BIOLOGIA PLANTARUM 38 (1): 1-18, 1996

REVIEW

Is there a GAS (general adaptation syndrome) response to various types of environmental stress?

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Abstract

A hypothesis of existence of a general adaptation syndrome (GAS), in which different types of stress evoke similar coping mechanisms, resulting in adaptations, is tested for plants. As stress coping mechanisms, oxy-free radical scavengers and anti-oxidants, osmoregulation, the role of abscisic acid, jasmonates, nitric oxide, synthesis of heat shock proteins and phytochelatins as heavy metal detoxifiers are discussed.

Additional key words: abscisic acid, adaptation, chaperonins, ethylene, heat shock proteins, jasmonates, nitric oxide, osmoregulation, oxy-free radicals, phytochelatin

Introduction

According to the classical mammalian "general adaptation syndrome" (GAS) hypothesis, different types of stress evoke similar adaptation responses (Selye 1936). Application of this hypothesis to plants implies that different types of stress as heat, cold, drought, salinity, anoxia, *etc.* would evoke similar or even identical stress coping mechanisms. The GAS hypothesis also implies that tolerance to one type of stress can be induced by sublethal exposure of the organism to a different type of stress. Drawing upon test cases involving osmoregulation, anti-oxidative pathways, abscisic acid (ABA) and jasmonic acid (JA) production, growth inhibition, heat shock proteins, ubiquitin and chaperonins, and endogenous coping with metal

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Received 24 July 1995, *accepted* 1 September 1995.

Abbreviations: ABA - abscisic acid; ACC - amino cyclopropane-1-carboxylic acid; GAS - general adaptation syndrome; HMM - high molecular mass; HSP - heat shock protein, JA - jasmonic acid; LAS - local adaptation syndrome; LMM - low molecular mass; MJ - methyl jasmonate; NO - nitric oxide; SOD - superoxide dismutase.

Acknowledgement: The authors would like to thank the Netherlands Organization for Scientific Research (NWO) which enabled their collaboration and the formulation of some of the concepts here presented.

pollution, the present authors conclude that application of the GAS hypothesis to plants provides insight into functioning of plants under stress.

The rationale behind the hypothesis of putative existence of a general adaptation syndrome in plants is that nature is not a controlled environment growth chamber. Any plant - be it perennial, annual or seasonal - during its life cycle is exposed to wide seasonal or diurnal vicissitudes of environmental conditions. One and the same plant during noon hours may be challenged with heat stress while at night with chilling or freezing stress. The same plant when young may develop and thrive in low temperatures when being exposed to a measure of root anoxia due to excessive soil moisture, while at a later stage it experiences heat shock and partial desiccation, but nevertheless develops normally to full fruition. Some evergreen perennials undergo cyclic changes of extremely cold winters and hot summers; several desert species undergo cyclic and marked changes of soil salinity which in a given location as in a wadi-bed, is inversely related to precipitation.

Over and above these, plants may be faced with 'climatic aberrations' in the form of hot dry winds (*e.g.*, chinook', 'föhn', 'sharav' or 'mistral') during cold spring weather or conversely may undergo exposure to spells of cold wintry weather during a mild autumn. Air pollutants are an increasing problem which also imposes acute or chronic stresses on plants. It thus appears that an inherent multiple stress resistance mechanism is developmentally advantageous and may be pleiotropically encoded by evolutionary selection.

In support of this contention, it can be seen that most of the individual stresses (Table 1), can be alleviated by virtually all of the GAS components. Also in combatting vastly different stresses, *e.g.*, heat and freezing, plants may employ identical stress-coping strategies. This table is by no means exhaustive but presents a typical cross-cut of pertinent documentation. Moreover, in addition to the five categories here highlighted, other GAS components unquestionably exist. Some of these will be discussed in later sections.

Concepts and definitions

The triphasic sequence of a typical stress event as envisaged in mammalian systems is indicated on Fig. 1. In tissues affected by stress, a "local adaptation syndrome" (LAS) develops at the site where the stressor is initially experienced. LAS and GAS are closely coordinated: directly stressed tissues send out chemical alarm signals, which induce adaptive responses of the organism in the form of hormones, enzymes, osmoregulants, *etc.* which in turn combat wear and tear in the stressed tissue. Thus, the generalized response (GAS) has a feedback effect upon the LAS region. We propose that the concept of a GAS syndrome is also applicable for plants.

In mammals, which are highly differentiated, the center of coordination acted upon by alarm signals is via the nervous system to endocrine glands, especially the pituitary and the adrenals which produce adaptive hormones. In plants the production of adaptive agents may be expressed at the level of specific organs, *e.g.* roots, shoots or buds, and is not as strictly localized as in mammals. However, a typical case of a

Table 1. Some putative GAS components in plants. It can be seen that the same tolerance component can be employed in plant adaptation to vastly different types of stress. Other GAS components are doubtlessly also involved. See text for details.

Stress	ABA	Free radical scavenging and antioxidative measures	Heat shock protein, ubiquitin and chaperone complex	Osmoregulation	NO$^{\cdot}$ and cytochrome P_{450} enzymes
Freezing	Macháčková *et al.* 1989, Heino *et al.* 1992, Lin and Tomashow 1992	Loubaresse *et al.* 1991, Andrews and Pomeroy 1989, McKersie *et al.* 1993	McElwain and Spiker 1992	Lin and Tomashov 1992	
Chilling	Rikin *et al.* 1993	Horiyadi and Parkin 1993	Cabane *et al.* 1993	Kovacs *et al.* 1994	
Drought	Leshem *et al.* 1986, Loveys 1991, Davies and Zhang 1991	Price and Hendry 1991, Pastori and Trippi 1992		Polyakoff Maayber and Lerner 1994	Leshem 1995
Desiccation	Black 1991	Simontacchi and Puntarulo 1992		Pages *et al.* 1993	
Salinity	Blatt 1993	Kalir and Polyakoff Mayber 1981	McElwain and Spiker 1992	Tarczynski *et al.* 1993, McKersie and Leshem 1994	
Flooding and anoxia	Voesenek *et al.* 1992	Jackson 1989, Crawford 1993, Leshem *et al.* 1986, Gudleifsson 1993	Donati *et al.* 1990		
Heat		Barna *et al.* 1993	Clark and Critchley 1992, Hernandez and Vierling 1993, Almoguera *et al.* 1995	Stoller 1977	
Heavy metals		De Kok and Stulen 1993	Neumann *et al.* 1994		
Herbicides		Malan *et al.* 1990			
Overall stress			Viestra 1993		Hendry 1985, Hansíková *et al.* 1995, Leshem and Haramaty 1996

LAS reaction which leads to a GAS in plants has been clearly indicated in drought stress by "split-root" experiments (Davies *et al.* 1990, Davies and Zhang 1991).

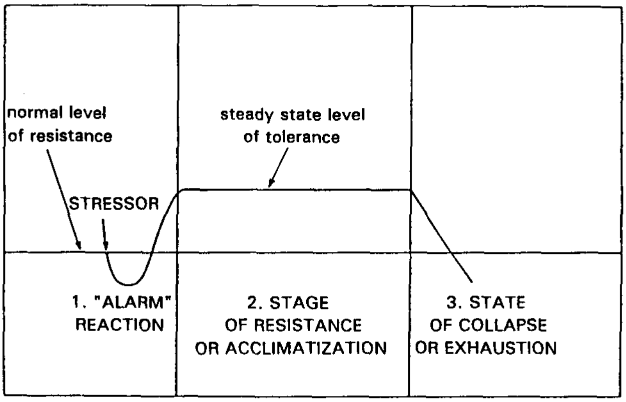

Fig. 1. Triphasic kinetics of the general adaptation syndrome (GAS). Modified from Selye (1975) to include plant systems. *1* - alarm reaction: this is the somatic response to the first exposure to a localized or general stressor and initially lowers basal state of resistance. If the 'stressor' is sufficiently strong (*e.g.* extremes of temperature, salinity, *etc.*), death may result; *2* - stage of resistance or acclimation: if continued exposure to the stressor is compatible with adaptation, resistance mechanisms of either a "syntoxic" (coexistence with stress) or a "catatoxic" (stressor-removal) nature ensues. The cellular manifestations characteristic of the alarm reaction have virtually disappeared or are strictly held in abeyance and resistance rises above normal; *3* - state of collapse or exhaustion: following long-term exposure to the stressor, adaptation capability is eventually exhausted. Signs of the alarm reaction reappear and the organ or the whole organism senesces and dies.

In these experiments, roots of intact maize plants were split (see Fig. 2), one half of which was exposed to water (drought) stress, while the other was maintained under adequate irrigation; the plant in its entirety undergoing no hindrance of normal stomatal behaviour nor of transpiration. After an initial stress period the localized root tissue produces ABA which promotes stomatal closure and induces drought resistance. As a consequence of the localized drought stress an overall increase in endogenous ABA is experienced throughout the whole plant, including parts which experience no water stress whatever.

Adaptive hormones and stimuli, according to the mammalian Selyean principle and as conceptualized by contemporary stress physiologists (Bensabat 1991) fall into two groups: (*a*) syntoxic stimuli which create a state of passive tolerance permitting symbiosis or peaceful co-existence with the stressors. In mammals, the β-endodorphins are such a factor. In parallel with mammals, in plants ABA, cytokinins, jasmonates, osmoregulation, *etc.*, may fulfill the same function (Leshem *et al.* 1993). In the case of general adaptation and acquired resistance to pathogens, again jasmonates [in connection with phytoalexin formation (Farmer and Ryan 1992)] and salicyclic acid (Cohen *et al.* 1993b, McKersie and Mehdy 1994) also have a GAS-related syntoxic effect; (*b*) catatoxic stimuli or agents which case biochemical changes mainly through the production of "detoxifying" enzymes, free radical scavengers, antioxidants, nitric oxide, *etc.*, which actively attack the stressor. In mammals, the "triple f" (fright, flight and fight) hormone - epinephrine (adrenaline) - is claimed to serve in this capacity. As shown below, similar cases will be presented for plants.

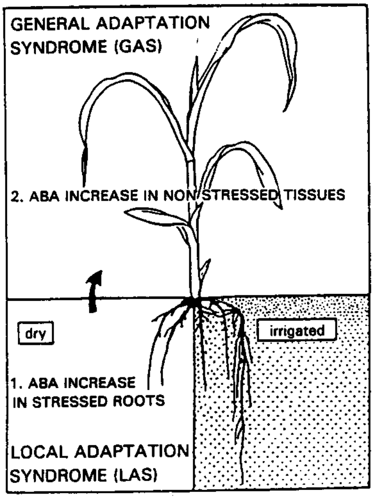

Fig. 2. 'Split-root' experiment with maize plants indicating an overall somatic 'GAS' response (see text for details). (After Davies and Zhang 1991).

Table 2. Syntoxic and catatoxic agents in mammals and plants.

	Syntoxic	Catatoxic
In mammals	cortisone	epinephrine (adrenalin)
	β-endodorphins	pregnenolone carbonitrile
	aspirin	anti-oxidants*
	valium	glutathione
	antipsychotic drugs	cytochromes P_{450}
	calmodulin inhibitors	NO'
	polyamines	
In plants	ABA, jasmonates	SOD
	cytokinins	*α-tocopherol (E)
	osmoregulants	*ascorbic acid (C)
	ubiquitin	glutathione
	HSPs	NO'
	Ca^{2+} (apoplastic)	cytochromes P_{450}
	flavonoids	
	polyamines	

Table 2 lists possible syntoxic and catatoxic factors in mammals and plants. However, it must be pointed out that the borderline between the two categories is not always clear-cut and a certain degree of overlapping - and in certain situations - even of interchange, may exist.

Oxy-free radical scavenging

There are numerous sites of oxygen activation in the plant cell, which are highly controlled and tightly coupled to prevent release of intermediate products. Under stress situations, it is likely that this control or coupling breaks down and the process "dysfunctions" leaking activated oxygen. This is probably a common occurrence in plants especially when we consider that a plant has minimal mobility and control of its environment. These uncoupling events are not detrimental provided that they are short in duration and that oxygen scavenging systems are able to detoxify various activated oxygen forms (Elstner 1990). If production of oxy-free radicals exceeds the plant's scavenging capacity, deleterious degenerative reactions occur, the typical symptoms being loss of osmotic responsiveness, wilting and necrosis. At the subcellular level, membrane disintegration and protein aggregation are typical symptoms. Therefore, the equilibrium between the production and the scavenging of activated oxygen is critical to the maintenance of active growth and metabolism and overall environmental adaptations.

As a group, these antioxidative and free radical and free radical quenching entities include the SOD family, catalase, tocopherols, ascorbic acid, glutathione, carotenoids, polyamines and flavonoids. Cytokinins have also been claimed to possess oxy-radical scavenging capacity (Leshem 1984). Following are but a few examples amongst many where one or more of the above have been documented in stress coping: drought (Price and Hendry 1991, Pastori and Trippi 1992), freezing (Loubaresse *et al.* 1991, McKersie 1991), chilling (Horiyadi and Parkin 1993), heat (Barna *et al.* 1993), desiccation (Simontacchi and Puntarulo 1992), oxidative stress (Meier *et al.* 1995), UV-B radiation, SO_2 and ozone stress (Kangasjarvi *et al.* 1994, Willekens *et al.* 1994, Jungblut *et al.* 1996), salinity (Kalir and Polyakoff-Mayer 1981), waterlogging (Crawford 1993), heavy metal pollution (De Kok and Stulen 1993), dipyrridilium herbicides (Malan *et al.* 1990) and pathogenic fungal infection (McKersie and Mehdy 1994).

Notwithstanding the stated above, oxidative damage in plant stress may be a consequence and not a primary cause of stress. If this is indeed so, then the transgenic manipulations to incorporate SOD isoforms (Scandalios 1993), *etc.* to enhance stress coping as *e.g.*, in the tomato (Perl *et al.* 1993), provide only a partial solution to the overall problem. Thus, these mechanisms of free radical scavenging and active oxygen deactivation may be palliative measures taken by the plant to mitigate damage already caused and may constitute a secondary line of defense. Consequently, the first front is to be found elsewhere. Logically, 'elsewhere' is incipient syntoxic prevention of stress damage, as will be detailed in the following sections.

Osmoregulation

Lowering of environmental water potential, *e.g.* by drought, low temperature, ice formation or salinity, results in a reduction of plant cell pressure potential, visible as wilting. Plant cells often respond to such cellular dehydration by synthesis of low molecular mass organic compounds (cytoplasmic compartment) and accumulation of ions in the vacuole (*e.g.* Na^+ in halophytes). Depending on the contribution of vacuolar ion accumulation and synthesis of organic compounds to the osmotic potential of the cell, pressure potential of the cell will be restored. This phenomenon has been called osmoregulation, though "turgor-regulation" would have been a more appropriate term. Osmoregulation follows the GAS hypothesis to a large extent: different stress signals like frost, drought and salinity induce an identical response - synthesis of osmoregulators. Moreover, acquired tolerance (hardening) is quite general in nature, enabling the plant to cope with all the above stress signals. Common to the above-mentioned stress signals is that they exert their effect by cellular dehydration. It should be emphasized that the stress signals - drought, salinity and freezing - strongly differ in intensity, cellular dehydration increasing in the above order: drought distress is manifested at values down to -2.0 MPa, salt stress to -3.5 MPa and freezing to even lower water potentials (*e.g.* -25.0 MPa at -20°C). Clearly, osmoregulation is a GAS response and for each stress signal more specific adaptations are required (Steponkus 1979).

One possible site of action of osmoregulants in stress coping is in association with the aqueous layers which are invariably present on either side of membrane bilayers, current opinion regarding the membrane as a galactolipid/protein bilayer "sandwiched" between two 1.0 - 1.5 nm thick aqueous layers. Osmoregulant presence in these membrane-encasing aqueous layers, as well as in intramembrane 'vicinal water', or in the 'trapped' water layer which has been documented to be present between each of the individual monolayers, may lend greater stability to the membrane and enable it to withstand various types of stress, either physiological or mechanical (Leshem 1992). Besides their contribution to the water potential, some osmoregulants such as sucrose or trehalose can replace water at bilayer interfaces and in this capacity fulfil a crucial role enabling biological organisms to withstand osmotic stress induced by drought or salinity (Crowe and Crowe 1986).

Table 3. Plant stress-associated saccharide osmoregulants.

Saccharide category	Species
Monosaccharides	glucose, fructose, mannose, galactose
Disaccharides	sucrose*, trehalose, lactose
Trisaccharides	raffinose
Tetrasaccharides	stachyose
Oligosaccharides	raffinose family oligosaccharides** (RFOs)

* - at high concentrations, tends to crystallize

** - retain "glass state" which prevents formation of ice nucleation centres (Stushnoff *et al.* 1993)

Organic osmoregulators predominantly fall into three groups, polyalcohols (polyols) such as glycerol, sorbitol, mannitol and arabitol; nitrogen-containing compounds such as proline and betaine; and saccharides (Table 3).

Maintenance of pressure potential under continued low water potential is facilitated by the low rate of metabolization of polyols. Rapid and adaptive responses occur: when the roots of the halophytic *Plantago coronopus* are exposed to moderate NaCl stress, respiration is reduced within hours and amount of saccharose salvaged in respiration, is quantitatively converted into sorbitol. Evidently respiration plays a role in regulation of energy metabolism under salinity stress, while growth is not affected by moderate salinity and no extra metabolic energy is required for functioning under salinity stress (Lambers *et al.* 1981). N-containing osmoregulators exhibit a further function - their synthesis counteracts stress-induced acidification of the cytoplasm (Steponkus 1979).

Osmoregulation is also expressed at the intact plant level. When plant roots are exposed to conditions which reduce water uptake, such as drought, salinity, frost, low root temperature and hypoxia by water-logging, a signal in the form of ABA (or other compounds) is transferred to the shoot, resulting in stomatal closure and re-establishment of pressure potential by foliar synthesis of osmotic compounds. Stomatal closure by the ABA signal from the roots, is caused by a reduced osmotic potential of the guard cells due to loss of K^+, Cl^- and malate. Again, the GAS hypotheses is evident: tolerance to limiting water supply of the roots occurs, irrespective of the nature of its limitation (Zeiger 1983). In a like manner, osmoticum and ABA interact to endow white spruce seedlings with drying and freezing tolerance (Attree *et al.* 1995).

Application of the GAS for long-term adaptation in the form of osmoregulation to stress demands more care: analysis of the time course of synthesis of osmoregulators and the corresponding development of tolerance indicates that other factors than osmotic compounds are involved. Reduction in shoot growth is obvious under limiting water potential and when for example growth percentage matches percentage increase in concentration of osmotic compounds, it is no longer possible to consider osmoregulation as an adaptive trait (Atwell 1989). Application of GAS is still valid for root elongation under water-limiting conditions when shoot growth has completely ceased. Under drought, growth of the primary root of maize is maintained, preferentially towards the root apex, and proline accumulation accounts for up to 50 % of the osmotic adjustment via an increased level of endogenous ABA (Ober and Sharp 1994). Leaf and root growth of *Eucalyptus* seedlings adapts to drought in a similar fashion by a combination of osmotic adjustment and extensibility of root as well as leaf cells (Rhizopoulos and Davies 1993).

Is ABA the plant's aspirin?

While most phytohormones are associated with stress, the most conclusive evidence of a GAS manifestation in plants applies to ABA. Typical examples include the alleviation of the following stress categories: - freezing (Heino *et al.* 1992), chilling (Rikin *et al.* 1993), drought and salinity (Loveys 1991), desiccation (Black 1991) and anoxia (see also Table 1). Moreover, ABA may be involved with the hypersensitive - and hence protective-response to fungal infection (Black 1991).

The mode of ABA action in each case may differ, *e.g.*, in water stress ABA causes stomatal closing which in turn may be associated with biophysical changes in guard cell membranes (Leshem *et al.* 1990), while in freezing tolerance ABA may serve to activate cold regulated (*cor)* genes which may produce cryoprotectant peptides (Lin and Tomashov 1992). Moreover, cDNA gene constituents for endogenous ABA synthesis have been found in various plants, these being activated upon exposure to a wide spectrum of stress-inducing conditions - a cDNA constituent, *BN8*, from *Brassica napus* whose coding region nucleotide sequence is 77 % homologous to the *At kin1* gene from *Arabidopsis thaliana* has been found; in both species activity being triggered by ABA treatment, low temperature or water stress, their amino acid transcript exhibits a close homology to the antifreeze protein found in flounder fish (Orr *et al.* 1992). Moreover, the characterization of ABA triggered *rab* genes suggests that they also play a role in desiccation tolerance (Pages *et al.* 1993). In addition to having a biological effect on plant tissue ABA may exert biophysical kosmotropic effect with stabilizes the quasi-crystalline form of cell water, with concomitant effects on soil/plant/atmosphere water relations (Leshem *et al.* 1990, 1993).

However, care should be taken not to overemphasize the role of this hormone in stress coping since ABA also induces senescence and the delicate balance between stress-coping and senescence-evoking effects may tend toward the latter, especially in phase III of the Selyean stress curve (Fig. 1). Cases of 'overshoot' of ABA production have been reported in which the levels of ABA remain elevated many days after relieval of stress conditions *e.g.* irrigation of drought-stricken plants (Itai and Benzioni 1976).

Jasmonates and GAS

Jasmonates - JA, MT and other derivatives to be mentioned later, are produced from α-linolenic acid (18:3) released from membranes when plants experience wounding or certain types of stress, by several mechanisms slow down several metabolic processes, thus favoring the onset of dormancy (Satler and Thimann 1981). Because dormant, nongrowing tissues are generally more resistant to stress injury than succulent, rapidly growing tissues, this series of effects is probably best viewed as a complex of protective processes designed to minimize further injury to the plant (Galston 1994). A dormancy-related stress-coping effect is winter or summer tuberization which precedes onset of seasonal-imposed climatic conditions which preclude above-ground plant growth. A close derivative of JA - tuberonic acid, has been shown to induce tuberization in several plant species including potatoes and dahlias (Koda *et al.* 1991).

Jasmonates act by regulating gene activity that induces novel proteins such as JSPs (jasmonate specific proteins) stored as seed reserves and which inhibit breakdown of other proteins which possibly play an overall role in disease resistance (Farmer and Ryan 1992, Cohen *et al.* 1993a). In light of the above mechanisms, methyl jasmonate alleviation of chilling stress in *Cucurbita pepo* (Wang and Buta 1994), of water stress in wheat (Leshem *et al.* 1994) and disease resistance may be understood. A proposed scenario for jasmonate intervention in the GAS response is as follows: jasmonate initially functions as a catabolic stressor, however at a later stage it provides a multifaceted GAS response which prevents further stress damage and injury by a syntoxic increase of threshold tolerance: in this respect, JA action may resemble that of ABA.

Interaction of stress ethylene with nitric oxide and ozone

As well documented elsewhere, ethylene production accompanies all of the various plant stress categories. It is tempting to suggest that the production of the endogenous ethylene evolution inhibitor isolated by Shih *et al.* (1989) from carnation petals, if found to be ubiquitous, would also be a component of the GAS complex. In keeping with this, it has been demonstrated that blocking ethylene precursor ACC conversion to ethylene is phenomenologically correlated with buildup of freeze resistance in wheat (Macháčková *et al.* 1989).

In senescing and water-stressed *Pisum sativum* tissue, it has recently been shown that low levels of the endogenously produced nitric oxide free radical ($NO^{\bullet}$) can inhibit ethylene emission (Leshem and Haramaty 1996). The mechanism suggested is via the inhibition of the 'ethylene forming enzyme' - ACC oxidase. At present, it is not known whether $NO^{\bullet}$ *per se* or its protonated peroxynitrite derivative (HOONO) is the direct ethylene inhibiting entity (Pryor and Squadrito 1995). Possibly in keeping with the overall concept are the findings of Langebartel's group (Betz *et al.* 1996) that triggering of a major ACC oxidase isozyme is O_3 dependent, hence $NO^{\bullet}$ inactivation of this enzyme by oxidation of its ascorbate substrate (Yang *et al.* 1993) could account for the $NO^{\bullet}$ stress-coping effect.

In evolutionary terms, it is perhaps more of passing interest that one isoform of the $NO^{\bullet}$ forming enzyme, nitric acid synthase contains realms of primary amino acid sequencing, which are identical to those of the xenobiotic pollution detoxifying enzyme cytochrome P_{450} (Feldman *et al.* 1993), the latter having been clearly demonstrated in detoxification processes in plants (Hendry 1985, Hansiková *et al.* 1995).

Application of various abiotic stresses such as: heat, cold, wounding, anoxia, high CO_2, ozone, UV-irradiation and methyl jasmonate to fruit and vegetables, could lead to acquisition of tolerance to different storage conditions. Many of the various stresses lead to formation of stress ethylene by induction of the ACC oxidase, ACC synthase or SAM synthase. In addition to induction of ethylene production, most of these stresses induce other enzymes which have a role in regulation of defense mechanism. For example, ionizing-irradiation applied to cherry tomatoes induces both specific and non-specific responses; including short term synthesis of ACC synthase and long term accumulation of chitinase (Triantaphylides *et al.* 1994). However, some of the stresses, *e.g.*, anaerobiosis, influence other systems which, in the plant, lead to inhibition of ethylene production, and also have beneficial effect on fruit quality by reducing senescence or stress inflicted damage. A typical example of GAS is the case of potential chilling injury which may develop when subjecting subtropical fruits such as tomato, avocado, papaya, pepper and citrus to low, non-freezing temperatures. Pretreatment with abiotic stress (anaerobiosis) or with short term exposure to heat induces defense mechanisms which enable these fruits to be stored at lower temperatures without appearance of injury symptoms (Pesis *et al.*

1994). A possibility broached by these and other workers is that besides deceleration of C_2H_4 emission, production of heat shock protein and aldehydes may also be involved (Klein and Luria 1994, Pesis *et al.* 1994, Sanxter *et al.* 1994)

GAS and heat shock protein, ubiquitin and chaperonin interaction

Despite the designation 'heat shock protein', it is now becoming increasingly evident that besides by heat (Nover *et al.* 1989), HSPs can be produced by exposure to other stresses as well, *e.g.* cold, and salt stress (McElwain and Spiker 1992), oxidative stress (Donati *et al.* 1990), chilling stress (Cabane *et al.* 1993, Collins *et al.* 1993) and heavy metal stress (Neumann *et al.* 1994). Moreover, certain types of HSPs also serve as ubiquitins which have been termed the "cellular housekeeper", purportedly functioning as a general stress-incapacitated protein disposal medium (Vierstra 1993) as well as in embryogenesis and regulation of the heat shock response (Almoguera *et al.* 1995). Several HSPs also function as cellular chaperonins which are a group of "match-making" proteins that ensure correct folding of other polypeptides and their assembly into multimeric units (Gething and Sambrook 1992). In addition, HSPs have been assigned a role in processes not connected with stress, *e.g.* flowering and seed development (Hernandez and Vierling 1993).

However, before providing more supportive evidence, we point out that a clear-cut general GAS role, spanning the broad spectrum of environmental stress is not as yet evident since several of the major stresses have not been conclusively associated with HSP-mediated coping. The last statement precludes the ubiquitin function, since in the final outcome all stresses cause dysfunction of proteins and since ubiquitin serves in their disposal, a presumptive overall GAS role, albeit secondary or tertiary, may well be assigned to HSPs. In our view, at the present stage of this comparatively recent avenue of environmental stress research, it transpires that synthesis of HSP is limb- or organ-localized, *i.e.* in Selyean terminology, LAS appears not to develop to GAS - local encounter with a stressor induces the LAS response, followed by adaptation which, in contrast to that produced by ABA, does not extend to other parts of the plant, *e.g.* when the leaves are stressed, their HSPs do not necessarily spread to other organs (Hernandez and Vierling 1993).

In general, HSPs active in thermo-tolerance belong to the LMW HSP class. Clarke and Critchley (1992) have classified plant HSPs into the following six groups, with the given mean kDa values:
a - 110 kDa; *b* - 90 kDa; *c* - 70 kDa; *d* - 60 kDa; *e* - 20 kDa (*b,c,d* and *e* also serves as molecular chaperonins); *f* - 8.5 kDa (identical to ubiquitin).

These HSPs are encoded by four (I - IV) discrete gene families, classes I - II encoding cytoplasm located HSPs and II - IV encoding chloroplast and endomembrane HSPs (Hernandez and Vierling 1993). Recently a group of HMW HSP (or HSP complexes) which may be as large as 260 kDa have been detected in heat stressed barley. This HSP species has been suggested to be a homogeneous octamer of a basic 32 kDa unit (Clarke and Critchley 1992). Mode of HSP mediated stress coping in pleiotropic and may involve mRNA protection, prevention of enzyme -

especially photosynthesizing - denaturation and/or their stress-induced aggregation and post-stress ubiquitin and chaperonin-aided repair (Gouloubinoff *et al.* 1989).

A remarkable degree of genetic homology exists between genes encoding HSP; this applies to resemblance of dicots to monocots (Clarke and Critchley 1992) and plant cDNA HSP encoding genes to those of *Drosphilla*, the latter manifesting *ca.* 75 % homology to the 70 kDa HSP structural genes in plant. A HSP protein which also function as a chaperonin in *E. coli* is homologous to the higher plant chaperonin binding protein which mediates correct assembly of the photosynthetic enzyme Rubisco (Gouloubinoff *et al.* 1989). In *E. coli* a single gene (DNA K) encodes a product which is homologous to plant HSP 70.

Metal pollution

In general, plant exposure to very recent environmental pollution stress will not elicit GAS reactions. However, GAS responses may develop under conditions of genetic selection for several generations. As shown below, GAS strategies in heavy metal tolerance and possible tolerance to Al in soils in the wet tropics, and under conditions of acid rain will be demonstrated.

There is a large genetic variation in heavy metal tolerance between plant species and between plant populations, the variation depending upon the metal composition of the soil and rock substrate. Populations may exhibit tolerance to a single metal species or to a large variety of metals. Heavy metals may enter plant cells via the same systems that carry essential metals like Cu and Zn (Steffens 1990). Possibilities for heavy metal tolerance are: (*1*) binding to pectin residues and carboxyl groups in cell walls, (*2*) complexing to organic acids followed by removal to the vacuole (De Knecht 1994). From the viewpoint of GAS detoxification of heavy metals by metal binding peptides, phytochelatins are most important (Grill *et al.* 1985, 1987).

As pointed out in the Oxy-free radical scavenging section, glutathione plays an important role in adaptation to oxidative stress. Its pivotal function in heavy metal detoxification as well, provides a link between the two apparently widely differing stress coping strategies. Phytochelatins consist of linear polymers of glutamyl-cysteine as secondary products of glutathione (Grill *et al.* 1987, Rauser 1993). All plant species studied respond to exposure to Cd or other heavy metals by activation of phytochelatin synthase and subsequent production of phytochelatins (Grill *et al.* 1993); synthesis of phytochelatins stops when all metals are chelated. Cu-induced synthesis of phytochelatins may deplete glutathione storage and thus cause oxidative stress (De Vos *et al.* 1992). It is thus apparent that phytochelatins act as detoxifying agents and assist in maintenance of cellular homeostasis of heavy metal concentrations. However, the participation of phytochelatins in heavy metal detoxification has recently been questioned. Research on phytochelatin deficient *Arabidopsis* mutants have clearly indicated that Cd sensitivity is not found in the wild type, thus confirming the heavy metal pollution (in this case, Cd) coping role of phytochelatins (Howden *et al.* 1995).

Interestingly, Cd sensitive clones of *Silene vulgaris* produced more phytochelatins upon exposure to Cd than Cd tolerant lines (De Knecht *et al.* 1994), an observation confirmed with similar results on Zn (Harmens *et al.* 1993). In conclusion, production of phytochelatins is a GAS reaction to heavy metal exposure; however, production of phytochelatins is unsuitable as a sole parameter for screening for a particular heavy metal tolerance since it probably goes hand-in-hand with other stress coping mechanisms.

At present possibilities for a GAS reaction to high Al levels in the soil under very wet conditions or imposed by acid rain is unclear. One possibility is an interaction between Al and Ca homeostasis in the growing root tip (Bennet and Breen 1991), since elevated Ca in the soil can relieve Al induced toxicity. There is no direct evidence for the involvement of Al via displacement of Ca on the root cell membrane surface or Ca-channels (Kinraide *et al.* 1994). Interference of Al with root growth via a signal perception and transduction system seems more promising (Bennet and Breen 1991), especially in view of the short lag required for tolerance induction after exposing roots to toxic Al concentrations (Llugany *et al.* 1995). Other factors like mucilaginous cap secretion and malate secretion and the response of Al to P-supply are probably involved in Al tolerance.

Conclusions and a few words of caution

The correlations between several of the major environmental stress categories - heat, drought, salinity, chilling, freezing, oxidative stress, desiccation, UV-B and O_3, manifest similar, if not identical, endogenous pleiotropic GAS responses whose final expression includes the concerted production of anti-oxidative and oxy-free radical control mechanisms, upsurge of ABA, JA, NO, osmoregulants, HSPs and phytochelatins. These measures may be either syntoxic or catatoxic and it may well be that the relative importance of each factor may differ for different types of stressor, plant species, plant organs, or stages of development in the same plant. In some cases, these GAS stress coping mechanisms may be primary - *i.e.*, incipiently preventing stress-induced damage, e.g., osmoregulation, while in other cases they may be secondary and serve to enhance post-stress repair - the free radical scavenging complex presumably belonging to the latter category, while others, *e.g.*, osmoregulation, to the former.

This essay mainly deals with physiological and biochemical aspects of GAS, however, brief mention is made of some anatomical adaptations. In this context, we mention presence of foliar trichomes (hairs) which have been found to function efficiently in coping with varying stress situations - in water stress by reducing transpiration ('boundary layer effects'); high-light intensity and UV-B stress by filtering out harmful solar spectra; alleviation of heat stress by light interception and shading; prevention of pest infection by preclusion of insect probosci insertion into mesophyll tissue; enhancement of freezing tolerance by reducing incidence of ice nucleation centres found in substomatal cavities. These and other anatomical adaptions relating *inter alia* to plant cuticulae, nature and chemical composition of the epidermis, degree of thylakoid thickness or curvature, *etc.*, all of which are beyond the scope of the present review, may be as important in the GAS mechanism as the biochemical/physiological adaptions detailed above.

On various plants and algae at a genetic level research is being conducted in an attempt to characterize the primary "master gene" which concomitantly induces or activates the volley of individual components of the GAS response in a manner similar to the function of the *Oxi R* gene in *E. coli.*

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