Chapter 6 Air Pollution and Its Role in Stress Physiology



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Abstract Environment plays a crucial role in the physiological processes of plants. The numerous biotic and abiotic stresses in the plant habitat trigger complex responses in vital processes like photosynthesis, respiration and stomatal function. In this chapter we discuss the effect of various air pollutants on the stress physiological parameters. These studies are crucial because one of the major responses to plant pollutants is the inhibition of photosynthesis. This inhibition of photosynthesis not only alters the growth pattern and longevity but also changes plant phenology. Besides, assimilation of pollutants into the plant processes ultimately leads to their inclusion in the animal community. All this leads to a vicious cycle wherein the ecological factors suppress plant growth and in turn plants hamper the ecology. In this chapter we have also reviewed and highlighted the mechanistic aspect of the pollutants on the vital physiological parameters. The major pollutants which are emphasized are sulphur dioxide (SO₂), nitrogen oxides (NO_x) and ozone (O₃) while physiological parameters reviewed are stomatal conductance, photosynthesis and respiration and photorespiration. These physiological processes are important parameters in governing growth and health of plants. Because all the natural processes are cyclic in nature, it is pertinent to observe that the stress in plants caused by the pollutants also directly and indirectly affects the human population.

Keywords Environmental stress · Physiological processes · Air pollutants · Mechanistic pathway

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6.1 Introduction

The equilibrium between ecosystem stability and socio-economic upgradation is dwindling day by day. The ecosystem stability and its dynamics are key parameters which determine the structure and function of any ecosystem. These parameters are maintained by various biotic and abiotic factors. The factors which negatively affect the agricultural and natural ecosystems include global climate change, deforestation, shifts in land use pattern and air pollution. It is important to note that these factors are interrelated and are not exclusive of each other.

In comparison to other factors, air pollution mostly affects flora and fauna. There are two ways by which airborne pollutants affect ecosystem, directly by toxicity and indirectly by altering soil nutrient availability. It is well established that a single factor does not affect terrestrial ecosystems but a multitude of factors result in chronic exploitation of ecosystem (Taylor et al. 1994). Increased concentrations of CO₂, elevated ultraviolet B (UV-B) radiation, high nitrogen deposition, nutrient deficiencies, drought or temperature extremes are the most emphatic stresses that degrade and hamper the plant characteristics.

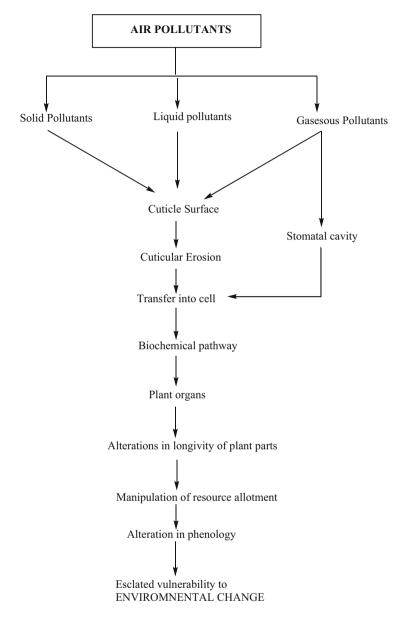
One can safely assume that the air pollutants concern the above-ground parts of the plants in a greater manner than the roots because they are directly exposed to the pollutants. The air pollutants including gaseous pollutants, dust particles and aerosols are adsorbed directly on the large leaf surfaces of vegetation and impact plant function and structure (Mukherjee and Agrawal 2018). The most important plant processes affected by the air quality deterioration are altering of species composition and structure, rate of decomposition, growth and morphology, physiological processes like photosynthesis, respiration, photorespiration and stomatal conductance, leaf functional traits and bioaccumulation of toxic chemicals. The pollutants penetrate from environment into the cells and act as an important carrier in the chain. This is represented in Scheme 6.1.

The pollutants affect the different physiological processes to different extent. The general parameters used to quantify these processes are tabulated in Table 6.1.

Air pollutants are classified as (a) primary pollutants and (b) secondary pollutants. The primary pollutants are the pollutants which are directly released from stationary and mobile sources. Figure 6.1 gives the provenance of primary pollutants.

The primary pollutants undergo chemical changes and reactions to generate secondary pollutants. The formation of secondary pollutants is depicted in Scheme 6.2.

Although there are several pollutants which generate stress in plant physiology, in this chapter we will be discussing only SO_2 , NO_x and O_3 . The deleterious effects of harmful atmospheric pollutant such as sulphur dioxide, ozone, oxides of nitrogen, peroxyacetyl nitrate, and fluoride on the physiological, morphological and biochemical aspects of flora have been widely reviewed (Baek and Woo 2010). These pollutants mainly disturb the biochemical and physiological processes and cellular structure of the plants (Saxena and Kulshrestha 2016a, b). It is also believed that the pollutants initially disturb the biochemical processes (photosynthesis, respiration,

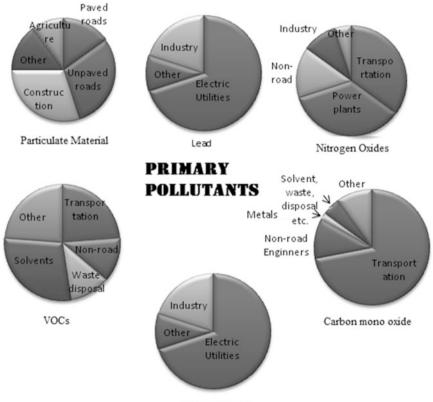


Scheme 6.1 Pathway of air pollutants: From air to the plant

lipid and protein biosynthesis, etc.), and then attack the ultrastructural level (disorganization of cellular membranes), and cellular level (cell wall, mesophyll and nuclear breakdown) (Saxena and Kulshrestha 2016a, b).

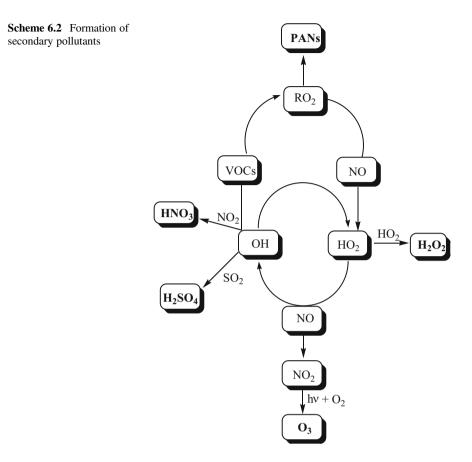
Process	Tested parameter
Photosynthesis	Chlorophyll fluorescence
-	CO ₂ Fixation
	Gas exchange/stomatal function
	Photosynthetic functions like ATP production, electron transport, enzymes
	and metabolites involved in Calvin Cycle
Respiration	Gas exchange
	Mitochondrial functions
	Enzymes involved in respiration
Water parameters	Transpiration
	Stomatal function
	Water potential
	Permeability of cuticle
Nutrients	N, P, K, S, Mg, Ca Iron contents
Biorhythms of	Electrical conductance in leaves
plants	

Table 6.1 Quantification of physiological parameters



Sulphur Dioxide

Fig. 6.1 Sources of primary pollutants



6.2 SO₂ and Its Effect on Plant Physiology

One of the most widespread and dangerous air pollutants is sulphur dioxide (SO₂). The main sources of its origin include the burning of sulphur containing fossil fuels and smelting of sulphur containing metals. Another prominent source of SO₂ in winters is crop cultivation using a greenhouse. Greenhouses are meant to keep warm by burning fuels like diesel oil, heavy oil, kerosene and by-product oil, all of which have high sulphur content and their combustion leads to high SO₂ emission (Park et al. 2010).

 SO_2 affect the environment both in gaseous as well as aqueous form. In aqueous form, SO_2 in the atmosphere results in acid rain, which is very damaging for plants, trees and forests. Acid rain leaches essential nutrients like calcium and magnesium from soil, which results in the plantation getting more prone to infection and damage by cold weather and insects. Not only this, aluminium also is removed from the soils which hinders the water up-taking capacity of the trees. Besides, acid rain destroys the outer coating of leaves, hampering the photosynthesis. In human beings even the

trace amount of acid particles leads to respiratory problems like asthma, chronic bronchitis and pneumonia. In the aquatic system, increase in acid content reduces the pH of water bodies leading to fish mortality.

In gaseous form, SO_2 affects the human health by entering through the respiratory tract. It causes irritation in the skin, and mucous membranes of eyes, nose, throat and lungs, which is responsible for throat irritation, coughing, wheezing and breathing difficulty. High concentration of SO_2 can affect lung function, worsen asthma attacks and heart disease in sensitive groups.

Apart from living organisms, SO_2 is equally hazardous to man-made materials. It severely damages a variety of carbonate-containing building materials like lime-stone, marble and mortar.

 SO_2 attacks on leather causing disintegration of leather goods. In case of metals though aluminium is almost noble to SO_2 attack, other metals like iron and steel get highly corroded by it. Various other materials like paper, wool, cotton etc. also deteriorate on SO_2 exposure leading to embrittlement and eventual loss of strength (Saxena et al. 2019).

Sulphur being a key constituent of amino acids, proteins and a few vitamins, is essential for plant metabolism. A low concentration of SO_2 is necessary for physiological growth of plants (Darrall 1989), especially in sulphur-deficient plants in which sulphate might be metabolized to sulphur to fulfill nutrition in plants (DeKok 1990). But at higher concentration of SO_2 , general disruption of photosynthesis, respiration and other fundamental cellular processes can occur. This can be understood as a chain of events wherein an increased uptake of SO_2 leads to a buildup of sulphites and sulphates which in turn are cytotoxic and stop the growth and productivity of plants (Darrall 1989; Agrawal and Verma 1997). SO_2 toxicity has a rather adverse effect on plant pigments and therefore SO_2 exposure reduces photosynthetic activities. SO_2 exposure also leads to tissue damage and the most affected areas are stomata, cell membranes and leaves while the most affected functions are transpiration, membrane transport and permeability. These all, in unison leads to reduced plant growth and a diminished yield (Crittenden and Read 1978; Unsworth and Ormrod 1982).

 SO_2 uptake can be both from root as well as shoot system. Sulphur is taken in the form of sulphate ions by the root and is assimilated into organic sulphur compounds. These sulphur compounds are employed in various biochemical processes and thus eventually become a part and parcel of the ecosystem (Omasa et al. 2002; De Kok et al. 2002).

The SO_2 uptake by the plant's shoot system can be shown as in the schematic representation in Fig. 6.2.

Plants do not show a uniformity in responses to SO_2 exposure due to their different absorption efficiency towards the gas as well as their capability to remove the excessive sulphur and detoxify the pollutants. Once the SO_2 enters in the plant through leaf, it dissolves in the moisture present in mesophyll cell and converts into sulphite and bisulphate (Kulshrestha and Saxena 2016). These toxic elements (sulphite and bisulphate) are then translocated to other parts of the plant. Several studies have been done during the past two decades to understand the effect of SO_2

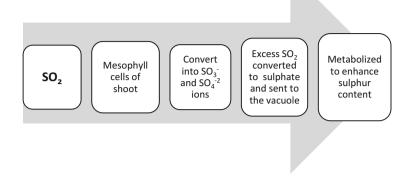


Fig. 6.2 SO₂ uptake by shoot of plants

Table 6.2 Classification of plants on the basis of extent of SO₂ exposure effects

Type of Plants	Species	Exposure effect
Herbs	Wheat, Barley, Pea, Beet, Bean, Carrot, Chilli, Petunea, Oat, Potato, Tobaco.	Immediate deterioration
	Croton, Opuntia, Nerium, Vinca	Slow, chronic effect
Shrubs and Trees	Mango, Arjun, Sisso, Jamun	Immediate deterioration
	Neem, Banyan, Bougainvillea, Chatim, Jarul, Sims, Pongamia pinnata	Slow, chronic effect

on various plants species. On that basis, a list of acute and chronic effects on plants is given in Table 6.2.

Exposure to SO_2 at even low concentrations may have several damaging effects on plants, such as:

- · Reduction in photosynthetic and transpiration rate
- Increase in respiration rate
- Increase in stomatal conductance
- · Reduction in chlorophyll content
- Membrane lipid peroxidation

6.2.1 SO₂ and Its Effect on Stomata

The pollutants enter into the plant through the leaf having abundant stomata on its surface. The response of stomata towards SO_2 depends upon species of plant, concentration of SO_2 , plant age and environmental conditions. It is also found that

exposure time of SO₂ affects opening and closing of stomata (Saxena and Sonwani 2019a, b, c). When a leaf gets exposed to SO₂ for a short time it causes stomatal opening, while for long-time exposure it causes stomatal closing (Abeyratne and Ileperuma 2006; Raschk 1975; Rao et al. 1983; Verma and Singh 2006; Robinson et al. 1998; Bytnerowicz et al. 2007). The effect of SO₂ concentration on stomatal opening is different in different plants (Biggs and Davis 1980). In one plant species it can cause stomatal opening while in another stomatal closing (Mudd 1975).

The SO₂ uptake depends upon the pore size and quantity of stomata, which affect the turgidity of guard cells. Long-term exposure of high concentration of SO₂ reduces the ability of guard cells to collect sulphur and open or close the stomata (Guderian 2012; Knabe 1976), which then alters the fabrication and supply of photosynthates (Khan and Khan 1993). There is decrease in stomata abundance (Olszyk and Tibbitts 1981; Kumari and Prakash 2015; Koziol and Whatley 2016), which is a necessary action to avoid entrance of high-level SO₂ into the leaf, due to which damaging of plant tissues can occur (Kumari and Prakash 2015).

Abeyrante and Ileperuma (2006) have studied the effect of SO_2 on stomatal pore width of *Argyreia populifolia* leaves at the three sampling sites of the Peradeniya University Park, Sri Lanka. Sampling site 1 was reported at high SO_2 concentration and other two locations (sampling site 2 and 3) were with moderate SO_2 concentration. A reduction (almost 50%) in the values of both length and width of stomatal pore were observed at sampling site number 1, whereas sampling sites 2 and 3 gave almost identical values of pore length and width (Abeyratne and Ileperuma 2006).

A decrease in cellular pH responsible for stomatal closure is also reported due to sulphur dioxide fumigation. This is due to the fact that SO₂ reacts with cellular water content and produces sulphuric acid according to the following reaction:

$$(SO_2 + H_2O \rightarrow [SO_2 \cdot H_2O] \rightarrow HSO_3^- + H^+ \rightarrow SO_3^{-2-} + 2H^+)$$

This may lead to inhibition of K^+ pump, responsible for stomatal closure (Dhir 2016) which thus affects the photosynthetic yield. Another reason for closing of stomata is the presence of abscisic acid (AbA) hormone in the leaf which is produced due to exposure to SO₂ (Hu et al. 2014). In case of high SO₂ exposure, stomatal conductance also gets reduced which affect the physiological processes of photosynthesis (Choi et al. 2014a; Liu et al. 2017).

Majemik and Mansfield (1971) found that SO2 does not affect the normal diurnal cycle of opening and closing of stomata, but increases the apertures during the day in plants (Majernik and Mansfield 1971). Similar results were found in another study on a plant species *Vicia faba*. The stomatal conductance was increased by 20-25% on exposure to low SO₂ concentrations (Black and Black 1979). This enhanced opening was responsible for damage of epidermal cells adjoining to the stomata.

In another study stomatal abundance and increase in epidermal cells in leaves of *Azadirachta indica* and *Polyalthia longifolia* (Pal et al. 2000), *Cassia siamea* (Aggarwal 2000), and *Nyctanthes arbortristis*, *Quisqualis indica* and *Terminalia arjuna* (Rai and Kulshreshtha 2006) on SO₂ exposure have been found. Along with

this, reduced stomata and epidermal cells size with exposure to SO_2 has also been found from other researchers' works (Aggarwal 2000; Kaur 2004; Dineva 2006). This may be due to inhibited cell elongation, leaf area and increase in cell occurrence (Rai and Kulshreshtha 2006).

6.2.2 SO₂ and Its Effect on Photosynthesis

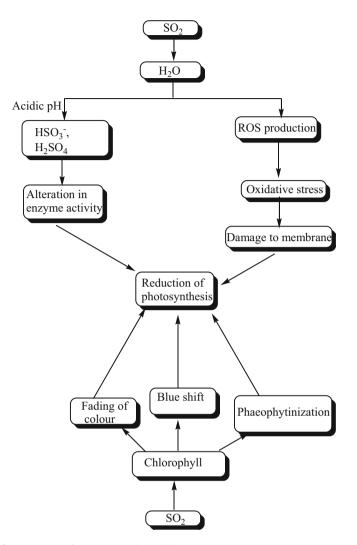
The vital physiological process of photosynthesis is highly sensitive to SO_2 concentration and duration of exposure (Saxena and Sonwani 2020). In various studies it was found that short-time exposure to low SO_2 concentrations generally stimulates photosynthesis, whereas long-time exposure even at low concentration of SO_2 was responsible for inhibition of photosynthesis (Gheorghe and Ion 2011).

 SO_2 destroys electron transport between photosystems, which decreases the rate of electron transport throughout the chain. The overall result of this is the reduced rate of photosynthesis (Gheorghe and Ion 2011). Another reason for reduced photosynthetic rate on SO_2 exposure may be due to reduced amount of chlorophyll (Aminifar and Ramroudi 2014; Hetherington and Woodward 2003). SO_2 exposure effect on chlorophyll can be trifurcated in three ways:

- 1. Fading of chlorophyll color
- 2. Phaeophytinization wherein chlorophyll molecules get degraded to phaeophytin (less active molecule))
- 3. Blue shift in pigment spectrum of lichens (Hetherington and Woodward 2003)

In a study on oak species, *Gracia* and coworkers found that decrease in photosynthetic rate could be due to reduction in protein contents and decreased carboxylation efficiency resulting in a reduced CO_2 uptake besides the chlorophyll factors (Farage et al. 1991). Because of its acidifying properties, a very high concentration of CO_2 acts as inhibitor. Reduction in leaf area and CO_2 -induced shift in the timing of the leaf ontogenetic processes (Miller et al. 1997; Rey and Jarvis 1998) may also be the additional factors for reduced photosynthesis. Similar results were found for rice and spinach.

 SO_2 deteriorates the height and girth of plant axis. It is well documented in literature that the photochemical efficiency of photosystem II in a healthy leaf ranges between 0.74 to 0.85, which gets drastically reduced when exposed to SO_2 (Choi et al. 2014b; Seyyednejad and Koochak 2011a; Lichtenthaler et al. 2005; Sobrado 2011). Furthermore, SO_2 exposure also inhibits the activity of essential Calvin cycle enzymes like Fructose bisphosphatase and Ribulose bisphosphate carboxylase (Chung et al. 2011). Reduction in the total chlorophyll content upon exposure to the gaseous SO_2 has also been documented in the literature. This may be due to the negative impact of SO_2 on chlorophyll metabolism (Choi et al. 2014b; Seyyednejad and Koochak 2011b). In addition to this, Seyyednejad and Koochak demonstrated that in *Prosopis juliflora*, the concentration of photosynthesis pigments like chlorophyll carotenoids Fwas decreased when leaf was exposed to SO_2 . The reason behind



Scheme 6.3 Reduction of photosynthesis on SO₂ exposure

this is the deposition of suspended particulate on leaf surface (Seyyednejad and Koochak 2011b).

The reduction in photosynthesis on SO_2 exposure is represented in Scheme 6.3.

6.2.3 SO₂ and Its Effect on Respiration and Photorespiration

Respiration also called dark respiration is a metabolic pathway which produces energy-rich molecules by the breaking of larger molecules like carbohydrates (Sonwani and Saxena 2016). In general, the rate of respiration increases when a plant is exposed to gaseous pollutants viz. SO₂, O₃, HF and NO₂. Some researchers have found that the rate of dark respiration increased when exposed to 35–380 ppb concentration of sulphur dioxide, while some other haves reported no change at 20–4000 ppb concentration of SO₂ (either short term, i.e., less than 8 h or long term, i.e., more than 1 day). Black and Unsworth (1979) studied the effect of SO₂ on one species, *Vicia faba* and they observed that the increase in the rate of dark respiration was not affected by the SO₂ concentration from 35 to 175 ppb (Black and Unsworth 1979). In addition to this, SO₂ exposure also affects the respiration rate in lichens and bryophytes. In some cases when certain lichens such as *C. impexa, Hypogymnia physodes, and Usnea fragiliscence* were exposed to a low concentration of aqueous solution of SO₂ with 23–27 ppm concentration, a decrease in rate of respiration was observed. On the basis of these findings, we can conclude that the change in respiration rate mainly depends on the concentration of SO₂.

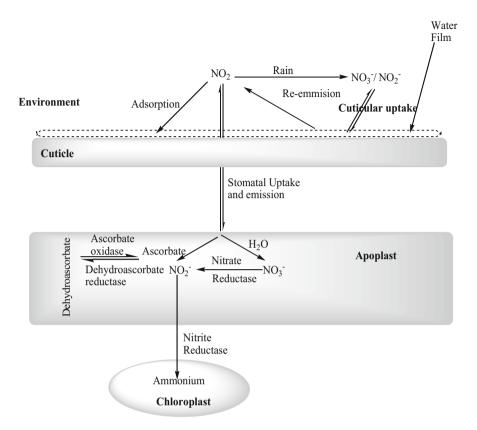
Photorespiration, also known as light respiration, occurs in chlorophyll tissues of plants in the presence of light and at higher O_2 concentration (Saxena and Naik 2018). It is a distinguished aspect of C_3 plants and essentially absent in C_4 plants. Generally, air pollutant has little effect on photorespiration. At high SO₂ concentration (1000 ppb), inhibition in photorespiration occurred. The effect of sulphur dioxide on photorespiration is also found in higher plants, due to which their productivity is greatly influenced (Black 1984).

6.3 NO_X and Its Effect on Plant Physiology

NOx, a primary air pollutant, enters into the environment through fuel combustion processes. The increase in automobile exhaust emissions from industrialized areas is responsible for increase in NO_x concentration (Munzi et al. 2009; Hu et al. 2015; Hultengren et al. 2004). NO_x is mainly composed of NO (>90%) and NO₂, which can covert into each other in sunlight and in the presence of some gases like O₃. NO₂ also releases some harmful pollutants in the environment like O₃ and particulate matters (Rahmat et al. 2013; Bermejo-Orduna et al. 2014; Marais et al. 2017).

Research studies have adopted two assumptions for plant response to NO_2 exposure. In one assumption it is proposed that NO_2 can produce nitrogenous compounds by its metabolism and incorporation in the nitrate assimilation pathway, which does not cause any visible injury (Stulen et al. 1998). Some other studies anticipated that the majority of the plants show evidence of fewer amounts of NO_2 (Middleton et al. 1958).

On the basis of a general hypothesis, it is believed that when NO_2 is present in high concentration it can cause extreme accumulations of NO_2^- (Okano and Totsuka 1986) and cell acidification (Schmutz et al. 1995). Due to this, deterioration of plant growth occurs by production of reactive oxygen species (ROS) and inhibition of absorption of N (Sonwani and Maurya 2018). On the other hand, some different physiological responses were obtained on NO_2 exposure. Therefore, there is a



Scheme 6.4 Assimilation of NO2 into chloroplast via stomata

disagreement on the effects of NO_2 exposure on plants and a united conclusion has not been reached.

Various environmental factors (Gebler et al. 2000; Chaparro-Suarez et al. 2006), stomatal dimension and conductance (Chaparro-Suarez et al. 2011; Breuninger et al. 2013) affect the foliar NO₂ uptake. NO_x is a free radical gas which transfers electrons crossways biological membranes due to which reactive oxygen species (ROS), a by-product of other biological reactions is generated (Xu et al. 2010). The NO₂ uptake in plants may be done directly through the stomata and/or through roots. The assimilation of NO₂ into chloroplast via stomatal route is given in Scheme 6.4.

The mechanism of absorption of gaseous NO_2 into leaf through stomata is proposed in two ways.

1. Either it is disproportionated to nitrate and nitrite in the apoplast

$$NO_2 + H_2O \rightarrow H^+ + NO_3^- + NO_2^-$$

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2. Or absorbed in leaf apoplast by ascorbate

$$Asc - OH + NO_2 \rightarrow Asc - O + H^+NO_2^-$$

In apoplast NO_2^- is converted to NO_3^- where it is metabolized by enzyme nitrate reductase (NaR) producing NO_2 , where it is taken up from the apoplast and then transported into the chloroplast (Eller et al. 2011). At high concentration NO_2 is capable of being stimulated upon nitrate reductase and responsible for more intense reduction of nitrite to ammonia and amino acids (Erisman et al. 2007)

It is pertinent to note that there are relatively few reports on effect of NO_x on plant physiology, perhaps because of the fact that it is less toxic as compared to SO_2 . It is also found that the effects of NO_x are most prominent when it is combined with SO_2 (Carlson 1983; Whitmore and Mansfield 1983; Freer-Smith 1985). In uncombined form NO_x is damaging only at high concentrations (Reinert et al. 1982). Furthermore, NO has less toxic effect than NO_2 , which may be attributed to its less solubility in water which in turn leads to lower uptake (Mansfield and Freer-Smith 1981). Another reason could be that NO gets easily converted to NO_2 ; therefore, the effects of NO are difficult to quantify. Nowadays, the concentration of NO_2 is steadily increasing and in some countries it exceeds the concentration of SO_2 (Lane and Bell 1984a; Martn and Barber 1984). It is also found that in rural areas the concentration of NO and NO_2 may be same, but in urban areas the NO concentration is high (Lane and Bell 1984b).

6.3.1 Effect of NO₂ on Stomatal Conductance

On foliar surface, the flow of NO_2 into the leaf has been a matter of intense discussion (Rogers et al. 1979; Fatima et al. 2018; Thoene et al. 1996; Teklemariam and Sparks 2006; Gebler et al. 2000). The exhaustive studies lead to the conclusion that the NO_2 deposition was much more than the cuticular deposition through stomatal contribution to the total leaf. Some studies suggested that cuticular contribution is upto 5% in most of the cases (Saxena and Sonwani 2019a, b, c). In 1900, Wellburn introduced that at 140 ppb NO_2 concentration, deposition through the stomata was higher than the deposition on the cutice (Wellburn 1990).

The NO₂ uptake process is highly influenced by the water films. It is proposed that absorption of water occurs through water film of plant surface. High humidity leads to deposition of water films on the leaf surface which in turn serves as sink for atmospheric NO₂ (Burkhard and Eiden 1994). Some researchers suggested that NO₂ consumption is solely depended on stomatal opening and that cuticular expulsion was entirely ruled out.

The stomatal dynamics as well as stomata-related physiological and biochemical processes are affected by the corrosive and oxidizing attributes of NO_2 (Takagi and Gyokusen 2004; Mazarura 2012). In a recent study on populous trees, Yanbo Hu

et al. (2015) showed that NO₂ gas has remarkable adverse influence on stomata connected with physiological processes of *Populus alba* and *P. berolinensis* leaves (Hu et al. 2015).

6.3.2 Effect of NO_x on Photosynthesis

Reduced photosynthesis is observed in various plants when exposed to gaseous NO_x , even at concentrations that do not produce visible injury (Hill and Bennett 1970; Capron and Mansfield 1976). It was also been observed that the effect of NO was much more rapid than the effect of NO_2 (Hill and Bennett 1970). In another study it was found that NO_2 concentration and exposure time were responsible for reduced photosynthesis (Srivastava et al. 1975). The effect of NO_x on photosynthesis is much less than other pollutants. Short-term exposure (< 8 h) of NO_2 between 500 to 700 ppb and continuing exposure (20-h period) at 250 ppb, can cause changes in photosynthetic rate (Hill and Bennett 1970; Capron and Mansfield 1976). In variation to above, nitric oxide disrupted four times like NO_x gets reduced to dioxide at 1000 ppb in a 4d ventilation of a variety of greenhouse plants (Saxe and Murali 1989).

Reduction of NO₂, into nitrite and ammonia was found when NO₂ entered into the plant, by reduced ferredoxin or by reduced nicotinamide adenine dinucleotide phosphate (NADPH) Reduction of NO₂ could be explained in the rate of photosynthesis as on the basis of presence of NADPH for nitrite reduction and absorb carbon in the chloroplast. Furthermore, the acidic behaviour of NO₂ can change the electron movement and photophosphorylation. As photoelectron systems are associated with chloroplast membranes, any changes in their structures would influence activities of the photosystems (Hill and Bennett 1970; Srivastava et al. 1975).

 NO_2 exposure is also responsible for swelling of chloroplast membranes (Wellburn 1990). This may result if NO_2 is reduced into ammonia, which is not rapidly incorporated into amino-forms and thus responsible for inhibition of photosynthesis by uncoupling electron transport (Avron 1960). Similarly, in some lichen species, reduced chlorophyll content was observed on NO_2 fumigation (Nash 1976). The inhibition in pigment synthesis on NO_2 exposure is also documented in the literature. This may be due to inhibition in photooxidative processes, which may affect the synthesis of chlorosis. Moreover, rise in percentage of chlorophyll by about 10% occurred in *Pisum sativum* with NO_2 exposure in some other study (Horsman and Wellburn 1975).

In some investigations, researchers found the effects of NO on photosynthesis rate of glasshouse crops, particularly the tomato (*Lycopersicon esculentum*). From the results, they concluded that in controlled fumigation, some NO is oxidized to NO_2 . So, it is difficult to interpret the effect of NO on photosynthesis since atmosphere will contain a blend of the oxides (Saxena and Sonwani 2019a, b, c). It is also found that it is not clear that which oxide is the more toxic. In a latest

research it has been reported that with NO rate of photosynthesis decreases rapidly as compared to NO_2 (Hill and Bennett 1970).

In comparison with the effect of NO₂ alone, spraying with a mixture of NO₂ and SO₂ has been found to show adverse effect on the rate of photosynthesis. At lower concentration (200-250 ppb), the combined effect of these gases on inhibition of net photosynthesis was much higher than with these gases individually. The study was done on various plant species like *Medicago sativa*, *alfalfa*, and *Glyeine max* (Carlson 1983). Thus, nitrogen dioxide and nitric oxide had reported good results only at high concentrations, that is 500–700 ppb and above, but when it combines with sulphur dioxide, effect of inhibition is high than that single gas.

6.3.3 Effect of NO₂ on Respiration and Photorespiration

Respiration is an important process for plant metabolism and growth, and also for rebuild and neutralization of the toxics (Koziol and Whatley 2016). Currently, there is no compatible way to recognize the effects of nitrogen dioxide on respiration. At concentrations between 40 and 400 ppb of nitrogen dioxide or nitric oxide, no effect was found on inhibition and stimulation, but high concentrations of these two gases, that is 1000–7000 ppb, showed effective behaviour for the same. Bengtson et al. (1982) have been studying the effect of NO and NO₂ on *Pinus sylvestris* at 40–400 ppb for 6 h. They found ineffective behaviour of NO_x on respiration in the absence of light at this concentration and time. In another study on pot plant cultivators, it was demonstrated that on 1000 ppb of NO fumigation for 4 h, there was inhibition in one cultivator (5.1%), while under similar conditions of NO₂ fumigation, there was an increase in two cultivators (8.2%) (Grennfelt et al. 1983).

Sabaratnam and Gupta investigated the effect of NO₂ on one-month mature soybean plants. The plants were treated with different specified limits of NO₂ concentrations from 0.1 μ l liter⁻¹ to 0.5 μ l liter⁻¹ for 5 days (7 hour per day), under controlled environment. The results showed that above the concentration from 0.3 μ l liter⁻¹ of NO₂, the rate of dark respiration was rapidly increased; this may be due to elevated activity of cellular physiology to metabolize the pollutant to non-toxic forms caused by NO₂ (Sabaratnam and Gupta 1988).

Oxides of nitrogen (NO and NO₂) are sometimes referred to as total reactive nitrogen oxides, which includes NO, NO₂, nitrous oxide (N₂O), nitric acid (HNO₃), nitrous acid (HNO₂), peroxyacetyl nitrate (PAN), organic nitrates, and other forms of oxidized nitrogen (Weller et al. 2002). Nitric oxide free radical is unstable and not easily deposited to surfaces in remarkable amounts (Horii et al. 2004). NOx species, mainly NO₂ a free radical, and a potent oxidant is related to deposition studies. It is principal constituent of urban air pollution (Jacobson et al. 2004). In atmosphere NO₂ is produced by the oxidation of nitric oxide (NO) which is formed by the oxidation of N₂ at high temperatures during combustion processes in energy production, burning of fossil fuels in automobiles by tropospheric ozone (O₃). O₃

rapidly converted NO to NO₂by oxidation process. NO₂ levels are used as an overall indicator of the atmospheric NOx status for U.S. EPA.

6.4 O₃ and Its Effect on Plant Physiology

The troposphere ozone is formed under sunlight via chain of chemical reactions with different intermediates of nitrogen oxides (NOx) and volatile organic compounds. Depending upon where it is found, ozone can be good or adverse. Good ozone forms a safety layer to shield us from harmful UV rays of sun (Sonwani and Kulshrestha 2016). The process of formation of ozone occurs naturally in upper atmosphere. Unfavourable ozone is formed in lower atmosphere, that is troposphere, where pollutants come in this level from man-made pollutants and from chemical reaction occuring in the presence of sunlight. Ozone at lower level is a destructive air pollutant. Ozone is a secondary pollutant formed in the presence of sunlight with nitrogen oxides (NOx), which comes mainly from automobiles and biomass burning, in the presence of volatile organic compounds as shown in Fig. 6.2.

Ozone in tropospheric region considered as a highly reactive pollutant, which produces adverse effects on plant development (Betzelberger et al. 2012; Wilkinson et al. 2012). Ozone goes into the plant through the stomata and reacts with different compounds connected with cell walls and membranes. The effect of ozone on plant development is determined with the concentration of ozone and the exposure time. Long-time exposures of ozone pollution on plant can change plant physiology, leading to changes in plant activities that can ultimately affect climate and atmospheric chemistry via transpiration, biogenic emissions, dry deposition, etc. Reduction of photosynthesis by dry deposition onto leaves is a major sink for ozone, but ozone exposure is also detrimental for the following phenomenon:

- Plant tissues \rightarrow impact on ecosystems and crops.
- Reduces stomatal conductance (damage).
- Surface ozone is a major air pollutant (causing ~0.7 M deaths/year).
- Reduces leaf Area Index (damage).
- Toxicity of ozone on plants shows symptoms comprising foliar damage, premature leaf erosion, decrease in growth and limited belowground of proportion of carbon.

The effect of O_3 exposure on plants and their eventual influence on ecosystem is given in Fig. 6.3.

6.4.1 Effects of Ozone Stress on Stomatal Conductance

The mechanistic pathway of ozone influence on stomatal conductance is by injuring the epidermal cells and causing them to break and open wide (Sonwani et al. 2016).

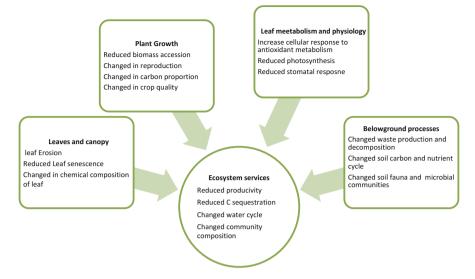


Fig. 6.3 Effect of O₃ exposure on plant ecosystem

This leads to closing of stomata and decrease in stomatal conductance. Besides stomatal functions, ozone exposure damages photosynthetic tissues and reduces photosynthetic pigments (Saxena et al. 2017).

The O_3 exposure goes hand in hand with the weather conditions. Stagnant weather conditions limit the dose of ozone absorption. Also, it is interesting to note that low humidity leads to low stomatal conductance.

On studying the effect of O_3 exposure on *B. nigra*, it was observed that even a short-term exposure reduced stomatal conductance and leaf transpiration, resulting in low quantities of intracellular CO_2 . A long-term exposure, on the other hand, increased intracellular CO_2 . The bleaching and chlorosis of the leaves was observed and was attributed to increase in CO_2 concentration (Paoletti and Grulke 2005).

 O_3 stress also brings about the appearance of *MYB44* gene. This gene takes a major role in responses to abioitc and biotic stress. It is believed that the appearance of *MYB44* elevates tolerance to low rainfall, by improving stomatal closure, leaf senescence and ROS scavenging. This is indicative of the extreme stress in plants because of O_3 exposure, matching draught- or famine-like situation (Baldoni et al. 2015; Jung et al. 2008; Jaradat et al. 2013).

6.4.2 Effects of Ozone on Photosynthesis

The plants exposure to ozone is the main internal factor which influences the rate of photosynthesis through multiple ways. The change in the photosynthetic rate on O_3 exposure depends on variety of plant, leaf age, O_3 concentration and exposure time,

and other environmental conditions (Moldau et al. 1993; Dizengremel 2001). Along with these factors, reduced carboxylation efficiency is also found as an important factor for reduced photosynthesis (Pell et al. 1992, 1994; Farage and Long 1999). Due to the strong oxidizing nature of O_3 , it significantly reduces photosynthesis and therefore responsible for reduction in ribulose 1.5-bisphosphate carboxylase/ oxygenase (Rubisco) activity (Dizengremel 2001), and decreases the CO_2 uptake of leaf (Farage et al. 1991).

Many researchers have found that ozone generally decreases photosynthetic rate of plants (Bagard et al. 2008) and also reduces plant productivity (Dizengremel 2001). Along with this, O_3 is also responsible for chlorophyll degradation and early leaf ageing (Bergmann et al. 1999; Ranieri et al. 2001). In a similar study on soyabean leaves, a reduction in chloroplast content, photolysis and oxygen of water was found when soyabean leaves was exposed to O_3 . This is due to the fact that this increased ozone accounts for reduced phosphorylation (Julia and Kangasjärvi 2015). Moreover, persistent O_3 exposure above 40 nL L⁻¹ concentration produces reactive oxygen species (ROS) which prevent uptake of O_3 through leaf by closing the stomata (Bergmann et al. 1999; Ranieri et al. 2001; Vahisalu et al. 2010).

Many researchers have studied the effect of concentrations and exposure time of O_3 on photosynthesis to know the effect of threshold concentrations and dose–response relationships. Some studies show reduction in photosynthesis when short-term exposed at 100 ppb, while others show reductions at 200–500 ppb. On long-term exposure to O_3 (<1 d) at 35–45 ppb also effects photosynthesis in crop plants (Reich and Amundson 1985).

Some studies reveal that the effect of O_3 exposure on tree species was only at higher concentrations or at long-time exposure than in herbaceous plants (Barnes 1972). Other species were more tolerant. In some cases, it was established that the O_3 exposure affects the newly enlarged foliage much more than mature foliage. It was evident when newly enlarged foliage of white pine was exposed to 150 ppb of O_3 for 19 days; it did not survive for 77 days long exposure.

The effect of O_3 on photosynthetic rate in another plant species was calculated at 85 and 125 ppb ozone exposure, and it was found that this affect the quantum yield, light dispersion value and the light damages point of the photosynthesis responses.

The O_3 exposure also affects photosystem I and II in plants. When *Spinacia* oleracea chloroplast was exposed to O_3 , the electron transport system in both photosystems was inhibited; however, photosystem I was found much more effected than photosystem II (Reich and Amundson 1985; Coulson and Robert 1974). This may be due to the reduced photophosphorylation which resulted from reduction in electron transport. O_3 affected the chlorophyll content of the treated plants (Leffler and Cherry 1974). In another research a strong connection was observed between chlorophyllioss and visible necrosis (Knudson et al. 1977). The reduction comparison of Chlorophyll a to Chlorophyll b was also observed on O_3 exposure. This may be due to the fact that chlorophyll a has much more affinity towards O_3 than chlorophyll b.

Schreiber et al. (1978) reported the effect of O_3 on the fluorescence characteristics in *Phaseolus vulgaris*. The results showed that a long-time exposure at low concentration was much more injurious than a short-time exposure at high concentration. On this basis it was concluded that the effect of O3 on fluorescence is due to its action on the donor site of Photosystem II. On further increase in O_3 exposure, it reduces the electron transfer from Photosystem II to Photosystem I (Schreiber et al. 1978).

6.4.3 Effects of Ozone on Respiration and Photorespiration

The respiration in plants is generally found to increase when exposed to ozone above a threshold concentration. The O_3 exposure can either raise (Todd 1958; Barnes 1972) or reduce respiration rate in plants. In a study, researchers observed no immediate effect on respiration after O_3 exposure on *Phaseolus vulgaris*, but after long exposure for about 24 h some adverse effects occurred (Pell and Brennan 1973). Furthermore, at 150 ppb concentration of ozone, decreased level of respiration occurred. Ozone exposure also inhibited respiration in *Nicotiana tabacum* leaf mitochondria (Lee 1967).

In several researches it is observed that the rate of photosynthesis also affects the rate of respiration in plants. If photosynthetic rate is very high, then a small change in the rate of respiration will not alter carbon balance of the plant, while low photosynthetic rate can cause changes in respiration and thus can affect the development of the plant.

6.4.3.1 Photorespiration

The photorespiratory pathway arises through the oxygenation of ribulose-1,5 (RuBP) by Rubisco that produced bisphosphate one molecule 3-phosphoglycerate and one molecule of the 2-carbon compound phosphoglycolate. The photorespiratory cycle permits the process of changing of this compound into 3-phosphoglycolate through a number of reactions that controls across three different compartments—chloroplasts, peroxisomes and mitochondria and releases CO₂ and NH_3 (Mouillon et al. 1999). Lots of studies show that photorespiration adversely affected leaf phenology in ozone-treated leaves during photosynthesis process (Bagarda et al. 2008).

Stromal CO₂ concentration reduced when low stomatal conductance will promote photorespiration, thus reducing the C:O ratio. In the light one of the factors activating stomatal closure, dry period and salt/osmotic stress are noted. Despite that, many bacterial pathogens that capture on the leaf through the stomata, such as *P syringae*, can also activate this response (Melotto et al. 2008).

6.5 Conclusion and Future Recommendations

The present review concludes that several morphological parameters do get affected by the air pollutant-induced stress. Stress caused by air pollution results in decreased photosynthetic rate, chlorophyll content, stomatal conductance, net photosynthetic carbon dioxide assimilation and carboxylation effectiveness. These parameters primarily include leaf characteristics like cuticle, stomata, etc. The leaf stats in turn influence gaseous exchanges including respiration and photorespiration in plants which further increase environmental stress. It is imperative to understand that effect of individual pollutants is quite different from each other and also from species to species. For instance, NO_x in low concentration acts as a growth promoter.

Environmental stress along with the plant response towards them leads to an eventual slow-down of total biomass growth rate. The need of the hour is to address the knowledge gap in quantification of effect of individual pollutants as well as in combined form on stress physiology. Even the changes observed are small, yet they play a critical role in existence of plant in stress. It should remain in mind that the overall effects of air pollutants on physiological parameters are not exclusive of each other. All of them are inter dependent and the remedial actions should include the holistic measures to balance the ecosystem stability and socio-economic upgradation.

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