

## Environmental stress influencing plant development and flowering

Aaram A Kumar<sup>1</sup>, Priyanka Mishra<sup>1</sup>, Khushbu Kumari<sup>1</sup>, Kishore CS Panigrahi<sup>1</sup>

<sup>1</sup>*School of Biological Sciences, National Institute of Science Education and Research, IOP campus, Sachivalaya Marg, Bhubaneswar, Orissa 751005, India*

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## 1. ABSTRACT

Plants are sessile organisms and unlike animals, cannot run away from adverse environmental conditions. Therefore, they have evolved sophisticated signaling and protective systems to overcome sub-lethal stress situations. Although, effect of stress on physiology and morphology were studied earlier, the research on molecular mechanisms of stress response is albeit new. Studies at the molecular level on stress physiology reveal that, many stress-induced pathways converge downstream or interact significantly. Abiotic stress factors regulate the extent and pattern of developmental programme. The timing of transition from vegetative to flowering phase, which is vital for survival and reproductive success, is often altered under various stresses. Unraveling the mechanisms by which different environmental stresses induce their effects and how tolerance to stress is achieved is an active area of research. Enhancing stress tolerance, especially in crop plants is an area of prime importance. In this review, we focus on stress responses induced by temperatures, high and low light intensities, UV radiation, drought and salinity stress and summarize the recent advancements by highlighting the underlying molecular pathways and processes.

## 2. INTRODUCTION

Plants survive in a wide range of fluctuating environmental conditions. Plants being sessile in nature, lack the ability to migrate from a sub-optimal environment to an optimal one. Therefore, the unpredictable abiotic factors impose them to cope up with different stressful conditions through adaptive mechanisms such as tolerance and resistance. A number of abiotic factors such as extremes of temperatures, salinity, high and low light intensity, UV, hypoxia, water deficit or drought can act as potential stressors and contribute to the generation of stress in plants. Variety of genetic and environmental parameters may influence the evolution and control of stress responses in plants. Hundreds of gene products are associated with the tolerance towards such abiotic stresses in plants. The environmental factors bring about variations in the genetic traits which in turn regulate the plants responding to stress. The genes controlling abiotic stress responses might act in cumulative or redundant fashions and activate common as well as unique downstream targets. It is still an intense area of research to study how plants respond to different combinations of stresses (1). The stress constraints severely affect plant development, both vegetative and reproductive.

The crop losses due to abiotic stresses have been estimated to be as much as 50% during some years (2-3). Hence, it is imperative that sufficient knowledge is gained to understand plant stress responses. One approach is to artificially induce stress conditions under laboratory situations. While this provides greater control of the parameters, it may not give a clear answer to how plants adapt to stressful environment in nature. Therefore, a combination of field studies and laboratory experiments would provide a deeper insight into this area of research. Much of the recent information in this regard has come out using molecular approaches. From the isolation and characterization of individual gene products to the creation of genome-wide screens, significant progress has been attained in this research field.

A good amount of the information available on various aspects in plant biology is based on research done in the model plant *Arabidopsis thaliana* (*At*). *At*, which belongs to the Brassicaceae family, is a weedy facultative long day plant. The full genome sequencing of *Arabidopsis* was completed in the year 2000. The information of entire genome provided scope to monitor and analyze global gene expression profiles induced by different stress using high throughput techniques like microarrays. It also helps in studying the epigenetic changes in DNA such as, different modification patterns, or at the level of RNA like alternate or differential splicing. Chromosomal modifications during stress adaptation have been studied in *At* by using analytical tools such as ChIP (Chromatin Immunoprecipitation) or ChIP on ChIP (4). Thousands of genes in *At* have been shown to be differentially expressed on the onset of stress conditions.

Many studies which focus on plant growth and physiological responses might not indicate how the survival and fitness of a plant is affected by a particular stress. However, reproductive traits could serve as a better indicator of stresses on plant fitness. Reproductive development in plants has been recognized to be significantly affected by various abiotic stresses and it has been reported to limit grain yield since long (5). Extensive reviews on stress sensitivity of the reproductive phase have been described in Barnaba's *et al.*, Hedhly *et al.* and Thakur *et al.* (6-8). By flowering at a time when adverse conditions, such as, very high or low temperatures, light intensity or drought are prevailing, plants would minimize their chances of propagation of viable seeds to the next generation. If the conditions are not favorable, producing more vegetative structures to support the later development of reproductive phase would be beneficial. However, delaying floral initiation under optimal environment may jeopardize the completion of life cycle of the plant. Tropical plants flower during cooler times of the year to avoid the high temperature and irradiance, while plants in the temperate region tend to enter the reproductive phase during the spring season to avoid cold stress. In this review, the impact of various environmental stresses on plant development, flowering time and the tolerance or resistance mechanisms/pathways

by which they overcome these are discussed and summarized.

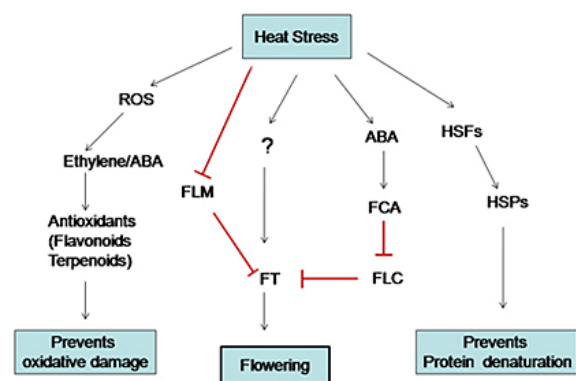
## 3. INFLUENCE OF DIFFERENT STRESSES

### 3.1. Temperature stress

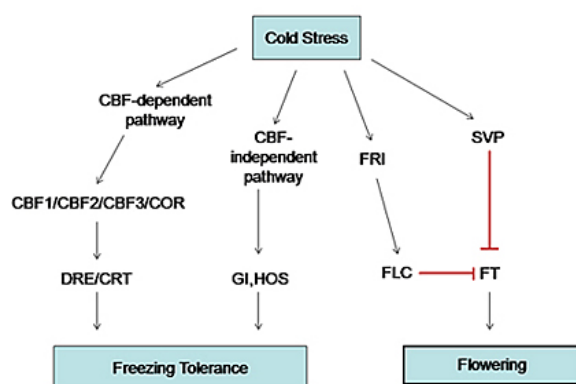
Extremely high or low temperatures can prove to be detrimental in plant development, especially in the reproductive phase, where, exposures to very hot or cold conditions even for a single day can prove to be hazardous. Temperature extremes affect not only the morphology and eco-physiology but, the cellular mechanisms of the plants as well. Cytoskeleton stability and pollen tube development were reported to be impaired in plants growing under cold stress. Plants have very robust temperature stress tolerance mechanisms. One such developmental precautionary measure is seed and pollen dormancy. Plants produce dehydrated pollens and embryos, which can remain dormant for long periods of cold/heat before germination upon the onset of favorable conditions. Whittle *et al* has reported that heat stress leads to a reduction in the total number of ovules and increased rates of ovule abortion (9). The transcript profiles in plants were also modified in response to heat/cold stress. Hormones and its signaling also play a key role in dealing with stress. Accumulation and signaling through abscisic acid (ABA), salicylic acid (SA) and ethylene are important in response to high temperature stress, while ABA, gibberellins (GA), auxin and ethylene signaling have been reported to be significant in inducing tolerance to low temperature (10-11).

At the molecular level, responses to heat and cold stresses vary and are mediated by different sets of stress-related genes, many of which are transcription factors. Under high temperatures, the Heat Stress transcription Factors (HSFs) are activated which in turn up-regulate the expression of many genes, such as, heat shock proteins (HSPs), some of which work as molecular chaperones that prevent the denaturation of other proteins and stabilize them (12). Cold specific transcription factors like CBF enhance the expression of cold tolerance genes like *CBF2* (*C-REPEAT-BINDING FACTOR 2*) and *COR* (*Cold-Regulated*). Many freezing tolerance genes act by stabilizing the membranes or increasing the expression levels of protective osmolytes (10). In addition to a CBF-mediated pathway (Figure 1), other signaling pathways are also involved in the regulation of the cold stress response (13). The *Arabidopsis* homeo-domain transcription factor *HIGH EXPRESSION OF OSMOTICALLY-RESPONSIVE* (*HOS*) genes for instance *HOS9*, regulates cold tolerance by affecting the activity of genes independent of the CBF pathway (14). *HOS1* is another gene which negatively regulates the expression of cold responsive genes like *RD29A*, *COR47*, *COR15A*, *KIN1*, and *ADH* and flowering time (15). *GIGANTEA* (*GI*), a circadian clock regulated gene involved in photoperiod flowering was also found to induce freezing tolerance by a CBF-independent mechanism (16-17). The stress-induced hormone, ABA was shown to act through a gene called *FLOWERING CONTROL LOCUS A* (*FCA*) (18). *FCA* is a RNA-binding protein that can regulate DNA methylation (19). ABA-induced *FCA* may regulate flowering

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**Figure 1.** Schematic representation of Heat-stress pathway in *Arabidopsis*.



**Figure 2.** Schematic representation of stress pathway induced by low temperature.

time and stress responses through regulation of FLC, a repressor of flowering, through chromatin remodeling (20). Mutant studies in *Arabidopsis* have recently revealed the role of another gene product CRYOPHYTE/LOS4 that influences the master regulator of cold response, CBF2. These plants which had mutations in a DEAD box RNA helicase gene were found to be hypersensitive to ABA and enhanced *CBF2* expression making *Arabidopsis* highly sensitive to chilling stress (21). Another *Arabidopsis* gene *SHORT VEGETATIVE PHASE* (*SVP*) plays an important role in the response of plants to ambient temperature changes. At low temperatures, the florigen FLOWERING LOCUS T (*FT*) is repressed by *SVP* via direct binding to the CArG motifs in the *FT* gene sequence (22).

Depending on the type of plant species (long day/ short day) and other environmental factors, temperature stress can delay or accelerate flowering. Duration of day-length or photoperiod is an environmental cue which provides seasonal information to plants and is the key regulator of flowering time in plants. Low temperatures cause delayed flowering while heat stress was recently reported to accelerate bolting and flowering in (23). Flowering Locus C (*FLC*) is a suppressor of thermal induction of flowering.

Prolonged cold temperature during the winter season (analogous to vernalization) usually inhibits *FLC* accumulation and promotes flowering. Another gene *FLOWERING LOCUS M* (*FLM*) also represses thermo-sensitive flowering in a quantitative manner (24). Plants defective in PHYTOCHROME B (*PHYB*) have been reported to flower early at 23 degree C, but such floral induction was not observed at 16 degree C (25). Role of autonomous pathway genes like *FVE* also has been recently unraveled (26). *FVE* delays flowering in response to intermittent cold stress by enhancing the expression of *FLC* (Figure 2).

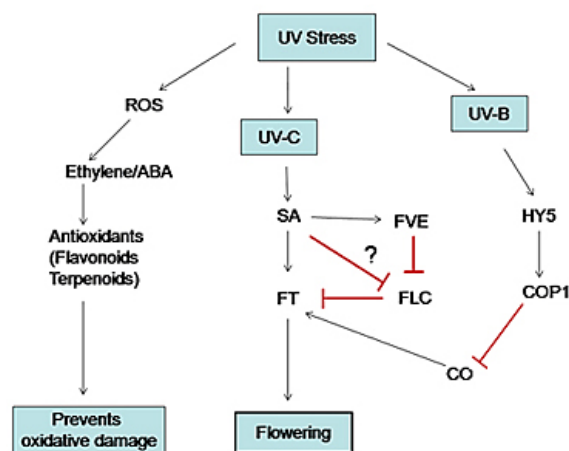
An *Arabidopsis* nucleoporin, *AtNUP160* has also been found to have a role in RNA export. *AtNUP160* mutant plants showed less tolerance to low temperature stress (27). This pathway is CBF-dependent. Loss of function of *AtNUP160* causes the plants to flower earlier irrespective of low or high temperature. Relatively recently, a gene *LONG VEGETATIVE PHASE 1* (*LOV1*), was identified which when mutated caused the plants to lose their ability to sustain in prolonged cold (28). *LOV1* also controls flowering time by negatively regulating the expression of *CONSTANS* (*CO*). The *LOV1* signaling for cold tolerance was through *COR* genes and not *CBF* genes. *LOV1* is NAC-domain protein (*NAM*, *ATAF1*, -2, and *CUC2*), which is a class of transcription factor known to control many different processes. This leads us to conclude that the cold responsive pathway and flowering pathway converge at a gene at some point and mutually control the flowering of plants. According to a recent finding, over-expression of *FTL1/DDF1* in *Arabidopsis* caused increased tolerance to cold (29). *DDF1* encodes for an AP2 type transcription factor which belongs to CBF/DREB1 family. Treatment of GA restores phenotype of the *ddf1* mutant, thus, indicating that *DDF1* belongs to the GA pathway or both the pathways converge downstream.

At lower temperature, the chlorophyll content in the plants is seen to decrease than at higher temperatures, suggesting that higher temperatures are stress to plants. Higher temperatures are seen to induce earlier flowering in plants as compared to lower temperatures (25, 30).

### 3.2. Light stress

Light is a vital factor controlling almost all physiological responses in plants. It has been documented to play a crucial role in determining the transition from vegetative to reproductive phase in plants. The timing of shifting to reproductive development is important as the reproductive stage is highly sensitive to the stress induced by extreme environments. A change from optimal conditions in light parameters such as photoperiod, light quality and intensity is detected by combined activity of the photoreceptors, plant molecular clock genes and other factors. The action of these cues need not be independent but rather are integrated by the activity of a number of floral genes to produce the flowering response. Light also controls the photo-morphogenetic development of seedling and plants. Since it interacts with the endogenous

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**Figure 3.** Schematic representation of UV-stress pathway in *Arabidopsis*.

developmental programs in the plant, it affects plant growth and development tremendously. Light can also be a stress factor, if it is not available in an optimal quantity. Excessive fluence leads to photo-oxidative damage in plant tissues. Plants harbor antioxidant pigment systems like carotenoids, xanthophylls and flavonoids to channel away the excessive radiation and prevent such damages. The expression of genes controlling the biosynthesis of these compounds is hence also mediated by photoreceptors (31). Light regulates the expression of circadian clock genes in plants and these genes in turn control the expression levels of the flowering time regulator gene *CONSTANS* (Figure 5). Besides this, light also plays a role in the regulation of the CO protein stability and activity. CO protein, a Zinc finger transcription factor, acts in a light dependent manner to facilitate the transcription of *FLOWERING LOCUS T (FT)* gene (32). It has been found that the E3-ubiquitin ligase, *CONSTITUTIVE PHOTOMORPHOGENETIC 1 (COP1)* facilitates the proteasomal degradation of CO in dark (33). So, under high light fluence the flowering time is altered. The physiology also changes in response to wavelength/light quality and duration/photoperiod. It is known that photoreceptors regulate flowering in many plants including *Arabidopsis* (34). It has been shown that flowering is accelerated by increased light intensity of far-red wavelength, mainly perceived by Phytochrome A. These can be considered as one among the survival and competition strategies. Photoperiod responses are different in long day and short day plants, but it is well established that flowering is dramatically delayed if the plants are kept under sub-optimal photoperiod conditions (35). In *Arabidopsis*, constant light leads to early flowering without accumulation of sufficient biomass and hence, the plants are weak. Changes in physiology and metabolite concentration at high light intensities have also been mentioned (36). Light also enhances thermo-sensitivity in plants. Overall, light influences the development of a plant at various levels to various degrees.

### 3.3. UV stress

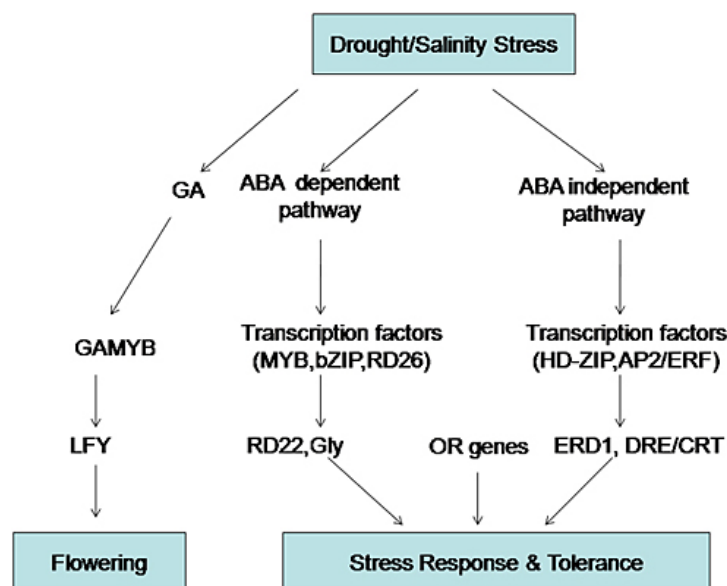
UV radiation can be detrimental to the plants as it can damage the DNA, induce severe stress and affect plant productivity (37). Plant responses to increased UV radiation may vary. However, many plants have developed protective mechanisms such as molecular UV filters, free radical quenchers, Reactive Oxygen Species (ROS) and DNA repair systems to cope with excess of UV stress (38-39).

One of the processes through which UV radiation adversely affects plants is the production of ROS. Similar to high light conditions, this leads to oxidative damage. The key mechanism in plants to prevent such damage to tissues is the production of antioxidants like flavonoids. Expression of genes like *CHALCONE SYNTHASE (CHS)*, the enzyme involved in flavonoid biosynthesis, are up-regulated by UV-B stress (31).

UV-B stress was shown to delay floral initiation and achievement of decreased rate of flowering, reduced flower retention and therefore, affecting the potential yield (40). But even though increased UV-B was found to be generally detrimental to growth and flowering; total seed production was actually enhanced at higher UV-B doses (41). The key players regulating UV-B responses in plants include genes such as *CONSTITUTIVE PHOTOMORPHOGENESIS 1 (COP1)*, which is an E3 Ubiquitin ligase, (Figure 3) and bZIP transcription factor HY5, both of which play a crucial role in regulating flowering. Such photomorphogenic responses to UV stress are also controlled by the genes *UVR8*, *REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1 (RUP1)* and *RUP2* which act as negative regulators of the UV-B response (42-43).

Plant responses to UV and other environmental stresses have been reported to be regulated by microRNAs (miRNAs). Some miRNA levels are altered under various stresses. For instance, in *Arabidopsis*, miR399 and miR395 were identified to be highly expressed under phosphate and sulfate starvation respectively (44-46) while miR393 was found to be induced under cold stress (47). In a more recent study by Zhou *et al.* (48), it was shown that 21 miRNA genes in 11 miRNA families are up-regulated under UV-B stress condition in *At*. These regulate many genes including transcription factors and, thus, control the expression of a wide range of downstream genes in UV-B stressed plants.

Irradiation of *At* seedlings with UV-C rays accelerated flowering. In UV stressed plants, the salicylic acid levels were observed to be high. The salicylic acid (SA) activated photoperiod and autonomous pathway genes but interestingly worked independent of key genes in these pathways such as *CO* or *FLC* (Figure 3). In *Arabidopsis*, SA works as a link between a number of stress responses and development pathways (49). The balance between growth and defending against negative effects of adverse



**Figure 4.** Schematic representation of Drought and salinity stress pathway.

conditions like UV stress, which is energy consuming, is vital to the survival and successful reproduction of plants.

### 3.4. Drought stress

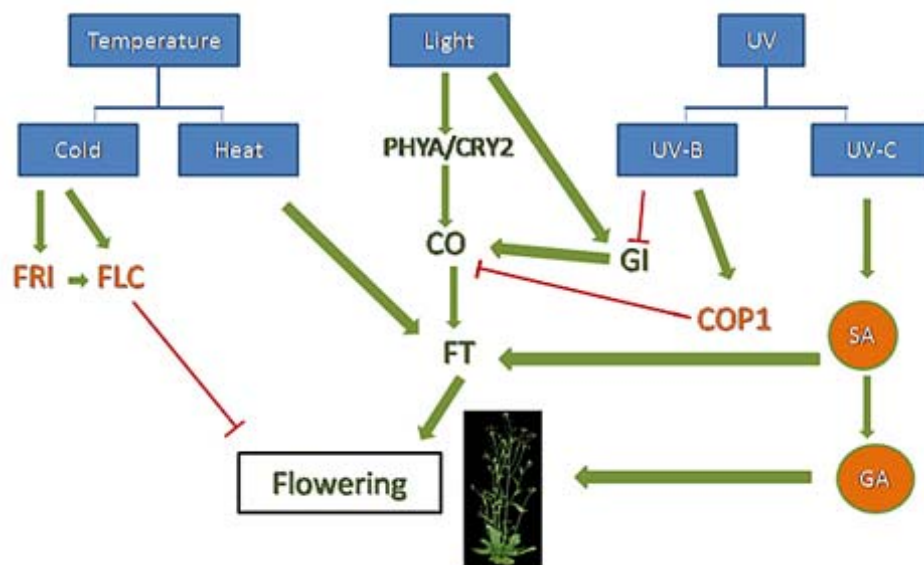
That water deficit conditions or drought promotes flowering was reported as early as 1949 by Prof. Went (50). Later, studies related this to water stress and an effort of the plants to maximize their size at the time of flowering (51). However, this hypothesis was questioned by, on grounds of lack of convincing evidence (52). On a molecular basis, water stress evokes oxidative damage in plants due to the build-up of reactive oxygen species owing to an imbalance in their production and metabolism. Changes in the photochemistry of chloroplasts in the leaves of drought-stressed plants result in the dissipation of excess light energy in the PSII core and antenna, thus generating active oxygen species ( $O_2^-$ ,  $O_2$ ,  $H_2O_2$ ,  $OH^\cdot$ ), which are potentially dangerous under drought stress conditions (53). This is followed by oxidative stress, which in turn leads to the production of oxidant species detoxifying enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), glutathione reductase (GR) and mono-dehydro-ascorbate reductase (MDAR). The levels of non-enzymatic antioxidants like flavonoids, carotenoids and ascorbic acid also go up in a bid to protect from the oxidative damage. A correlation between oxidative stress tolerance and longevity exists. Oxidative stress accelerates flowering response and the late flowering *gi-3* mutants, where *GIGANTEA* (*GI*) (Figure 1), a plant clock gene controlling flowering, is not expressed, were shown to show increased tolerance as compared to wild type accessions (54) (Figure 4). GA is expressed during drought conditions and enhances flowering apparently by GA-MYB, LEAFY-dependent manner (55) (Figure 4). Photosynthetic rates and ribulose-1,5-bisphosphate carboxylase activity among cultivars of mulberry (*Morus alba*) subjected to water stress were also observed to vary markedly (56).

### 3.5. Salinity stress

Salt is a major stress factor contributing to both ionic and osmotic stress. Salinity can act as an indirect agent leading to dehydration and water stress, thus paving the way to oxidative damage. It can also cause ion toxicity. These can lead to tissue destruction, incomplete development and premature senescence. Plants evade salinity stress by various tolerance mechanisms which include ion homeostasis, regulation of transpiration, anatomical changes and osmotic adjustments (57). Understanding the underlying mechanisms of salt tolerance in plants is crucial to tailor the crop plants which are tolerant, since, a significant area on earth has soil with higher saline concentration and hence, unfit for cultivation. A variety of classical and molecular genetic approaches have been adopted to identify stress tolerance genes using *At* as a model system. A number of genes whose products are involved either directly or indirectly in salt stress plant protection are expressed/up-regulated in response to high-salinity stress (Figure 4).

These genes code for a variety of products such as enzymes for osmolyte synthesis, ion channels, receptors, and components of calcium signaling or some other regulatory signaling molecules which are able to confer salinity-tolerant phenotypes when transferred to salinity-sensitive plants (58). A plasma membrane  $Na^+/H^+$  antiporter (*SOS1*), a vacuolar  $Na^+/H^+$  antiporter (*NHX1*) and a plasma membrane  $Na^+$  transporter (*HKT1*) have come up through genetic studies as essential genes required for salt tolerance (59-61). Many *osmotic response* (*OR*) genes are expressed downstream as a result of converging ABA dependent and independent pathways which regulate salinity and drought stress responses (Figure 4) (62). Information about salt tolerance mechanisms in *Arabidopsis* has been accumulating. However, the acquisition of natural salt-tolerance in plants and its interaction with other stresses

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**Figure 5.** Schematic representation of Interactions of various abiotic stresses in flowering response in *Arabidopsis*. An arrow-head indicates promotive effect while a dash-head indicates the negative regulation.

still remains poorly understood and is an open area for further research.

Cytoplasmic calcium concentration rises by high salinity resulting in osmotic imbalances in the cell. As a consequence,  $\text{Na}^+$  and  $\text{Cl}^-$  ions are compartmentalized into the vacuole to minimize the cytotoxic effect (63-64). Since plant cell growth also occurs by directional cell expansion mediated by an increase in vacuolar volume, this kind of compartmentalization of ions effects the development.

### 3.6. Combined stress responses

Under natural conditions, most, if not all of the stresses, do not act in isolation. One of the best examples is a plant growing under field conditions, where heat and drought stresses would be faced together. Many tropical plants are said to be under constant stress from high light and temperature. Though individual stress responses are better characterized, effect of combination of different stresses has been studied less extensively. Various stresses control how the plants respond to their combined effects in an interactive manner which may be additive, synergistic or inhibitory. Many of the stress response pathways converge downstream. (Figure 2) For instance, both UV stress and drought stress leads to oxidative damage of tissues and evoke similar responses. There may be specific genes, which are activated only when a set of stresses are applied. Metabolic profiling of plants subjected to drought, heat stress, or a combination of drought and heat stress revealed accumulation of sucrose and other sugars (65). Such genes can be identified and characterized using microarrays, RNA blots etc. (66). Effect of one stress may decrease or nullify the effect of the other one. As an example, while drought accelerates flowering, a combination of drought with UV stress delays phenology (67).

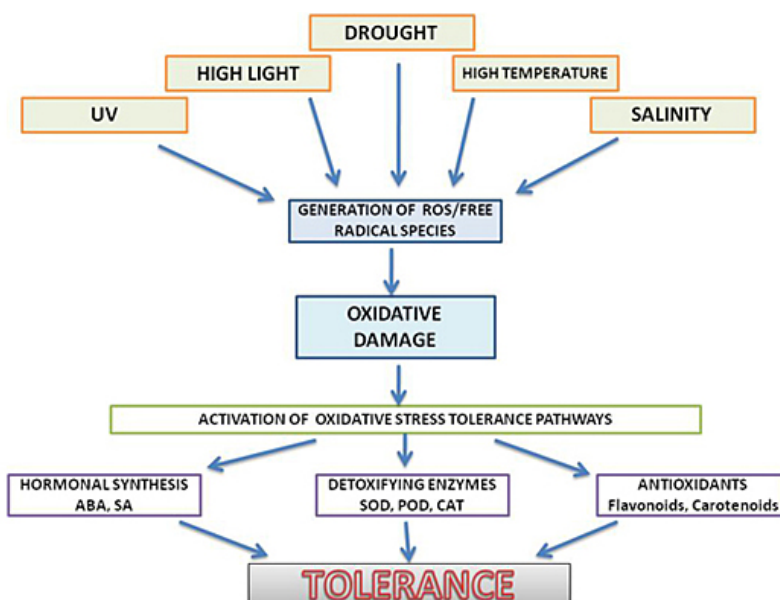
Many stress-responsive genes induced by cold, drought, and high salinity have a strong association in their expression. Stress hormones like SA, ABA and GA are mediators of plant response common to combination of stresses (68). These hormones play an important role in the tolerance of plants to a variety of stresses in nature by induction/repression of a number of genes. They also exert their effect by epigenetic regulations such as through histone modifications, DNA methylation and acetylation (69). These can lead to the retention of heritable stress memory in plants, leading to acclimation under persistence of the stress factor.

## 4. SUMMARY

The endogenous developmental programs and decision to flower are both crucial for the reproductive success of plants. They are influenced by various environmental stresses. Temperature is a crucial factor regulating plant development and flowering. Both low and high temperatures induce stress in plants and consequently trigger a number of tolerance mechanisms. Those mechanisms are orchestrated by the combined action of transcription factors namely HSFs and CBFs, plant hormones such as ABA and flowering time regulators like FLM, FLC, GI etc.

However, light as a stress generally induces the accumulation of antioxidant pigments like carotenoids, xanthophylls and flavonoids. Besides light, other radiation such as UV also induce oxidative stress, influence developmental rate and floral transition. Antioxidants like, flavonoids and terpenoids accumulate along with photomorphogenic genes such as *UVR8* and distinct miRNAs. Drought or water deficiency leads to the generation of Reactive Oxygen Species (ROS) and also are mediated by flowering time genes like *GI* (54).





**Figure 6.** Converging Pathways in Environmental Stress sensing and effect in plant.

Salinity can induce water stress indirectly. It also causes ion toxicity leading to the induction of ion channels, transporters and hormones such as ABA and GA. The different stress response pathways often cross-talk amongst themselves in order to bring a collective response. These pathways may also act redundantly to provide flexibility to the plants to survive in adverse environment. On a molecular level, a number of genes are differentially induced by various stresses. While many are specific to the kind of stress, some are activated in response to different stresses indicating a convergence of various pathways to produce integrated responses. For instance, almost all abiotic stressors such as high light, temperature, drought, UV radiation and salinity lead to the generation of free radicals which can induce oxidative damage. Such an effect is mitigated by the activation of various stress tolerance pathways. The synthesis of stress tolerance hormones like ABA and antioxidants such as flavonoids is common during a number of stresses. The effect of different stresses on flowering time and reproductive development are species specific and depends on environmental and/or epigenetic factors. Various stresses up-to various degrees activate or repress gene networks that in turn interact. This flexible interaction brings a complex trait of stress adaptation and is an emerging area in plant biology research and needs more attention since it is directly related to crop productivity and yield.

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**Send correspondence to:** Kishore CS Panigrahi, School of Biological Sciences, National Institute of Science Education and Research, IOP campus, Sachivalaya Marg, Bhubaneswar, Orissa 751005, India, Tel: 91 9439863130, Fax: 91 674 2304070, E-mail: panigrahi@niser.ac.in