Pollution, 6(4): 827-848, Autumn 2020
DOI: 10.22059/poll.2020.303151.821
Print ISSN: 2383-451X Online ISSN: 2383-4501
Web Page: https://jpoll.ut.ac.ir, Email: jpoll@ut.ac.ir

Physiological and Growth Responses to Pollutant-Induced Biochemical Changes in Plants: A Review

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Received: 19.05.2020 Accepted: 01.07.2020

ABSTRACT: Industrial activities compromise the ambient air quality at a local, regional and global level through gaseous and dust emissions. This study reviews uptake mechanisms and the associated phytotoxicity of pollutants in plants, focusing on heavy metals and SO_2. It further describes detoxification mechanisms and the resultant biochemical and physiological changes in plants. Finally, the morpho-physiological and growth responses to stress-induced biochemical changes are discussed. Heavy metals and SO_2 enter the plant tissue through the stomata, cuticular layers, lenticels and root hairs. In the plant cells, SO_2 converts to SO_3^{2-} or SO_4^{2-} ions upon reacting with water molecules, which in excess are toxic to plants. However, the detoxification process of SO_3^{2-} increases the production of reactive oxygen species (ROS). ROS are toxic to plants and damages biomolecules such as lipids, proteins, carbohydrates and DNA. On the other hand, heavy metals, such as Cu and Fe catalyse the Fenton/Haber-Weiss reactions, breaking down H_2O_2 into $OH^{\bullet}$. Additionally, Pb and Zn inhibit the activities of ROS-detoxifying enzymes, while other heavy metals bind to cellular layers making them rigid, thereby reducing cell division. Therefore, pollutant toxicity in plants affects biochemical parameters damaging organic molecules and limiting cambial activity. Damaged biomolecules inhibit the plant's capacity to carry out physiological functions, such as photosynthesis, stomatal functions, transpiration and respiration while impaired cambial activity reduces cell division and elongation resulting in reduced plant growth and productivity.

Keywords: Heavy metals, SO_2, biomolecule damage, physiological functions, cambial activity.

INTRODUCTION

Industrial pollution sources produce a wide range of pollutants in a combined form including gases and dust emissions depending on the industrial processes of a particular site. Gaseous pollutants may account for Sulphur dioxide (SO_2), Nitric oxides (NO_x), Carbon dioxide (CO_2) and Carbon monoxide (CO). Comparatively, the composition of dust emissions may include heavy metals, such as Zinc (Zn), Manganese (Mn), Copper (Cu), Iron (Fe), Nickel (Ni), Mercury (Hg), Cadmium (Cd), Chromium (Cr), Lead (Pb) and Aluminium (Al). Most pollutants emanating from industrial processes are aerodynamic (Ncube et al.,

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2014) and are therefore dispersed by wind and the constituents deposited across the nearby landscape. Gaseous pollutants and particulate matter become available for uptake by plants via the leaf stomata and cuticles, bark lenticels and root hair.

Heavy metals, such as Mn, B, Fe, Mo, Ni, Cu and Zn are required in trace amounts as plant micronutrients (Etienne et al., 2018; Tripathi et al., 2015), while non-essential elements like Pb, Hg, Al, Cr, and Cd are toxic to plant life even in traces (Emamverdian et al., 2015). Conversely, research has shown that even those required in traces may become toxic to plants at elevated levels (Emamverdian et al., 2015; Kulshrestha & Saxena, 2016). According to Tripathi et al. (2015), Fe in excess of 2000 mg/kg in plants is considered toxic, while Cu, Zn, Mn and B toxicity threshold stands at 25 mg/kg, 120 mg/kg, 200 mg/kg and 80 mg/kg, respectively. Further, non-essential elements exhibit phytotoxicity at such low concentrations as 3 mg/kg (Al), 10 mg/kg (Cd), 28 mg/kg (Pb) and 100 µg/kg (Cr) (Amari et al., 2017; Shanker et al., 2005). Similarly, at low concentration SO_2 stimulates physiological processes and growth of plants growing in sulphur (S) deficient soil where sulphate is metabolised to meet the demand for S as a nutrient (Khan & Khan, 2011). On the other hand, excess sulphite (SO_3^{2-}) or sulphate (SO_4^{2-}) ions resulting from increased uptake of SO_2 by plants are toxic and affect plant growth and productivity (Brychkova et al., 2007).

Studies show that exposure to air pollution alters the biochemical (Seyyednejad et al., 2013; Wang et al., 2009; Woodward & Bennett, 2005), morphological (Ahmed et al., 2016; Leghari & Zaidi, 2013; Pourkhabbaz et al., 2010; Salam et al., 2016; Saleem et al., 2019) and physiological (Gupta & Sarkar, 2016; Sen et al., 2017; Thakar & Mishra, 2010; Pourrut et al., 2011) characteristics of plants. Ultimately, the pollutant-induced changes affect the growth and productivity of plants growing in air polluted environments. Seyyednejad & Koochak (2013) argued that plant response to environmental toxicities depends on factors, such as plant species and age, the pollutant type and exposure conditions, such as duration, levels and season. The observed changes in morphological and physiological characteristics suggest the activation of strategic adaptation mechanisms in mitigating the detrimental effects of toxicants in a stressful environment (Leghari & Zaidi, 2013).

The phytotoxicity of SO_2 and heavy metals in plants can be traced from biochemical reactions at the cellular level. However, most reviews focus on the growth and yield changes as a response to pollution stress. This manuscript delineates the plant morpho-physiological and growth alterations in response to pollutant-induced biochemical stress. It first reviews uptake mechanisms and the associated phytotoxicity of pollutants in plants focusing on heavy metals and SO_2. Subsequently, enzymatic and non-enzymatic attempts at pollutant detoxification and the resultant changes in biochemical and physiological reactions are described and finally, the morpho-physiological and growth responses to stress-induced biochemical changes are discussed.

Uptake Mechanisms and Phytotoxicity of Sulphur Dioxide and Heavy Metals

Sources and Dispersion of Environmental Pollutants

There are two primary sources of pollutants in the environment, namely natural and anthropogenic sources. Putrefying organic matter, volcanic eruptions and solar action on seawater constitute the natural sources (Cullis & Hirschler, 1980; Singh et al., 2012), while processes, such as smelting, refining and fossil fuel combustion account for human-induced sources (Gheorghe & Ion, 2011). Figure 1 shows the most common sources of environmental pollutants, such as SO_2, NO_X, VOC_s, heavy metals, CO and CO_2.

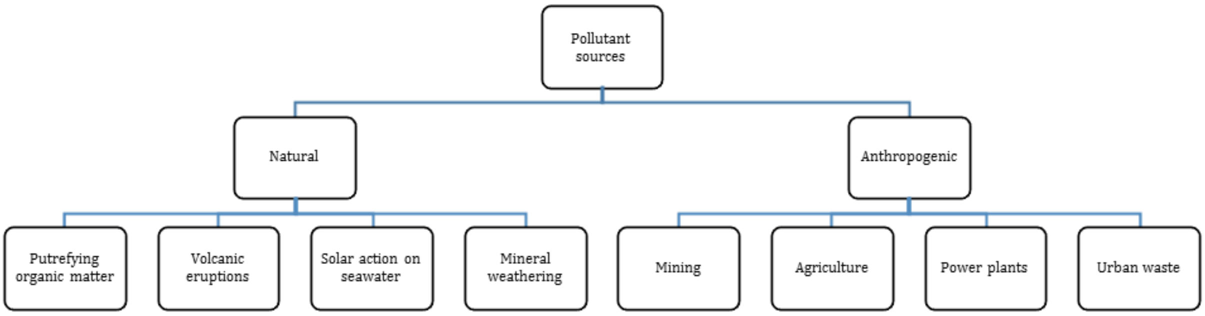

Fig. 1. Common sources of natural and anthropogenically-induced environmental pollutants

Environmental pollutants such as SO_2 and heavy metals emanating from industrial activities are aerodynamic and dispersed by the wind across a given landscape (Ncube et al., 2014). Therefore, weather conditions and topography play an essential role in dispersing these pollutants across landscapes around fixed pollutant sources (Cassiani et al., 2013).

Uptake and Toxicity of Sulphur Dioxide in Plants

SO_2 enters the plant tissue either through leaves or roots (Lee et al., 2017). In leaves, it penetrates through the stomata regulated by the guard cells. It further diffuses into the mesophyll cells and converts to SO_3^{2-} or SO_4^{2-} ions upon reacting with water molecules (Khan & Khan, 2011). The internal (mesophyll) resistance to SO_2 is low, because it is highly soluble and dissolves rapidly in the cell sap. Slow conversion of SO_2 to SO_3^{2-} leads to their oxidation to SO_4^{2-} and consequently utilisation by plants (Brychkova et al., 2007; Friend, 1973; Khan & Khan, 2011). Excess $SO^{2-}{}_4$ or $SO^{2-}{}_3$ is toxic to plant life, although the latter is about 30 times more toxic (Thomas et al., 1943).

According to Omasa et al. (2008), the detoxification process of SO_3^{2-} to SO_4^{2-} increases the production of toxic reactive oxygen species (ROS), hydrogen peroxide (H_2O_2) and superoxide radicals ($O_2^{\bullet-}$). Furthermore, stomatal closure triggers an insufficient concentration of intercellular CO_2, which instigates the formation of singlet oxygen atoms-$^1O_2$ (Das & Roychoudhury, 2014) another family member of the toxic ROS, which also includes hydroxyl radicals ($OH^{\bullet}$). Singlet oxygen causes severe damage to proteins, lipids, pigments and nucleic acids (Dogra & Kim, 2020) putting photosystems and photosynthetic machinery into jeopardy (Das & Roychoudhury, 2014). On the other hand, $O_2^{\bullet-}$ transforms into the more toxic and reactive $^1O_2$ and $OH^{\bullet}$, which causes lipid peroxidation (Halliwell, 2006).

H_2O_2 has two roles, depending on its intercellular concentration. It regulates the signal for physiological processes such as photorespiration, photosynthesis and senescence (Das & Roychoudhury, 2014; Tanou et al. 2009) at low concentration. At high intercellular concentration, H_2O_2 oxidises methionine ($-SCH_3$) and cysteine ($-SH$) residues and inactivated Calvin cycle enzymes iron superoxide dismutase (Fe-SOD) and Cu/Zn-SOD by oxidising their thiol groups. Bienert et al. (2007) noted that the longer half-life of H_2O_2 enables it to traverse long distances and across cell membranes through aquaporins covering significant lengths within the cell and cause oxidative damage. They further argued that H_2O_2 is responsible for programmed cell death and 50% loss of enzymatic activities at a high cellular concentration.

Additionally, $OH^{\bullet}$ is generated by the Fenton and Haber-Weiss-type reactions and is the most toxic and reactive among the members of the ROS family (Barceló &

Gómez Ros, 2009). According to Das & Roychoudhury (2014), $OH^{\bullet}$ destroys cellular compartments through protein destruction, lipid peroxidation and membrane damage.

Furthermore, Pinto et al. (2003) observed that the lack of enzymatic mechanisms to scavenge $OH^{\bullet}$ triggers its excess accumulation in plant tissues and cause cellular death.

Uptake and Translocation of Heavy Metal in Plants

Heavy metals penetrate the foliar surfaces through the stomata, lenticels, ectodesmata and cuticular cracks (Fernández & Brown, 2013; Shahid et al. 2016). Therefore, particle size plays an essential role in the adsorption of heavy metals into the leaves. Smaller particles penetrate the plant leaves more quickly compared to the larger ones remaining stuck on the surface wax. Eichert et al. (2008) reported the penetration of small size nanoparticles (43 nm) of Cu into *Vicia faba* leaves, while the larger sized particles (1.1 µm) failed to penetrate through the stomata.

Heavy metals exist in the soil solution as ions where plant roots can access them. Heavy metals together with micronutrients are then absorbed by the root hair and transported via the symplastic and apoplastic pathways and loaded onto the xylem for upward translocation along the transpiration stream (Luo et al., 2016; Page et al., 2006). The transpiration stream transports heavy metals through the xylem from root tissues to different parts of the plant (Page & Feller, 2015). The rate and extent of translocation are dependent on many factors, including the tree age and species as well as metal speciation (chemical form-free ion or complexed to a ligand) (Adriano, 2001; Roberts et al., 2005). Therefore, transporters - mainly proteins - of essential micronutrients in the soil solution facilitate the uptake of toxic metals into the plant roots. Shi et al. (2019) noted that transporters of trace elements include the family members of the natural resistance-associated macrophage protein (NRAMP), zinc-iron permease (ZIP) and heavy metal ATPases (adenosine) (HMA) localised in different parts of the root compartments. Studies on *Arabidopsis thaliana* and *Noccaea caerulescens* show that each family member from the three main categories of transporters is involved in the transportation of different ions depending on its affinity (Milner et al., 2013, 2014). For example, AtZIP2 is localised in the plasma membrane and is involved in the uptake and transport of Mn^{2+}/Zn^{2+} into the root stellar cells while AtZIP1 acts as a vacuolar exporter. According to Lin et al. (2016), NcZNT1, a homolog of AtZIP4 is a plasma membrane-localised transporter of Zn^{2+} and Cd^{2+} while (IRT1) absorbs Fe^{2+}, Fe^{3+}, Cd^{2+} and Zn^{2+} in the same plant species (Lombi et al., 2002). NcZNT1's promoter is mainly active in the cells of the cortex, endodermis and pericycle of *Noccaea caerulescens* roots.

Additionally, the NRAMP family members specialise in transporting bivalent metal ions into the root cells (Milner et al., 2014). On the other hand, HMAs transports both monovalent and divalent heavy metal ions in plants. Localised in the chloroplast (AtHMA1) and plasma membranes (AtHMA2 and AtHMA4), these HMAs family members export ions from the chloroplast across the cytosol into the vascular cylinder facilitating their movement from roots to shoots (Cun et al., 2014).

Further, some toxic metal ions form complexes with phytochelatins, which include malate, citrate and histidine (Kozhevnikova et al., 2014; Kozlov et al., 1999). According to Richau et al. (2009) and Fourcroy et al. (2014), heavy metal ions in the complex form are then absorbed into the root cells by oligopeptide and ATP-binding cassette transporters (ABC). Luo et al. (2016) argued that there is scant information on the mechanisms governing the uptake of heavy metals by woody plants. They noted that scientific information suggests that the influx of toxic metals into woody plant roots is higher than into herbaceous plants. For example, He et al. (2011) reported a 100 times higher Cd^{2+} influx into the roots of woody *Populus tremula* x *Populus alba* than the herbaceous *Triticum aestivum*.

Phytotoxicity of Heavy Metals and Biochemical Responses in Plants

The bioactivity of heavy metals partly depends on their physicochemical properties grouped as redox-active and non-redox active (Emamverdian et al., 2015; Jozefczak et al., 2012). Bielen et al. (2013) explained that non-redox active heavy metals have an indirect action on the toxification of plant life as compared to the direct role redox-active heavy metals plays. Non-redox active metals cause oxidative stress by inducing ROS-producing enzymes, glutathione depletion, antioxidative enzymes inhibition and binding to sulfhydryl groups of proteins. On the other hand, redox-active metals generate oxidative injury by undergoing Fenton reactions, thereby producing ROS toxic to plant macromolecules.

Excess heavy metal concentrations trigger the formation of ROS toxic to plant cells injuring the macromolecules required for healthy plant functioning. Upon interacting with cytoplasmic proteins, heavy metals reduce the concentration of the protein pool in plants (Gupta et al., 2010; Pourrut et al., 2013, 2011). Pourrut et al. (2013) and Gupta et al. (2010) observed that a protein pool reduction causes ROS-induced acute oxidative stress, protease activity stimulation, gene expression modification and free amino acid reduction. Yadav (2010) noted the generation of ROS is a well-known attribute of heavy metal toxicity in plants. He argued that ROS targets cellular antioxidants reserves, and upon exhaustion, they quickly attack and oxidise all types of biomolecules, especially lipids, proteins and nucleic acids.

In addition to their influence on the generation of the ROS, heavy metals are capable of singularly or in combination causing adverse effects on the cell compartments. Pourrut et al. (2011) observed that Pb induces its phytotoxicity through binding the Pb^{2+} to cell membranes and cell wall producing rigidity in these cellular components leading to a reduction in cell division. It further promotes the production of abnormal cells at the colchicine-mitosis stage through the induction of disturbances in the cell division stages M and G_2. Further, Baran (2013) deduced that the phytotoxicity of Zn depends on the bioavailability factors, plants species and plant development stage. Zn reduces the photosynthetic pigments including total chlorophyll by disturbing Mg and Fe absorption and translocation into the chloroplasts (Emamverdian et al., 2015). The disturbance affects the efficiency and functionality of the entire photosynthetic machinery. In addition, the toxicity of Cu reduces total chlorophyll and carotenoid content compromising the plant photosynthetic competence and reduce cell elongation (Li et al., 2018; Nicholls & Mal, 2003). Ni creates an artificial deficiency of Zn^{2+} and Fe^{2+} by outcompeting them during plant uptake resulting in chlorosis expression in plants (Aydinalp & Marinova, 2009; Emamverdian et al., 2015). Fe and Zn deficiency affects plant growth parameters leading to poor nodulation and reduced yield.

Further, studies have shown that Mn toxicity reduces CO_2 assimilation, total chlorophyll content, root and shoot growth depending on plant species and levels of light (Li et al. 2010). Other metals, such as Al^{3+} binds to DNA and hinders cell division in roots due to improved rigidity of double helix in cells walls and DNA (Steiner et al., 2012). In the process, it leads to perturbations in the absorption and translocation of Ca, Mg, P and K nutrients. It further causes necrosis and chlorosis in young and older leaves, respectively and decreases stomatal regions and photosynthetic activity (Batista et al., 2013; Trevizan et al., 2018).

Additionally, the phytotoxicity of Arsenic (As) depends on its bioavailability and speciation (Mohan & Pittman, 2007). In the oxidation state, Arsenate (AsO_4^{3-}) and Arsenite (AsO_3^{3-}) also referred to as As(V) and As(III), respectively, are the main species of As in the environment (Joseph et al., 2015). In plant tissues, As(V) is converted to mobile, soluble and toxic As(III); a process leading to the production of ROS through the utilization of O_2 as the final receptor of electrons (Talukdar, 2013). Sharma (2012) added that electron leakage and enzyme inhibition during the conversion of As(V) to As(III) create pathways for ROS production in plants. Furthermore, As(V) conversion is followed by the biomethylation of As generating methylated forms of As such as tetramethylarsonium ions, monomethylarsonic and arsenobetaine, which are more reactive with O_2 favouring the formation of ROS (Abbas et al., 2018). In addition to ROS generation, As(III) toxicity disrupts plant metabolism by reacting with sulfhydryl groups of proteins and enzymes, thereby causing detrimental effects on plant cells (Akter et al., 2006). On the other hand, remnant As(V) interferes with the ATP molecule by generating unstable ADP-As which affects energy flow in cells and causes cell death (Manzano et al., 2015).

Several studies have demonstrated that As exposure in plants inhibit root extension and promote stunted growth (Nel et al., 2006), reduces gaseous exchange and damage chloroplast membranes (Anjum et al., 2011; Debona et al., 2017) and damage cellular membranes leading to reduced stomatal conductance, photosynthesis, transpiration, water transport and nutrient uptake (Gill & Tuteja, 2010; Sharma et al. 2012).

Pathway and Detoxification of Reactive Oxygen Species in Plants

Heavy Metal-Induced Generation of ROS

ROS are produced under natural and pollutant-induced conditions in various locations, including the plasma membranes, chloroplasts, peroxisomes, mitochondria and the cell wall (Gurda et al., 2012; Pucciariello et al., 2012). Under natural conditions, incomplete reduction of oxygen (O_2) lead to the generation of ROS as unavoidable byproducts of aerobic metabolism (Asada, 2006). The reduction of O_2 to water (H_2O) during the healthy cellular metabolism produces $O^{\bullet-}$, H_2O_2 and $OH^{\bullet}$ through energy or electron transfer reactions (Shahid et al., 2014). Several studies (Kumar et al., 2012; Achary et al., 2012; Sheng et al., 2015; Sun et al., 2010; Valko et al., 2005) reports increased production of ROS in plants exposed to heavy metal-induced stress. The reported increase in ROS under pollutant-induced conditions is attributed to the imbalance between its generation and elimination (Kováčik et al., 2010). Furthermore, Pourrut et al. (2011) observed that heavy metals deplete ROS scavenging glutathione (GSH) and many other antioxidants, thereby disrupting the ROS balance through its enhanced production and accumulation in plant tissues.

Specifically, the metal-induced generation of ROS in plants is dependent on the nature of the metals involved. Redox-active heavy metals, e.g. Cu and Fe, catalyse the Fenton and Haber-Weiss reactions, respectively (Barceló & Gómez Ros, 2009). On the other hand, redox-nonactive metals, e.g. Pb and Zn, inhibit the activities of enzymes (Opdenakker et al., 2012). For example, Pourrut et al. (2011) and Shahid et al. (2014) noted that Fe and Cu catalyse the Fenton reaction at neutral pH breaking down H_2O_2 into $OH^{\bullet}$, whereas Pb and Zn have a high affinity for -SH groups, affecting the healthy functioning of enzymes.

In the initial stages, ROS are unable to cause damage, because different antioxidant mechanisms scavenge them. However, the balance between ROS production and elimination is easily disturbed by factors ranging from abiotic to biotic stresses. Abiotic stress factors include: gaseous pollutants, drought (water deficiency conditions), high light intensity and temperature, soil salinity (excess Na^+, K^+ and Cl^- ions) and heavy metals, while pests and diseases cause biotic stress.

According to Choudhury et al. (2013), peroxisomes and chloroplasts are the leading producers of ROS in the presence of light and mitochondria take charge under dark reactions. In the chloroplast, ROS are produced by the core light-harvesting system composed of photosystems, PSI and PSII. As a consequence, water stress, low CO_2 and excess light necessitates the formation of $O_2^{\bullet-}$ at the PS through a Mehler reaction (Das & Roychoudhury, 2014) and $O_2^{\bullet-}$ then converts into the more toxic $OH^{\bullet}$ via the Fenton reaction. Furthermore, Das & Roychoudhury (2014) noted that mitochondrial ETC (mtETC) houses electrons with sufficient energy to reduce oxygen and generate ROS. Complex III and Complex I are the primary components of mtETC responsible for ROS production (Noctor et al., 2007). Mitochondria generally produce ROS in normal conditions, but are significantly boosted under stressful conditions (Pastore et al., 2007). Peroxisomes are the main production sites of intercellular H_2O_2 hydrogen peroxide generation, because of their integral oxidative metabolism (Río & Puppo, 2009). Wrzaczek et al. (2011) further noted that like mitochondria and chloroplast peroxisomes produce $O_2^{\bullet-}$ during various metabolic processes.

The ROS-Induced Destruction of Organic Molecules

The three significant biomolecules at the receiving end of ROS attack in plants are: DNA, proteins and lipids. According to Das & Roychoudhury (2014), ROS causes extensive damage to proteins, DNA, lipids and carbohydrates. Pourrut et al. (2011) argued that the indirect effect of heavy metals on plants via organic molecules-damaging ROS generation are rapid and toxic than their direct effect.

Lipids provide energy for cellular metabolism, cell membrane building and organelle maintenance, among other functions (Møller et al., 2007; Xiao & Chye, 2011). However, through the production of excess ROS, heavy metals trigger lipid peroxidation (LPO). LPO is the worst form of heavy metal phytotoxicity, because it deteriorates cell membranes. Das & Roychoudhury (2014) noted that lipid radicals initiated by the LPO chain reaction and oxidative stress causes damage to DNA and proteins. The polyunsaturated fatty acids (PUFA) are the hotspots for ROS-induced damage. PUFAs are prone to ROS attack, especially $^1O_2$ and $OH^{\bullet}$, but the latter is more destructive as it triggers cyclic chain reactions causing further peroxidation of several PUFAs.

Additionally, heavy metal-induced ROS affects the structure and synthesis of proteins in plants by changing the protein quality and quantity through several mechanisms. The mechanisms include: 1) binding metal ions to free protein functional groups and 2) replacing micronutrients in metal-dependent proteins with free heavy metal ions (Shahid et al., 2014). Ultimately, heavy metal-induced ROS quantitatively reduces the total protein content in cells. The quantitative reduction of proteins results from the modification of gene expression, reduced amino acid content, consumption of ROS-scavenging amino acids and increased ribonuclease activity (Gupta et al., 2010).

Although the mechanisms governing the heavy metal-induced genotoxicity is not fully understood, research has shown that ROS instigates the propagation of heavy metal-induced DNA damage in plant cells (Barbosa et al., 2010; Shen et al., 2012). According to Das & Roychoudhury (2014), ROS severely attacks mitochondria and chloroplast DNA due to a lack of histones and associated proteins and the proximity to the ROS generation machinery. The $OH^\bullet$ is the most reactive member of the ROS family and damages all components of DNA molecules upon interaction (Hirata et al., 2011). For example, the interactions between DNA and ROS lead to the destruction of DNA-protein cross-links, base modifications and deletions, as well as pyrimidine dimers damage and strand breaks (Pourrut et al., 2013). Barbosa et al. (2010) and Pourrut et al. (2011) reported DNA damage in response to heavy metal stress.

Detoxification of ROS through Enzymatic Antioxidants

The ubiquitous superoxide dismutase (SOD) forms the first line of defense against ROS-induced phytotoxicity. As a catalyst, SOD promotes the breakdown of $O_2^{\bullet-}$ into H_2O_2 and O_2 avoiding the formation of the more toxic and reactive $OH^\bullet$ (Hossain et al., 2015). SOD are common ROS-scavenging antioxidants found in different cellular components and are classified based on the ions binding them. Examples are manganese-SOD in the mitochondria, iron-SOD in the chloroplast and copper/zinc-SOD found in the peroxisomes, chloroplasts and cytosol (Das & Roychoudhury, 2014; Kim et al., 2009). Other known ROS-eliminating antioxidant enzymes include guaiacol peroxide (GPX) catalase (CAT), glutathione reductase (GR), dehydroascorbate reductase (DHAR), monodehydro- ascorbate reductase (MDHAR) and ascorbate peroxidase (APX).

Das & Roychoudhury (2014) argued that CAT has a high affinity for H_2O_2 catalysing the dismutation of $6x10^6$ molecules of H_2O_2 to O_2 and H_2O under a minute. They further noted that APX eliminates H_2O_2 in the chloroplast and cytosol reducing it to H_2O and dehydroascorbate (DHA). In this process, ascorbic acid (AA) is used as a reducing agent. The AA cellular pool is replenished by MDHAR and DHA using NADPH and DHAR as reducing agents, respectively (Shi et al., 2019).

Detoxification of ROS through Non-Enzymatic Antioxidants

Non-enzymatic antioxidants are other plant defense mechanisms utilised to detoxify the stress-induced ROS. These include: α-tocopherol, proline, ascorbic acid, flavonoids, carotenoids and GSH. Shi et al. (2019) and Das & Roychoudhury (2014) argued that ascorbic acid is the most abundant antioxidant capable of donating electrons to a range of both non-enzymatic and enzymatic reactions. The substantial accumulation of ascorbic acid in the cytosol and apoplast places it first in the defense line against ROS attack (Omasa et al., 2002; Smirnoff & Wheeler, 2000). It protects cell membranes from ROS-induced damage by reacting with $OH^\bullet$, H_2O_2, and $O_2^{\bullet-}$ to regenerate α-tocopherol from tocopheroxyl radical. At a cellular level, ascorbic acid plays a role in cell division, cell wall synthesis and protection (Seyyednejad & Koochak, 2013). Studies have shown that in air polluted environments, the content of AA is higher for tolerant plants than sensitive species (Sen et al., 2017; Seyyednjad et al., 2011).

As a free radical scavenger, proline protects plants from ROS-induced damage (Seyyednejad et al., 2011) by scavenging $OH^\bullet$, and $^1O_2$ and inhibits the damages caused by LPO. Studies have reported elevated concentration of proline in plants exposed to pollution stress. The accumulation of proline in stressful environments is attributed to either its reduced degradation or enhanced production (Das & Roychoudhury, 2014). Kameswaran et al. (2019) argued that its ability to accumulate in plants during pollutant stress is beneficial to plants for the role it plays in ROS elimination than the other more effective amino acids, e.g. tyrosine, tryptophan and histidine.

Seyyednejad et al. (2009) and Wang et al. (2009) report that because of the positive correlation between proline content and SO_2 concentration in some species, there is need to re-designate SO_2 toxicity threshold for particular species. For example, significant accumulation of soluble sugar and proline have been reported in *Eucalyptus camaldulensis* in a polluted site compared to reference samples (Seyyednejad & Koochak, 2011). Furthermore, Wang et al. (2009) explained that there is a positive correlation between lipid peroxidation and proline accumulation in plants exposed to air pollutants. Earlier studies (Tankha & Gupta, 1992; Woodward & Bennett, 2005), reported increased proline accumulation in the leaves of plants subjected to SO_2, heavy metals and salt stresses. Therefore, proline accumulation plays a vital role in inhibiting pollutant-induced toxification in plants.

According to Das & Roychoudhury (2014), carotenoids are localised in both non-photosynthetic and photosynthetic plant tissues. Carotenoids are natural fat-soluble pigments and play a role in the plant's photosynthetic processes (Seyyednejad et al., 2011). Like chlorophyll, carotenoids gather light energy in chloroplasts and protect chlorophyll from photooxidative destruction (Seyyednjad et al., 2011). Furthermore, carotenoids protect the photosynthetic machinery by scavenging $^1O_2$ and generating heat energy as a byproduct (Shahid et al., 2014). They also react with LPO products, thereby ending the chain reaction and transferring energy to chlorophyll molecules (Das & Roychoudhury, 2014). Some researchers (Kováčik et al., 2012; Prajapati & Tripathi, 2008; Seyyednejad et al., 2011) have reported a reduction in the content of carotenoid pigments in leaves in response to pollution stress. For example, Kováčik et al. (2012) reported reduced water content, sugar, chlorophyll_a, chlorophyll_b and carotenoids in *Tillandsia albida* exposed to Cd and Ni stress.

GSH is involved in cell division, differentiation, growth, senescence and death (Shahid et al., 2014). It is found in most plant cellular compartments and performs multiple functions, such as regulating sulphate transport, enzymatic activities and synthesising proteins, nucleotides, phytochelatins, detoxifying xenobiotics and protection against abiotic stress (Mullineaux & Rausch, 2005). They noted that GSH participates in both enzymatic and non-enzymatic activities and scavenges on all types of ROS to protect different organic molecules. Furthermore, GSH is involved in the regeneration of AA, which is a ROS scavenger.

Morpho-Physiological Responses to Stress-Induced Biochemical Changes

Photosynthesis

There is overwhelming evidence documenting the changes in the photosynthetic activity of plants grown in polluted environments. The decrease in the photosynthetic processes results from the damage caused by biochemical reactions in plant leaves (Enete et al., 2013; Joshi & Swami, 2007; Sen et al., 2017). Thakar & Mishra (2010) and Joshi et al. (2009) reported a correlation between photosynthesis rate and specific biochemical parameters. They reported reduced chlorophyll, water content, ascorbic acid and leaf extract pH with decreasing photosynthetic activity in plants. Similarly, Ali et al. (2015) and Ahmad et al. (2015) cited heavy metal interference with chloroplast replication and cell division. They noted that Cd, Cu and Pb reduce the number of chloroplasts per cell, resulting in inhibition of chlorophyll biosynthesis or impairment in the supply of essential micronutrients. Therefore, the inhibition of chlorophyll biosynthesis deprives leaves of photoreceptors required during photosynthesis.

Respiration and Transpiration

Prolonged exposure of plants to excessive SO_2 and heavy metals leads to the development of symptomatically visible injury to tissues and hidden physiological disturbances. According to Koziol & Whatley (1984), respiration taking place in several sites of the cell (mitochondria, cytoplasm and peroxisomes) is either stimulated or inhibited depending on the degree of tissue injury. Notably, the repair process uses energy from the non-damaged adjacent tissues to the necrotic ones, thereby increasing the rate of transpiration in different cell sites (Gupta & Sarkar, 2016). In the process, energy and carbohydrates required for cell division and growth are wasted through enhanced respiration in response to pollution. Plant exposure to higher SO_2 concentration reduces the net photosynthesis, while increasing the respiration rate (Addison et al., 1984; Gheorghe & Ion, 2011; Koziol & Whatley, 1984). The trade-off affects the plant carbon balance and causes acute visible damage and reduces growth rates (Ashraf & Harris, 2013). According to Miller (1988), the balance between CO_2 required for respiration and photosynthesis expresses the net CO_2 exchange during the light period. He further argued that this measurement singularly does not account for respiratory processes during the dark period nor help identify the complete physiological basis of the effect of air pollution stress on plants.

Stomatal Function and Erosion of the Cuticular Layer

Exposure to air pollutants undermines the ability of guard cells to close and open due to accumulating sulphur, heavy metals and suspended particulate matter on the leaf surface (Lee et al., 2017). Consequently, excess accumulation of pollutants on leaf surfaces affects gas exchange and reduces biochemical activities, inhibits photosynthesis and impairs reproductive processes in plants (Chaurasia et al., 2013). Therefore, alterations in the stomatal function reduce plant growth by changing the production and translocation of photosynthates. The reported decrease in stomatal frequency is an adaptive measure aimed at preventing SO_2 entry into the leaves (Lee et al., 2017). In addition, the erosion of epicuticle wax structures around the stomata facilitates SO_2 entry into internal leaf spaces causing tissue damage and plant death (Lee et al., 2017; Taylor, 1978).

According to Gupta & Sarkar (2016), most pollutants can upset the water balance in leaves, because they interfere with the function of the stomatal aperture. They argued that although the cuticle acts as a barrier to the exchange of gases and water between the atmosphere and plant leaves, gaseous pollutants and acidic water molecules reduce the integrity of the cuticular layers. Loss of cuticular integrity leads to a considerable flux of ions between cytoplasmic solutions and depositions on the leaf surfaces and cytoplasmic solutions (Winner & Atkinson, 1986). The cuticular layer of leaf and needle surfaces consists of waxes and cutin, offering the plant protection against air pollutants, insect attack, pathogen infection and hostile environmental conditions, such as frost and wind (Weigel et al., 1989). These surfaces present the initial contact and point of attack between pollutants and plants. The reaction between oxygen radicals and aromatic compounds destroys the wax layer, thereby compromising its ability to protect plants (Dhanyalakshmi et al., 2019; Shepherd & Wynne, 2006). Studies in on fir and spruce trees show that the early signs of plant exposure to gaseous pollutants are the erosion of wax layers on stomatal regions (Harrington & Carlson, 2015).

Foliar Dimensions and Injury

Leaf morphology has been used over the years to study the effects of environmental pollution on plant growth. Changes in leaf length, breadth and petiole length are indicative of biochemical and physiological disturbances caused by air pollution (Seyyednejad et al., 2009). Several studies report significant reductions on leaf dimensions and the number of leaves on trees growing in polluted sites (Assadi et al., 2011; Chukwuka & Uka, 2014; Leghari & Zaidi, 2013; Pourkhabbaz et al., 2010; Sen et al., 2017; Seyyednejad et al., 2009; Seyyednejad & Koochak, 2013). Seyyednjad et al. (2011) attributed the reduction in leaf size and frequency to reduced leaf production and enhanced premature senescence. Leaf area reduction leads to reduced absorbed radiation culminating in decreased photosynthesis (Seyyednjad et al., 2011; Tiwari et al., 2006).

The decline in plant foliar characteristics is an adaptive measure providing reduced leaf contact area with air pollutants, thereby improving the plant resistance against pollutant-induced stress. Besides, reduced leaf area balances the leaf tissue water content and increases the leaf tolerance levels under stressful conditions (Kuddus et al., 2011; Leghari & Zaidi, 2013). Furthermore, research has shown that significant morphological changes caused by environmental pollutants - including heavy metals and SO_2 - in woody plants are reductions in the growth of aerial parts and leaf size, stomatal damage and leaf injury, necrosis and chlorosis (Dumčius et al., 2011; Salam et al., 2016; Seyyednjad et al., 2011).

Further to foliar dimensions, other symptoms, such as necrotic spots and defoliation appear on leaves and tree branches following exposure to air contaminants at different concentrations and duration of exposure (Ncube et al., 2014). These symptoms are indicative of changes to plant biochemical reactions damaging the leaf pigments (Lee et al., 2017). Depending on the exposure conditions and plant species, significant symptomatic damage may range from a change in leaf colour to leaf injury. Studies have reported brown or white spots as the primary symptoms further adding yellow spots, discolouration and necrotic appearance of leaf surfaces (Ahmed et al., 2016; Lee et al., 2017).

Effect of Stress-Induced Physiological and Morphological Changes on Plants

Plant Growth and Yield

Thompson (1981) studied the impact of copper smelting activities on the growth of *Pinus monophyla*. He established three distinctive periods, i.e. a low copper production period between 1840 and 1908, higher production from 1910 to 1930 and low mining activity from 1935 until 1970. Before the intermediate period, radial growth recorded on polluted and control sites were not significantly different. However, lower mean ring widths were observed at the pollutant-stressed site. The growth rate reduced significantly during the period of increased mining activities, yielding hardly reconstructable small rings in some trees at polluted sites. The growth patterns of *P. monophyla* during this period were attributed to increased pollution emanating from enhanced mining activities. However, significant increases in tree ring widths were observed after the high production period from 1935 until 1970. The accumulative deposition of mineral nutrients, which could have been inadequate before the pollution peak period may have contributed to this unexplained growth pattern between 1935 and 1970. Unfortunately, there was no follow-up study undertaken to confirm the results and establish factors, which contributed to increased tree growth in the aftermath of excessive mining pollution.

Battipaglia et al. (2010) studied the effects of exhaust pollution on the growth of *Pinus pinea* along a high traffic road. They evaluated the correlations between the concentration of C and N stable isotopes and ring widths between 1955 and 2005. The period between 1955 and 1979 before the road construction was marked as unpolluted and the polluted period characterised the time after the road construction between 1980 and 2005. A positive correlation was detected, showing significant differences between ^{13}C mean values and tree radial growth before road construction. Furthermore, the ^{13}C increased with decreased tree ring width after 1980, post road construction period.

Safdari et al. (2012) assessed the growth response of *Pinus elderica* to air pollution. For the three sites studied (non-polluted, semi-polluted and polluted), the average highest and lowest ring widths were reported at the pollutant-stressed and non-polluted sites, respectively. They further observed the presence of false rings in samples extracted from polluted and semi-polluted sites. The transition from earlywood to latewood was abrupt at the polluted and semi-polluted sites, while control samples recorded a gradual transition. The reported abrupt transition in pollutant-stressed locations was affected by the formation of false rings around the latewood.

Fox et al. (1986) reported significantly lower growth rates for periods corresponding to peaks in SO_2 emissions. Furthermore, the resumption of the average growth in *Larix occidentalis* was observed immediately after a reduction in the emission levels. Other studies have reported similar growth patterns of *Quercus pubescens* and *Pinus sylvestris* exposed to stressful environmental conditions (Kincaid & Nash, 1988; Perone et al., 2018; Seftigen et al., 2013; Singh et al., 2017). Seftigen et al. (2013) noted adverse growth effects in *Pinus sylvestris* than *Picea abies* after nitrogen deposition. They argued that the reduction in nitrogen and other acidifying compounds resulted in improved pine growth without significant impact on the growth of spruce. The results suggest that *Pinus sylvestris* is more susceptible to changes in the acidification and nitrogen levels of forest ecosystems than *Picea abies.* Table 1 shows observed growth adjustments on selected species on exposure to certain stress conditions.

Table 1. Species-specific observed growth and yield alterations after exposure to different environmental stresses

Stress and source	Plant species	Observed changes	Author(s)
Dose-response experiment (Pb, Cd)	*Fagus sylvatica*	*root elongation and biomass production *root hair formation **root branching system **root secondary and primary laterals	(Breckle & Kahle, 1992)
Copper smelter (SO_2, NO_x, HM, PM)	*Pinus monophyla*	*ring width during higher Cu production ** ring width during low Cu production after the higher Cu mining period	(Thompson, 1981)
Vehicular exhausts (Pb, Hg, CO_2, NO_x, PM, VOCs, CO, SO_2)	*Pinus pinea*	*tree ring width after the road construction	(Battipaglia et al., 2010)
	Pinus elderica	**ring widths **false rings **abrupt transition from earlywood to latewood	(Safdari et al., 2012)
Lead-Zinc smelter (SO_2)	*Larix occidentalis*	*radial growth	(Fox et al., 1986)
Steel factory (HM)	*Quercus pubescens*	*radial growth	(Perone et al., 2018)
Sulphate, Nitrate and Ammonium	*Picea abies* *Pinus sylvestris*	*radial growth in Pinus Sylvestris without significant effects on Picea abies	(Seftigen et al., 2013)

*Reduced **Increased

Table 1 illustrates that plant species respond differently to varying environmental stresses. Tolerant species are capable of withstanding more extreme exposure conditions compared to sensitive ones. Generally, plant growth and yield are profoundly affected by biochemical and morpho-physiological alterations caused by pollutant-induced stress. The photosynthetic activity is affected by damaged biomolecules (Chaurasia et al., 2013; Thakar & Mishra, 2010), increased transpiration and respiration (Gupta & Sarkar, 2016; Koziol & Whatley, 1984; Lee et al., 2017) and reduced foliar dimensions (Tiwari et al., 2011). Reduced photosynthetic activity affects the cambial activity leading to reduced cell division, elongation and differentiation (Ahmad et al., 2015). Furthermore, the affinity of some heavy metals for binding to cell membranes and cell walls compromises the ability of wood cells to divide and expand (Steiner et al., 2012; Pourrut et al., 2011). The reduction in cambial activity limits ring widths and plant growth, resulting in reduced biomass production and plant productivity.

On the other hand, the reported (Safdari et al., 2012; Thompson, 1981) increase in growth and false rings, as well as the abrupt transition from earlywood to latewood can be attributed to an unexpected increase in the growth rate of plants. In nutrient deficient soil, SO_2 and selected heavy metals can be utilized as sulphate and micronutrient ions respectively to meet the demand of the required nutrients (Khan & Khan, 2011; Tripathi et al., 2015). The availability of the initially lacking nutrients may improve the soil nutrition value, thereby enhancing or exacerbating the growth rate of plants.

Wood Formation and Characteristics

Studies on woody plants suggest air pollution has devasting effects on wood formation and characteristics. The impact of gaseous and heavy metal stresses on cambial activity and characteristics of wood cells both under laboratory and field conditions were evaluated. Iqbal et al. (2010) and Rajput et al. (2008) observed confluent vasicentric axial parenchyma cells, tri-to multi-seriate ray and multiple vessels in *Prosopis spicigera* and *Ailanthus excelsa* exposed to stressful conditions. Other studies reported significant increases in vessel width and frequency, fibre length, tangential tracheid and lumen diameter in *Cassia occidentalis*, *Abutilon indicum*, *Abies religiosa*, *Calendula officinalis* and *Croton sparsiflorus* growing in SO_2, NO_x and particulate matter environment (Bernal-Salazar et al., 2004; Sukumaran, 2014; Wali et al., 2007).

On the other hand, research on *Pinus sylvestris, Mangifera indica*, *Prosopis cineraria* and *Syzygium cumini* exposed to heavy metals, SO_2, particulate matter, NOx and CO_2 reported reductions in fibre and vessel diameter, length and lumen (Dmuchowski et al., 1997; Gupta & Iqbal, 2005; Iqbal et al., 2010; Mahmooduzzafar et al., 2010). Reduced fusiform and ray initials, tracheid cell walls, diameter and increased tracheid length and lumen, as well as resin ducts, were observed in *Juglans regia* and *Pinus elderica* growing in an air polluted environment (Ahmad et al., 2015; Safdari et al., 2012; Wani & Khan, 2010). Another laboratory-based study reported reduced vessel length, area, width and frequency in the stems and roots of *Trigonella foenum graecum Linn* treated with Cd and Pb separately at different stages of plant growth (Ahmad et al., 2005). The reductions were noted with increased concentration of individual heavy metals applied. Table 2 shows pollutant-induced changes in the anatomic characteristics of selected plants species under field and laboratory conditions.

Table 2. Field and laboratory-based observed pollutant-induced changes in wood characteristics of selected herbaceous and woody plants.

Stress and source	Plant species	Observed changes	Author(s)
Industrial plant (PM, N, NO_X, CO_2, CO and SO_2)	*Mangifera indica*	*fibre length and width * vessel diameter, length and width **vessel frequency per mm^2	(Gupta & Iqbal, 2005)
	Prosopis cineraria	*vessel length and diameter *fibre length **vessel frequency **vasicentric axial parenchyma **tri-to multi-seriate rays	(Iqbal et al., 2010)
	Syzygium cumini	*vessel length and width *fibre length and width *vessel and axial parenchyma frequency **fibre and ray frequency	(Mahmooduzzafar et al., 2010)
	Ailanthus excelsa	*vessel lumen diameter *vessel frequency **multiple vessel elements	(Rajput & Rao, 2005)
	Pinus elderica	*tangential tracheid cell walls and diameter. **ray and resin duct frequency per mm^2 **tracheid fibre length and lumen diameter	(Safdari et al., 2012)
Cement dust	*Juglans regia*	*fusiform and ray initials	(Wani & Khan, 2010)
Dose-response experiment (SO_2)	*Calendula officinalis*	*vessel diameter **fibre and vessel length	(Wali et al. 2007)
Dose-response experiment (Cd, Pb)	*Trigonella foenum graecum Linn*	*vessel element length, width, area and frequency *fibre length and width	(Ahmad et al., 2005)

*Reduced **Increased

Table 2 demonstrates that pollution-induced stress affects wood cells dimensions and distribution patterns. According to Mahmooduzzafar et al. (2010) and Wali et al. (2007), wood fibres occupy a larger transectional area of wood in stressful environments. Attributed to the mechanical function of fibres, woody plants require more fibres as an adaptive mechanism against the extreme growing conditions. Furthermore, the production of shorter and narrower vessels offers resistance against collapse and deformation required for plant safety (Gupta & Iqbal, 2005; Zimmermann, 1983). On the other hand, narrower vessels assure a smooth and facilitated flow of sap throughout the plant (Husen & Iqbal, 1999). Increased frequency of vessels in plants growing in stressful environments is considered as the plant response/strategy to mitigate high negative tension in the transpiration stream caused by pollutant induced stresses (Rajput et al., 2008).

Forest Productivity and Sustainability in Polluted Landscapes

Over the years, studies on the effects of heavy metals and SO_2 on plant growth focused mainly on herbaceous plants. Herbaceous plants account for the majority of hyperaccumulators and crops. Increased interest in hyperaccumulators is aimed at identifying plants for phytoremediation purposes to restore massively polluted landscapes through phytoextraction of pollutants using plants (Singh et al., 2016; Tangahu et al., 2011). Studies on agricultural crops facilitate strategic measures to improve the productivity and yield of farm produce in polluted environments. On the other hand, studies on woody plants are mostly concentrated on the impact of climate change-induced stresses, such as temperature, CO_2, O_3 and water availability on plant growth and yield at the macroscale.

However, there is limited information on the effect of SO_2 and heavy metal stress on the growth and characteristics of woody plants. As discussed earlier, heavy metals and SO_2 cause direct or indirect damage at plant molecular level, thereby instigating changes in biochemical and physiological parameters of plants. Additionally, there is a generalised understanding that pollution reduces forest growth and productivity. Therefore, there is a need for studies to establish the pollutant and species-specific effects in woody plants growing in stressful environments. In this regard, priority research areas may include spatial and temporal distribution of pollutants from emitting sources, effects on tree growth and wood quality attributes, such as chemical composition, anatomical characteristics, mechanics and machinability. Such studies would lead to the generation of scientific information required for management plans to assure sustainable utilisation of both exotic and natural forests around polluted environments.

CONCLUSIONS

Increased industrial operations account for the emission of a wide range of pollutants including heavy metals, CO_2, SO_2, NO_x and CO into the atmosphere. The emitted pollutants are available for uptake by plants through different organs. For example, heavy metals and SO_2 enter the plant tissue through the leaves penetrating the stomata and cracked cuticular layers and finally diffuse into the mesophyll cells. Further, heavy metals accumulated in the soil solution are absorbed by root hairs and transported into the transpiration stream through symplastic and apoplastic pathways. In the plant tissue, pollutants are then translocated and redistributed throughout the plant by hydrostatic pressure and transpiration.

In plant cells, SO_2 and heavy metals participate in several biochemical reactions producing ROS and inhibiting the normal functioning of enzymes involved in the detoxification of ROS. ROS are destructive to plants as they cause damage to organic molecules such as proteins, DNA, lipids and carbohydrates. In addition, some heavy metals bind the cell membranes and cell walls, making them rigid, thereby reducing cell division and elongation.

Increased production of ROS in stressful environments is attributed to the pollutant-induced stress on the biochemical reactions instigated by the imbalance between the generation and elimination of ROS in plant tissues. Therefore, the imbalance triggers physiological and morphological alterations. Pollutant-induced phytotoxicity compromises the functionality and efficiency of photosynthetic systems, stomatal functions and cambial activity.

Finally, pollution-induced stresses in plants affect biochemical parameters inhibiting the plants capacity to carry out its physiological functions, such as photosynthesis, transpiration and respiration. The effects could be severe depending on plant species and exposure conditions, such as pollutant type, concentration level, duration and season. Ultimately, pollutant-induced toxification may result in visible plant injuries, reduced growth and yield, thereby affecting the productivity of plants.

GRANT SUPPORT DETAILS

The present research has been financially supported by the Department of Forest and Wood Science, Stellenbosch University.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interests regarding the publication of this manuscript. In addition, the ethical issues, including plagiarism, informed consent, misconduct, data fabrication and/or falsification, double publication and/or submission, and redundancy has been completely observed by the authors.

LIFE SCIENCE REPORTING

No life science threat was practiced in this research.

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