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Review Article

Chilling Stress Effects on Structure, Function and Development of Different Plant Processes

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Abstract

The unprecedented climate change has become a major issue around the globe. Abiotic stress which includes salt, drought, nutrient deficiency, pesticide contamination, light intensity as well as extreme low or high temperature inhibits or slow down many plant processes and ultimately cause the decreased or abnormal growth of the plant. These stresses reduce performance of four complex present in thylakoid membrane photosystem, cytochrome b6-f complex and ATP synthase. In chloroplasts, chilling stress may change the lipid membrane state and enzyme activity. The efficiency of photosynthesis then decreases, resulting in an overabundance of reactive oxygen species (ROS). There is a decline in antioxidant enzyme production, coupled with increased ROS accumulation in plants under environmental stress. A major negative effect has been observed on the activity of RuBisCo with increasing intensity of a range of environmental factors. The reduction in RuBisCo activity is due to the enzyme's activation state being downregulated in response to low temperature (e.g., by de-carbamylation and/or binding of inhibitory sugar phosphates). Chilling stress inhibits RuBisCo activation via a rapid and direct effect on RuBisCo activase. The present review tells how chilling stress can create serious effects on cellular membrane, biosynthesis of photosynthesis pigments, electron transport chain as well as RuBisCo activity.

Keywords: Chilling Stress; Low Temperature; Stress; Rubisco Activity; Environmental Stress

Introduction

Abiotic stress is the most common cause of crop failure, reducing the average yields of most main crops by more than 50% on average and endangering the long-term viability of agriculture around the globe. Temperature is one of the abiotic elements that has an impact on the development of plants. When plants are exposed to cold temperatures, they experience a loss in membrane fluidity, which has an impact on enzyme kinetic parameters and protein folding. As a result, developmental, morphological, physiological, and biochemical processes are disrupted, resulting in decreased yield, decreased quality, and decreased survival [1].

The production of ice inside plant cells may be very damaging. Even when the surrounding air temperature drops under 0 degrees Celsius, freeze-tolerant plants use a range of methods to limit the chance of this happening. Sustaining intracellular solute concentrations and stimulating ice nucleation outside the cells are two of these ways. The xerophytic adaptations that these plants have developed to cope with the decreased water availability both inside the plant and in the soil are also widespread. Temperatures as low as 5°C may kill a winter wheat plant that has not been hardened, despite its inherent ability to acclimate, stiffen, and acquire tolerance to freezing temperatures as low as -20 °C.

Carbon balance in plants is the primary factor influencing crop production. Plant productivity is measured by the difference between photosynthetic CO_2 uptake and respiration rates. It is now well accepted that *in vivo* RuBisCo activity may be rapidly controlled in order to manage flow through the photosynthetic carbon reduction cycle in response to changes in the environment [2]. The enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo) is responsible for CO_2 fixation during the photosynthetic process. It is predicted that plants fix more than 1011 tonnes of CO_2 from the atmosphere each year, which has a significant impact on primary output.

Warm-climate plants' photosynthesis is considerably reduced when they are cooled. Tropical and subtropical species provide an excellent opportunity to investigate the effects of low temperature on photosynthetic processes that are not obscured by the abundance of protective responses observed in temperate species, thanks to the abundance of protective responses observed in temperate species. Low temperature, which is one of the most important abiotic stressors affecting the development and productivity of plants, severely depresses plant growth and results in a large decrease in grain output [3]. It causes a number of metabolic alterations, including the deactivation of numerous metabolic enzymes and the disruption of metabolic regulatory mechanisms, among other things [4], Osmolytes (e.g., proline and glycinebetaine) build-up [5], variations of glucose metabolism, and changes in photosynthetic characteristics are all possible outcomes [6].

Low temperature stress has a deleterious influence on a number of components of photosynthesis. It may, for example, impede thylakoid electron transport by increasing membrane viscosity and limiting plastoquinone diffusion, both of which are harmful to the process. It has been shown that low temperature stress has a negative effect on the activities of scavenging enzymes in the body [7]. As a result, the mitochondrial and chloroplastic electron transport processes are inefficient at counterbalancing the formation of ROS [8]. The review focuses on the effect of chilling stress on different plant processes like chloroplasts, RuBisCo activity, electron transport chain and photosynthetic efficiency as well as their structure, function and development.

Effect of low temperature on chloroplast ultrastructure

Low temperature is one of the abiotic variables that affects plant life and development. Low-temperature, or chilling, stress (damage produced by temperatures below freezing but above freezing) has been identified as a distinct environmental influence on agricultural plant physiology for more than 70 years. Many plant organisms experience physiological or cellular changes when exposed to low temperatures, which is referred to as low-temperature injury [9]. As a result, evolutionary, morphological, biochemical and physiological, mechanisms are influenced in many plants, influencing growth, efficiency, and survival [10].

While several variables determine the severity and duration of chilling damage, the ultrastructural consequences are almost identical across species. Chromatin condensation, lipid droplet aggregation, thylakoid dilatation, starch granule reduction, thylakoid swelling and disorganisation, chloroplast and mitochondrial swelling and disorder, and thylakoid swelling and disorganisation are some of the symptoms. Despite the fact that protective components (for example free proline, carbohydrates, and carotenoids) aggregate at low temperatures, a succession of detrimental repercussions will follow [11]. Typically, the most vulnerable targets are photosynthetic components, since their reaction is obvious as changes in pigment complexes, a fall in photosynthetic rates, loss of the chloroplast structure, or decreased electron transport and activity of enzymes [12]. The development of reactive oxygen species (ROS) is the most critical case when plants are subjected to low temperature.

Under favourable temperatures, chloroplasts have many starch granules and well-developed granal stacks that are intertwined by stromal thylakoids, and the chloroplast envelope's two membranes are intact. Chloroplast swelling, thylakoids deformation and swelling, and a reduction in the size and number of starch granules are often the first indicators of low temperature stress and the creation of tiny vesicles of the chloroplast membrane termed the peripheral reticulum. Additionally, low temperature stress might inhibit photosynthate transport out of the chloroplast. It is unknown if triose phosphate export from chloroplasts is prevented directly. Protein absorption by chloroplasts, which needs energy, is impaired in the cold owing to a deficient trans-envelope proton motive power [13]. As a result, another energy-intensive activity, photosynthate export from chloroplasts, is likely to be impeded as well. Indirectly, a reduction in phloem loading caused by cold may also limit photosynthate export [14]. It was also observed that the leaf soluble sugars can also rise during low temperature [15].

Figure 1: Effect of different levels of low temperature on chloroplast ultrastructure.

In cold temperatures, chloroplast pigments, including carotenoids and both chlorophylls, are impacted. Phenylpropanoid metabolism and flavonoid biosynthesis enzymes (phenylalanine ammonia-lyase enzymes) are stimulated by low ambient temperatures, resulting in an increased production of phenolic compounds that can tolerate stress conditions [16] recorded anthocyanin buildup was seen in maize leaves subjected to temperatures of 5 °C, 10 °C, and 15 °C [17] and [18] noted elevated total phenolic content in the leaves of Lactuca sativa (exposed at 4 °C for 1 day) and Olea europaea (exposed at 4 °C for 12h).

In addition to their role in photoprotection, carotenoids serve as light pigments and ROS scavengers [19]. A major role is played by xanthophyll cycle pigments, a key subgroup of carotenoids, in the response to stress. When there is excess excitation energy that cannot be utilised for photosynthesis, the deep oxidation cycle converts violaxanthin into zeaxanthin and antheraxanthin. Low temperature stress has been associated to an increase in zeaxanthin concentration [20]. Reduced chlorophyll concentration indicates oxidative stress, as does a decrease in chlorophyll content after cooling. Low temperatures affected the pigment makeup of maize plants, resulting in a decrease in -carotene and an increase in zeaxanthin [21].

Cells of the mung bean that are susceptible to low temperatures show condensation and chromatin fragmentation [22]. Early observations (within 6 hours) indicated vesiculation of cellular membranes, including the ER and tonoplast, as well as vacuolation of plastids and mitochondria. Chilling damage proceeded in these cells in an orderly and predictable way. This was followed by the formation of enormous Golgi vesicles and parallel arrays of dilation of the endoplasmic reticulum (ER). Vesicles merged with vacuolar membranes and their contents were released after 72 - 96 hours of cytoplasm condensation. As the cooling progressed, the cytoplasm shrank away from the cell membrane, and organelles were digested, until the cell was digested completely. Because the cells were grown in culture, there were no physical signs to worry about.

Decline in RuBisCo activity

RuBisCo is biologically significant because its catalysis the main chemical reaction that allows inorganic carbon to release into the biosphere. One of the non-stomatal causes for the decline in photosynthesis rate was found to be a decrease in RuBisCo activity. Photosynthesis was impacted by a 90% fall in O_2 content at cold temperatures (16 °C) because RuBisCo's activation state reduced at higher CO_2 concentrations. Reducing the pressure gradient of $_{CO2}$ at cold temperatures increased the activation state of RuBisCo as well. It is necessary for the RuBisCo activation protein RuBisCo activase to be present. The rate at which $_{CO2}$ is absorbed by plants depends heavily on the growth temperature [23].

As a general rule, plants that grow at relatively low temperature are more efficient in absorbing $_{CO2}$ than plants that grow at normal room temperatures, but at high temperatures, they are less efficient. At roughly 17 °C, the Arrhenius plot of RuBisCo activity shows a thermal split [24]. Because RuBisCo isn't being produced at low temperatures, photosynthesis suffers. The RuBisCo activase isoform is under redox regulation, and as a result, this enzyme becomes inactive during the hot midday and cool night [25].

At low temperatures, RuBisCo activation state recovers following CO_2 decrease, which is linked to an indication of restrictions in RuBP regeneration. The CO_2 saturation threshold of C3 and C4 photosynthesis falls below the present atmospheric CO_2 levels below 20 degrees Celsius [26]. Stomatal closure is caused by a breakdown in the structure of guard cells, which influences the concentration of CO_2 in the leaf, resulting in a drop-in RuBisCo activity [27]. Due to a decrease in oxygenase activity and decreased photorespiration, RuBisCo carboxylase activity should be controlled. Photorespiration, which reduces stomatal conductance in response to cooling, serves as a defense mechanism [28].

The photochemical efficiency of photosynthesis was considerably lowered when Phaseolus vulgaris was subjected to intense light and cooling temperatures [29]. Rice seedlings exposed to

chilling stress produce more ROS, which raises the activity of the antioxidant catalase, suggesting that photorespiration plays a role in low temperature metabolism [30]. Due to slow CO_2 fixation rate (kcat c, 2 - 3 s1) and competitive O_2 fixation, which forms 2-phosphoglycolate and requires photorespiration recycling, the generation of RuBisCo is limited in C3 plants. Cold-treated seedlings had decreased levels of RuBisCo large subunits and RuBisCo binding protein, suggesting chloroplast injury.

Effect on electron transport chain

Temperature changes in plant mitochondria and chloroplast energy transducing membranes have attracted a lot of interest lately. Due to the adverse effects of low temperature stress on the photosynthetic electron transport system, photosynthesis is inhibited [31]. There are two large protein complexes in the thylakoid membrane known as photosystems I and II that employ incoming light energy to support a series of electron transfer processes. As early as the earliest biological research [32], cryogenic temperatures have been thoroughly studied in regard to this process.

In terms of a rate map, the temperature consequences on electron transport can be more readily visualized. In recent years the temperature has been increasingly influenced in the structure and operation of the energy-transducing membranes of plant mitochondria and chloroplasts. Most of this attention was based on the molecular comprehension of the cold sensitivity or chills of various plant species [33,35].

A study of thylakoids extracted from midday leaves found that oxygen production was significantly reduced. This clearly shows that strong irradiance impacted leaf variations more severely on the decreasing side of PS2 than it did on CN leaves. Mitocryphal membranes obtained from cooling plants showed an increase in Ea' for respiratory enzymes and a decrease in lipid fluid at temperatures between 10 and 15 C, but not from cooling-resistant plants. [33,35]. PSII activity was strongly hindered and NPQ and photosynthetic electron transport were decreased when the shoots were chilled, but not the roots [36].

In plants from which mitochondria were extracted, the presence or absence of temperature-induced alterations to mitochondrial membranes is linked to cooling sensitivity and resistance, although studies from chloroplast membranes do not reveal an obvious relationship of this kind [37,40]. After removing or bypassing the rate-limiting processes, chloroplast membranes separated from both cold sensitive and cold resistant plants showed temperature-induced Ea alterations [39]. There was a difference at a higher temperature not only in the chilling-temperature spectrum but in the chloroplast extracted from each plant.

If the major electron transfer process, photosynthetic linear transport, is hindered, then other mechanisms, like cyclic electron flow around PSI and chlororespiration, may be promoted [41], as plant health and survival are dependent on the ability to regulate photosynthetic electron transport. When the photosynthetic system is under low-temperature stress, these alternative ways of linear electron transport may assist to safeguard it [42].

Decrease photosynthetic efficiency of both photosystem (PS I and PS II)

Photosynthesis requires the activities related to electron transfer and energy capture. Photodamaging can occur here as a result of these reactions, which use redox chemistry and light intensity. A very sensitive to suboptimal environmental factors, as examples include the plant's geographic origin and to fluctuations of temperature, such as those that exist in the plants of the tropical or subtropical regions [43]. RuBP restoration lowers $_{CO2}$ uptake in plants, which in turn reduces Rubisco activity, and this in turn reduces the rate of photosynthesis [44]. Photosynthesis's key activities, including as thylakoid electron transport, carbon reduction, and stomatal conductance control, would be impaired by these stimuli. Because NPQ (non-photochemical quenching) dispersion as heat of the excess energy suppresses photochemical performance at low temperatures, considerable levels of ROS accumulate in cells [45].

It is known that the PSII reaction center is affected when the architecture of related protein components is disrupted. It has been concluded that ROS does not actively trigger oxidative stress in the PSII operational centre but rather amplifies this photoinhibition by restricting protein synthesis, particularly the D1 protein, which is required for the PSII repair mechanism in the newly approved two-step system for PSII photoinhibition. ROS may be eliminated by plants' antioxidant systems, such as the water-water cycle [46]. The photosynthetic machinery may build up more free radicals as a result of cells becoming phototoxic when confronted with a cold discomfort [47].

PSII photoinhibition is minimal in chilling-sensitive plants such as cucumber (*Cucumis sativus* L.) and Arabidopsis thaliana when subjected to short-term chilling-light tension. This is especially true in cases when tropical tree species are exposed to chilly temperatures that are associated with modest light intensity [48]. Chilling-sensitive plants have different responses to cold temperatures in terms of PSII activity. As a result, nothing is known about the impact of these pressures on PSII behavior in the Paphiopedilum species.

Figure 2: Effect of chilling stress on photosynthesis in thermophilic plants.

Weak electron transmission via linear electron few from PSII to PSI delays $_{CO2}$ assimilation, resulting in hydroxyl radical generation and acceptor side over-reduction at PSI. This makes the PSI vulnerable to oxidative hydroxyl radicals at the electron acceptor end [49]. Tropical tree PSI activity is unaffected by cooling temperatures and moderate light intensity, despite the fact that PSI activity in sensitive cucumbers and Arabidopsis is reduced. PSI's performance varies from species to species, as is obvious [48].

Photoinhibition is a term used to describe the gradual and reversible limitation of photosynthetic activity caused by both harmful and regulating factors. A combination of stress elements, including bright light and heat, cold and dehydration, inhibits photosynthesis because plants absorb lighter than they utilise in photosynthetic energy [46]. The PSII photoinhibition site is well-known. In chilling-sensitive and chilling-resistant species, PSII photoinhibition has been intensively researched for its detrimental and protective effects [50].

It has been believed that excessive irradiation *in-vivo* has little effect on PSI in general or has a negligible effect on it [27]. Even so, emerging research suggests that PSI can remain inhibited in response to light stress, especially at chilling temperatures (0 - 10°C). When leaves of cold-sensitive cucumber (*Cucumis sativus* L.) and common bean (*Phaseolus vulgaris* L.) were cooled under low sunlight, photo-inhibition of PSI happened. When exposed to bright light, potato leaves (*Solanum tuberosum* L.) showed a considerable change [51]. Electron transport between PSII and PSI is required for PSI photoinhibition because of the need for molecular oxygen and PSI photo-inhibition. In the absence of oxygen, or even when diuron inhibited electron transmission from PSII to PSI, PSI inhibition was not seen. Active oxygen species (AOS) have been discovered to impede PSI [52].

Many thermophilic species are observed that if temperature getting low in dark and immediate chilling occurs then the photodamage process initiated. By contrast, the confluence of low temperature and high light can cause chronic photoinhibition of PSII [53]. Photorespiration and $_{CO2}$ fixation are two examples of processes that utilise light as a source of excitation energy (light) but are slowed by lower temperatures. Smaller sinks for inhibitory energy used boost PSII's oxidative damage potential [54]. It is possible that decreasing fatty acid saturation by genetic alteration of thylakoid lipids might decrease high-light-low-temperature photoinhibition by enhancing diffusion and aiding repair even more. Additionally, light-chill-induced photosynthetic inhibition in thermophilic species is usually not the result of PSII photodamage [50].

Photosystem I (PSI) have been shown to be more effective at cooling than photosystem II (PSII) (PSII). In isolated thylakoid membranes, this is often evaluated using artificial electron donors or acceptors. PSI electron transport in intact plants may be measured using 820 nm absorption measures of the chlorophyll P700

reaction cluster and the redox phase. [27]. This absorption of $_{CO2}$ has been researched under freezing circumstances to see what effects PSI, PSII, and other processes have.

Even though PSI activity declines more rapidly than PSII activity, this does not mean that PSI is the main target for relaxation. Due to the fact that improved PSI or PSII behaviour reported as a secondary response, the ultimate cold sensitive systems that have not been examined are not eliminated as a main target. As a consequence, complete leaf data is insufficient to pinpoint PSI as the principal focus of a terrifying set of events [47].

A drop in PSII quantum efficiency that can be reversed rapidly is essential for leaf photoprotection. Rearranging the xanthophyll pigments and creating an electrochemical potential variation in the transthylakoid molecule is a crucial defence against the more severe consequences of photodamage, as this procedure includes [55]. Detecting variations in the quenching of excitation energy in the antennae of PSII is straightforward owing to chlorophyll fluorescence [56]. This downregulation of PSII electron transport is frequently measured using quantum yields Fv′/Fm′ (excitation energy transfer efficiency to accessible PSII reaction centres and non-photochemical quenching) [57].

Heat is released from the reaction Centre when photosynthetic sinks cool down (simultaneously with or after cooling). This occurs because the light accumulation complex's transmission efficiency into the reaction centre is reduced. The thermophilic crops like maize and tomato, when exposed to light and cold, exhibit these phenomena. Tomatoes and mangoes, for example, don't have complicated photoinhibition to blame for their decline in photosynthesis after a frost [52].

It is fascinating to see some impacts of chilling on photosynthesis induced by failing to execute some circadian rhythms and the implications of chilling on carbohydrate metabolites can be underlined [47]. Light energy cooling has the potential to affect PSII photo-damage as well as redox modulation of stromal bisphosphatases, FBPase, SBPase, and presumably rubisco activase, although these effects are less apparent [58].

Conclusion

Many species, including essential agricultural crops, have productivity and geographic spread limitations because of low temperatures. Nonfreezing temperatures (0 - 12°C) are typical throughout the growing season in temperate countries and may significantly reduce plant production, which is discussed here. Low temperature, which is one of the most important abiotic stresses impacting plant development and productivity, slows plant growth and reduces grain yield significantly. Photosynthetic transport out of the chloroplast is hindered by low temperature stress. Chilling stress obstructs thylakoid electron transport by increasing membrane viscosity and restricting plastoquinone diffusion, both of which are detrimental to the process. A reduction in RuBisCo activity was discovered to be one of the non-stomatal explanations of the fall in photosynthesis rate. Because of cells becoming phototoxic when faced with chilling stress the photosynthetic machinery may store up more free radicals. The effects of chilling on photosynthesis generated by failure to execute specific circadian cycles are significant, and the consequences of chilling on carbohydrate metabolites cannot be emphasized. In general, low temperature or chilling stress reduce development of chloroplast ultrastructure, RuBisCo activity, disturb electron transport chain and one of the major abiotic stresses in reduction of photosynthesis.

Conflict of Interest

The authors declare no conflict of interest.

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