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RESEARCH ARTICLE

EFFECT OF DECREASING OXYGEN CONCENTRATION ON PLANT METABOLISM IN RESPONSE TO DIFFERENT ENVIRONMENTAL STRESSES.

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Abstract

The use word "stress" when everything seems to have become too much. It causes significant crop losses. The stresses are numerous and often crop- or location-specific. They include increased UV-B radiation, water, high salinity, metal toxicity, herbicides, fungicides, air pollutants, light, temperature, topography and hypoxia (restricted oxygen supply in waterlogged and compacted soil). Research in this area is driven by the hope of improving crop yield in afflicted areas. The balance between the production of activated oxygen species and the quenching activity is upset which often results in oxidative damage. Many metabolic processes produce active oxygen species. This review concluded that the stress study must begin with a panoramic overview of the field from its medical and physiological origins in the early stages through its psychological elaborations during the mature stages of the crops and its current application and practice in organizations.

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Introduction:-

Most environmental stresses are affecting on the production of active oxygen species in plants, causing oxidative stress (1, 2, 3). Also, there is growing evidence that in plants subjected to environmental stress. The balance between the production of activated oxygen species and the quenching activity of antioxidant is upset, which often results in oxidative damage (4, 5, 1, 6).

Environmental stress causes significant crop losses. The stresses are numerous and often crop- or location-specific. They include increased UV-B radiation, water, high salinity, temperature extremes, hypoxia (restricted oxygen supply in waterlogged and compacted soil), mineral nutrient deficiency, metal toxicity, herbicides, fungicides, air pollutants, light, temperature and topography. Research in this area is driven by the hope of improving crop yield in afflicted areas. Currently, real, but slow advances are being made by crop breeders and agronomists using tried-and-tested methodology; however, biotechnology will increasingly have a role as genes involved in stress resistance are cloned and their mode of action elucidated (7).

It is apparent that many environmental stresses exert at least part of their effect by causing oxidative damage (8). Consequently, the antioxidant defense system of plants has been attracting considerable interest (9). Characterization of mutants and transgenic plants with altered expression of antioxidant is a potentially powerful approach to understanding the functioning of the antioxidant system and its role in protecting plants against stress, and significant progress is now being made in this area.

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Atmospheric oxygen has been recognized for more than 100 years as the agent responsible for the deterioration of organic materials exposed to air. The parallel role of oxygen, a molecule essential for many forms of life, as a destructive (toxic) agent for living tissues has been discovered much more recently. Even under optimal conditions many metabolic processes produce active oxygen species. Among the four major active oxygen species [superoxide radical $O_2^{\cdot-}$, hydrogen peroxide H_2O_2 , hydroxyl radical OH and singlet oxygen 1O_2] H_2O_2 and the hydroxyl radical are most active, toxic and destructive (1). In plants the most important of these are driven by or associated with light dependent events. Photosynthetic cells are prone to oxidative stress because they contain an array of photosensitizing pigments and they both produce and consume oxygen. The photosynthetic electron transport system is the major source of active oxygen species in plant tissues (10), have the potential to generate singlet oxygen 1O_2 and superoxide $O_2^{\cdot-}$.

Olga et al. (11) concluded that generation of reactive oxygen species (ROS) is characteristic for hypoxia and especially for reoxygenation. Of the ROS, hydrogen peroxide (H_2O_2) and superoxide ($O_2^{\cdot-}$) are both produced in a number of cellular reactions, including the iron-catalysed Fenton reaction, and by various enzymes such as lipoxygenases, peroxidases, NADPH oxidase and xanthine oxidase. The main cellular components susceptible to damage by free radicals are lipids (peroxidation of unsaturated fatty acids in membranes), proteins (denaturation), carbohydrates and nucleic acids. Consequences of hypoxia-induced oxidative stress depend on tissue and/or species (i.e. their tolerance to anoxia), on membrane properties, on endogenous antioxidant content and on the ability to induce the response in the antioxidant system. Effective utilization of energy resources (starch, sugars) and the switch to anaerobic metabolism and the preservation of the redox status of the cell are vital for survival (12). The formation of ROS is prevented by an antioxidant system: low molecular mass antioxidants (ascorbic acid, glutathione, and tocopherols), enzymes regenerating the reduced forms of antioxidants, and ROS-interacting enzymes such as SOD, peroxidases and catalases (12).

In plant tissues many phenolic compounds (in addition to tocopherols) are potential antioxidants: flavonoids, tannins and lignin precursors may work as ROS-scavenging compounds (11). Antioxidants act as a cooperative network, employing a series of redox reactions. Interactions between ascorbic acid and glutathione, and ascorbic acid and phenolic compounds are well known. Under oxygen deprivation stress some contradictory results on the antioxidant status have been obtained. Experiments on overexpression of antioxidant production do not always result in the enhancement of the antioxidative defense, and hence increased antioxidative capacity does not always correlate positively with the degree of protection (12). Here we present a consideration of factors which possibly affect the effectiveness of antioxidant protection under oxygen deprivation as well as under other environmental stresses. Such aspects as compartmentalization of ROS formation and antioxidant localization, synthesis and transport of antioxidants, the ability to induce the antioxidant defense and cooperation (and/or compensation) between different antioxidant systems are the determinants of the competence of the antioxidant system (11).

In this review my aim is to concentrate on current investigations of the environmental stresses, basis of stress resistance and on the potential of plants to improve functions by making stress resistance.

Environmental stresses impact:-

Ultraviolet stress:-

Sunlight contains energetic short wavelength ultraviolet (UV) photons which are potentially detrimental because of their destructive interactions with many cellular molecules, such as the amino acids of essential proteins, nucleic acids bases or membrane lipids (1). Intense light has long been known to disrupt metabolic processes in plants, including photosynthesis, respiration glucose assimilation, and phosphorylation (13). Approximately 4% of the total energy contained in sunlight occurs in the ultraviolet region (wavelengths shorter than 400 nm). The intensity of UV irradiance at the earth's surface varies greatly with season, time of day, latitude) ozone layer thickness, altitude, and cloud cover. Distinctions are sometimes made between the UV-A (400-320nm) and the UV-B (320-290nm) regions. In both cases, however, the fundamental mechanisms of photochemical damage are similar although different receptor molecules (chromophores) may be involved.

UV-B damages DNA by causing oxidative cross linking between adjacent pyrimidine bases forming cyclobutane pyrimidine dimers and pyrimidine pyrimidone dimers (14). Unless repaired, these block transcription and replication. Repair is achieved by light-activated photolyases which reduce the dimers in a light-dependent manner. Mutants deficient in photolyase activity have been isolated in rice (15) and Arabidopsis (*uvr2*) (16). Both are UV-B sensitive and unable to repair cyclobutane pyrimidine dimers. The photolyase (PHR1) from Arabidopsis has been

cloned by PCR using primers based on animal type II photolyases. Furthermore, PHR1 and uvr2 were shown to be the same by PCR, the mutant having a single base pair deletion (17). Identification of the photolyase gene opens the way for investigating the consequences of its overexpression on UV-B resistance.

There have been many reports on deleterious physiological effects on plants exposed to high levels of UV-B which may increase if stratospheric ozone concentrations decrease. The destructive action of UV irradiation results from both direct and indirect mechanisms involving endogenous sensitizers and the generation of active oxygen species. Physiological and biochemical effects of UV-B radiation include effects on enzymes, stomatal, resistance concentrations of chlorophyll, protein and lipid, reduction in leaf area, and tissue damage (18,19).

Some plants, however, appears to be quite resistant to increased UV irradiation. The differential susceptibility of plants to UV stress is clearly an important factor in their competitive relationships in terrestrial ecosystems (18); experiments with agriculturally important species pairs grown in pots have indicated that significant effects on biomass production took place when UV-B was present either at ambient or artificial increased levels. Photochemical damaging events in cells are initiated by the uptake of the electronic energy of a photon by a UV absorbing molecule (19). In the UV region of the electromagnetic spectrum, the energy of such photons is sufficient to break covalent bonds, although it is unusual for their energy converts the target molecules in its ground state to an electronically excited state whose excess energy manifests itself in a different and often quite unstable electron configuration. The initial excited state, a short-lived singlet having, fully paired electrons, may be deactivated by fluorescence (emission of a photon having a longer wavelength than the exciting radiation) and return to the ground state, it may react with neighboring molecules (although this is not common with singlet since their lifetime are normally too short for them to diffuse over very many molecular diameters) or it may undergo internal rearrangement to a longer lived excited state. The triplet state is much more likely to react chemically with surrounding molecules (18,19).

Water stress:-

Water stress is perhaps the most prevalent cause of crop yield loss but also the most difficult to tackle because of the strong link between transpiration and photosynthesis. Gene expression and signal transduction in water stressed plants has been recently reviewed (20). There is evidence for a mitogen-activated protein kinase type system in plants analogous to that involved in yeast osmoregulation. In support of such a system, a protein kinase is rapidly activated in maize roots exposed to low water potential (21). The role of dehydrins, late embryogenesis proteins and related proteins, which accumulate in seeds and water-stressed vegetative tissues, has been reviewed (22). Transgenic rice expressing HVA1, a gene encoding a late embryogenesis abundant protein from barley, has increased tolerance to drought and NaCl as shown by simple growth analysis (23). Aquaporins (water channel proteins) are clearly involved in controlling water movement between cells (24) and may be a target for manipulating water flow through the plant with potential for improving water relations and water use efficiency.

On exposure to osmotic stress as a result of drought, high salinity and low temperature plants accumulate a range of metabolically benign solutes, collectively known as compatible solutes or osmolytes. Their primary function is turgor maintenance but they may have other protective effects on macromolecules in dehydrating cells. The solutes accumulated vary between species and include proline, betaines, dimethylsulfoniopropionate (DMSP), polyols (mannitol, sorbitol, and pinitol), trehalose, and fructans. Over the past five years, a number of transgenic plants have been produced in which overaccumulation occurs (e.g. proline) or in which the ability to accumulate osmolytes not previously present has been introduced. The results suggest that they can improve plant growth during osmotic stress even at osmotically-insignificant levels (8).

Glycine betaine (GB) is accumulated by a taxonomically restricted range of species. In higher plants, it is synthesised from choline via betaine aldehyde using choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BALDH) in chloroplasts (25). Some bacteria, however, convert choline to betaine in a one-step reaction catalysed by choline oxidase. CodA, which encodes choline oxidase from *Arthrobacter globiformis*, has been expressed in *Arabidopsis*, a non-betaine accumulator. The gene had a chloroplast targeting sequence. The average leaf concentration was low but, if chloroplast localised, would be 50 mM, which approaches an osmotically-significant concentration. The transgenic plants, judged by photographs and measurement of plant length, were more tolerant to NaCl and continuous light at 5°C (26). Cytoplasmic targeting had less effect on tolerance. The same group also showed that the cyanobacterium *Synechococcus*, transformed with the same gene, was also more tolerant

to low temperature-induced photo-inhibition and provided evidence that GB affected membrane phase transitions and accelerated recovery of photo-inhibition (27).

There is a report that expression of *Atriplex hortensis* BALDH in rice increases GB content and salinity tolerance (28). Application of GB in foliar sprays is reported to improve the growth of water-stressed tobacco in laboratory experiments and maize, sorghum and soybean crops in the field (29, 30, 31). These interesting observations need more investigation, perhaps, to rule out the possibility that improved growth is caused by improved nitrogen supply. Contrary to this, exogenous GB is apparently toxic to *Brassica napus*, a non accumulator (32). Higher plant BALDH has been cloned and this has now been followed by cloning of CMO. Like BALDH, CMO expression is upregulated by NaCl. It has a Rieske-type [2Fe-2S] cluster and it is ferredoxin-dependent and, therefore, it represents a novel type of plant oxidase (25). It is suggested that metabolic engineering of GB synthesis with plant BALDH and CMO would be preferable to using choline oxidase because the plant-derived genes may also have promoters, which could drive increased expression during water stress (25). Furthermore, CMO uses chloroplast ferredoxin as reductant, thus linking timing of high stress in the light to betaine synthesis (25). BALDH is equally efficient at catalysing oxidation of 3-dimethylsulfoniopropionaldehyde to DMSP a compatible solute of even narrower distribution than GB (33) and ability to synthesise DMSP could have evolved by co-opting this enzyme. Transgenic tobacco expressing beet BALDH also had enhanced dehydrogenase activity towards 3-dimethylsulfoniopropionaldehyde and two other aldehydes, confirming the view that BALDH is a multisubstrate enzyme (34). BALDI-I expression may be more widespread than GB accumulation. BALDH is expressed in rice (non-GB accumulator) and the rice gene has high homology to barley BALDH. Unlike BALDH in betaine accumulating plants, the rice enzyme is located in peroxisomes. Feeding betaine aldehyde dehydrogenase to rice plants increases their GB content, and on the basis of photographic evidence, improves the growth of the plants at high salinity and low water content (35).

Evidence suggests that drought causes oxidative damage through generation of oxygen radicals or inhibition of antioxidant systems in plant (36, 37, 38). Drought related physiological changes such as a decrease in leaf water and stomatal closure, result in limited CO₂ availability to the channeling of reducing equivalents to the production of active oxygen species rather CO₂ fixation (39). Among the four major active oxygen species [superoxide radical O₂⁻, hydrogen peroxide H₂O₂, hydroxyl radical OH and singlet oxygen ¹O₂] H₂O₂ and the hydroxyl radical are most active toxic and destructive (1). Hydrogen peroxide can be produced by either dismutation of O₂⁻ by SOD or photorespiration.

Salinity Stress:-

Height salt concentration normally impair the cellular electron transport within the different subcellular compartments and lead to the generation of reactive oxygen species (ROS) such as singlet oxygen, superoxide, hydrogen peroxide and hydroxyl radicals (40, 45, 46). Excess of ROS triggers phytotoxic reactions such as lipid peroxidation, protein degradation and DNA mutation (47, 48, 49).

Mannitol is accumulated by a wide range of species in response to salinity (50). Mannitol synthesizing ability was introduced into transgenic tobacco by the *E. coli* mtlD gene encoding Mannitol dehydrogenase. These plants accumulated modest amounts of mannitol but were said to be more salt-tolerant (51). Bohnert and co-workers (52) have now produced transgenic tobacco in which mtlD expression is targeted to the chloroplast. A concentration of 100mM was estimated. It has been suggested that compatible solutes, including mannitol, could be antioxidants by scavenging hydroxyl radicals (OH) (56, 58). This might be significant for plants exposed to drought and high salinity as there is strong evidence that oxidative generation of active oxygen species increases under such conditions (59).

The chloroplast-targeted mannitol accumulating tobacco has been used to test this hypothesis. Mannitol accumulation did not affect photosynthesis. The transgenic plants were more tolerant to OH* generated in chloroplasts by methyl viologen treatment. The OH* content of transgenic plants was also lower (52) suggesting that the protection could result from OH* scavenging by mannitol. In a further paper (53), the same group have provided convincing evidence that a key target for OH* produced by illuminated thylakoids is the Calvin cycle enzyme phosphoribulokinase (regulated by thiol-disulfide interconversion). This inactivation, in mixtures containing thylakoids and phosphoribulokinase, was prevented by mannitol and could explain the in vivo protective effect of mannitol. Further support for the efficiency of mannitol acting as an OH* scavenger in vivo has been provided by transformation of *Saccharomyces cerevisiae* with the same mtlD gene. A mutant unable to grow at high osmolarity because of inability to synthesize glycerol, the normal osmoregulatory solute of yeast, had this ability restored by

introduction of mannitol synthesis capacity. Furthermore, the transgenic yeast was also more tolerant to chemically-generated OH^* in the growth medium (60). These studies suggest osmolytes could indeed have multiple functions and could explain the protective effects observed at osmotically insignificant concentrations (61).

Metals stress:-

Accumulation of phytotoxic metal results from industrial and agricultural practices. The Zn, Cu, and Cd are widespread pollutants resulting in stunted growth, chlorosis and necrosis (63, 65). Copper Cu_2 ions cause light mediated lipid peroxidation and pigment bleaching (66, 67). Prolonged exposure to CuSO_4 resulted in chlorophyll bleaching in rye and the endogenous CAT level declined (70). Thus enhanced susceptibility to photooxidative damage was related to the rapid loss of CAT activity, Cu_2 ions are redox active and catalyze fentonperoxides also originate from the induction of lipoxygenase in the presence of Cu_2 . This enzyme is known to initiate lipid peroxidation.

Cadmium treatment, decrease the chlorophyll levels of germinating mung bean seedlings by induction of lipoxygenase with the simultaneous inhibition of the antioxidative enzyme SOD and CAT (71). Such inhibition results from binding of the metal to the important sulfhydryl groups of enzymes, which exacerbates the phytotoxic action of metals (72).

Pang et al. (74) studied improving the plant ability to resist lead stress, effect of 0.05 mg/L La (NO_3)₃ on the activities of catalase (CAT), superoxide dismutase (SOD), the level of malondialdehyde (MDA) in wheat seedlings under lead stress were studied. The effect of La⁺³ on plant growth, chlorophyll content in wheat seedlings after adding 0, 50, 100 mg/l Pb (NO_3)₃ to the nutrient solution for 12 days was observed. The plants were grown in nutrient solution in a strictly controlled climate growth room. Effects of La⁺³ (with La treatment) compared with check groups was evidently observed. The activities of SOD and CAT in root were enhanced 0.45–1.69 times and 33.20–77.77% respectively and MDA content was reduced 11.05–27.49% in root after treatments from the second day till the end of the experiment. The activities of SOD and CAT was found to be increased slightly ($P < 0.05$) and MDA content decreased in shoot and root of wheat seedlings by La⁺³ under lead stress within five days after treatments compared with Pb₁ and Pb₂ groups. It was assumed that antioxidant enzymes was found to be increased by La (NO_3)₃, the antioxidant potential of the wheat seedlings to resist lead stress enhanced. It is suggested that La⁺³ could be used to resist lead stress at the beginning under stress while the stress was not so serious.

Herbicides stress:-

Several herbicides have been found to generate active oxygen species, either by direct involvement in radical production or by inhibition of biosynthetic pathways. The generation of the hydrocarbon gas ethane, the production of malonaldehyde and changes in electrolytic conductivity has frequently been used as sensitive markers for herbicide action in plants (75, 76). The bipyridinium and diphenyl ether herbicides have been the most insensitively investigated in terms of their oxidative action in plants.

The bipyridinium herbicides generate oxygen radicals directly in the light. Compounds such as paraquat (also known as methyl viologen) induce light dependent oxidative damage in plants. Members of this group are called total kill herbicides (77). The di-cationic nature of these compounds facilitates their reduction to radical cation. The PSI-mediated reduction of the paraquat di-cation results in the formation of a mono-cation radical which then reacts with molecular oxygen to produce O_2^- with the subsequent production of other toxic species, such as H_2O_2 and OH^* (44). The diphenyl ethers, cyclic imides and lutidine derivative, act by inhibition biosynthetic pathways with the subsequent accumulation of reactive radical-forming intermediates. These compounds cause severe toxicological problems and results in peroxidation of membrane lipids and general cellular oxidation.

The mode of action of these herbicides is based on the ability to induce the abnormal accumulation of photosensitizing tetrapyrroles specifically protoporphyrin IX (67). This pigment is able to cause light dependent generation. These herbicides can also catalyze the oxidation of protoporphyrinogen to protoporphyrin IX. The penultimate step of both heme and chlorophyll biosynthesis is recorded (79). It is somewhat anomalous that the reaction product protoporphyrin IX accumulates in condition where the enzyme which catalyses its formation is expected to be inhibited.

Other compounds such as diuron, that block photosynthetic electron transport and inhibitors of carotenoids biosynthesis, such as norflurazon, initiate photooxidative processes most probably via the generation of 1O_2 (78,

80). Herbicides which block photosynthesis cause increased excitation energy transfer from triplet chlorophyll to oxygen while those inhibit carotenoid biosynthesis eliminate important quenchers of the triplet chlorophyll and $1O_2$.

Fungicides stress:-

A number of agricultural chemicals such as fungicides (91) and herbicides (92) have been shown to possess antiozonant properties. However, most of these investigations have concentrated on the effectiveness of agrochemicals in preventing plants from ozone injury, and relatively little work has focused on the physiological and biochemical modes of action.

The strobilurins are an important new class of fungicides with a unique mode of action which targets mitochondrial respiration in fungi. Few studies on the physiologic effects of strobilurins on and in plants showed that strobilurins increased grain yields, dry matter, chlorophyll and protein contents and delayed senescence (95).

Air pollutant stress:-

Atmospheric pollutants such as ozone (O_3) and sulfur dioxide (SO_2) have been implicated in free radical formation (96, 99) and are considered to be one of the major factors influencing modern forest decline. Ozone, which originates from a natural photochemical degradation of nitrous oxides (NO_2), seems to be a greater threat to plants than pollution (102). Mehlhorn et al. (99) suggested that the phytotoxicity of O_3 is due to its oxidizing potential and the consequent formation of radicals that induce free radical chain reactions. The O_3 concentration in the intercellular air spaces of leaves is close to ozone (103). Ozone is, thus unlikely to reach the chloroplast but it nevertheless, causes pigment bleaching and lipid peroxidation (104,105). Stimulation of both synthesis and degradation of the PSII-D1 protein occurs in spruce trees following O_3 treatment (106,107) and a decrease in the activity and quantity of rubisco has been found in poplar following exposure to O_3 (108).

Exposure to SO_2 results in tissue damage and release of stress ethylene from both photosynthetic and non-photosynthetic tissues (110,111). Fumigation with SO_2 causes a shift in cytoplasmic pH. The proton concentration of the cytoplasm is one of the most important factors regulating cellulase activity. When cells are exposed to SO_2 an appreciable acidification of the cytoplasm occurs because this gas reacts with water to form sulfurous acid which may then be converted into sulphuric acid (112, 113, 114). These results, in loss of photosynthetic function caused by inhibition of the activity of SH-containing light-activated enzymes of the inhibition of the activity of SH- containing light-activated enzymes of the chloroplast (115, 116, 117).

The oxidation of sulfite to sulfate in the chloroplast also gives rise to the formation of O_2^- (96). The oxidation of sulfite is initiated by light and is mediated by photosynthetic electron transport. Navari-Izzo et al. (120) reported that the degradation of membrane lipid components possibly by de-esterification rather than peroxidation with SO_2 . They found no evidence to support the view that free radical attack on polyunsaturated fatty acids occurred at low pollutant concentrations.

Light stress:-

A wealth of evidence shows that antioxidants are responsive to photooxidative stress (9, 83). In bacteria, signal transduction systems involved in responses to oxidative stress have been identified (121); however, very little is known in plants. An important step forward has been made in identifying a possible mechanism of detecting oxidative stress in chloroplasts of leaves exposed to high levels of light. Transfer of Arabidopsis leaves from low light to high light causes rapid induction of mRNA for two nuclear-encoded cytosolic ascorbate peroxidase genes (APX1 and APX2). Also, within this 15 minute period the ratio of reduced to oxidized glutathione decreases, indicating that the leaves are under oxidative stress as a result of exposure to excess excitation energy. The induction of the APX genes was prevented by treatment with 3-(3,4-dichlorophenyl)-l, l-dimethylurea, which blocks photosynthetic electron transport before plastoquinone (PQ). Conversely, 2, 5-dibromo-3-methyl-6- isopropyl-p-benzoquinone, which blocks electron transport at the cytochrome b/f complex, causes higher APX expression in low light. The results can be interpreted as suggesting that the redox state of PQ has a role in acting as a sensor of excess light. Interestingly, glutathione feeding also blocked the response and it was suggested that extra glutathione swamps a signal generated by the redox state of the endogenous pool (6). These observations require further investigation because it is clear that there is a rapid signal transduction process leading to induction of APX when leaves are exposed to excessive light.

Evidence of similar redox signaling in controlling light-mediated phosphorylation of light harvesting complexes and expression of photosynthesis enzymes exists (122,123). Signal transduction via increased cytosolic Ca^{2+} has been suggested (124) and this observation has been extended by demonstration of elevated cytosolic Ca^{2+} in stomatal guard cells by methyl viologen and hydrogen peroxide treatment, which then causes closure (127).

Temperature stress:-

Various tolerance mechanisms have been suggested on the basis of the biochemical and physiological changes related to chilling injury (63, 42, 128). Levitt has suggested that a major target of chilling injury is cell membranes (130). As temperature is reduced, a specific temperature determined by the ratio of saturated to unsaturated fatty acids accelerates the conversion of lipids of a liquid-crystalline condition into that of a solid condition in plant cell membranes (131). The conversion of fatty acid may give rise to chilling resistance at lower temperatures in the plant cells. However some plants, which show a similar fatty acid ratio under chilling conditions, are very sensitive to chilling injury compared to others; thus other mechanisms may also be necessary for chilling injury. In previous studies it has been suggested that oxidative stress induced by chilling stress may play a pivotal role for chilling injury in plant cells (132,133).

Dong and Chin (134) were investigated in the following: the antioxidant defense system and chilling stress-induced changes of antioxidant enzymes in the leaves of cucumber (*Cucumis sativus* L.). Chilling stress preferentially enhanced the activities of the superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR) and peroxidase specific to guaiacol, whereas it induced the decrease of catalase activity. In order to analyze the changes of antioxidant enzyme isoforms against chilling stress, foliar extracts were subjected to native PAGE. Leaves of cucumber had four isoforms of Mn-SOD and two isoforms of Cu: Zn-SOD. Fe-SOD isoform was not observed in this plant. Expression of Cu: Zn-SOD and Mn-SOD was preferentially enhanced by chilling stress. Expression of Mn-SOD-2 and -4 was enhanced after 48 h of the poststress period. Five APX isoforms were presented in the leaves of cucumber. The intensities of APX-4 and -5 were enhanced by chilling stress, whereas that of APX-3 was significantly increased in the poststress periods after chilling stress. Gel stained for GR activity revealed six isoforms in the plant. Activation levels for most of GR isoforms were higher in the stressed-plants than the control and poststressed-plants, but that of GR-1 isoform was significantly higher in the poststressed-plants than chilling stressed-plants. Dong and Chin (134) results collectively suggest that chilling stress activates the enzymes of an SOD: ascorbate-glutathione cycle under catalase deactivation in the leaves of cucumber, but the response timing of enzyme isoforms against various environmental stresses is not the same for all isoforms of antioxidant enzymes.

Topography Stress:-

High mountain plants must have a very effective carbon assimilation mechanism due to a very short growing period. The extreme climatic conditions of high mountain zone, high irradiance, low temperature, rapid temperature change and a reduced CO_2 partial pressure creates unfavorable conditions for photosynthesis (64, 69, 135). Previous studies revealed that alpine plants are highly efficient in photosynthesis at low temperatures and are also adapted to high irradiance (135). The biggest damage caused by the high light intensity in plants is the inactivation of D1 protein (located on PSII) and the catalase (CAT) enzyme. Low temperature stress has a similar effect upon PSII and CAT (69). The alpine plants have a much more effective protection mechanism against oxidative damage compared with the plants growing in lower altitude regions (69,136,137). The steppe plants are also affected by the combination of high light intensity, high temperature and drought stresses.

The steppe regions have very poor vegetation and a very short vegetative period since these conditions limit plant growth (68,138). The high light intensity, high temperature and the temperature difference between night and day increases the generation of reactive oxygen species and thus the risk of oxidative damage. The plants may have developed two strategies to adapt to these severe conditions: antioxidant protection and avoidance from oxidative stress (68). The damage from the electron transfer system results in the formation of free radicals (singlet oxygen, superoxide radical and hydroxyl radicals). It is necessary to activate the biochemical protection mechanism of the plant in order to eliminate these extremely hazardous radicals (140).

The antioxidant protection requires high amounts of carotenoids, ascorbic acid, α -tocopherol, glutathione, phenolics and flavinoids (139) and the increased activities of CAT, superoxide dismutase (SOD) ascorbate peroxidase, dehydroascorbate reductase and glutathione reductase (GR) enzymes (80,141). The antioxidant defense mechanism protects the unsaturated membrane lipids, nucleic acids, enzymes and other cellular structures from the harmful

effects of free radicals (84,140,142). The tolerance of *Homogyne alpina*, an alpine plant, to light stress is explained by the presence of a stable CAT enzyme. *Ranunculus glacialis* growing at the same altitude has a weak antioxidant system (69,137). The activity of antioxidant enzymes and amount of carotenoids in *Retama raetam*, a desert plant, has been found to be higher than in non-desert plants (68).

Lack of oxygen stress:-

Lack of oxygen or anoxia is a common environmental challenge which plants have to face throughout their life. Winter ice encasement, seed imbibitions, spring floods and excess of rainfall are examples of natural conditions leading to root hypoxia or anoxia. Low oxygen concentration can also be a normal attribute of a plants' natural environment. Wetland species and aquatic plants have developed adaptative structural and metabolic features to combat oxygen deficiency. A decrease in adenylate energy charge, cytoplasmic acidification, anaerobic fermentation, elevation in cytosolic Ca^{2+} concentration, changes in the redox state and a decrease in the membrane barrier function, are the main features caused by lack of oxygen (143, 144, 147, 148, 149, 150). Regulation of anoxic metabolism is complex and not all the features are well established. In the recent paper by Gout et al. (12) a cytoplasmic acidification process has been temporally resolved in sycamore (*Acer pseudoplatanus*) cell culture by NMR (nuclear magnetic resonance). The immediate response of cytoplasmic pH was solely dependent on proton-releasing metabolization of the nucleoside triphosphate pool; the long-term regulation (after 20 min of anoxia) involves lactate synthesis, succinate, malate, amino acid metabolism and ethanolic fermentation (12).

Under natural conditions anoxic stress includes several transition states (hypoxia, anoxia and reoxygenation) characterized by different O_2 concentrations (Table 1). Excessive generation of reactive oxygen species (ROS), i.e. under oxidative stress, is an integral part of many stress situations, including hypoxia. Hydrogen peroxide accumulation under hypoxic conditions has been shown in the roots and leaves of *Hordeum vulgare* (151) and in wheat roots (153). The presence of H_2O_2 in the apoplast and in association with the plasma membrane has been visualized by transmission electron microscopy under hypoxic conditions in four plant species (154).

Table 1:- ROS scavenging and detoxifying enzymes

Enzyme	EC umber	Reaction catalyzed
Superoxide dismutase	1.15.1.1	$\text{O}_2^- + \text{O}_2^- + 2\text{H}^+ \leftrightarrow 2\text{H}_2\text{O}_2 + \text{O}_2$
Catalase	1.11.1.6	$2\text{H}_2\text{O}_2 \leftrightarrow \text{O}_2 + 2\text{H}_2\text{O}$
Glutathione peroxidase	1.11.1.12	$2\text{GSH} + \text{PUFA-OOH} \rightarrow \text{GSSG} + \text{PUFA} + 2\text{H}_2\text{O}$
Glutathione S-transferases	2.5.1.18	$\text{RX} + \text{GSH} \leftrightarrow \text{HX} + \text{R-S-GSH}^*$
Phospholipid-hydroperoxide glutathione peroxidase	1.11.1.9	$2\text{GSH} + \text{PUFA-OOH} (\text{H}_2\text{O}_2) \leftrightarrow \text{GSSG} + 2\text{H}_2\text{O}^{**}$
Ascorbate peroxidase	1.11.1.11	$\text{AA} + \text{H}_2\text{O}_2 \leftrightarrow \text{DHA} + 2\text{H}_2\text{O}$
Guaiacol type peroxidase	1.11.1.7	$\text{Donor} + 2\text{H}_2\text{O}_2 \leftrightarrow \text{oxidized donor} + 2\text{H}_2\text{O}^{***}$
Monodehydroascorbate reductase	1.6.5.4	$\text{NADH} + 2\text{MDHA} \leftrightarrow \text{NAD}^+ + 2\text{AA}$
Dehydroascorbate reductase	1.8.5.1	$2\text{GSH} + \text{DHA} \leftrightarrow \text{GSSG} + \text{AA}$
Glutathione reductase	1.6.4.2	$\text{NADPH} + \text{GSSG} \leftrightarrow \text{NADP}^+ + 2\text{GSH}$

* R may be an aliphatic, aromatic or heterocyclic group; X may be a sulfate, nitrite or halide group.

**Reaction with H_2O_2 is slow.

*** AA acts as an electron donor (100).

In these experiments H_2O_2 was probably of enzymatic origin considering the low oxygen concentration in the system and the positive effects of the various inhibitors of H_2O -producing enzymes. Indirect evidence of ROS formation (i.e. lipid peroxidation products) under low oxygen has been detected (145, 155, 157, 158, 159).

The phenomenon of cross-tolerance to various environmental stresses suggests the existence of a common factor, which provides crosstalk between different signaling pathways. ROS have recently been considered as possible signaling molecules in the detection of the surrounding oxygen concentration (167). It has been suggested also that ROS and oxygen concentration (including hypoxia) can be sensed via the same mechanism. Several models employ direct sensing of oxygen (via hemoglobin or protein SH oxidation) or ROS sensing. There are two models which suggest either a decrease in ROS under oxygen deprivation (low NADPH oxidase activity) or an increase in ROS due to the inhibition of the mitochondrial electron transport chain.

Molecular oxygen is relatively unreactive (41) due to its electron configuration. Activation of oxygen (i.e. the first univalent reduction step) is energy dependent and requires an electron donation. The subsequent one-electron reduction steps are not energy dependent and can occur spontaneously or require appropriate e^-/H^+ donors. In biological systems transition metal ions (Fe^{2+} , Cu^+) and semiquinones can act as e^- donors. Four-electron reduction of oxygen in the respiratory electron transport chain (ETC) is always accompanied with a partial one- to three-electron reduction, yielding the formation of ROS. This term includes not only free radicals (superoxide radical, $O_2^{\cdot-}$, and hydroxyl radical, $OH\cdot$), but also molecules such as hydrogen peroxide (H_2O_2), singlet oxygen (1O_2) and ozone (O_3). Both $O_2^{\cdot-}$ and the hydroperoxyl radical HO_2^{\cdot} undergo spontaneous dismutation to produce H_2O_2 . Although H_2O_2 is less reactive than $O_2^{\cdot-}$, in the presence of reduced transition metals such as Fe^{2+} in a chelated form (which is the case in biological systems), the formation of $OH\cdot$ can occur in the Fenton reaction.

A potential route for the formation of a damaging species from a photochemical activated triplet state is the transfer of triplet energy to molecular oxygen. The product of the energy transfer reaction is singlet oxygen 1O_2 . The chlorophyll pigments associated with the electron transport system are the primary source of 1O_2 . The 1O_2 may also arise as a byproduct of lipoxygenase activity, like the hydroxyl radical; 1O_2 is highly destructive reacting with most biological molecules at near diffusion controlled rate (78,168). Several classes of biological molecules are susceptible to attack by 1O_2 including several protein amino acids (cysteine, methionine, tryptophan and histidine) which react with it at quite rapid rate (85). Polyunsaturated fatty acids also react at much slower rate, increasing with the number of double bonds in the molecule, to form lipid hydroperoxides and $O_2^{\cdot-}$ radicals (169,170) this take place by enzyme lipoxygenase. Primary radical ($R\cdot$) formed as a result of UV irradiation lead to formation of lipid radicals ($L\cdot$). Lipid radicals react with O_2 (a reaction limited only by the rate of diffusion) to produce lipid peroxy radicals ($LOO\cdot$). This peroxide is likely contributors to damage and dysfunction of cell and organelle membranes. The subject of singlet oxygen and plants has been reviewed by Knox & Dodge, (78).

Non-photochemical routes for oxidative damage in plants usually involve the interaction of molecular oxygen with free radicals to produce new, potentially harmful free radical species containing oxygen. This type of reaction may occur directly, or it may be promoted by enzyme catalysts normally present in the plant cell such as the enzyme lipoxygenase (171). Atmospheric oxygen is unusual in that its ground state has two unpaired electrons; it is a triplet state with considerable diradical character. These penults are to enter into energetically favorable chain reactions with many organic free radicals.

The formation of organic (usually carbon centered) free radicals $R\cdot$ from non radical precursors is called the "initiation phase" of the autooxidation. This process, which is often quite slow, results in the characteristic lag period of a radical chain reaction. In the propagation phase of the reaction there is a buildup of peroxy radicals, $ROO\cdot$, and the subsequent reaction of peroxy radicals with compounds ($R'H$) having extractable hydrogen atoms. The new radicals are then available for further reaction with molecular oxygen. Finally when all the oxygen or active hydrogen species are used up the 'termination phase' begins. In this phase, the radicals recombine with each other to produce inactive, nonradical products. Synthetic organic chemists have created many effective inhibitors of oxidative damage for rubber, hydrocarbon fuels, plastics foodstuffs and many other materials.

Summary:-

The stress study must begin with panoramic overviews of the field from its medical and physiological origins in the early stages through its psychological elaborations during the mature stages of the crops and its current application and practice in organizations. The panoramic overviews are the examine sources of stress; the psychophysiology of the stress response and individual moderators that condition vulnerability for distress; the psychological, behavioral, and medical forms of individual distress; and the organizational costs of distress. At the heart of the stress studies is a framework for preventive stress management. Specific examine methods and instruments for diagnosing organizational and individual stress; ways to redesign work and improve professional relationships; and methods for managing demands and stressors, altering how one responds to inevitable and necessary demands are also included. Organizational and individual prevention methods are designed to enhance health and performance at work while averting the costs and discomfort of distress.

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