RESEARCH ARTICLE

ANTIOXIDATIVE DEFENSE IN PLANTS IN RESPONSE TO SEASONAL ENVIRONMENTAL STRESS

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ABSTRACT

Exposure of plants to stressful environments can cause disruption of cellular homeostasis and uncoupling of major metabolic processes, such as photosynthesis and photorespiration, leading to enhanced production of reactive oxygen species, ultimately leading to drastic reduction in growth, yield and yield quality. The increased production of toxic oxygen species is a feature commonly observed under certain stress conditions, when the equilibrium of formation and detoxification of active oxygen species can no longer be maintained. To counter the hazardous effects of oxygen radicals, all aerobic organisms have evolved a complex antioxidative defense system composed of both enzymatic constituents and free radical scavengers, such as ascorbate and glutathione. The scavenging enzymes consist of superoxide dismutase (SOD), catalase, peroxidase, glutathione reductase, dehydroascorbate reductase, monodehydroascorbate radical reductase and ascorbate peroxidase. A positive correlation exists between increased antioxidant activity and different abiotic tolerance. Total peroxide and MDA content are highest in the unfavourable conditions indicating environmental stress. The antioxidant enzymes showed maximum activity in the stressful seasons for crops. Ascorbate peroxidase and Glutathione reductase enzyme activities and higher carotenoid, total phenols, Ascorbic acid and sulfhydryl content under optimum seasonal conditions provide the plants strong defense against ROS ensuring higher and quality yield.

INTRODUCTION

The growth and physiological behaviour of plants, especially of those growing under natural conditions is strongly influenced by factors of the environment. Of the different factors *viz.* climatic, topographic, edaphic and biotic which are most likely to influence plant behaviour, the *climatic* or *environmental* factors are of paramount importance. These are the factors which are concerned with temperature, light, atmospheric humidity, rainfall and others. The behaviour, duration and intensity of these factors constitute the *climate* of a region. The seasonal cycles of temperature, daylength, rainfall, humidity and wind exert a profound influence over the physiological and reproductive processes which is reflected in the ecosystem structure and function. These seasonal changes provide the organisms with a calendar to which developmental changes are "physiologically locked" (Sen and Mukherji 1997, 1998 a,b,c,d,e 1999 a,b).

Sources of Variation: The "weather machine" is driven by a combination of solar radiant energy input and the motions and relative motions of earth, moon and sun.

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As a hemisphere facing the sun, the earth has twice the illuminated area of a disc and the distribution of surface irradiance varies as the cosine of the zenith angle (sine of the angle of incidence). Because of this, about half the instantaneous radiant income falls on 14.6% of the earth's surface and the remainder is spread unevenly over 35.4% (50% is in darkness). The presence of the atmosphere exaggerates the geometrical effect. The earth spins on its axis once in 24 hours and circles the sun every 365.25 days: because the axis is "set" in space and is tilted at an angle of $66^1/_2$ degree to the orbital plane, each pole apparently tilts toward and then away from the sun during the year. The result of this axial tilt and orbital effect is to impose a *seasonal variation* of *daylength* and *radiant income.* It represents a winter reduction of mean radiant income by 40% of the maximum in mid-latitudes, and 10% in the equatorial belt. The seasonal impact becomes even greater as the poles are approached. All plant species are under environmental conditions that limit their performance (Osmond et al. 1980). In general, crops are limited to about 25% of their potential yield by the impacts of environmental stress (Boyer 1982). Stress occurs when the stressor induces enough physiological change to result in reduced growth, reduced yield, physiological acclimation, species adaptation or a combination of these (Sen 2019).

Thus, a stressor is considered to be an aspect of the environment that can induce an alteration in plant physiology (Nilsen and Orcutt 1996, Ramakrishna and Ravishankar 2011, Hasanuzzaman et al. 2013, Sen and Mukherji 2002, 2004, 2006 a,b,c 2007). The influence of a particular stressor on the physiological processes of a particular plant species is not always equal. At different times during its life cycle a plant will be differentially sensitive to a particular stressor. Thus, climatic effects are excessively complex as they interact differently at various stages in the plant life cycle. Sensitivity of plants is also known to vary with seasonal patterns of physiology (Sen and Mukherji 2002, 2004, 2006 a,b,c 2007). Hence, the developmental status of plants, the age of the plant parts and the impact of seasonal environmental patterns all significantly influence the physiology of plants (Sen and Mukherji 1997, 1998 a,b,c,d,e 1999a,b). Different plant species are highly variable with respect to their optimum environments, and a harsh environmental condition, which is harmful for one plant species, might not be stressful for another (Larcher 2003, Munns and Tester 2008, Sen 2014).

Stress tolerance is the potential of a plant to acclimate to a stressful condition. For example, in summer, trees and herbaceous plants in northern latitudes cannot withstand freezing. Exposure to chilling temperatures, however, induces hardening and acclimated plants survive winter temperatures far below freezing. Plants can increase their resistance to various stresses including heat, saline, and drought conditions in response to a period of gradual exposure to these constraints. Acclimation is plastic and reversible. The physiological modifications induced during acclimation are diverse and are usually lost when the adverse environmental condition does not persist (Krasensky and Jonak 2012). Though there are reports of seasonal variations in tree species, detailed information of the seasonal impact on the physiology of crop plants is limited. The study of seasonal effects on the morphology, physiology and biochemical characteristics could explain the differences in productivity and yield obtained in crop plants in different seasons. The reactions or responses of the plants to different seasonal conditions might also serve in the determination of suitable bio-indicator species, besides giving an idea of their adaptability potential in the changing environment. The study of plant responses to environmental stress could provide important information about how crops cope with less than optimum growing conditions. Complex interactions exist between plants and their environments and by studying the physiological responses of plants to changing seasonal conditions, it becomes known how plants serve to adapt or acclimate to particular seasons, and hence the underlying physiology is revealed which ultimately leads to differences in growth and productivity.

Seasonal Stress Impact On Metabolism: Plants influence the environment and are in turn influenced by the environment. Environmental factors affect vegetative as well as reproductive growth of a plant. Plant survival, growth and productivity are intimately coupled to the aerial environment through the processes such as uptake of CO_2 in photosynthesis, loss of water vapour in transpiration and energy exchange (Grace et al. 1981). Even though physiological processes like photosynthesis and photorespiration are genetic in nature, they are strongly influenced by the environment (Austin 1989). Winter occupies the greater part of the year for plants growing in boreal and arctic regions, and it is therefore not surprising

that there are a number of adaptations that are specific for this season. Strategies for surviving an environmental stress in winter can differ from those that provide protection from the same stress when it occurs in summer (Crawford 2003). Seasonal variation in growth in *Bupleurum falcatum* has been studied by Minami et al. (1997). The growth of the shoot was maximum in October and then decreased. Both the maximum diameter and the dry weight of the main root increased from August to October and reached a plateau in November. Changes in morphological characteristics in different seasons in *Ecklonia kurome* were recorded by Tsutsui and Ohno (1992). Plants attained maximum length in spring and minimum length in autumn. Thickness of the central lamina became maximum in winter. In a study of *Laminaria saccharina,* the length-to-width ratio of newly grown lamina tissue was observed to vary throughout the year (Sjotun 1993). A period of rapid lamina growth during late winter and spring was observed, while both length and width growth declined in the summer. Seasonal change in specific needle weight in *Pinus thunbergii* was studied by Kimura (1992). Specific needle weight showed distinct seasonal changes, as it increased from autumn to early spring, followed by a decrease in mid - summer. Photosynthetic characteristics of an alpine and a subalpine population of *Nephroma arcticum,* assumed to represent different ecotypes, were measured by Sonesson et al. (1992) to investigate possible seasonal patterns. The light compensation levels in the alpine population were consistently higher than those in the subalpine ones, and the chlorophyll contents of the former were, on average, about half those of the latter, reflecting the differences in light regimes between sites. The influence of climatic conditions on seasonal and diurnal variations in gas exchange of banana *(Musa sp.)* leaves was studied by Eckstein and Robinson (1995). Highest rate of photosynthesis, transpiration and stomatal conductance were measured in winter, while constraints on gas exchange in summer, were due to high temperatures and high vapour pressure deficit, causing stomatal closure. Seasonal changes in CO_2 assimilation of cranberry leaves were studied by Hagidimitriou and Roper (1995). CO_2 assimilation rates increased from May to early June and declined from August to October. Seasonal variations in photosynthetic rate have also been reported by Chaumont et al. (1994), Flores-Moya et al. (1995), Lacointe et al. (1995), Fredericksen et al. (1996), Sobrado (1996), Weng et al. (2005), Pollet et al. (2010) in a variety of plant species.

The effects of seasonal changes on the chlorophyll 'a' content of *Fucus vesiculosus* were studied by Ruokolahti and Ronnberg (1988), who reported lowest chlorophyll contents in spring - early summer and the highest in late autumn-winter. Seasonal variation of chlorophyll content (a, b and total) and chlorophyll a:b ratio in *Zea mays* leaves were reported by Kumar and Singh (1996). Ribulose 1,5-bisphosphate carboxylase activity exhibited seasonal variations in its activity which correlated with protein content, but not with net photosynthetic rate in tropical deciduous tree species (Naidu and Swamy 1995). Pilon-Smits et al. (1991) reported seasonal variation in Phosphoenol pyruvate carboxylase activity in 12 *Sedum* species with a maximum during the summer - from 8 to 30 fold higher than winter values. For most species, the seasonal fluctuation correlated significantly with temperature, and to a lesser extent, with irradiation. Seasonal changes of nitrogenous compounds and carbohydrates were monitored from one year old seedlings of *Diospyros kaki* by Yoon

(1996). Soluble sugars in the leaves increased during the growing season while starch contents increased from July to August and then decreased. Protein in all seedling parts increased from July to September while amino acids in the leaves accounted for about 50% of the total in July. Seasonal changes in the utilization and turnover of assimilation products of *Pinus sylvestris* were studied by Hansen and Beck (1994). During summer, assimilates of the old needles were utilized for secondary growth of the axial system while growth of the recent year's shoots was supported by their own photosynthesis. In autumn, soluble carbohydrates were produced instead of starch, a major part of which in addition to recent photosynthates was utilized for root growth during the cold season. Seasonal changes in nonstructural carbohydrates in *Vaccinium macrocarpon* were studied by Hagidimitriou and Roper (1994). Total non-structural carbohydrate concentration in above-ground tissues increased early in the season, reached a maximum in late May, decreased as flowering approached and remained low from late June to late August, - the latter period corresponding to flowering, fruit set, floral initiation and fruit development stages. Seasonal patterns of nonstructural carbohydrates were also studied by Pavel and Dejong (1995) in apple *(Malus pumila)* fruits. Estimated contribution of soluble carbohydrates to fruit solute potential declined over the growing season, while fructose contributed the largest amount to the solute potential, followed by sucrose. Seasonal variations in pH, carbohydrate and nitrogen of xylem exudate of *Vitis vinifera* were studied by Campbell and Strother (1996). Exudate pH varied inversely with daily exudate flow while exudate NH_4^+ and NO_3^- concentrations increased directly with exudate flow. Variations in exudate carbohydrate concentration were also consistent over the 2 years of the study. Seasonal changes of starch content in the shoots and leaves of lilac were determined by Pilarski (1995). In winter, the starch content in the shoot decreased, with the smallest amounts in spring (1%). In the following period, the starch content increased; its greatest amounts in the shoots were found in July (13%), and in leaves in June (11 %).

Nitrate metabolism was studied by Sarjala et al. (1987) in *Pinus sylvestris.* Nitrate content increased from June to October while nitrite was not detected in the seedlings during the growing season. Total nitrogen content decreased towards autumn, whereas protein content initially decreased but increased again in autumn. Fischer and Feller (1994) reported total proteins to increase considerably between February and May, before the emergence of the new leaf generation in the ivy plant. Marked seasonal changes in the peptide hydrolase pattern were observed. Clausen and Apel (1991) studied the seasonal changes in the concentration of the major storage protein and its mRNA in the xylem ray cells of poplar trees. In autumn, large amounts of a major storage protein accumulated, which was stored in the xylem ray cells during the winter season and was degraded in late spring. Protein accumulation was preceded by a dramatic but transient appearance of the corresponding mRNA. Seasonal patterns in cold tolerance and proteins were studied in the leaves of sibling deciduous and evergreen peach by Arora et al. (1996). Bark storage proteins progressively disappeared from summer through fall, in leaves of deciduous peach but accumulated to a high level in bark tissues. Studies on the seasonal patterns of dehydrins and 70-kDa heat-shock proteins in bark tissues of 8 species of woody plants revealed that some proteins, immunologically related to dehydrins, appeared to be constitutive; however, distinct

seasonal patterns associated with winter acclimation were also observed in all species. The molecular masses of the proteins varied widely, although similarities were observed in related species. Among the 8 species examined, the seasonal patterns exhibited by the proteins were highly variable (Wisniewski et al. 1996). Polyamines (PA) are small aliphatic molecules positively charged at cellular pH. Various stresses, such as drought, salinity and cold, modulate PA levels, and high PA levels have been positively correlated with stress tolerance (Yang *et al.* 2007, Cuevas *et al.* 2008, Groppa and Benavides 2008). Seasonal fluctuations in the free polyamines were monitored by Sarjala and Savonen (1994) in the needles of *Pinus sylvestris.* The highest putrescine values were measured in winter and lowest in summer, while spermidine concentrations were highest in spring. Low spermine values coincided with low temperatures in winter. The seasonal and geographical variation of terpenes, resin acids and total phenolics in *Pinus sylvestris* were studied by Nerg et al. (1994). Seasonal variation was remarkable in monoterpene, resin acid and total phenolic concentrations. Seed origin had no significant effect either on the resin acids or total phenols, suggesting that the origin of the seed material was not as important in affecting the concentrations of secondary compounds as were the environmental factors. Schoenwitz et al. (1990) investigated seasonal variation in monoterpenes in the needles of *Picea abies.* In juvenile needles, the amounts of oxygenated terpenes increased constantly with age during the first 2 months of needle growth. The terpene levels of the one year old needles were considerably lower in spring at the time of bud burst than in autumn.

In eucalypts studied by McKiernan et al. (2015), drought effects were different for secondary metabolites synthesized via shikimate and isoprenoid synthesis pathways. Isoprenoids, mono- and sesquiterpenes, were unaffected by drought, but the concentration of condensed tannins was enhanced, and concentrations of macrocarpals, the condensation products of shikimic acid and isoprenoid pathway intermediates specific to eucalypts, decreased upon drought (McKiernan et al. 2015). Seasonal changes of plant growth regulators in *Corylus avellana* were measured by Rodriguez et al. (1991). The endogenous IAA level showed a maximum in May, coinciding with the highest rate of shoot elongation and leaf expansion, decreasing afterwards, although a minor increase was observed in November, perhaps having a certain role in leaf abscission. The highest ABA levels occurred in winter, whereas the minimum was in March, coinciding with bud burst, suggesting a role for ABA in the induction and maintenance of winter dormancy. Loveys et al. (1987) reported that the leaves of *Prunus armeniaca* largely lost the ability to synthesize ABA in response to zero turgor between November and March, although this ability was partly regained in April. Seasonal changes in the effects of auxin on rooting in stem cuttings of *Ficus infectoria* were studied by Anand and Heberlein (1975). They reported that the auxin treated cuttings root profusely in June when cambial activity was high, but not in October when cambial activity was low, suggesting a close correspondence of seasonal variation between the rooting activity of auxin and cambial activity. The seasonal influence of auxins (IAA, IBA and NAA) on adventitious root formation in the branch cuttings of *Pongamia pinnata* was examined by Palanisamy and Kumar (1997). 800 ppm IBA induced 100% rooting and more number of roots in the month of March. Exogenously applied auxins were able to activate the cambium resulting in

adventitious root formation in a particular season, probably when the cambium was in active phase. The changes in the contents of free β- indolyl-acetic acid (IAA) in the needles of 10 year old specimens of *Picea abies* were studied by Psota et al. (1992). The breaking of endogenous dormancy, budding and the growth of annual shoots was associated with a gradual rise in the content of IAA, reaching the maximal value in July. The content of 1AA decreased after a decrease in the growth activity. The changes in the content of IAA were investigated in the needles of dwarf pine by Psota et al. (1995). In newly formed needles, the content of 1AA increased, starting from July and reaching its maximum in August to October. The 1AA content decreased with a decline in the intensity of apical dominance during dormancy, but no changes were observed in bud break (May and June). Tromp and Ovaa (1990) recording seasonal changes in the cytokinin composition of xylem sap of apple, reported that the total cytokinin concentration was low from mid-summer until late in winter. Starting in February, a number of concentration peaks were found. After leafing out, a rapid decline occurred until the original low level was reached in July.

Abscisic acid (ABA) is an integral regulator of abiotic stress signalling (Cutler *et al.* 2010). ABA quickly accumulates in response to different environmental stress conditions and ABA-deficient plants have an altered stress response. ABA promotes stomatal closure, inhibits stomatal opening to reduce water loss by transpiration, induces the expression of numerous stress-related genes, and recent studies indicate a role in regulation of stress-induced metabolic adjustments. Seasonal variations in the activity of cambium and radial growth of wood formation in *Pinus roxburgii* were studied by Khattak and Majeed (1993). The cambial zone showed marked periodic changes and became 3 to 4 layered during the dormant period and 7 to 10 layered during the active period. The initiation of cambial activity was associated with the emergence of new crops of leaves, and the cambium was highly active in the months of July and August, when the tree was with mature foliage and rainfall was the highest.

More time was required for the completion of radial growth phase in the beginning of the growing season than at the end. Cambium has been reported to divide actively in mid-April and cease to divide by early-November in *Pterocarya stenoptera* (Zhang et al. 1992). In *Ficus religiosa*, extension and radial growth occurred in late July and early August respectively (Siddiqi 1991). The derivative tissue differentiated into xylem and phloem simultaneously in August, while cell size and the relative proportion of fusiform and ray initials varied with season. The original features of cambial cells and their immediate derivatives in temperate tree species were reviewed by Catesson (1994). Seasonal changes in the cell wall structure and composition implied variations in cell wall plastic properties and growth potential while detailed studies of nucleic acid metabolism during the seasonal cycle showed that the nuclei of dormant cells were blocked in the G$_l$ phase, as expected from previous results with apical meristems. Prasad and Guelz (1990) analyzed the development and seasonal variations in the epicuticular waxes of *Fagus sylvatica*. The folded leaves in buds contained hydrocarbons, wax esters, benzyl acyl esters, alcohols and fatty acids while aldehydes were identified after 10 days of leaf unfolding. The biosynthesis of wax lipids was rapid till May during which they doubled quantitatively.

From June to October, the composition of the wax lipid classes remained constant with the exception of fatty acids. Seasonal variations in fatty acids in developing *Mentha piperita* leaves were analyzed by Maffei and Scannerini (1992). A decreasing trend in both total and unsaturated fatty acids was observed with leaf development. Winter leaves of *Euphorbia acanthothamnos* and *Phlomis fruticosa* contained higher amounts of lipids than summer leaves (Meletiou-Christou et al. 1992*)*. Seasonal variation was analyzed in *Ficus carica* leaf nutrient concentrations, to be used as preliminary norms for the interpretation of tree nutrient status for high-yielding commercial fig orchards (Brown 1994). Macroelement dynamics were analysed in *Rubus idaeus* by Kowalenko (1994). The plants accumulated N, P, K, Ca, Mg and Na rapidly during May to June and more slowly in September and October. Macroelement uptake was nearly complete by mid-summer, which was followed by a period of senescence with nutrient loss. Seasonal changes in minerals, proteins and amino acids were studied in *Salvadora persica* (Joshi et al. 1993). The seasonal variations in ion concentrations (Ca, Mg, Na, K and Cl) in the soil and plant samples of *Halopeplis perfoliata* were determined (Hajar and Al-Zahrani 1997). The results indicated higher ionic concentrations in the plant shoots during winter and summer, while the soluble ions were lower in the soil during spring.

Seasonal changes in the concentrations of cadmium, copper, lead and zinc were measured in the leaves of *Aesculus hippocastanum.* The temporal trends in the concentrations of the metals could be related to their dominant source (Kim and Fergusson 1994). Marked seasonal variations of mineral (cadmium, lead and zinc) concentrations were observed by Hagemeyer et al. (1992) in *Fagus sylvatica.* Seasonal changes in trace element concentrations in *Pinus densiflora* forest communities were studied by Nashimoto et al. (1986). Mercury and strontium concentrations in leaves and branches were high in summer. Boron concentrations in leaves tended to be high in summer, but were high in winter in the branches. Seasonal variations in edaphic factors *viz.* water holding capacity, electrical conductivity, major and minor elements of two different forest ecosystems in Gujarat were studied by Pandit et al. (1998), revealing the importance of edaphic factors in determining the soil-vegetation correlation in a forest ecosystem. A significant relationship was observed between physico-chemical parameters *viz.* alkalinity, hardness, pH and electrical conductivity and distribution of fungi during different seasons in aquatic systems in Tiruchirapalli (Ravikumar et al. 1998). The variations of the essential oils in *Acorus calamus* and their major compositions with seasons were investigated (Li and Jiang 1994). The results indicate that June was the best season for the cropping of *A. calamus.* Monthly quantitative and qualitative changes in the essential oils of *Thymus capitatus* and their antimycotic activity against *Penicillium italicum* and *Alternaria alternata* were examined by Arras and Grella (1992). Maximum oil yield occurred in August and proved to be fungistatic to *P. italicum* and fungicidal to *A. alternata.* The essential oil from leaves of *Virola surinamensis* showed seasonal variation (Lopes et al. 1997). The monoterpenes represented 50% of the total volatile compounds during the dry season (June), while sesquiterpenes were predominant (50%) in the early rainy season (October). Chalchat et al. (1997) observed a marked inversion of the menthol/menthone ratio, depending on the time of harvest in *Mentha piperita.* A late blooming period gave oils rich in

menthol. Kamalam and Jegadeesan (1998) found that wedelolactone, a hepatoprotective principle isolated from the leaves of *Eclipta prostrata* showed considerable seasonal variation in its content, being highest in July and August, and lowest in November and December. Seasonal variation of peroxidase activity in chestnut trees was observed by Havir and Anagnostakis (1998). Total amount of peroxidase activity was highest in December and April for most trees. The effects of environmental conditions on changes in dormancy and germination of seeds of *Sisymbrium officinale* were studied by Bouwmeester and Karssen (1993). Temperature proved to be the most significant factor, as dormancy was relieved in periods of low temperatures and induced in periods of high temperature. Studies were carried out on the year's season on the mobilization of easily soluble seed proteins of some legumes which serve as a protein reserve in the early hours of their germination (Nikolova et al. 1993). The dependence on the season was manifested by enrichment of the electrophoretic spectra of proteins isolated from cotyledons and embryos of dry pea seeds in the summer. On the other side, a more intensive mobilization of easily soluble proteins was observed during seed germination in this season, leading to the decrease of the quantity or extinction of some of the minor protein bands.

Bai et al. (2015) indicated the occurrence of metabolic biorhythms in germinating and dehydrating seeds associated with seasonal changes in germination and, more pronouncedly, in seed dehydration tolerance. Increased biosynthesis of protective compounds (polyphenols) in dehydrating seeds during the winter season at the expenses of central metabolites likely contributes to the respective enhanced dehydration tolerance monitored. Climatic changes induced a seasonal variation in the fruit setting ability of *Solanum melongena* (Sun et al. 1990). Fruit setting was affected by the average maximum temperature and precipitation during the first 5 days after the flowers opened. Seasonal dynamics in the process of maize seed ageing was studied by Klisurska et al. (1990). Initial seed moisture content appeared to be the decisive factor of seed ageing as compared to storage temperature. The rate and degree of seed ageing depended on the yearly seasons. Seed ageing was the slowest in summer, while the loss of viability was fastest in the period of February to March. A significant influence of season on green matter yield in hybrid grasses was observed by Vanangamudi et al. (1989). The seasonal variation for dry weight differences indicates that solar radiation and mean air temperature during crop growth period were important climatic requirements for a good yield of *Vigna radiata* (Singh et al. 1985a). A significant effect of weather on leaf biomass of *Pinus taeda* has been reported (Dougherty et al. 1995). Nanda et al. (1997) observed variations in biomass in *Brassica campestris* and *Brassica juncea* in different seasons to be associated with interception of radiation. Time of sowing seemed to be an important factor in improving the yield of rapeseed - the yield being the highest for the October sown crop, and declined drastically as the sowing was delayed (Pradhan et al. 1997).

Reactive Oxygen Species: Utilization of oxygen represents an efficient mechanism for aerobic organisms to generate energy, but reactive oxygen species as the by-products during this process and other unfavourable events are also produced within the biological system (Tian et al. 1998). Under environmental stress conditions, which reduce the capacity to assimilate C (Fryer et al. 1998), it has been suggested by Asada (1996) that photosynthetic electron flux to O_2 will increase, resulting in the increased production of superoxide anion radical ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2) and hydroxyl ($^{\cdot}OH$) radicals. These active oxygen species are highly reactive and capable of damaging many biological macromolecules such as DNA, RNA, protein and lipids (Tian et al. 1998). The schematic representation of the formation of active oxygen species as reported by Elstner (1982) is as follows. $O_2^{\cdot-}$ can be produced either by the univalent reduction of O_2 or by the univalent oxidation of H_2O_2. In the leaves, the major site of $O_2^{\cdot-}$ formation is the chloroplasts (Elstner 1982, Halliwell 1984). $O_2^{\cdot-}$ is also generated in the plant mitochondria at the expense of NADH (Rich and Bonner 1978). $O_2^{\cdot-}$ in aqueous solution is a nucleophilic reactant with both oxidizing and reducing properties. It can reduce cytochrome f, cytochrome c, plastocyanin but can oxidize ascorbic acid, ferredoxin, sulfur compounds and NADPH (Elstner 1982, Halliwell 1984).

H_2O_2 is one of the non-radical species resulting from the stepwise reduction of oxygen to water. It is produced *in vivo* as a consequence of normal cellular metabolism and of oxidant generating agents (Hoffschir et al. 1998). H_2O_2 may be generated directly by divalent reduction of O_2 or indirectly by univalent reduction of O_2 followed by dismutation of $O_2^{\cdot-}$. In plant mitochondria, there are some oxidases which transfer two electrons to each oxygen molecule forming H_2O_2. These are glycolate oxidase, urate oxidase and amino acid oxidases. H_2O_2 is also formed by the enzymatic dismutation of $O_2^{\cdot-}$ by superoxide dismutase. H_2O_2 formation has been reported from all parts of plant cell such as cell walls (Gross et al. 1977, Halliwell 1978), peroxisomes (Tolbert 1981), mitochondria (Rich et al. 1976) and chloroplasts (Mehler 1951, Elstner 1982). H_2O_2 can cause the oxidation of sulfhydryl compounds (Fridovich 1976) and inactivates several enzymes of the CO_2 reduction cycle (Kaiser 1976, 1979, Charles and Halliwell 1980, 1981). At physiological pH, the long life of H_2O_2, its ability to traverse lipid bilayers, and its reactivity with membrane or protein-bound Fe^{2+} (which initiates hydroxyl radical formation) combine to make H_2O_2 an extremely dangerous form of activated oxygen (Yasminah and Theologides 1993, Liochev and Fridovich 1994). Apart from exerting their direct toxic effects, $O_2^{\cdot-}$ and H_2O_2 can react together to generate $^{\cdot}OH$ in the 'Haber-Weiss reaction.' There are several reports that this reaction is occurring in the cell, specifically in the active chloroplasts (Asada et al. 1977, Halliwell 1984). $^{\cdot}OH$ is far more reactive than either $O_2^{\cdot-}$ or H_2O_2 and can oxidise almost every molecule in the cell. This radical can initiate lipid peroxidation and damage the cellular membranes (Fridovich 1976, Halliwell 1984). $^{\cdot}OH$ is extremely aggressive and thus reacts at the very site of its formation. The increased production of toxic oxygen species is a feature commonly observed under certain stress conditions (Foyer et al. 1994), when the equilibrium of formation and detoxification of active oxygen species can no longer be maintained. To counter the hazardous effects of oxygen radicals, all aerobic organisms have evolved a complex antioxidative defense system composed of both enzymatic constituents and free radical scavengers, such as ascorbate and glutathione (Biemelt et al. 1998, Gill and Tuteja 2010). The scavenging enzymes consist of superoxide dismutase (SOD), catalase, peroxidase, glutathione reductase, dehydroascorbate reductase, monodehydroascorbate radical reductase and ascorbate peroxidase (Asada 1996).

A positive correlation exists between increased antioxidant activity and different abiotic tolerance. Antioxidative enzyme activities play an important role against stress. When plants are subjected to environmental stresses such as salinity, drought, temperature extremes, herbicide treatment and mineral deficiency, the balance between the production of reactive oxygen species (ROS) and the quenching activity of antioxidants is upset, often resulting in oxidative damage (Hussain et al. 2016; Kusvuran et al. 2016). Oxidative stress is crucial in relation to chilling- and drought-induced injuries in plants (Hussain et al. 2016; Lamaoui et al. 2018). Biological processes involving light may have both beneficial (photosynthesis) and destructive (photosensitization) consequences. Singlet molecular oxygen ($^1O_2$) and other reactive oxygen species such as H_2O_2 and $^•OH$ arise during the interaction of light with photosensitizing chemicals in the presence of molecular oxygen. Singlet molecular oxygen ($^1O_2$) oxidises macromolecules such as lipids, nucleic acids and protein depending on its intracellular site of formation; and promotes detrimental processes such as lipid peroxidation, membrane damage and cell death (Ryter and Tyrrell 1998). $^1O_2$ also damages chlorophyll by a process known as chlorophyll photo bleaching (Halliwell 1984). Complex interactions exist between plants and their environments and there are several instances of functional specialization, which may serve to adapt or acclimate specific plants to specific environmental conditions.

Seasonal Variations in Antioxidative Stress: Emergence of intricate stress combinations and their impacts on crop growth and productivity in modern day agriculture are the outcomes of global climate change. Climate change is a multi-facet field that could have long-term impacts in the form of different abiotic stresses (Hussain et al. 2018). Agricultural productivity depends on increasingly extreme weather phenomena, and the use of germplasm that has to be continuously improved by plant breeders to become tolerant to various biotic and abiotic stresses. (Dresselhaus and Hückelhoven, 2018). Abiotic stressors including soil temperature, moisture, pH, and trace metal availability, all play a role in inducing oxidative stress towards irrigated cropped plants in the form of ROS. The two primary ways abiotic stressors cause oxidative stress towards plants is either by creating imbalance in the metabolic pathways or a reduction in the efficiency of antioxidant enzymes (Enez et al. 2018). The antioxidant defense machinery protects plants against oxidative stress damages. Plants possess very efficient enzymatic (superoxide dismutase, SOD; catalase, CAT; ascorbate peroxidase, APX; glutathione reductase, GR; monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR; glutathione peroxidase, GPX; guaicol peroxidase, GOPX and glutathione-S-transferase, GST) and non-enzymatic (ascorbic acid, ASH; glutathione, GSH; phenolic compounds, alkaloids, non-protein amino acids and α-tocopherols) antioxidant defense systems which work in concert to control the cascades of uncontrolled oxidation and protect plant cells from oxidative damage by scavenging of ROS (Caverzan et al. 2016, Filiz et al. 2019). Subsequently, with the development of molecular cloning technology, researches on the functions of antioxidant genes generated many new insights into this area. The dynamic transcription activity of ROS-scavenging enzymatic genes has been widely characterized (Xie et al. 2019).

Indicators of Oxidative Stress: In my work with two crop plants, total peroxides estimated from the leaf samples increased in winter in *Abelmoschus* and rainy in *Lycopersicon*. Lipid peroxidation can be estimated by measuring malondialdehyde (MDA), a decomposition product of the oxidation of polyunsaturated fatty acids. MDA content was also found to be increased in winter in *Abelmoschus* and rainy in *Lycopersicon*, thus indicating free-radical induced damage. The increase of total peroxides and MDA in any season indicates that those particular seasons are not optimum for growth. Thus winter for *Abelmoschus* and rainy for *Lycopersicon* are the periods of seasonal stress. MDA mediates photoperoxidative destruction of chlorophyll. It also inhibits amino acid incorporation into proteins, reacts with and modifies the properties of proteins and nucleic acids (Dhindsa 1982). The increase of MDA produced by lipid peroxidation reflects the accumulation of superoxide radical toxicity (Wang et al. 1989). There have been reports on the increase of lipid peroxidation under a variety of stresses including osmotic, drought, radiation and temperature extremes (Jiang et al. 1994, Zhang and Kirkham 1994, Klebanov et al. 1996, Fryer et al. 1998, Sen et al. 2014, Sen 2016a). H_2O_2 has also been reported to increase under stress conditions (Jiang et al. 1994).

Antioxidative Defense

Non-Enzymatic Antioxidants: Carotenoids help in maintaining the conformation of the chlorophyll - protein complexes (Hladik et al. 1982). Besides, they play an all important role in antioxidant defence and can effectively inactivate electronically excited molecules such as $^1O_2$ and triplet chlorophyll (process termed "quenching") to protect the chlorophyll and the photosynthetic membrane against lethal oxidation and photooxidative damage (Goodwin and Mercer 1983, Hladik and Sofrova 1983, Mayfield et al. 1986, Siefermann-Harms 1987). A reduction in carotenoid (both carotene and xanthophylls) indicates stressful environmental conditions. Thus, a decrease in carotenoid content in the winter season in *Abelmoschus* (Sen and Mukherji 2006a) and rainy in *Lycopersicon* (Sen and Mukherji 2009, Sen 2016b) implies a reduced capacity to help maintain the conformation of the pigment-protein complexes as well as a decreased efficiency of the leaves to scavenge the harmful free radicals (activated oxygen species). A similar condition can be expected also in the postflowering stages of plants or in aging leaves (which may be taken as natural stress) when carotenoid content is low. In my work with crop plants, both carotene and xanthophyll increased in the summer season in *Abelmoschus* and winter season in *Lycopersicon*. Both contents remained higher in the preflowering stage as compared to the postflowering as was observed by Sen and Mukherji (2006a, 2009, 2016b) and in *Vigna* radiata (mung bean) by Sen et al. (2014). Lycopene, a carotenoid mainly responsible for the characteristic red colour in tomato (Sharma and Le Maguer 1996) is a more potent inhibitor of human cancer cell proliferation than either α-carotene or β-carotene (Levy et al. 1995). Lycopene, a carotenoid may protect against the development of cancer by preventing free radical damage at the cellular level (Helzlsouer et al. 1996). The anti proliferative properties of lycopene are due to its ability of preventing free radical damage at the cellular level (Arab and Steck 2000, Takeoka *et al.* 2001). Lycopene content like the other carotenes are higher in optimum seasonal conditions and was hence found to be the maximum in the winter season, Sen and Mukherji 2000, Sen

2013. In an early work, Iycopene synthesis was shown to be inhibited at temperatures above 30°C (Goodwin and Jamikorn 1952). As phenols offer resistance to diseases and pests in plants, their low content in the months of seasonal/climatic stress indicates greater susceptibility to diseases and/or pests and hence an increase in biotic stress. The highest phenol content was at the end of the vegetative season (Gugnacka-Fiedor and Siedlewska 1989). It was also reported earlier that phenol concentrations decline as the growing season progressed (Wagner et al.1990). Both these reports are similar to my observations, as phenol content in my selected plants was higher in the young preflowering leaves as compared to the postflowering. Phenolic compounds have been associated with antioxidant activity (Larson 1995). They form an important part of the plant defense system that aid in the scavenging of the reactive oxygen species such as singlet oxygen, hydroxyl radical and organic oxyradicals, which have been implicated in causing damage to plant organs and biopolymers such as chloroplasts, cell membranes, proteins and even DNA. Thus, a low phenol content indicate poor antioxidative defense. Thus the seasons when phenol content is low there is a weaker defense system in plants and a poor scavenging of the harmful active oxygen species.

Metabolism of proteins is one of the fundamental cellular events. If protein synthesis is adversely affected, it would directly influence the operation of metabolic pathways. Bernstam (1978) suggests that the high sensitivity of protein synthesis to environmental stress resides primarily at the level of the initiation step in translation. Polysome disassembly and mRNA run off occur before impairment of RNA synthesis. Inhibition of protein synthesis by environmental stress may be a major factor contributing to the exacerbation of inhibition by a variety of environmental stresses including drought and temperature stresses (Powles 1984). In my work, protein content increased in the young plants (preflowering stages), but declined in their postflowering counterparts. Ontogenetic and age-dependent changes in protein and free amino acids have been reported in leaves (Weinberger 1975, Viana and Metivier 1980). Higher protein and amino acid contents have been reported during the period of active growth (Yoon 1996). The highest amounts of amino acids have been detected during the period of bud break and leaf expansion (Schneider et al. 1994), while a sharp fall in the amount of proteins accompanied by a general increase in proteolytic activity with approaching senescence was reported by Stoddart and Thomas (1982). Both these reports are similar to my observations (Sen and Mukherjee 1998d). The occurrence of maximum protein concentration is indicative of intense metabolic activity of the leaves during those periods (Sen and Mukherji 1998d).

Ascorbic acid is a ubiquitous antioxidant playing a key role in the detoxification of activated oxygen. It acts as an antioxidant either by reducing O_2^{-}, H_2O_2 and $^{\cdot}OH$, or by quenching singlet oxygen (Sharma et al. 1997). Higher ascorbic acid is present in the preflowering leaf samples and during optimum environmental conditions. Ascorbic acid acts as a potent and probably the most important hydrophilic antioxidant (Etsuo et al. 1995), and is a good reducing agent and scavenger of O_2^{-}, $^{\cdot}OH$ and $^{1}O_2$ (Bodannes and Chan 1979). However, under conditions of stress, there is a decrease in the content of ascorbic acid (Jiang et al. 1994, Sen et al. 2014). Decline in the ascorbic acid content during stress or in senescence as evidenced by my findings, imply decreased capacity of the

leaves to scavenge the free radicals and maintain the general reducing environment. Ascorbic acid concerns one of the main important anti-oxidant that protect plants from **oxidative stress** by regulating complex sequences of biochemical reactions such as activation or suppression of various key enzymatic reactions, induction of stress responsive protein synthesis and production of various chemical defense compounds beside its role in ascorbate-glutathione cycle through donating or losing electrons to produce the reducing form and regulating of flowering and senescence (Marzouk et. al 2018).

Enzymatic Antioxidants: Polyphenol oxidase oxidizes phenolic substrates. During periods of stress following cell injury, this plastidial enzyme is released into the cytoplasm, and it oxidizes phenols to lower their level to produce quinones, which are quite toxic in nature (Mayer and Harel 1979, Vaughn and Duke 1984). Thus, an increase in the activity of polyphenol oxidase may indicate a protective measure adopted by the plants in response to the prevailing conditions of environmental stress. It is evident that an increase in polyphenol oxidase activity always resulted in lowering of phenol content. Polyphenol oxidase was found to be more active in the postflowering stages and unfavourable seasons of crop plants (Sen and Mukherji 2006a, 2009). Ascorbic acid oxidase is a multi-copper enzyme which catalyzes the oxidation of ascorbic acid to dehydroascorbate. From my work and a previous work on *Vigna radiata* (Sen et al. 2014) it is evident that ascorbic acid content and ascorbic acid oxidase activity are inversely related to one another. The enzyme was more active in the postflowering stages of both plants. The role of this enzyme has been thought to be important in regulating the levels of reduced and oxidised glutathione and NADPH (Malik and Singh 1980). Like SOD, catalase activity showed an increase in the early phase of drought in wheat (Zhang and Kirkham 1994). Catalase is the potent H_2O_2 destroying enzyme whose activity increases manifold to scavenge the free radicals in the periods of environmental stress, as evidenced by the findings of the present work. Catalase activity in general, has always been found to decline during the senescence of leaves of various plants (Patra et al. 1978, Parida et al. 1981, McRae and Thompson 1983, Pauls and Thompson 1984, Li and Mei 1989). Catalase activity was significantly higher in winter in *Abelmoschus* and rainy in *Lycopersicon* and the enzyme was more active in the preflowering stages of both plants (Sen, 2016a). Peroxidase has been found to be highly active under various conditions of stress. In fact, the activities of enzymes involved in the H_2O_2 - scavenging pathway were also observed to increase under various stress conditions (Gossett et al. 1994, Kampfenkel et al. 1995, Mishra et al. 1995, Knorzer et al. 1996), and the present findings lend support to such observations. Increase in peroxidase activity during senescence has been well documented in different plant species (Parida et al. 1981, McRae and Thompson 1983, Mukherjee and Rao 1993). Catalase and peroxidase activities may be taken as indices of leaf senescence and stressful environmental conditions (Sen 2016a, Sen et al. 2014). Activity of SOD increased in those seasons in which lipid peroxidation and free radical formation were maximum, and this may well be assumed as an effort to scavenge and detoxify the active oxygen species (Sen 2016a). Activity of SOD has been reported to be elevated in the early phase of drought stress and also in temperature stress (Zhang and Kirkham 1994, Fryer et

al. 1998). SOD activity has been reported to decrease in maturing or senescent leaves (Li and Mei 1989, Wang et al. 1989, Sung and Jeng 1994, Li et al. 1995a, 1995b). In fact, SOD activity might be employed as one of the physiological parameters in studying leaf senescence (Li et al. 1995b), and along with the activities of catalase and peroxidase serve as effective indicators of prevailing environmental stress (Sen, 2016a) including arsenic toxicity (Sen 2016c). In plants, the SOD genes are regulated by development, tissue-specific and environmental signals (Scandalios 2005; Menezes-Benavante *et al.*, 2004). SOD has been associated with a variety of abiotic stresses (Saibi and Brini 2018, Berwal and Ram 2018). Decrease in ascorbate peroxidase activity during the periods of seasonal stress indicates the reduced efficiency of the chloroplasts to scavenge H_2O_2. Spruce seedlings under an abiotic stress like temperature stress, exhibited declining ascorbate peroxidase activity, which corresponded to a sudden upsurge in lipid peroxidation (Polle *et al.* 1996). Aging has been shown to inhibit the activity of ascorbate peroxidase (Sung and Jeng 1994). Ascorbate peroxidase activity declined in the winter season of *Abelmoschus* and rainy in *Lycopersicon*. The enzyme was more active in the preflowering stages of both crops (Sen 2016a).

Esterbauer and Grill (1978) reported that glutathione reductase activity showed an annual rhythm. It is known that reduced glutathione stabilizes protein-SH groups either by scavenging oxidising agents or by reducing formed S-S bonds in a nonenzyme reaction. These authors are of the opinion that since reduced glutathione is oxidised in both cases, it is evident that the protecting action of reduced glutathione is effective only as long as oxidised glutathione is reduced as soon as it is formed. Thus a decline in glutathione reductase activity in the winter of *Abelmoschus* and rainy of *Lycopersicon* (Sen 2016a) implied a diminished capacity to regenerate reduced glutathione leading to poor scavenging of the free radicals. Results reported elsewhere suggest that changes in the physiological and environmental conditions affect the interaction of ascorbate - related enzymes *viz.* ascorbate peroxidase, mono-dehydroascorbate radical reductase, dehydroascorbate reductase and glutathione reductase in plants (Polle and Morawe 1995). Diminished activities of ascorbate peroxidase and glutathione reductase correlate with the general inhibition of metabolism as indicated by, for example, stunted growth in wheat (Biemelt et al. 1998) and conform to my results (Sen 2016a) exactly. High sulfhydryl content, in general, is characteristic for young, physiologically active tissue (Pilet and Dubois 1968). It has been observed that plants older than three months are practically unable to accumulate sulfhydryl compounds (Kok et al.1981). Glutathione is the most abundant sulfhydryl compound, comprising more than 95% of the total sulfhydryl content (Grill et al. 1979). The function of glutathione in plants appears to be dual: regulation of S nutrition and defence against oxidative stress (Lappartient and Touraine 1997). Glutathione is a metabolite which protects the photosynthetic apparatus. The principal function of glutathione is to maintain the intracellular redox balance, detoxifying ROS, xenobiotics, and heavy metals (Soengas et al. 2018).

Conclusion

- Abundant production of free radicals accompanied by poor scavenging and detoxification of the active oxygen species by the non-enzymatic antioxidants and scavenging enzymes by the plant defense system marked the periods of seasonal environmental stress.
- Effects of unfavourable seasons (environmental stress periods) were more pronounced in the postflowering stages of plants.
- The parameters (morphological, physiological and biochemical) under study exhibited significant seasonal changes and can be taken as useful *bioassay indices* of environmental stress, while the plants by their extreme sensitivity to changing seasons act as a measure of the prevailing environmental conditions, and may thus serve as *efficient bioindicator species*.

Future Trends: Reverse genetics studies in crops that alter antioxidant enzyme profiles for stress tolerance are an important approach for crop improvement and to improve our understanding of basic cellular mechanisms. Moreover, the application of exogenous protectants such as plant nutrients, antioxidants, osmolytes, phytohormones, signaling molecules, and others have been employed and may contribute to mitigating the toxic effects of a high ROS level through increasing the antioxidant defenses in crops (Caverzan et al. 2019). The manipulation of scavenging enzymes is a worthwhile approach to produce transgenic plants with wide tolerance to a variety of stresses. However this requires more exploration and research as multiple enzymes and pathways may be involved and ROS scavengers, both enzymatic and non-enzymatic are only potential parameters for increasing plant tolerance to both abiotic and biotic stress.

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