Effect of sub-optimal conditions on Cardinal Plant Growth and Development Process

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Introduction:

Plants in their life time come across different types of stresses and condition which are not favourable to the growth and development of the plant, such conditions are known as the suboptimal condition. These conditions generally involve drought conditions, heat stress, cold stress and salt stress.

Drought stress

Conditions like drought involve different adaptive changes or deleterious effects. Under field conditions these responses can be synergistically or antagonistically modified by the superimposition of other stresses. Plant strategies to cope with drought normally involves a mixture of stress avoidance and tolerance "strategies" that vary with genotype. Early response to water stress aid intermediate survival, whereas acclimation, calling on new metabolic and structural capabilities mediated by altered gene expression helps to improve plant functioning under stress. Some of these responses occur at the leaf level in response to stimuli generated in the leaf itself or elsewhere in the plant. They have negative influence on carbon assimilation and growth. They have a negative influence on carbon assimilation and growth. However, it is the integrated response at the whole plant level, including carbon assimilation and the allocation of photoassimilated to different plant parts and reproductive ability, finally dictates survival and persistence under environmental stress. Some of the differences among species in growth and survival can be traced to different capacities for water acquisition and transport rather than to drastic differences in metabolism at a given water status. Neverthless, carbon assimilation at the whole plant level always decrease as a consequence of limitations to CO_2 diffusion in the leaf, diversion of carbon allocation to non-phtosynthestic organs and defence molecules or changes in leaf biochemistry that result in the down regulation of photosynthesis. Acclimatory changes in the root-shoot ratio or

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the temporary accumulation of reserve in the stem under water deficit are accompanied by alteration in carbon-nitrogen metabolism. In the perennial plants, when leaves have to withstand frought, the dissipation of excitation energy at the chloroplast level through processes other than photosynthetic C-metabolism is an important defence mechanism, which is accompanied by down-regulation of photochemistry and in the longer term of photosynthetic capacity and growth.

The different plant strategies to cope with drought are as follows-

1. Keeping the water balance right
2. Stomatal closure
3. Matching biochemical capacity for carbon assimilation with CO_2 availability
4. Small and thick leaves
5. Accumulating reserves of water and sugars

Heat stress:

There are three cardinal points for the types of temperatures that are vital for plant activity:

- Minimum temperature below which no plant growth and development occurs.
- Optimum temperature at which maximum plant growth and development occurs
- Maximum temperature above which plant growth and development stops

Temperature requirement of different plants vary for the cardinal points as it is related to the duration of exposure, age of the plant, previous history and such externalities. Generally, it is the air temperature or the ambient temperature that affects the crop in several ways. The normal physiology of the plant gets affected and plant maturity is accelerated. In some cases, plants shed leaf/flower/fruit or dry-up non-productive tillers and even become sterile to overcome the unprecedented stress. Surpassing the high temperature peak, various enzymes get inactivated, decreasing the photosynthetic efficiency. The high temperature coupled with high respiration and evaporation pushes the plant to permanent wilting when the temperature exceeds 46°C. Short periods of very high temperature (>35°C) are of common occurrence in many wheat-growing areas of the world. Such sudden exposure to heat stress affects the yield and quality of the wheat grain. Maturing kernel is highly sensitive to heat stress at milk and dough stages of grain development. The kernel becomes progressively less sensitive as the grain hardens. Reduction in kernel weight results primarily due to the shortening of the grain filling duration than due to the reduction in the rate of grain filling.

The grain filling is seriously impaired and translocation processes get affected due to early senescence of the leaf and ear, and the reduction in chlorophyll content adversely affects photosynthesis. Since the photosynthetic source is affected and the sink duration is reduced, filling of the kernel is poor, resulting in small grain size having less grain weight. Under such situations, alternate sugar sources, stored as stem reserves, get mobilized so as to fill the kernel.Genotypic variation in the mobilization of stored stem reserves to support grain filling is an important consideration in selecting wheat lines for heat tolerance. Also, it is widely acknowledged that in wheat, under heat stress situations, kernel number per spike is a reliable measure for heat tolerance.

High temperature during seed development is associated with a reduction in total oil yield. Under field conditions the negative effect of high temperature gets amplified if there is also a moisture stress. Both temperature and moisture stress together influence the yield of oil in Brassica by interfering with seed growth and development. At elevated temperatures, with high night temperatures, a marked reduction in the percentage of linoleic acid occurs, apparently due to desaturase enzymes that are essential for the conversion of oleic to linoleic acid.

Heat stress leads to the synthesis of normal proteins and the accelerated transcription and translation of heat shock proteins (HSPs), the production of phytohormones (ABA) and antioxidants and changes in the organization of cellular structures, including organelles, the cytoskeleton, and membrane functions.

Impact of heat on photosynthesis:

Numerous components of the photosynthetic apparatus display heat lability, it has long been proposed that PSII is the most heat-sensitive component of the photosynthetic apparatus. Other parameters during heat stress include components that facilitate CO_2 transfer from the intercellular space to the chloroplast, photosynthetic electron transport and loss of ribulose bisphosphate (RuBP) regeneration capacity.

The heat lability of various photosynthetic components is secondary to the failure of cells to maintain RuBP carboxylase/oxygenase (Rubisco) in an optimally activated state. Under conditions of heat stress Rubisco activity declines as a consequence of the association of catalytic 'misfire products' at the active site rather than temperature- induced enzyme inactivation. It is the well-characterized temperature sensitivity of Rubsico activase that precludes adequate reactivation of these dead-end complexes during periods of heat stress. The main effect

of heat stress after/during floral initiation is observed on kernel number. The number of kernels per unit area decreases at a rate of 4% for each degree increase in mean temperature during the 30 d preceding anthesis. Drought and high temperature together, 3–4 weeks prior to flowering, caused asynchrony in the tasselling and silking of maize, while the growth and receptivity of the style were also inhibited.

Cold stress:

Plants differ in their tolerance to chilling (0-15˚C) and freezing (<0˚C) temperatures. Plant from temperate climatic regions are considered to be chilling tolerance with variable degree and can increase their freezing tolerance by being exposed to chilling, non freezing temperatures, a process known as cold acclimation. Low temperature inhibits chlorophyll accumulation in actively growing leaves. Cold snaps cause a reaction in the plant that prevents sugar getting into the pollen. Without sugar there is no starch build up for pollen to germinate. Low temperature changes the gene expression and protein products leading to symptoms like necrosis or growth retardation. Membrane damage can occur as a consequence of freeze induced cellular dehydration including expression induced lysis, lamellar-to-hexagonal-II phase transition and fracture jump lesions. The increase of cellular solute concentration during

frost is capable of reducing cell volume by osmotic dehydration and may inhibit photosynthesis. The poikilohydrous, that are usually subjected to drastic change of molar concentrations and volume at any time reveal a combination of extremely high freezing tolerance and maintenance of photosynthetic capacity.

The freezing process in plant tissues is affected by the following facts:

- Plant cells are not immersed in an aqueous solution but are surrounded by a water saturated environment;
- The amount of osmotically available extracellular water is small relative to the amount of water inside living cells
- The apoplastic solution has a much lower solute concentration than the cell
- Cellular water, because of the higher solute concentration, has a greater freezing point depression
- A functionally intact cell membrane is an effective barrier to the propagation of ice crystals
- The effectiveness of the cell membrane as a barrier to ice may vary with CA or temperature
- The presence of heterogeneous nucleators inside cells is minimized, excluded, or masked and

- In many tissues a portion of the internal extracellular volume is free air space, normally saturated with water vapor. The other major factor in the freezing of plant cells is the rate of cooling.

Impact of snow coverage on plants:

Potential efficiency of PSII increases markedly by snow cover. Snow reduces temperature extremes, provides a moist environment and allows light transmission that is sufficient for moderate photosynthetic activity. Plant activity has been observed mainly in late winter or early spring. Spring "ephemerals" (mostly geophytes) have a remarkable capability to grow, to produce leaves and flowers or even to germinate under a layer of snow up to 50 cm.

- Winter desiccation stops under the snow covered conditions Additionally, complete snow cover protects plants from wind exposure and wind abrasion of surface wax that was found to decrease resistance to cuticular transpiration.
- Vascular plants are generally assumed to have no photosynthetic activity under the snow because of the severity of the subnivean environment.
- Significant photosynthetic activity was facilitated by favourable conditions in the subnivean environment, where CO_2 concentrations are elevated,

temperatures are often above freezing, and light levels are sufficient to drive photosynthesis.

- Diurnal changes in CO_2 concentration under the snow and light responses of snow-covered ecosystem CO_2 fluxes provide supporting evidence of carbon gain at the ecosystem level.
- This activity allows plants to rapidly increase photosynthesis upon snowmelt and reduces wintertime losses of carbon from arctic ecosystems.

Salt stress:

In addition to alterations in photosynthesis and cell growth, salt stress when slowly imposed, often induce osmotic adjustment which is considered an important mechanism to allow the maintenance of water uptake and cell turgor under stress conditions. The restriction on CO_2 diffusion into the chloroplast, via limitations on stomatal opening mediated by shoot- and root-generated hormones, and on the mesophyll transport of CO_2, to alterations in leaf photochemistry and carbon metabolism. These effects vary according to the intensity and duration of the stress as well as with the leaf and the plant species. Some plants are able to prevent salt entry (salt exclusion at the whole plant or the cellular level) or to minimize its concentration in the cytoplasm (by compartmentalizing salt

in the vacuoles), thus avoiding toxic effects on photosynthesis and other key metabolic processes.

In salt- acclimated plants, it was also shown that primary metabolites linked to amino acid and nitrogen or carbohydrate and polyol metabolism do increase; these compatible solutes play a role in osmotic adjustment, membrane and protein protection or scavenging of reactive oxygen species (ROS) and of excess accumulated ammonium ions. Interestingly, in those plants a depletion of organic acids is also observed following the decreased carbon assimilation as stomata close. The reduced content of organic acids under salt stress may be involved in compensating for ionic imbalance. Stomata close in response to leaf turgor decline, to high vapour pressure deficit in the atmosphere or to root generated chemical signals, the latter being common to both drought and salinity. Supply of CO_2 to Rubisco is therefore impaired, what predisposes the photosynthetic apparatus to increased energy dissipation and down-regulation of photosynthesis when plants are subjected to high light and temperature. Under mild stress, a small decline in stomatal conductance may have protective effects against stress, by allowing plant water saving and improving plant water-use efficiency by the plant.

Case Studies-

Ploeg et al. (2015) reviewed the influence of suboptimal temperature on tomato growth and yield and concluded that

1. Leaf initiation rates decrease linearly with decreasing temperature.
2. Young plants grown at sub-optimal temperatures produce thicker leaves, so they intercept less light and therefore have a lower relative growth rate.
3. At sub-optimal temperatures, fruit set is reduced as a result of poorer pollen quality.
4. The period between anthesis and ripening of the fruit increases and, as the growth rate of the fruit at a certain developmental stage is independent of temperature, fruits become larger at sub-optimal temperature.
5. Higher temperature leads to an increase in early yield, at the cost of vegetative growth, but may also cause a delay in later trusses.
6. Breeding for cultivars with equal production at lower temperatures is hampered by the limited variation for temperature response in cultivated tomato. Therefore breeders have to look for other sources of variation, as in related wild *Lycopersicon* species.

Wolfe (1991) studied the low temperature effects on early vegetative growth, leaf gas exchange and water potential of chilling-sensitive and chilling-tolerant crop species

1. Two chilling-sensitive (*Phaseolus vulgaris* L., *Zea mays* L.) and two chilling-tolerant (*Pisum sativum* L., *Spinacia oleracea* L.) species were raised in growth chambers under warm (28/18°C day/night cycle) and cool (18/12°C) temperature regimes

2. Chilling-tolerant species *P. sativum* and *S. oleracea* showed relatively minor delay in emergence, a higher net assimilation rate (NAR) and less than a 10% reduction in relative growth rate (RGR) at 18/12°C.

3. Chilling-sensitive species (*Phaseolus vulgaris* L., *Zea mays* L.) showed 40–50 % reductions in RGR, and for *P. vulgaris* this was most associated with lower specific leaf area (SLA) and photosynthetic area at 18/12°C.

4. A significantly lower SLA at the cooler temperature was also observed in Z. mays, but factors controlling NAR and photosynthesis per unit leaf area (Pnet) dominated growth response for this species.

5. Visibly thicker leaves and increased leaf density (i.e. lower SLA) were observed in all species when grown at 18/12°C.

6. The greatest response to short-term chilling was measured in P. decline in visible

wilting in some cases, and 60–80% reductions in Pnet and stomatal conductance.

7. Severe water stress was not observed in *Z. mays*, and Pnet reductions were only 5–30%.

8. For both chilling-sensitive species, those grown at the cooler regime had a less negative response to chilling than those grown at 28/18°C.

9. Exposure of *P. sativum* and *S. oleracea* to 8/4°C had little impact on leaf water status or Pnet regardless of growth temperature. *P. sativum*, *S. oleracea* and to a lesser extent, *Z. mays*, had more negative leaf solute potential when grown at 18/12°C compared to 28/18°C. This osmotic adjustment minimized chilling-induced water stress in these species.

Thermal sensitivity of primary photochemical reactions occurring in the thylakoid membrane system limits the response of plant to high temperature. Light causes an increase in tolerance to heat, and this stabilization is related to the light-induced proton gradient. CO_2 assimilation may be limited, in part, at high temperature by an imbalance in the regulation of the carbon metabolism, which is reflected in a 'down-regulation' of the ribulose-1,5-bisphosphate carboxylase/oxygenase (**Weis E and Berry JA 1988).**

Brassica rapa was more sensitive to heat stress than *B. napus* and *B. juncea*. Although observation did not indicate the exact developmental phase when the reproductive organs were susceptible to heat stress, pods that passed a critical threshold developmental phase tolerated heat stress, which explained the smaller effect of high temperature stress at pod development. A direct temperature effect on reproductive organs appeared to be responsible for the reduction in yield. All genotypes began to recover from the stress by continuing flowering after returning to 20/15°C. *Brassica napus* was least able to recover from severe stress a flowering, as evidenced by the formation of many abnormal pods during recovery. Per-plant yield response of canola-quality *B. juncea* line J90-4316 was similar to oriental mustard Cutlass. Thus, heat stress effect depends on the growth stage of canola and mustard and *Brassica* species differ in heat stress response **(Angadi et al. 2000)**.

Drought stress progressively decreases CO_2 assimilation rates due to reduced stomatal conductance. Drought stress also induces reduction in the contents and activities of photosynthetic carbon reduction cycle enzymes, including the key enzyme, ribulose-1,5-bisphosphate carboxylase/oxygenase **(Reddy et al. 2004).**

Oxygenic photosynthesis in plants involves highly reactive intermediates and byproducts that can damage the photosynthetic apparatus and other chloroplast constituents. The potential for damage is exacerbated when the amount of absorbed light exceeds the capacity for light energy utilization in photosynthesis, a condition that can lead to decreases in photosynthetic efficiency. A feedback de-excitation mechanism (qE), measured as a component of nonphotochemical quenching of chlorophyll fluorescence, regulates photosynthetic light harvesting in excess light in response to a change in thylakoid lumen pH. qE involves de-excitation of the singlet excited state of chlorophyll in the light-harvesting antenna of photosystem II, thereby minimizing the deleterious effects of high light via thermal dissipation of excess excitation energy **(Holt et al. 2004).**

In C_3 plants, Rubisco capacity is the predominant limitation on across a wide range of temperatures at low CO_2 (<300 microbar) . At elevated CO_2 P(i) regeneration is the limitation. In C(4) plants, Rubisco capacity limits instantaneous net CO(2) assimilation rate below 20 degrees C in chilling-tolerant species, but the control over instantaneous net CO(2) assimilation rate at elevated temperature remains uncertain. In many C(4) species from warm habitats, acclimation to cooler growth conditions increases levels of Rubisco and C(4) cycle enzymes which then

enhance instantaneous net CO(2) assimilation rate below the thermal optimum while in C_3 it is associated with a disproportional enhancement of the P(i) regeneration capacity **(Sage RF and Kubien DS 2007).**

The primary sites of targets of high temperature stress are Photosystem II (PSII), ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) while Cytochrome b559 (Cytb559) and plastoquinone (PQ) are also affected. As compared to PSII, PSI is stable at higher temperatures. ROS production, generation of heat shock proteins, production of secondary metabolites are some of the consequences of high temperature stress **(Mathur et al. 2014)**.