [79], *Corylus colurna* and *Tilia cordata* 'Greenspire' trees were found to possess high and the *Ulmus × hollandica* 'Lobel' low cooling potential.

High / low irradiance and chilling

High/low irradiance and chilling stress are other limiting factor for Urban plants that inhibit their photosynthetic activities and other metabolic functions [107,108]. Chilling stress disrupts photosynthetic components including stomatal conductance, transpiration rate, carbon reduction cycle, and thylakoid electron transport [109]. Low light causes decrease in photosynthesis, carboxylation capacity, reduced electron transport, and reduced carbon and nitrogen metabolism [110,111]. Under high irradiance (1000 μmol m⁻²s⁻²) also, degradation of D1 protein has been commonly reported e.g. in barley leaves [108]. Under this intense light *Dunaliella salina* also showed photodamage [112]. Low temperature may lead to stomatal closure, in turn, reducing the photosynthesis via CO₂ depletion at rubisco carboxylation site [107].

High CO₂

During all of the cycles between ice ages and warm periods over the past million years, atmospheric carbon dioxide never increased beyond 300 ppm, however the current concentration is 410 ppm. CO₂ is increasing at a regular pace due to natural causes and anthropogenic activities. It is predicted to reach upto 550 ppm by the middle of the 21st century. Due to vehicular exhaust, wood and coal burning and industrial processes, CO₂ concentration has increased gradually in urban areas. High CO₂ in general causes an increase in photosynthesis. In several C₃ plants i.e. brassica, wheat, rice, soybean etc., when grown in a FACE facility, elevated CO₂ increased photosynthesis rate [113, 114], leaf area index and yield [114–116]. In some plants, the PS I, PSII, whole chain photosynthetic electron transport rates, increased in eCO₂ [114]. High starch accumulation in leaves as a result of eCO₂ was observed in many plants [117–119]. The specific responses of each crop may be different [115,120] and many differences are even observed among the different varieties/cultivars of the same species [119,120].

Usually increased photosynthesis is sustained over long

periods i.e. there is no decrease in photosynthesis and yield [114,118,121,122]. Maintenance of photosynthesis with no decrease in yield over long periods have been observed in fast growing trees [121], and in soybean and poplar [116, 118, 123]. In deciduous forest trees photosynthesis increased consistently for 8 consecutive years in eCO₂ [122]. Changes in protein expression is one of the responses to elevated CO₂.

However contrasting reports of decrease of photosynthesis and yield to previous levels, after a few generations, have also been reported [117,119,124] and is equally important. This process is called photosynthetic acclimation [116,124]. Photosynthetic acclimation happens due to decrease in abundance, carboxylation capacity (V_{max})/efficiency, activation state [117,119] and total activity of rubisco. A lesser than normal concentration of CO₂ at rubisco active site as a result of lower stomatal and mesophyll conductance may also lead to decreased CO₂ fixation [125]. The stomatal conductance (g_s) is generally reduced in elevated CO₂ and is also subject to feedback regulation [126]. Reduced g_s in response to elevated CO₂ may be due to altered stomatal density [127] and stomatal development by down-regulation of genes [127–129]. The mitochondrial respiration is usually increased in eCO₂ and is attributed to increased mitochondria and abundance of mitochondrial proteins [118,130]. Sugar accumulation in an elevated CO₂ environment is known to cause modulation of transcription of chloroplast proteins [131] leading to the speculation for acclimation.

Nitrogen supply and the form of Nitrogen available in soil also influence the growth and yield of plants in presence of eCO₂. Carbon and nitrogen assimilation are co-regulated. Under nitrogen (N) limiting conditions, elevated CO₂ failed to increase biomass and economic yield of *Arabidopsis*, wheat and rice plants [132–134].

Sulphur dioxide

SO₂ is an important gas that is produced as a result of heating system and burning of fuel in greenhouses in winter season in colder countries. SO₂ can enter the plant tissues either from soil via the roots or from the atmosphere via the leaves. Photosynthesis is one of the first processes affected by SO₂ [135]. SO₂ response on physiological activities is mediated through the stomatal conductance [136]. At low concentrations, SO₂ is oxidized and used to synthesize proteins [137]. Therefore plants had shown initial increase in photosynthesis and increase in respiration in response to low SO₂ [138]. However, at high concentrations, SO₂ cause leaf injury, disrupts the functioning of thylakoid membranes and electron transport chain [139,140], reduce photosynthetic activity, destroy pigments, cause stomatal damage, interfere with membrane permeability, and reduce plant growth and yield [141]. Interestingly, compared to youngest and oldest leaves, mature leaves are more susceptible to SO₂ injury [142]. In *Glycine max* photosynthesis decreased with increasing concentrations of SO₂ [143]. In *Vicia faba*, photosynthesis reduced in proportion to the SO₂ concentration. Stomatal resistance was regulated through the feedback loop between photosynthesis and internal CO₂ [144]. In the succulent plant *Augea capensis*, photosynthesis was inhibited only when SO₂ fumigation (with 1.3 and 0.6 ppm) was performed in the dark [145]. Here carboxylation efficiency inhibited by 38% and CO₂ saturated rates of photosynthesis by 62%. However, this inhibition was fully reversible, indicating no permanent metabolic damage [145]. Elevated CO₂ was reported to reduce the inhibitory effect of SO₂ on photosynthesis by reducing SO₂ injury and SO₂ absorption via inducing stomatal closure [143]. Upon

treatment with different gases including SO₂, strawberry plants showed closure of stomata, reduced photosynthesis and accumulation of ROS (singlet oxygen and hydrogen peroxide) [146].

Conclusion and future perspectives

The green spaces in urban environments especially mega cities have a tremendous importance in terms of cleaning the air, reducing the temperature, mitigating pollutant effects, decreasing localized CO₂ concentrations as well as providing aesthetic values. Therefore preserving such areas should be of utmost importance to the public as well as policymakers. Although, exulted cost of the land discourages the allocation for green spaces, the future scenario of climate change make it imperative to reconsider green space allocation in cities. Second equally important aspect is to plants trees that are able to perform better under urban environments in terms of stress tolerance and are able to provide maximum above-mentioned benefits.

The plants in urban environments are subjected to various stresses. Photosynthesis is a highly sensitive process and is affected by most of these stresses. To make the photosynthesis process active in plants, chlorophyll, carotenoids and xanthophyll pigments need to be synthesized, and assembled with proteins to make functional electron transport chain complexes. The plants have to deal with lesser or excess light and altered diurnal rhythms through manipulation of leaf orientation, reflectance, xanthophyll cycle changes (increased non photochemical quenching) and photoinhibition. The stomata need to be tightly adjusted in response to the external environment and the CO₂ after being diffused or actively transported to rubisco is fixed. The fixed CO₂ has to be removed from the site of production and transported to sink in temporal and spatial separation. All these processes may be affected by various stresses. Plants respond to stresses by adjustments of metabolic processes e.g. osmolytes accumulation [147,148], membrane permeability, antioxidant synthesis and chaperon synthesis etc. [37,39,116]. Therefore understanding these processes at molecular level and in terms of responsible QTLs and adopting breeding strategies to transfer the respective QTLs to the novel varieties and transgenic approaches may help in application of the generated knowledge.

References

1. Claeys H, Inzé D. The agony of choice: How plants balance growth and survival under water-limiting conditions. *Plant Physiol.* 2013; 62(4): 1768-79.
2. Munia HA, Guillaume JHA, Wada Y, Veldkamp T, Virkki V, et al. Future transboundary water stress and its drivers under climate change: A global study. *Earth's Futur.* 2020; e2019EF001321.
3. Albanese P, Nield J, Tabares JAM, Chiodoni A, Manfredi M, et al. Isolation of novel PSII-LHCII megacomplexes from pea plants characterized by a combination of proteomics and electron microscopy. *Photosynth Res.* 2016; 130(1): 19-31.
4. Hurt E, Hauska G. A cytochrome f/b6 complex of five polypeptides with plastoquinol-plastocyanin-oxidoreductase activity from spinach chloroplasts. *Eur J Biochem.* 1981; 17(3): 591-9.
5. Lam E, Malkin R. Reconstruction of the chloroplast noncyclic electron transport pathways from water to NADP with three integral protein complexes. *Proc Natl Acad Sci U S A.* 1982; 79(18): 5494-8.
6. Caspy I, Nelson N. Structure of the plant photosystem I. *Biochem. Soc. Trans.* 2018; 46(2): 285-94.
7. Chen X, Wang L, Tong L, Sun S, Yue X, et al. Mode selection of China's urban heating and its potential for reducing energy consumption and CO₂ emission. *Energy Policy.* 2014; 67: 756-64.
8. Stone B. Urban heat and air pollution: An emerging role for planners in the climate change debate. *J Am Plan Assoc.* 2005; 71(1): 13-25.
9. Sjöman H, Gunnarsson A, Pauleit S, Bothmer R. Selection approach of urban trees for inner-city environments: Learning from nature. *Arboricul Urban For.* 2012; 38(5): 194.
10. Terzaghi E, Wild E, Zacchello G, Cerabolini BEL, Jones KC, et al. Forest Filter Effect: Role of leaves in capturing/releasing air particulate matter and its associated PAHs. *Atmos Environ.* 2013; 74: 378-84.
11. Li Y, Wang S, Chen Q. Potential of thirteen urban greening plants to capture particulate matter on leaf surfaces across three levels of ambient atmospheric pollution. *Int J Environ Res Public Health.* 2019; 16(3): 402.
12. Siqueira-Silva AI, Pereira EG, Modolo LV, Paiva EAS. Leaf structural traits of tropical woody species resistant to cement dust. *Environ Sci Pollut Res.* 2016; 23(16): 16104-14.
13. Hirano T, Kiyota M, Aiga I. Physical effects of dust on leaf physiology of cucumber and kidney bean plants. *Environ Pollut.* 1995; 89(3): 255-61.
14. Prajapati SK, Tripathi BD. Seasonal variation of leaf dust accumulation and pigment content in plant species exposed to urban particulates pollution. *J Environ Qual.* 2008; 37(3): 865-70.
15. Taheri Analogeh A, Azimzadeh HR, Mosleh Arani A, Sodaiezhadeh H. Investigating and comparing short period impact of dust on physiological characteristics of three species of *Pinus eldarica*, *Cupressus sempervirens*, and *Ligustrum ovalifolium*. *Arab J Geosci.* 2016; 9(4): 244.
16. Maletsika PA, Nanos GD, Stavroulakis GG. Peach leaf responses to soil and cement dust pollution. *Environ Sci Pollut Res.* 2015; 22(20): 15952-60.
17. Pourkhabbaz A, Rastin N, Olbrich A, Langenfeld-Heyser R, Andrea Polle A. Influence of environmental pollution on leaf properties of urban plane trees, *Platanus orientalis* L. *Bull Environ Contam Toxicol.* 2010; 85(3): 251-5.
18. Zia-Khan S, Spreer W, Pengnian Y, Zhao X, Othmanli H et al. Effect of dust deposition on stomatal conductance and leaf temperature of cotton in Northwest China. *Water (Switzerland).* 2015; 7(1): 116-31.
19. Zhang R, Zheng G, Li P. Effects of foliar trichomes on the accumulation of atmospheric particulates in *Tillandsia brachycaulos*. *Open Life Sci.* 2019; 14(1): 580-7.
20. Karabourniotis G, Liakopoulos G, Nikolopoulos D, Bresta P. Protective and defensive roles of non-glandular trichomes against multiple stresses: structure–function coordination. *J. For. Res.* 2020; 31(1): 1-2
21. Javanmard Z, Kouchaksaraei MT, Bahrami H, et al. Dust collection potential and air pollution tolerance indices in some young plant species in arid regions of Iran. *iForest.* 2019; 12(6): 558.
22. Kuddus M, Kumari R, Ramteke PW. Studies on air pollution tolerance of selected plants in Allahabad city, India. *J Environ Res Manag.* 2011; 2(3): 042-6.
23. Roy A, Bhattacharya T, Kumari M. Air pollution tolerance, metal accumulation and dust capturing capacity of common tropical trees in commercial and industrial sites. *Sci Total Environ.* 2020; 722: 137622.

24. Sheppard LJ. Causal mechanisms by which sulphate, nitrate and acidity influence frost hardiness in red spruce: review and hypothesis. *New Phytol.* 1994; 127(1): 69-82.
25. Grantz DA, Garner JHB, Johnson DW. Ecological effects of particulate matter. *Environ. Int.* 2003; 29(2-3): 213-39.
26. Buchner P, Takahashi H, Hawkesford MJ. Plant sulphate transporters: Co-ordination of uptake, intracellular and long-distance transport. *J Exp Bot.* 2004; 55(404): 1765-73.
27. Thompson JR, Mueller PW, Flückiger W, Rutter AJ. The effect of dust on photosynthesis and its significance for roadside plants. *Environ Pollution Ser A, Ecol Biol.* 1984; 34(2): 171-90.
28. Nanos GD, Ilias IF. Effects of inert dust on olive (*Olea europaea* L.) leaf physiological parameters. *Environ Sci Pollut Res.* 2007; 14(3): 212-4.
29. Shukla J, Pandey V, Singh SN, M Yunus, N Singh, et al. Effect of cement dust on the growth and yield of *Brassica campestris* L. *Environ Pollut.* 1990; 66(1): 81-8
30. Murugesan M, Sivakumar A, Jayanthi N, Manonmani K. Effect of cement dust pollution on physiological and biochemical activities of certain plants. *Pollut Res.* 2004.
31. Cook RJ, Barron JC, Papendick RI, Williams GJ. Impact on agriculture of the Mount St. Helens eruptions. *Science.* 1981; 211(4477): 16-22.
32. Darley EF. Studies on the effect of cement-kiln dust on vegetation. *J Air Pollut Control Assoc.* 1966; 16(3): 145-50.
33. Kameswaran S, Gunavathi Y, Krishna PG. Dust pollution and its influence on vegetation-a critical analysis. *Res J Life Sci Bioinfo Pharm Chem Sci.* 2019; 5(1): 341-63.
34. Khalaim O, Zabarna O, Kazantsev T, Panas I, Polishchuk O. Urban green infrastructure inventory as a key prerequisite to sustainable cities in Ukraine under extreme heat events. *Sustain.* 2021; 13(5): 2470.
35. Wang XM, Wang XK, Su YB, Zhang HX. Land pavement depresses photosynthesis in urban trees especially under drought stress. *Sci Total Environ.* 2019; 653: 120-30.
36. Percival GC, Keary IP, AL-Habsi S. An assessment of the drought tolerance of *Fraxinus* genotypes for urban landscape plantings. *Urban Forest Urban Green.* 2006; 5(1): 17-27.
37. Lawlor DW, Tezara W. Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: A critical evaluation of mechanisms and integration of processes. *Ann. Bot.* 2009; 103(4): 561-79
38. Osakabe Y, Osakabe K, Shinozaki K, Tran LSP. Response of plants to water stress. *Front Plant Sci.* 2014; 5: 86.
39. Pinheiro C, Chaves MM. Photosynthesis and drought: Can we make metabolic connections from available data? *J. Exp. Bot.* 2011; 62(3): 869-82
40. Kaur G, Asthir B. Molecular responses to drought stress in plants. *Biol. Plant.* 2017; 61(2): 201-9.
41. Singh LR, Poddar NK, Dar TA, Rahman S, Kumar R, et al. Forty years of research on osmolyte-induced protein folding and stability. *J Iran Chem Soc.* 2011; 8(1): 1-23
42. Dalal VK, Tripathy BC. Water-stress induced downsizing of light-harvesting antenna complex protects developing rice seedlings from photo-oxidative damage. *Sci Rep.* 2018; 8(1): 1-6
43. Dalal VK, Tripathy BC. Modulation of chlorophyll biosynthesis by water stress in rice seedlings during chloroplast biogenesis. *Plant, Cell Environ.* 2012; 35(9): 1685-703.
44. Behnam B, Iuchi S, Fujita M, Fujita Y, Takasaki H, et al. Characterization of the promoter region of an arabidopsis gene for 9-cis-epoxycarotenoid dioxygenase involved in dehydration-inducible transcription. *DNA Res.* 2013; 20(4): 315-24.
45. Miyazawa SI, Yoshimura S, Shinzaki Y, Maeshima M, Miyake C. Deactivation of aquaporins decreases internal conductance to CO₂ diffusion in tobacco leaves grown under long-term drought. *Funct Plant Biol.* 2008; 35(7): 553-64.
46. Tezara W, Mitchell VJ, Driscoll SD, Lawlor DW. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature.* 1999; 401(6756): 914-7.
47. Giardi MT, Cona A, Geiken B, J Masojádek, AK Mattoo. Long-term drought stress induces structural and functional reorganization of photosystem II. *Planta.* 1996; 199(1): 118-25.
48. Zhou Y, Lam HM, Zhang J. Inhibition of photosynthesis and energy dissipation induced by water and high light stresses in rice. *J Exp Bot.* 2007; 58(5): 1207-17.
49. Liu WJ, Yuan S, Zhang NH, T Lei, HG Duan, et al. Effect of water stress on photosystem 2 in two wheat cultivars. *Biol Plant.* 2006; 50(4): 597-602.
50. Wang Z, Li G, Sun H, Ma L, Guo Y, et al. Effects of drought stress on photosynthesis and photosynthetic electron transport chain in young apple tree leaves. *Biol Open.* 2018; 7(11): bio035279.
51. Batra NG, Sharma V, Kumari N. (2014) Drought-induced changes in chlorophyll fluorescence, photosynthetic pigments, and thylakoid membrane proteins of *Vigna radiata*. *J Plant Interact.* 2014; 9(1): 712-21.
52. Ruban AV. Light harvesting control in plants. *FEBS Lett.* 2018; 592(18): 3030-9.
53. He JM, Wang J, Liang HG. Effects of water stress on photochemical function and protein metabolism of photosystem II in wheat leaves. *Physiol Plant.* 1995; 93(4): 771-7.
54. Toivonen P, Vidaver W. Variable chlorophyll a fluorescence and CO₂ uptake in water-stressed white spruce seedlings. *Plant Physiol.* 1988; 86(3): 744-8.
55. Kim SH, Yan Y Bin, Zhou HM. Role of osmolytes as chemical chaperones during the refolding of aminoacylase. *Biochem Cell Biol.* 2006; 84 (1): 30-8.
56. Ivanov BN, Borisova-Mubarakshina MM, Kozuleva MA. Formation mechanisms of superoxide radical and hydrogen peroxide in chloroplasts, and factors determining the signalling by hydrogen peroxide. *Functional Plant Biology.* 2018; 45(2): 102-10.
57. Schmitt FJ, Renger G, Friedrich T, Kreslavski VD, Zharmukhamedov SK, et al. Reactive oxygen species: Re-evaluation of generation, monitoring and role in stress-signaling in phototrophic organisms. *Biochim. Biophys. Acta - Bioenerg.* 2014; 1837(6): 835-48.
58. Hasanuzzaman M, Bhuyan MHMB, Zulfiqar F, Raza A, Mohsin SM, et al. Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants.* 2020; 9(8): 681
59. Huseynova IM, Rustamova SM, Suleymanov SY, Aliyeva DR, Mammadov AC, et al. Drought-induced changes in photosynthetic apparatus and antioxidant components of wheat (*Triticum durum* Desf.) varieties. *Photosynth Res;* 130(1): 215-23.
60. Masojádek J, Trivedi S, Halshaw L, Alexiou A, Hall DO. The synergistic effect of drought and light stresses in sorghum and pearl millet. *Plant Physiol.* 1991; 96(1): 198-207.

61. Giardi MT. Phosphorylation and disassembly of the photosystem II core as an early stage of photoinhibition. *Planta*. 1993; 190(1): 107-13.
62. Yordanov I, Velikova V, Tsonev T. Plant responses to drought, acclimation, and stress tolerance. *Photosynthetica*. 2000; 38(2): 171-86.
63. Tamburino R, Vitale M, Ruggiero A, Sassi M, Sannino L, et al. Chloroplast proteome response to drought stress and recovery in tomato (*Solanum lycopersicum* L.). *BMC Plant Biol*. 2017; 17(1): 1-4.
64. Das A, Eldakak M, Paudel B, Dea-Wook K, Hemmati H, et al. Leaf proteome analysis reveals prospective drought and heat stress response mechanisms in soybean. *Biomed Res Int*. 2016; 2016: 1-23.
65. Azri W, Cosette P, Guillou C, Rabhi M, Nasr Z, et al. Physiological and proteomic responses to drought stress in leaves of two wild grapevines (*Vitis sylvestris*): a comparative study. *Plant Growth Regul*. 2020; 91(1): 37-52.
66. Ali GM, Komatsu S. Proteomic analysis of rice leaf sheath during drought stress. *J Proteome Res*. 2006; 5(2): 396-403.
67. Faghani E, Gharechahi J, Komatsu S, Mirzaei M, AliKhavarinejad R, et al. Comparative physiology and proteomic analysis of two wheat genotypes contrasting in drought tolerance. *J Proteomics*. 2015; 114: 1-5.
68. Xu C, Huang B. Comparative analysis of proteomic responses to single and simultaneous drought and heat stress for two Kentucky bluegrass cultivars. *Crop Sci*. 2012; 52(3): 1246-60.
69. Zhou S, Li M, Guan Q, Liu F, Zhang S, et al. Physiological and proteome analysis suggest critical roles for the photosynthetic system for high water-use efficiency under drought stress in *Malus*. *Plant Sci*. 2015; 236: 44-60.
70. Hayano-Kanashiro C, Calderón-Vásquez C, Ibarra-Laclette E, Herrera-Estrella L, Simpson J. Analysis of gene expression and physiological responses in three Mexican maize landraces under drought stress and recovery irrigation. *PLoS One*. 2009; 4(10): e7531.
71. Perdomo JA, Capó-Bauçà S, Carmo-Silva E, Galmés J. 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. *Front Plant Sci*. 2017; 8: 490.
72. Ji K, Wang Y, Sun W, Lou Q, Mei H, et al. Drought-responsive mechanisms in rice genotypes with contrasting drought tolerance during reproductive stage. *J Plant Physiol*. 2012; 169(4): 336-44.
73. Hajheidari M, Eivazi A, Buchanan BB, Wong JH, Majidi I, et al. Proteomics uncovers a role for redox in drought tolerance in wheat. *J Proteome Res*. 2007; 6(4): 1451-60.
74. Demirevska K, Zasheva D, Dimitrov R, Stamenova M, Feller U, et al. Drought stress effects on rubisco in wheat: Changes in the rubisco large subunit. *Acta Physiol Plant*. 2009; 31(6): 1129.
75. Caruso G, Cavaliere C, Foglia P, Gubbiotti R, Samperi R, et al. Analysis of drought responsive proteins in wheat (*Triticum durum*) by 2D-PAGE and MALDI-TOF mass spectrometry. *Plant Sci*. 2009; 177(6): 570-6.
76. Peng Z, Wang M, Li F, Lv H, Li C, et al. A proteomic study of the response to salinity and drought stress in an Introgression strain of bread wheat. *Mol Cell Proteomics*. 2009; 8(12): 2676-86.
77. Santamouris M, Ban-Weiss G, Osmond P, Paolini R, Synnefa A, et al. Progress in urban greenery mitigation science – assessment methodologies advanced technologies and impact on cities. *J. Civ. Eng. Manag*. 2018; 24(8): 638-671.
78. Kleerekoper L, Van Esch M, Salcedo TB. How to make a city climate-proof, addressing the urban heat island effect. *Resour Conserv Recycl*. 2012; 64: 30-8.
79. Gillner S, Vogt J, Tharang A, Dettmann S, Roloff A. Role of street trees in mitigating effects of heat and drought at highly sealed urban sites. *Landsc Urban Plan*. 2015; 143: 33-42.
80. Gill SE, Handley JF, Ennos AR, Pauleit S. Adapting cities for climate change: The role of the green infrastructure. *Built Environ*. 2007; 33(1): 115-33.
81. Demuzere M, Orru K, Heidrich O, Olazabal E, Geneletti D, et al. Mitigating and adapting to climate change: Multi-functional and multi-scale assessment of green urban infrastructure. *J Environ Manag*. 2014; 146: 107-15.
82. Santamouris M, Cartalis C, Synnefa A, Kolokotsa D. (2015) On the impact of urban heat island and global warming on the power demand and electricity consumption of buildings - A review. *Energy Build*. 2015; 98: 119-24.
83. McPherson G, Simpson JR, Peper PJ, Maco SE, Xiao Q. Municipal forest benefits and costs in five US cities. *J For*. 2005; 103(8): 411-6.
84. Moss JL, Doick KJ, Smith S, Shahrestani M. Influence of evaporative cooling by urban forests on cooling demand in cities. *Urban Fores Urban Green*. 2019; 37: 65-73.
85. Upmanis H, Eliasson I, Lindqvist S. The influence of green areas on nocturnal temperatures in a high latitude city (Goteborg, Sweden). *Int J Climatol*. 1998; 18(6): 681-700.
86. Shashua-Bar L, Hoffman ME. Vegetation as a climatic component in the design of an urban street. An empirical model for predicting the cooling effect of urban green areas with trees. *Energy Build*. 2000; 31(3): 221-35.
87. Wang C, Wang ZH, Yang J. Cooling effect of urban trees on the built environment of contiguous United States. *Earth's Futur*. 2018; 6(8): 1066-81.
88. Allakhverdiev SI, Kreslavski VD, Klimov VV, Los DA, Carpentier R, et al. Heat stress: An overview of molecular responses in photosynthesis. *Photosynth. Res*. 2008; 9 8(1): 541-50.
89. Sharkey TD. Effects of moderate heat stress on photosynthesis: Importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. *Plant, Cell Environ*. 2005; 28(3): 269-77.
90. Sun AZ, Guo FQ. Chloroplast retrograde regulation of heat stress responses in plants. *Front Plant Sci*. 2016; 7: 398.
91. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: An overview. *Environ Exp Bot*. 2007; 61(3): 199-223.
92. Wang QL, Chen JH, He NY, Guo FQ. Metabolic reprogramming in chloroplasts under heat stress in plants. *Int. J. Mol. Sci*. 2018; 19(3): 849.
93. Wang W, Vinocur B, Shoseyov O, Altman A. Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. *Trends Plant Sci*. 2004; 9(5): 244-52.
94. Ghatak A, Chaturvedi P, Bachmann G, Valledor L, Ramšak Z, et al. Physiological and proteomic signatures reveal mechanisms of superior drought resilience in pearl millet compared to wheat. *Front Plant Sci*. 2021; 11: Art-600278.

95. Yamane Y, Kashino Y, Koike H, Satoh K. Effects of high temperatures on the photosynthetic systems in spinach: Oxygen-evolving activities, fluorescence characteristics and the denaturation process. *Photosynth Res.* 1998; 57(1): 51-9.
96. Havaux M. Characterization of thermal damage to the photosynthetic electron transport system in potato leaves. *Plant Sci.* 1993; 94(1-2): 19-33.
97. Havaux M, Tardy F. Temperature-dependent adjustment of the thermal stability of photosystem II in vivo: Possible involvement of xanthophyll-cycle pigments. *Planta.* 1996; 198(3): 324-33.
98. Anjana J, Allakhverdiev SI. High-temperature stress in plants: consequences and strategies for protecting photosynthetic machinery. *Plant Stress Physiol.* 2017; 2017: 138-54.
99. Salvucci ME, Crafts-Brandner SJ. Relationship between the heat tolerance of photosynthesis and the thermal stability of rubisco activase in plants from contrasting thermal environments. *Plant Physiol.* 2004; 134(4): 1460-70.
100. Schrader SM, Wise RR, Wacholtz WF, Ort DR, Sharkey TD. Thylakoid membrane responses to moderately high leaf temperature in Pima cotton. *Plant, Cell Environ.* 2004; 27(6): 725-35.
101. Wise RR, Olson AJ, Schrader SM, Sharkey TD. Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. *Plant, Cell Environ.* 2004; 27(6): 717-24.
102. Yamamoto Y, Aminaka R, Yoshioka M, Khatoon M, Komayama K, et al. Quality control of photosystem II: Impact of light and heat stresses. *Photosynth. Res.* 2008; 98(1): 589-608.
103. Dutta S, Mohanty S, Tripathy BC. Role of temperature stress on chloroplast biogenesis and protein import in pea. *Plant Physiol.* 2009; 150(2): 1050-61.
104. Narayanan S, Prasad PVV, Welti R. Wheat leaf lipids during heat stress: II. Lipids experiencing coordinated metabolism are detected by analysis of lipid co-occurrence. *Plant Cell Environ.* 2016; 39(3): 608-17.
105. Narayani M, Srivastava S. Elicitation: a stimulation of stress in *in vitro* plant cell/tissue cultures for enhancement of secondary metabolite production. *Phytochem. Rev.* 2017; 16(6): 1227-52.
106. Brugnoli E, Scartazza A, De Tullio MC, Llio DT, Rmelo MC, et al. Zeaxanthin and non-photochemical quenching in sun and shade leaves of C3 and C4 plants. *Physiol Plant.* 1998; 104(4): 727-34.
107. Allen DJ, Ort DR. Impacts of chilling temperatures on photosynthesis in warm-climate plants. *Trends Plant Sci.* 2001; 6(1): 36-42.
108. Pandey DM, Yeo UD. Stress-induced degradation of D1 protein and its photoprotection by DCPIP in isolated thylakoid membranes of barley leaf. *Biol Plant.* 2008; 52(2): 291.
109. Hou W, Sun AH, Chen HL, Yang FS, Pan JL, et al. Effects of chilling and high temperatures on photosynthesis and chlorophyll fluorescence in leaves of watermelon seedlings. *Biol Plant.* 2016; 60(1): 148-54.
110. Demao J, Xia L. Cultivar differences in photosynthetic tolerance to photooxidation and shading in rice (*Oryza sativa* L.). *Photosynthetica.* 2001; 39(2): 167-75.
111. Wang L, Deng F, Ren WJ, Yang WY. Effects of shading on starch pasting characteristics of indica hybrid rice (*Oryza sativa* L.). *PLoS One.* 2013; 8(7): e68220.
112. Xu Y, Ibrahim IM, Harvey PJ. The influence of photoperiod and light intensity on the growth and photosynthesis of *Dunaliella salina* (chlorophyta) CCAP 19/30. *Plant Physiol Biochem.* 2016; 106: 305-15.
113. Cai C, Yin X, He S, Jiang W, Si C, et al. Responses of wheat and rice to factorial combinations of ambient and elevated CO₂ and temperature in FACE experiments. *Glob Chang Biol.* 2016; 22(2): 856-74.
114. Ruhil K, Sheeba, Ahmad A, Iqbal M, Tripathy BC, et al. Photosynthesis and growth responses of mustard (*Brassica juncea* L. cv Pusa Bold) plants to free air carbon dioxide enrichment (FACE). *Protoplasma.* 2015; 252(4): 935-46.
115. Ainsworth EA, Rogers A, Nelson R, Long SP. Testing the "source-sink" hypothesis of down-regulation of photosynthesis in elevated [CO₂] in the field with single gene substitutions in *Glycine max*. *Agric For Meteorol.* 2004; 122(1-2): 85-94.
116. Ainsworth EA, Rogers A. The response of photosynthesis and stomatal conductance to rising [CO₂]: Mechanisms and environmental interactions. *Plant, Cell Environ.* 2007; 30(3): 258-70.
117. Ainsworth EA, Long SP. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol.* 2005; 165(2): 351-72.
118. Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, et al. Elevated CO₂ effects on plant carbon, nitrogen, and water relations: Six important lessons from FACE. *J Exp Bot.* 2009; 60(10): 2859-76.
119. Long SP, Ainsworth EA, Rogers A, Ort DR. Rising Atmospheric Carbon Dioxide: Plants FACE the future. *Annu. Rev. Plant Biol.* 2004; 55: 591-628.
120. Zhu C, Ziska L, Zhu J, Zeng Q, Xie Z, et al. The temporal and species dynamics of photosynthetic acclimation in flag leaves of rice (*Oryza sativa*) and wheat (*Triticum aestivum*) under elevated carbon dioxide. *Physiol Plant.* 2012; 145(3): 395-405.
121. Davey PA, Olcer H, Zakhleniuk O, Calfapietra C, Long SP, et al. Can fast-growing plantation trees escape biochemical down-regulation of photosynthesis when grown throughout their complete production cycle in the open air under elevated carbon dioxide? *Plant, Cell Environ.* 2006; 29(7): 1235-44.
122. Bader MKF, Siegwolf R, Körner C. Sustained enhancement of photosynthesis in mature deciduous forest trees after 8 years of free air CO₂ enrichment. *Planta.* 2010; 232(5): 1115-25.
123. Leakey ADB, Bernacchi CJ, Dohleman FG, Ort DR, Long SP. Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future [CO₂] rich atmospheres? An analysis of diurnal courses of CO₂ uptake under free-air concentration enrichment (FACE). *Glob Chang Biol.* 2004; 10(6): 951-62.
124. Gutiérrez E, Gutiérrez D, Morcuende R, Verdejo AL, Kostadinova S, et al. Changes in leaf morphology and composition with future increases in CO₂ and temperature revisited Wheat in field chambers. *J Plant Growth Regul.* 2009; 28(4): 349-57.
125. Jauregui I, Aroca R, Garnica M, Zamarreño AM, García-Mina JM, et al. Nitrogen assimilation and transpiration: Key processes conditioning responsiveness of wheat to elevated [CO₂] and temperature. *Physiol Plant.* 2015; 155(3): 338-54.
126. Bunce JA. Carbon dioxide effects on stomatal responses to the environment and water use by crops under field conditions. *Oecologia.* 2004; 140(1): 1-0.
127. Clifford SC, Black CR, Roberts JA, Stronach IM, Singleton-Jones PR, et al. The effect of elevated atmospheric CO₂ and drought on stomatal frequency in groundnut (*Arachis hypogaea* (L.)). *J Exp Bot.* 1995; 46(7): 847-52.
128. Kim SH, Sicher RC, Bae H, Gitz DC, Baker JT, et al. Canopy photosynthesis, evapotranspiration, leaf nitrogen, and transcription

- profiles of maize in response to CO₂ enrichment. *Glob Chang Biol.* 2006; 12(3): 588-600.
129. Watson-Lazowski A, Lin Y, Miglietta F, Edwards RJ, Chapman MA, et al. Plant adaptation or acclimation to rising CO₂? Insight from first multigenerational RNA-Seq transcriptome. *Glob Chang Biol.* 2016; 22(11): 3760-73.
130. Gomez-Casanovas N, Blanc-Betes E, Gonzalez-Meler MA, Azcon-Bieto J. Changes in respiratory mitochondrial machinery and cytochrome and alternative pathway activities in response to energy demand underlie the acclimation of respiration to elevated CO₂ in the invasive *Opuntia ficus-indica*. *Plant Physiol.* 2007; 145(1): 49-61.
131. Van Oosten J-J, Wilkins D, Besford RT. Regulation of the expression of photosynthetic nuclear genes by CO₂ is mimicked by regulation by carbohydrates: a mechanism for the acclimation of photosynthesis to high CO₂? *Plant Cell Environ.* 1994; 17(8): 913-23.
132. Seneweera SP, Conroy JP, Ishimaru K, Ishimaru K, Okada M, et al. Changes in source - Sink relations during development influence photosynthetic acclimation of rice to free air CO₂ enrichment (FACE). *Funct Plant Biol.* 2002; 29(8): 947-55.
133. Bloom AJ, Burger M, Asensio JSR, Cousins AB. Carbon dioxide enrichment inhibits nitrate assimilation in wheat and arabidopsis. *Science.* 2010; 328(5980): 899-903.
134. Asensio JSR, Rachmilevitch S, Bloom AJ. Responses of Arabidopsis and wheat to rising CO₂ depend on nitrogen source and nighttime CO₂ levels. *Plant Physiol.* 2015; 168(1): 156-63.
135. Ziegler I. The effect of SO₂ pollution on plant metabolism. *Residue Rev.* 1975: 79-105.
136. Madhusudana Rao I, Amundson RG, Alschner Herman R, Anderson LE. Effects of SO₂ on stomatal metabolism in *Pisum sativum* L. *Plant Physiol.* 1983; 72(2): 573-7.
137. Robinson MF, Heath J, Mansfield TA. Disturbances in stomatal behaviour caused by air pollutants. *J Exp Bot.* 1998: 461-9.
138. Florentina I, Io B. The effects of air pollutants on vegetation and the role of vegetation in reducing atmospheric pollution. In: *The Impact of Air Pollution on Health, Economy, Environment and Agricultural Sources.* 2011: 241-80.
139. Addison PA, Malhotra SS, Khan AA. Effect of sulfur dioxide on woody boreal forest species grown on native soils and tailings. *J Environ Qual.* 1984; 13: 333-336.
140. Heber U, Hüve K. Action of SO₂ on plants and metabolic detoxification of SO₂. *Int Rev Cytol.* 1997; 177: 255-86.
141. Almohisen I. Response of free amino acids in four legumes plants to air pollution. *J Biol Today's World.* 2014; 3(8): 169-73.
142. Bhat MS, Afeefa QS, Ashok KP, Bashir AG. Brick kiln emissions and its environmental impact: A Review. *J Ecol Nat Environ.* 2014; 6(1): 1-1.
143. Carlson RW. The effect of SO₂ on photosynthesis and leaf resistance at varying concentrations of CO₂. *Environ Pollution Ser A, Ecol Biol.* 1983; 30(4): 309-21.
144. Kropff MJ (1987) Physiological effects of sulphur dioxide. 1. The effect of SO₂ on photosynthesis and stomatal regulation of *Vicia faba* L. *Plant Cell Environ.* 1987; 10(9): 753-60.
145. Swanepoel JW, Krüger GHJ, van Heerden PDR. Effects of sulphur dioxide on photosynthesis in the succulent *Augea capensis* Thunb. *J Arid Environ.* 2007; 70(2): 208-21.
146. Muneer S, Kim TH, Choi BC, Lee BS, Lee JH. Effect of CO, NOx and SO₂ on ROS production, photosynthesis and ascorbate-glutathione pathway to induce *Fragaria×annasa* as a hyperaccumulator. *Redox Biol.* 2014; 2: 91-8.
147. Dalal VK, Biswal AK, Patel D, Subramanyam R, Raghavendra AS. *In vitro* stability of various enzymes by proline from H₂O₂ mediated oxidative damage. *Ind J Biochem Biophys* 2022; 59: 1-15.
148. Dalal VK. Modulation of photosynthesis and other proteins during water-stress. *Mol Biol Rep* 2021; 48(4): 3681-3693