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Impacts of climatic changes on agronomically and physiological processes in plants: A review

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ABSTRACT

Climate change is threatening crop productivity worldwide and new solutions should urgently adapted the crops to these environmental changes. High temperatures always affect the developmental and physiological plant processes that, ultimately, influence crop yield and quality. Xylem and phloem consider as plant vascular tissues, affected by the climatic changes. Their formation are critical for the transpiration phenomena, besides photosynthesis, however impacts on the transpiration stream are well studied, interactive effects of multiple stress factors are underrepresented. Climate changes will result in plants experiencing multiple co-occurring environmental stress factors, which require further studies. Due to drought stress will gradually influenced the diameter and density of xylem vessels or tracheid's. All of these factors are expected to increase vascular cell wall thickness, due to increasing carbon allocation to these tissues. Roots are responsible for uptake both water and nutrients by plants. However changing in soil temperatures will alter the mechanisms that caused limiting crop growth. Variable climatic forecast will affect the development of root efficient system to better adapt the changing soil and environmental conditions for enhancing crop productivity. Studies of improving root for facing high temperatures are important to obtain more adapted suitable crop varieties. This review, will summarize the current knowledge about the effect of increasing temperatures on root growth and their impact on crop yield. The coordinated physiological and metabolic changes will be considered in roots and aerial parts that response of the plant to increased temperatures. The main regulatory mechanisms controlling root adaptation to warmer soils, including the activation of heat and oxidative pathways to prevent damage of root cells and disruption their growth as well as the interplay between hormonal regulatory pathways and the climatic changes on gene expression and protein homeostasis. Considering also that increasing temperatures are usually associated with other abiotic and biotic stresses such as drought, salinity, nutrient deficiencies, and pathogen infections as well. We will present recent advances on how the ability of root system to integrate and respond to complex and different stimuli in order to adapt to an increasingly changing environment as well as the initiation of vascular of both xylem and phloem , the transpiration stream through them , and photosynthesis. Finally, we will discuss the new prospects and challenges in this field as well as the more promising pathways for future research.

Keywords: Environmental factors; higher temperature; drought stress; elevated carbon dioxide;, roots vascular cambium hydraulic conductivity, wood anatomy, nutrient uptake

1. Introduction

Atmospheric carbon dioxide (CO_2), air temperature, and drought are the main components of climate changes Qaderi *et al.* (2006), Stocker *et al.* (2013). As reported, global mean surface air temperatures have already risen by 1–2^{-o}C, and are expected to rise another 2–3^{-o}C by 2050 (Stocker *et al.*, 2013), with one of the greatest degrees of warming projected for Northern latitudes Rossi *et al.* (2011). Due to the abnormal activity and industrial revolution, atmospheric CO_2 has been steadily increasing, with a current concentration of over 400-µmol mol^{-1}, and a projected concentration of 700-µmol mol^{-1} by the end of the century Stocker *et al.* (2013), Flexas *et al.* (2014). While one-third of the

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world is currently facing some form of water deficit, water availability is predicted to further decrease by 20%–70% Irigoyen *et al*. (2014), leading to increased incidences of drought and a need for improvements in plant water use efficiency (WUE). In order to properly adjust to climate changes, photosynthetic processes and WUE of plants must be increased substantially (Flexas *et al*., 2013). Plant photosynthesis depends on both atmospheric CO_2 and the presence of sunlight, and along with related processes, such as transpiration and respiration, it is sensitive to changes in global climate Centritto, *et al*. (2011). Uptake of CO_2 occurs through stomata, small pores on the epidermal cells of plants Woods (1896), Pittermann (2010). Guard cells surround each stoma and regulate uptake of CO_2 and release of water vapour by opening and closing of the stomata Fig. (1) Woods (1896) Haworth *et al*. (2010).

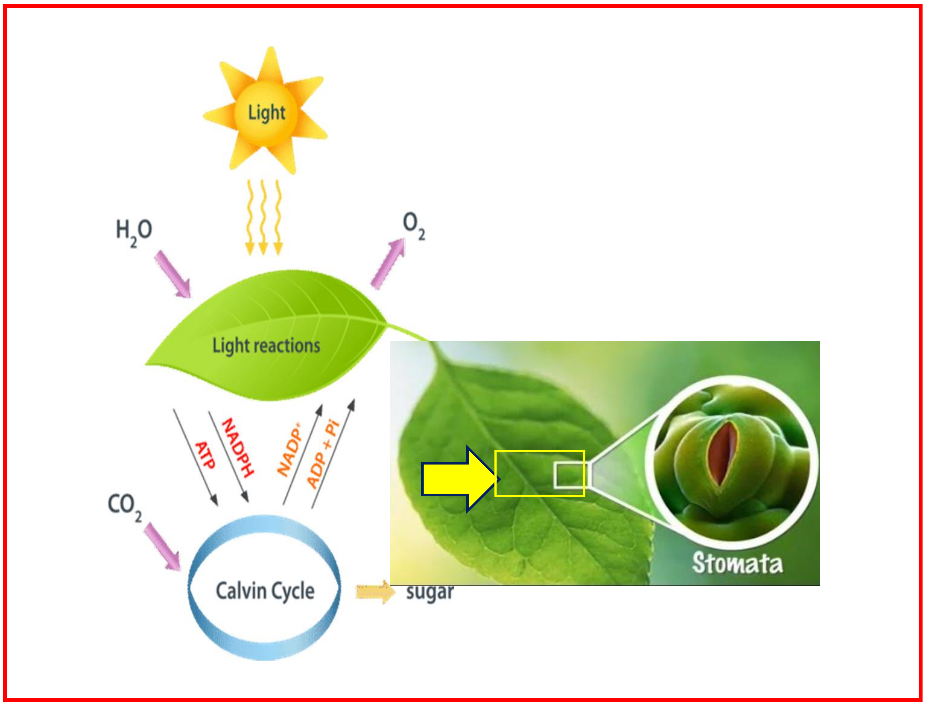


Fig. 1. Illustrates carbon dioxide process of photosynthesis through guard cells that surround each stoma and regulate uptake of CO_2 (present quite naturally in the atmosphere in an approximate proportion of 0.038%, or 380 ppm) and release of water vapour by opening and closing of the stomata.

Stomata are sensitive to external factors, and water transport and stomatal regulation both depend strongly on the development of vascular tissues Milhinhos and Miguel (2013), hydraulic conductance, and water potential Buckley (2015). Plant water transport can be disrupted by environmental factors Suzuki *et al*. (2015), which adversely affect plant metabolism, growth, or reproduction Lichtenthaler (1996), Reddy *et al*. (2004). Many studies have examined the individual and two-way interactive effects of temperature, CO_2, and drought on plant functions Irigoyen *et al*. (2014), Centritto *et al*. (2011), Dhirendra and Venugopal (2011), , Zwieniecki and Secchi (2015), Kumar *et al*. (2020) such as transpiration stream and photosynthesis Song *et al*. (2011), Nabeshima *et al*. (2015); however, few studies have considered the effects of all these factors together Irigoyen *et al*. (2014), Dhirendra and Venugopal (2011), Medeiros *et al*. (2013), Erice *et al*. (2006), Qaderi *et al*. (2013). Fig. (2)

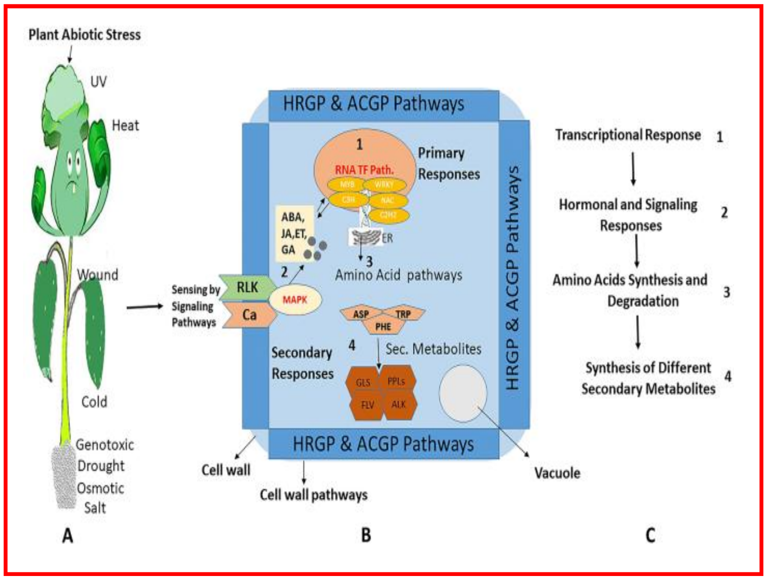


Fig. 2: Represents the plant abiotic stress and cellular level responses. **A** Plant under environmental stress. **B** Cellular level defense mechanism of plant during progression of abiotic stress and production of primary and secondary metabolites. **C** Representation of physiological responses in their order. RLK receptor-like kinase, Ca Calcium, NAC NAM ATAF, and CUC transcription factor, ABA abscisic acid, JA jasmonic acid, GA gibberellic acid, ET ethylene, ASP aspartic acid, TRP tryptophan, PHE phenylalanine, GLS glucosinolate, PPLs phenylpropanoid, ALK alkaloids, FLV favonoids. HRGP hydroxy proline-rich O-glycoproteins, ACGP arabinogalactan-proteins. After Kumar *et al*. (2020).

Kumar *et al*. (2020) stated that understanding the mechanisms of plant responses to multiple simultaneous abiotic stresses, it is crucial to develop broad spectrum of stress-tolerant crops. This process also reveals the production of different kinds of metabolites substances that help in the survival of plants during these adverse conditions. In the different challenging climatic conditions plant starts physiological response at the transcription level that activates post-translational protein modifications further effecting on metabolite alteration and accumulation, which leads to a particular physiological response against abiotic stresses Fig. (2) Yadav *et al*. (2016).During the progression of various abiotic stress, the plant produces secondary metabolites kind of excretory material, which are extracted from leaves, roots, shoots, bark at different stages of the life cycle of the plant. Plant metabolism can be disturbed due to limitation of enzymes or substrate; sometimes, it is also perturbed because of the higher requirement of a particular compound or a combination of these factors. The amount of secondary metabolite products is more or less dependent on the growing environmental condition as well, as how the other entity like transcriptome and proteome affects the metabolic pathways, which control the synthesis of related metabolites. During the progression of abiotic stress several intermediate signaling cascades have been dissected, the intersection points between different signaling pathways, as well as the identity of the signaling key regulators is already characterized but most of them are still largely unknown Baena-González *et al*. (2007). All of these major secondary metabolites could be used as metabolic fingerprinting to recognize metabolic signatures allied with a particular stress response without quantification. Pattern identification study is then executed on the data to find features specifc to a fingerprint because each stress has its specifc metabolites.

Studies on the effects of these factors on the development of vascular tissue are particularly scarce. In a changing climate, it is important to understand how environmental factors interact and affect plants. The in-depth effects of these three factors on vascular tissue and water regulation have yet to be examined Irigoyen *et al*. (2014). The main objectives of this review are: (a) to synthesize available information regarding the effects of the main climate change components on plant vascular system and (b) to predict possible changes in vascular tissue and water regulation of plants, as they are influenced by multiple environmental factors. In this review, we first discuss plant transpiration and its regulating factors, and then the individual and interactive effects of three components of climate change on plants and the form and function of their vascular system.

Plant transpiration and their regulating Factors

Beerling, and Franks, (2010), reported that about 30. 10^3 billion tonnes of water vapour to the atmosphere because of transpiration, each year, contributing about 30% of annual precipitation. Pittermann (2010) stated that each molecule of CO_2 gained through the stomata, about 200 to 400 molecules of water were loses by plant, therefore water uptake is critical for proper plant functioning. Boehm *et al*. (1894), Dixon, and Joly (1894), reported that Transpiration creates tension, leading to a tug-of-war process that drives a continuous stream of water molecules from the roots to the leaves, known as the cohesion-tension theory Fig. (3).

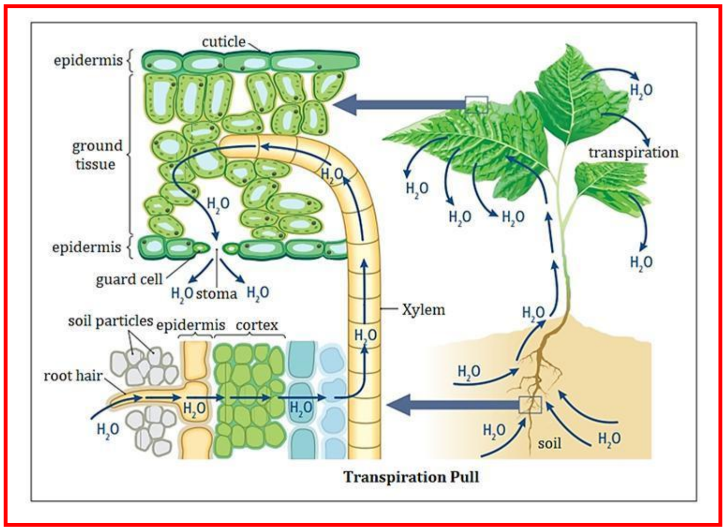


Fig. 3. Illustrates the transpiration process creates tension, leading to a tug-of-war process that drives a continuous stream of water molecules from the roots to the leaves, known as the cohesion-tension theory.

This process pulls water through the transpiration stream, where it mainly evaporates from the stomatal pore Pittermann (2010), Kim *et al*. (2014). Boyer (2015) stated that though most of exchangeable gas gradually occurs through stomata when they are open, the cuticle controls the transpiration rate when stomata are closed, for instance, due to drought stress or elevated CO_2 concentration. Chaumont and Tyerman (2014) stated that water movement is also driven by water potential, with water moving from an area of higher potential to an area of lower potential Pittermann (2010), stated that transpiration can occur at high rates and, therefore, water must effectively be replaced through root uptake and transported through vascular tissue; this is a passive process requiring little energy.

Adrijana filipovic, (2020) reported that water movement in the plant occurs predominantly regarding the passive or active transport of osmotic active substances along with water across the membrane. Main trigger for such solutes moving through the plant cells is difference in water potential followed by a difference in pressure Fig. (3). The entry of water into the root cells occurs passively, that is, diffusely, and the solution moves freely through the apoplasmic space. Since the water molecule uncharged, it can very easily cross the membrane without hindrance and continue to move upward through the conductive elements of the xylem by mass flow. Mass flow is also a passive mode of water transport, which is used for long-distance transport. While diffusion is a way of moving water and solutes over shorter distances which mainly occurs at the entry of water into the root cells and the exit of water through the stoma into the atmosphere, which occurs mainly in nonvascular tissues. In the rhizosphere layer, water generally moves by mass flow to the site of adsorption. However, after contact of water and solutes with the root hairs, the mode of uptake changes significantly as other forces occur that affect the uptake mechanism. Water movement trough the rhizosphere layer depends on the texture and structure of the soil. Since more permeable, sandy soils have weaker buffering capacity, so they tend to dry out quickly, while compacted, clayey soils have very limited capacity to receive and conduct water and nutrients, and transitional soil types are in terms of permeability and moisture retention and nutrients mobility of moderate capacity

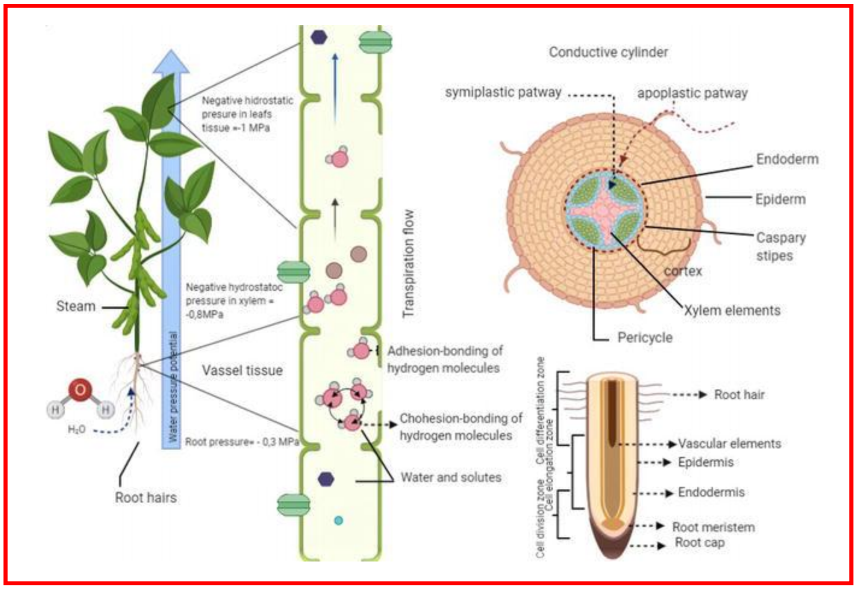


Fig. 4: Water movement through the plant root and root elements.
After Adrijana filipovic, (2020)

2.1. Structure of plant vascular and their function

Pittermann (2010), stated that water transport during xylem is always more efficient than through plasmodesmata of parenchyma. Sperry *et al*. (2006) reported that when water reaches the xylem, it enters conducting elements of both conifer tracheid's or angiosperm vessels and gradually flows upwards through the stem to the leaves Kim *et al*. (2014). The conduit diameter of xylem gets smaller and tapered with plant height, indicating the widening aspect of xylem anatomy from apex to the base of plant as illustrated by Kim *et al*. (2014). Plants that have an increased number of xylem conduits per cross-sectional area can maintain hydraulic conductance by reducing effects of path length Fig. (5).

Iakimova *et al*. (2017) illustrated that xylogenesis, the process by which conduits are formed through programmed cell death. Resulting in a long-distance, low-resistance pathway composed of non-living cells acting as a water pipeline as reported by Kim *et al*. (2014), Payvandi *et al*. (2014).Since it is composed of non-living cells that cannot adapted to the climatic changes , therefore xylogenesis are important at this time . Moreover, earlier studies have suggested that vascular anatomy is important in plant adaptation potential. For example, common oak (*Quercus robur* L.) trees that died in response to a widespread drought had a greater xylem vessel diameter than trees that survived, so these anatomical traits may increase drought susceptibility Levanic *et al*. (2011). In addition, vegetation shifts due to climate change lead to ecological drought Tietjen *et al*. (2017) and can affect plants and their vascular system in the new environment.

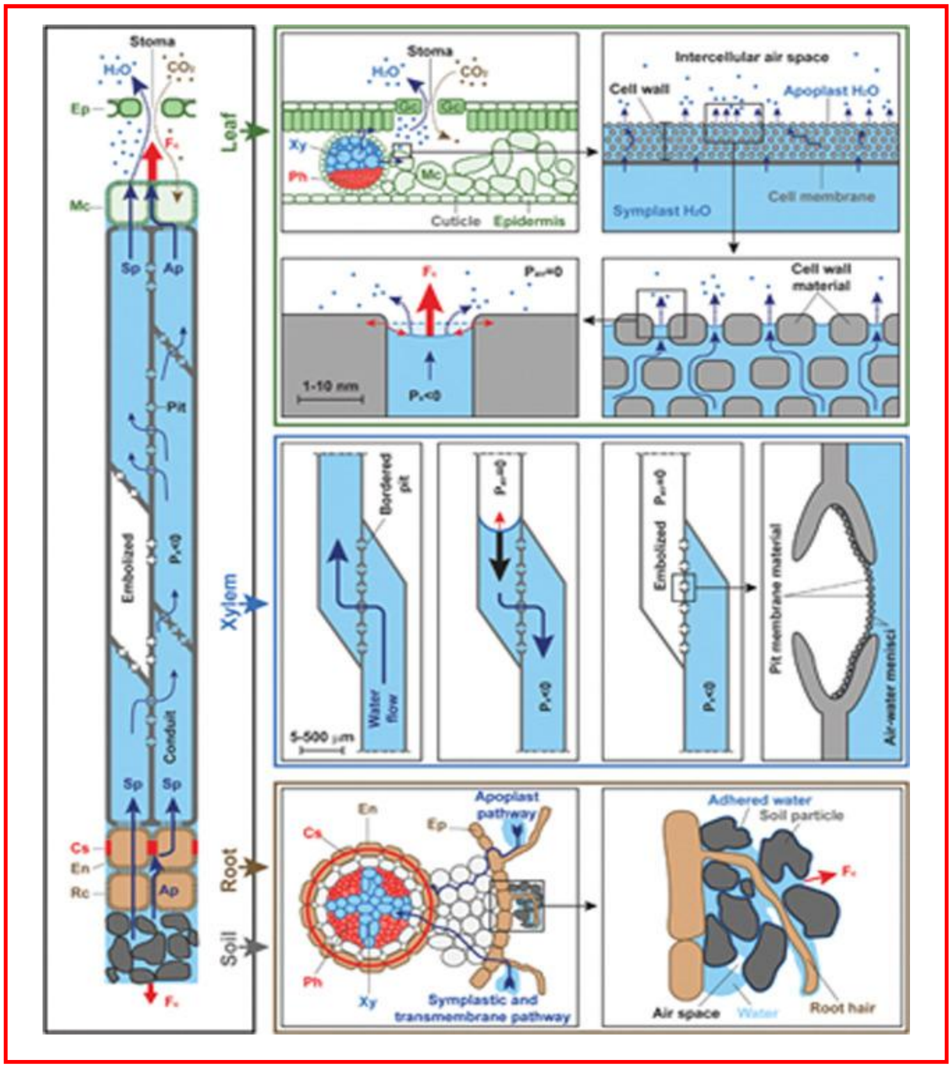


Fig. 5: Cohesion-tension mechanism of ascent of sap in plants (A) Schematic water column from soil to leaf cells After Sperry (2011). Liquid water is pulled (solid) from the soil to the evaporating surface of leaf cell walls by negative water pressure (**P x <0**) created by cell wall capillary forces (red Fc arrow). This force moves water through the mesophyll (**Mc**) from the xylem via a symplastic and transmembrane pathway (**Sp**), an apoplastic pathway (**Ap**), or a combination of both. Water moves up the xylem through a network of conduits that must be full of water to function (not gas-filled or "embolized"). Water moves through root cells (**Rc**) from soil to root xylem via **Ap** and Sp pathways except where it is filtered at the endodermis (**En**) because the Casparian strip (**Cs**) blocks the apoplastic pathway. The epidermis (**Ep**) and stomata control H_2O vapor loss (broken blue arrow) and CO_2 uptake (broken brown arrow) by diffusion from higher to lower partial pressures.(**B**) Leaf cross section, showing that the rate of evaporation from leaf cell walls (and hence potential for CO_2 uptake) is largely controlled by stomatal guard cell (**Gc**) aperture.(**C**) The evaporating surface of the leaf cell wall. (**D**) The air-water menisci held by surface tension and hydrophilic cell wall material. (**E**) Close up of a single meniscus illustrating the origin of the capillary pulling force (**Fc**). Adhesion of water to the wall (horizontal red arrows) anchors the meniscus edges. Evaporation (dashed blue arrows) causes the meniscus to retreat, increasing its curved surface area (curved meniscus surface relative to flat dashed surface). Surface tension resists the curvature, pulling the meniscus back to its equilibrium surface (dashed blue line), thereby exerting a pulling force that lowers the liquid pressure behind the meniscus (**P x <0**).This force is propaged through the continuum in (**A**), moving water up from the soil. (**F**) Conduits in the xylemare connected to each other through pits which offer resistance toflow but provide safety to the system.(**G**) If air gets into these conduits, capillary forces are not strong enough to retain the water column because conduit diameters are too large, and (**H**)water recedes into the adjacent tissue and the vessel becomes embolized andnon functional to water transport .(**I**) Pit"membranes"of modified primary cell wall material avoid the spread of air throughout the xylem network by generating the same capillary forces as the menisci of mesophyll cell walls.(J)Root cross section detailing water flow from soil to root xylem. The endodermis (**En**) with its

Casparian strip (**Cs**) interrupts apoplastic flow, forcing water through the En cell membranes by reverse osmosis. (**K**) Detail of water held in the soil by the same capillary forces that pull the water up the plant. Cohesion-tension is a tug of war on a rope of water by capillary forces in leaf vs. soil. After Martin *et al*. (2017)

2.2. Vascular cambium and plant Growth

Rossi *et al*. (2011), Medeiros *et al*. (2013), reported that cell division of active, vascular cambium contributing to secondary growth of xylem and phloem, which representing the largest carbon sink in vascular plants Fig. (6). Jae-Heung *et al*. (2004), stated that development of Secondary Xylem Was Correlated with the Height of the Plant. When this facultative long-day plant is grown for 8 weeks under the short-day (8 h light/16 h dark) condition, the Arabidopsis plant sustains vegetative growth and grows very large compared to the long day (16 h light/8 h dark) grown plants (data not shown). In order to produce large quantities of secondary xylem tissues, we induced thick inflorescence stems by subjecting short-day grown plants to a brief long-day treatment. It is possible to obtain same-age plants with various stem heights by adjusting the long-day treatment period Fig. (6A) 5 to 10 d). The stem area located immediately above the rosette (basal level) was cross-sectioned by hand and stained with 2% phloroglucinol-HCl, which selectively reacts with cinnamaldehyde in the lignified secondary xylem cells. The red color staining in the interfascicular region was used as our primary estimation of the secondary xylem tissue. Since the parenchyma cells in the interfascicular region undergo lignification and form primary fibers that can be stained with the chemical Turner and Somerville, (1997), Lev-Yadun and Flaishman, (2001), we confirmed the wood formation in the stems by using confocal laser microscopy Fig. (6B). from the synchronized plants, we learned that the development of secondary xylem was correlated with the height of the plant Fig. (6A). Secondary xylem development did not occur in stems shorter than 10 cm, regardless of stem thickness.

Medeiros *et al*. (2013) stated that cambial zone refers to all layers of meristematic cells and their derivatives between the xylem and phloem. Therefore increasing cambial division leads to increased production of xylem biomass. Dié *et al*. (2012) stated that cell developing have different stages of both primary and secondary cell wall formation and lignification. Through primary growth stages, procambial cells promote upward growth of vascular tissue, Medeiros *et al*. (2013). Patterns of radial growth are positively correlated with the width of the cambial zone Pate *et al*. (2014), which varies among individuals of a species Dié *et al*. (2012). Pittermann (2010), Medeiros *et al*. (2013), Pate *et al*. (2014) reported that developing of Cambium can controlled by the interactions of phytohormones, such as auxins, gibberellins, cytokinins, and ethylene . Pramod *et al*. (2013) observed that low concentration of ethylene can have a stimulatory effect on cambial cell division in young shoot of white lead tree (Leucaena leucocephala (Lam.) de Wit.) . While low concentration of cytokinin caused the impaired cambial growth of poplar (Populus trichocarpa Torr. and A. Gray ex. Hook.) Nieminen *et al*. (2008). Atkinson, and Urwin, (2012), Wilkinson *et al*. (2010), stated that environmental factors could influence hormone levels and transport, Wilkinson *et al*. (2010) reported that developing of cambium might be indirectly affected; for example, drought reduces transport of cytokinins from root to shoot but increases transport of an ethylene precursor

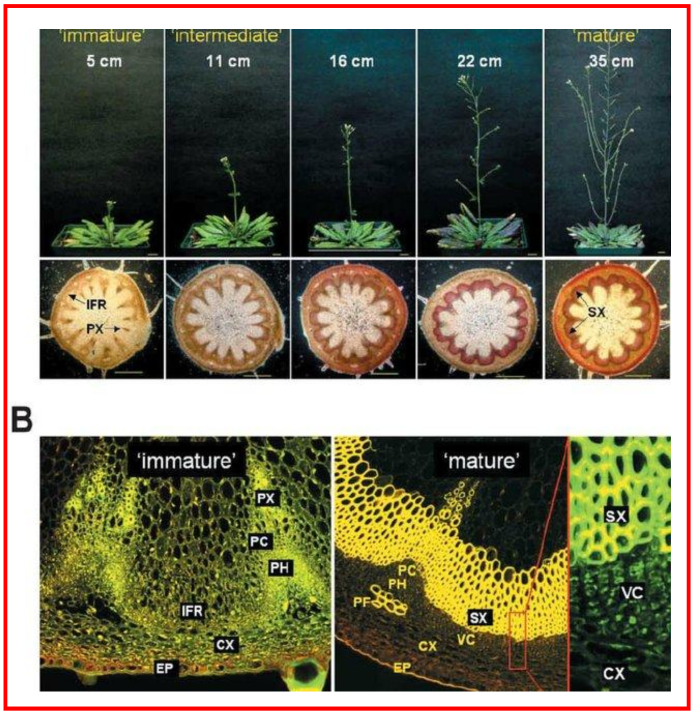


Fig. 6: Represents the secondary xylem tissue development of Arabidopsis stem. A, Secondary xylem development is related to the plant stem height. All plants are the same age (8 weeks old) and have similar stem thickness, but differ in the height growth of inflorescence stems. The heights of the stems are indicated in upper panels. Basal level of the stem was cross-sectioned and stained with 2% phloroglucinol-HCl to visualize secondary xylem as red color in the lower section. Scale bars represent 1 cm in upper sections and 0.5 cm in lower sections. B, Secondary xylem developed from vascular cambium of the mature Arabidopsis stem. Detailed structure of immature and mature stem cross-section was obtained from confocal laser microscopy (see ''Materials and Methods''). EP, epidermis; IFR, interfascicular region; PC, procambium; PH, phloem; PX, primary xylem; VC, vascular cambium; PF, phloem fiber; SX, secondary xylem. Bar indicates 0.2 mm of length.

2.3. Plant hydraulic conductance

Gradient of water pressure on the either side of the stomata for generating transpiration, and water from the soil into the roots without any energy (passively action). Pittermann (2010) reported that due to water lost by transpiration; hydraulic conductance is required to replace the adequate transpired water. Pivovaroff *et al*. (2014) calculated the hydraulic conductance for plant as water flow divided by the difference in pressure or water potential. Considering the relationship between transpiration and hydraulic conductance, anatomical gradually influence stomatal regulation can also affected. Buckley (2019) stated that stomatal responses to humidity, soil moisture and other factors that influence plant water status are critical drivers of photosynthesis, productivity, water yield, Ecohydrology and climate forcing, yet we still lack a thorough mechanistic understanding of these responses. Here I review historical and recent advances in stomatal water relations. Clear evidence now implicates a metabolically mediated response to leaf water status ('hydro active feedback') in stomatal responses to evaporative demand and soil drought, possibly involving abscisic acid production in leaves. Other hypothetical mechanisms involving vapor and heat transport within leaves may contribute to humidity, light and temperature responses, but require further theoretical clarification and experimental validation. Variation and dynamics in hydraulic conductance, particularly within leaves, may contribute to water status responses. Continuing research to fully resolve mechanisms of stomatal responses to water status should focus on several areas. Validating and quantifying the mechanism of leaf-based hydro active feedback, identifying where in leaves water status is actively sensed, clarifying the role of leaf vapor and energy transport in humidity and temperature responses, and verifying foundational but minimally replicated results of stomatal hydromechanics across species. Clarity on these matters promises to deliver modelers with a tractable and reliable mechanistic model of stomatal responses to water status. He also reported that Stomatal regulation consists of much more than guard cell signaling, however. It also involves tissue- and leaf-scale biophysical factors that translate guard cell function into changes in stomatal conductance (Fig. 7). For example, the water potential of guard cells may be affected by vapor exchange with relatively dry air within the stomatal pore channel Peak & Mott, (2011), or with relatively moist air in the airspaces between sun-warmed mesophyll cells Pieruschka *et al*., (2010). Water status may be actively sensed in guard cells Bauer *et al*., (2013), or in other tissues such as mesophyll McAdam & Brodribb, (2018) or phloem companion cells Endo *et al*., 2008), which experience different degrees of water stress. Understanding of stomatal function in intact leaves thus rests not only on guard cell biology, but also on features of leaf and plant biophysics such as fine scale gradients in temperature and water potential. Some of those features are poorly resolved. Some vary widely across taxa, and may therefore drive diversity in the ecophysiology of gas exchange and stress resilience. My objective here is to stimulate and focus progress on these issues. Summarizing the general features of plant water relations and stomatal function, in the context of longstanding theories of how stomata respond to humidity and drought. Then we discuss recent work and new ideas bearing on our understanding of how stomata in intact leaves respond to changes in soil moisture, evaporative demand, humidity, temperature and water transport. Finally, we identify several pathways for continuing research that are critical to enabling confident, mechanistic understanding of stomatal responses to water status in intact leaves

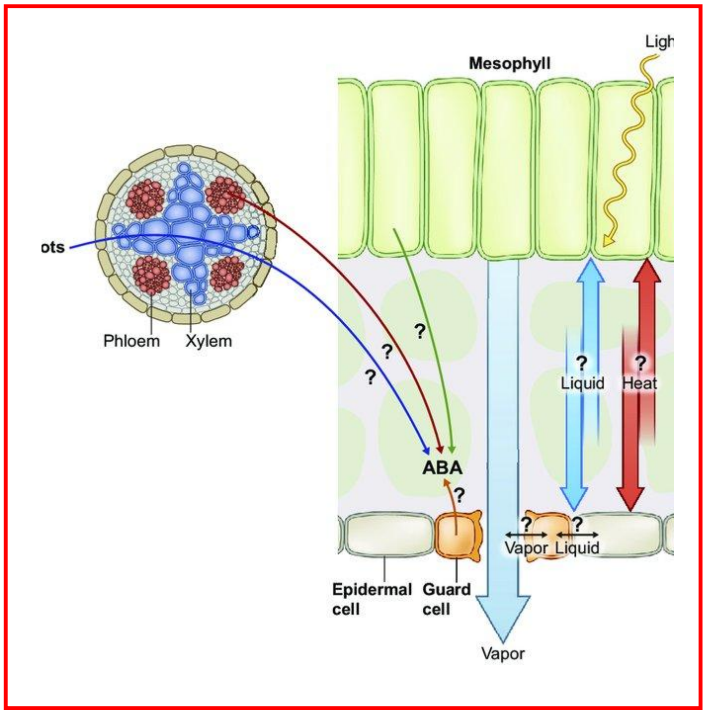


Fig. 7: Illustrates Stomatal conductance is regulated not only by guard cell biology, which governs guard cell osmotic content, but also by numerous biophysical factors that influence guard and epidermal cell water potentials and link these cells to other tissues across the leaf and plant. Abscisic acid and other signaling compounds may be synthesized in guard cells or synthesized elsewhere and transported to guard cells, but may have little impact on stomata in some species. The potential ABA source tissues are located at different positions along the soil-plant-atmosphere continuum, and are thus differentially sensitive to soil drought and evaporative demand. Guard cells may or may not exchange vapor with air in the stomatal pore channel and liquid water with epidermal cells , and heat and liquid water may move in either direction between the mesophyll and epidermis .After Buckley, (2019).

Buckley *et al*. (2015) stated that leaf anatomy parameters, can help and determine the sites of water evaporation and flow resistance patterns, and furthermore affect stomatal regulation, small variations in leaf water potential can affect stomatal regulation and water flow coordination. Recent work suggests that the transport of water vapour between mesophyll and epidermis may contribute to the regulation of stomatal movement Buckley *et al*. (2015), Pieruschka *et al*. (2010), Peak, and Mott (2011). Lignin content of cell wall consider as another factor influencing the hydraulic conductance. Pittermann (2010) observed that cell walls that contain a significant amounts of lignin, is required for structural support and affects water transport**.** Voelker *et al*. (2011) reported that xylem conductance was related to lignin content, decreasing lignin content gradually increased the xylem conductance in poplar (Populus spp.) Fig. (8), (9)

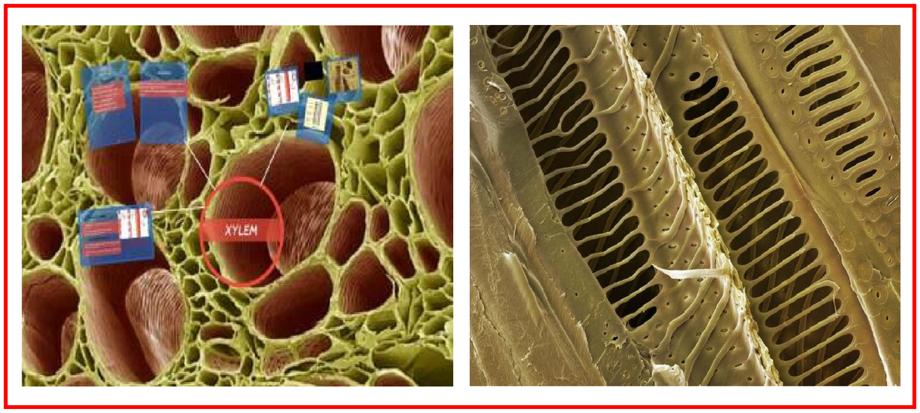


Fig. 8: Illustrates Xylem vessels showing the different patterns of lignification

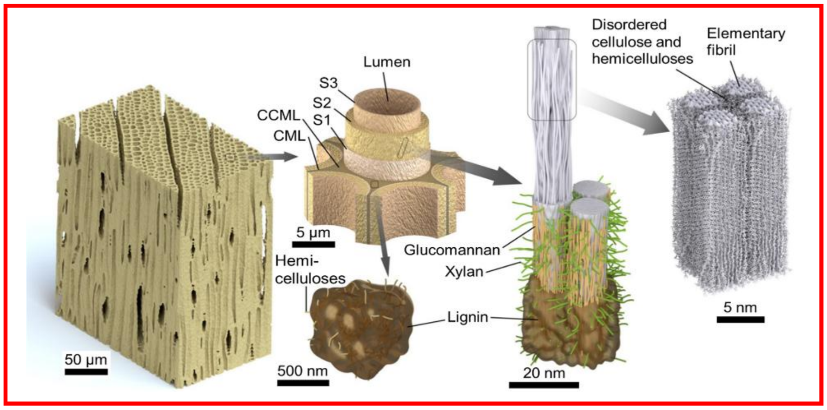


Fig. 9: Schematics illustrating the breakdown of softwood from the cellular to nanoscale. Secondary cell walls (S1, S2, and S3) are nanofiber reinforced composites of cellulose fibrils embedded in an organized matrix of amorphous cellulose, hemicelluloses (glucomannan and xylem), and lignin after Terashima (2009). Cellulose organizes into highly ordered elementary fibrils approximately 3nm across after Jakob *et al*. (1995), which organize into bundles that form microfibrils with amorphous polysaccharides between them after Fernandes (2011). Individual cells are adhered to each other by the compound middle lamella (CML), which is made of an open-cellular hemicelluloses structure encrusted with lignin after Hafren *et al*. (2000) At the corsners between multiple cells, the large volume of CML is termed the corner CML (CCML). After Joseph *et al*. (2020)

Meyer, and Peterson, (2011) stated that suberin, a fatty polymer, can influence the water movement which preventing water movement in the roots, due to layers of differentiated Casparian may prevented water movements . Such phenomena may impede horizontal water flow through the apoplastic pathway Steudle (2000); Fig. (10).

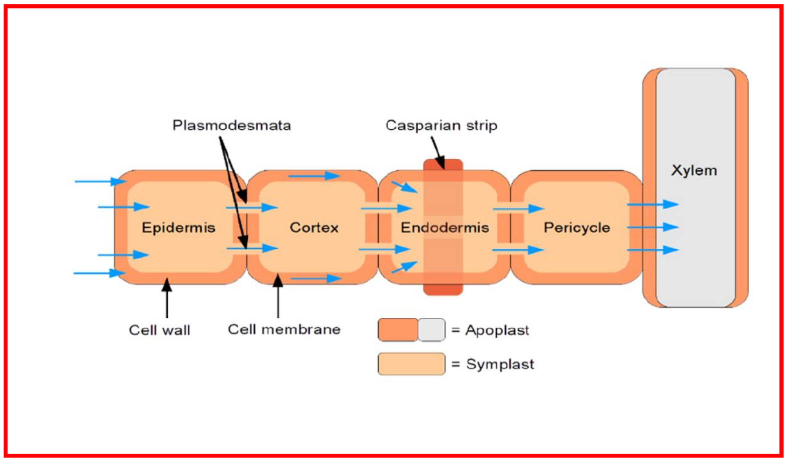


Fig. 10: Illustrates the diagram of symplastic and apoplastic water uptake by a plant root
The Casparian strips forces water into the symplast at the root endodermal

Their deposition is extremely specific Meyer, and Peterson, (2011) and may be controlled by environmental factors Okazaki, and Saito, (2014). Hydraulic conductance can be affected and disrupted due to climatic changes environmental factors, under extreme climate such as high temperature and drought, creating unsustainable level of xylem tension, leading to a process called cavitation breaking of water column Fig. (11) Jingmin *et al*. (2012). This leads to separation of air from water, resulting in a gas bubble called an embolism that blocks the conduit and prevents water movement Pittermann (2010).

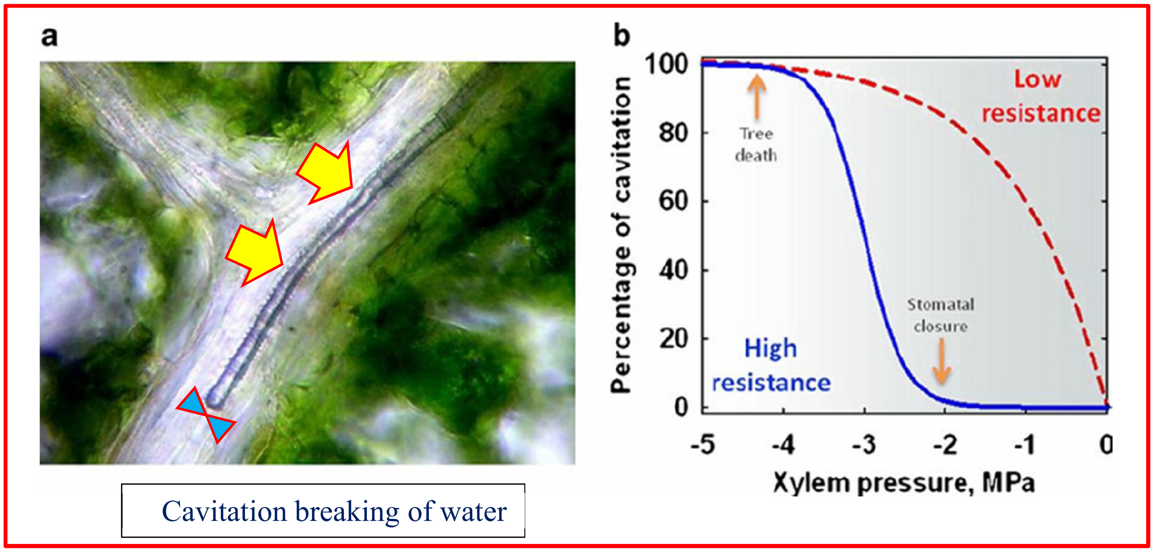


Fig. 11: Cavitation in plants. (**a**) Light micrograph showing an air bubble formed by cavitation in the vein of a walnut leaf. (**b**) Vulnerability curves showing the increase in cavitation with decreasing xylem pressure during drought. Cavitation was initially thought to occur only in conditions of intense drought stress after stomatal closure (plain blue curve). Studies carried out in the last decade suggested that cavitation might be much more common than previously thought (dashed red curve). However, this view should now be overturned as major biases have been reported with the techniques used in recent years. After Hervé Cochard and Sylvain Delzon (2013) (INRA, Clermont-Ferrand, France)

Hervé Cochard and Sylvain Delzon (2013) reporting that cavitation occurs as soon as xylem pressure falls below zero. Jacobsen and Pratt (2012) reported instance 50 % of cavitation at −0.16 MPa for Vitis vinifera cv. Glenora. These trees are thus routinely exposed to high levels of cavitation even when well watered (Zwieniecki and Holbrook 1998). As a corollary, cavitation was found to be rapidly repaired by a mechanism that remains a matter of debate Holbrook and Zwieniecki (1999). Under this low-cavitation-resistance paradigm, cavitation is seen as a process with beneficial effects on tree growth, possibly due to the release of water into the sap stream to sustain stomatal opening during the day. Drought tolerance may, therefore, be linked more to the ability of trees to repair cavitation than to their capacity to avoid cavitation in the first place. Clearly, our perception of cavitation resistance in trees has changed dramatically in the last decade. A phenomenon that was once thought to occur only in extreme conditions is now considered very common.

Jingmin *et al*. (2012) Sperry and Tyree, (1988), besides the tension-driven embolism, the freeze–thaw events can also lead to embolism; in this case, small gas bubbles are formed in the frozen liquid Fig. (12), (13). Stefan Mayr (2007) stated that freeze-thaw events could cause embolism in plant xylem. According to classical theory, gas bubbles are formed during freezing and expand during thawing. Conifers have proved to be very resistant to freeze-thaw induced embolism, because bubbles in tracheids are small and dissolve during thawing. In contrast, increasing embolism rates upon consecutive freeze-thaw events were observed that could not be explained by the classical mechanism. In this study, embolism formation during freeze-thaw events was analyzed via ultrasonic and Cryo-scanning electron microscope techniques. Twigs of *Picea abies* L. Karst. Were subjected to up to 120 freeze-thaw cycles during which ultrasonic acoustic emissions, xylem temperature, and diameter variations were registered. In addition, the extent and cross-sectional pattern of embolism were analyzed with staining experiments and Cryo-scanning electron microscope observations. Embolism increased with the number of freeze-thaw events in twigs previously dehydrated to a water potential of 22.8 MPa. In these twigs, acoustic emissions were registered, while saturated twigs showed low, and totally dehydrated twigs showed no, acoustic activity. Acoustic emissions were detected only during the freezing process. This means that embolism was formed during freezing, which is in contradiction to the classical theory of freeze-thaw induced embolism. The clustered pattern of embolized tracheids in cross sections indicates that air spread from a dysfunctional tracheid to adjacent functional ones.

Zwieniecki and Secchi (2015). Moreover, pathogen infection can changes in sap chemistry and can induce embolism Fig. (14) Brodersen, and Mc Elrone, (2013). All these stress conditions increase the frequency of embolism, leading to decreased plant productivity Zwieniecki, and Secchi (2015). In order to cope with embolism, plants can re-route water through nearby xylem, create new xylem Pittermann (2010), Jingmin *et al*. (2012) or refill vessels to force the air bubbles to dissolve in water Brodersen *et al*. (2010). Refilling requires hydraulic isolation from tensions, which prevent embolism repair; as shown hydraulic conductivity in the xylem can be, restored in the presence of tensions in the bulk xylem Brodersen *et al*. (2010). Aquaporins also play a role in the repair of embolism during its refilling Kaldenhoff *et al*. (2008), Chaumont, and Tyerman, (2014), Hachez *et al*. (2013), Martínez-Ballesta (2014). Pittermann (2010). Pratt *et al*. (2015), reported that the failure to fix embolism can resulted in reducing both hydraulic capacity, limited photosynthesis, or sometimes runaway embolism and even plant death particularly under extreme drought conditions Klein *et al*. (2018).

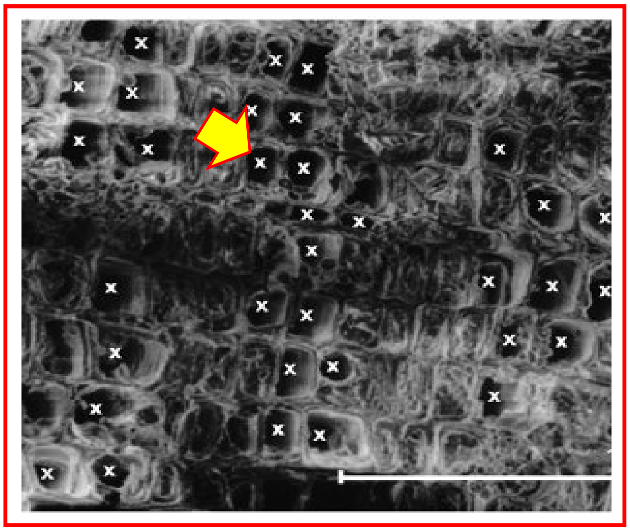


Fig. 12. Cross-section of P. abies twigs dehydrated to a c of 22.8 MPa and exposed to 60 freeze-thaw cycles. White crosses mark-embolized tracheids. After Stefan Mayr (2007).

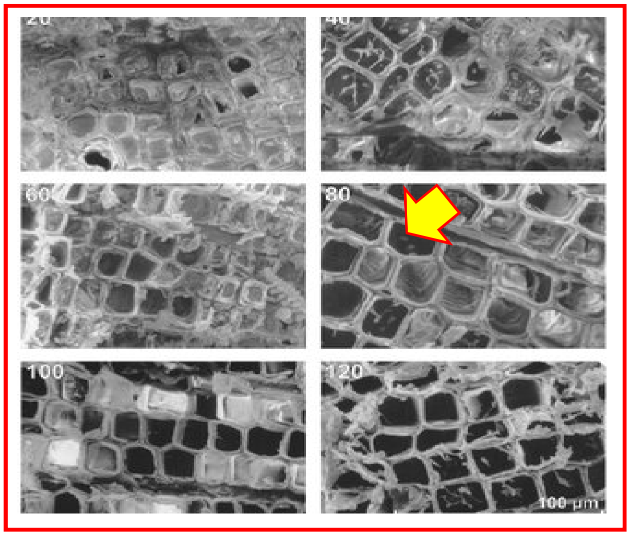


Fig. 13: Illustrates Cryo-SEM analysis of P. abies twigs dehydrated to a c of22.8MPa and exposed to consecutive freeze-thaw cycles. The number of freeze-thaw cycles is indicated at the top of each photo. In cross sections, empty tracheids appear black, while intact tracheids are ice-filled .After Stefan Mayr (2007)

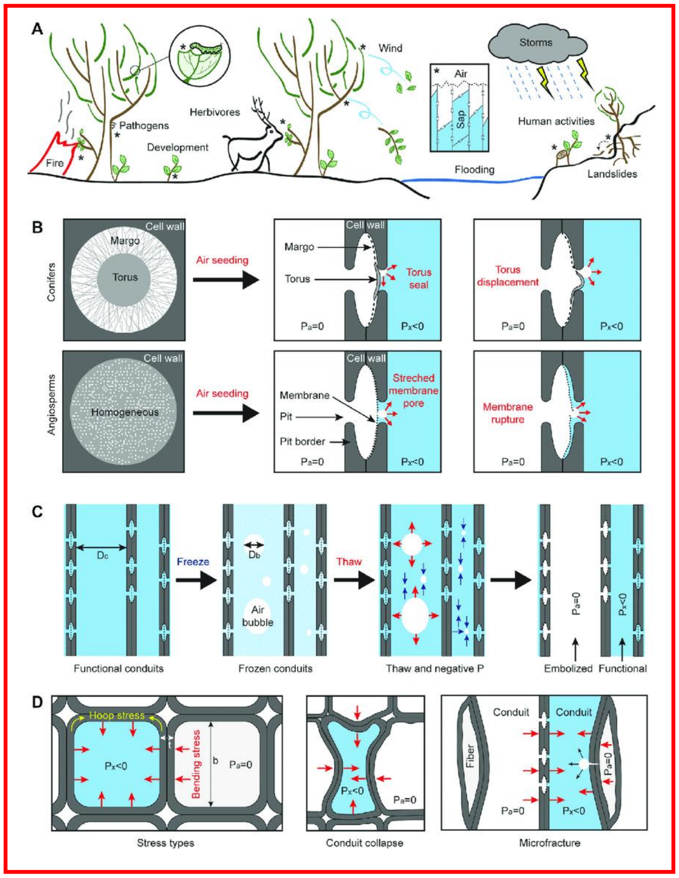


Fig. 14: Illustrates the mechanisms of xylem dysfunction (A) Mechanical damage and xylem rupture and exposure to air is something that plants face commonly due to storms, wind, herbivores, pathogens, fires, landslides, floods and human activities among many other factors. Inter-conduit pits arrest the leakage of air (insert). (B) Air-seeding mechanism under drought stress conditions for conifers and angiosperms. The pressure difference (DP) between an air-filled conduit (Pa? 0) and a contiguous functional sap filled one (P x < 0) causes the pit membrane to be deflected against the bordered pit wall of the functional conduit. In conifers air is aspirated into the functional conduit when DP is greater that the pressure that can be sustained by the torus-bordered pit seal or when DP is large enough to displace the torus. After Martin *et al.* (2017).

3. Impact of climatic changes on plant water status

Climatic changes have common impact on plants, including growth inhibition, decreasing photosynthesis, hormone fluctuations, and accumulation of stress-related compounds. Imbalance between water uptake in roots and water loss through leaf transpiration related to the environmental factors such as drought. Aroca, *et al* (2012) stated that local weather extremes holding the highest impact on plant survival and productivity. Physiological function of xylem is highly vulnerable as tree survival always depending on their ability to sustain water supply for crown particularly under variable environmental conditions. Zwieniecki, and Secchi (2015) reported that stomatal is the first line of defense against drought stress, both stomatal conductance and water transport are affected to each other, furthermore changes on plant photosynthetic processes. Patel *et al* (2014), Köcher *et al* (2012) stated that climatic changes have an important effect on the initiation and differentiation of vascular cambium. Humidity and rainfall are the most important factors for rate of cambial cell division and, xylem development, which related to temperature. Higher rainfall leads for reactivation of cambial these processes are negatively correlated with temperature. Cambial activity of woody plants is very sensitive to water deficits and drought that decreases or delays cell division of vascular cambium by reducing turgor pressure of cambial cells, leading to reduced plant growth Patel *et al.* (2014). Environmental stress can be increased by accumulation of metabolites, such as glycinebetaine Kurepin *et al.* (2015). It is important to understand the components and role of climate change, for affecting the growth, vascular systems, and water status of plants.

3.1. Temperature their effect on plant physiology

Lobell and Gourdji (2012) stated that photosynthesis and water use efficiency (WUE) are gradually decreased by increasing the air temperature, however transpiration and stomatal conductance were increase, creating a shorter growth period and faster development. At short-term in C_3 plants, are increases in air temperature and affecting the photosynthesis by altering either the catalytic properties of Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) or the ratio between CO_2 and O_2 at Rubisco active sites, resulting in increased photorespiration Fig.(15).

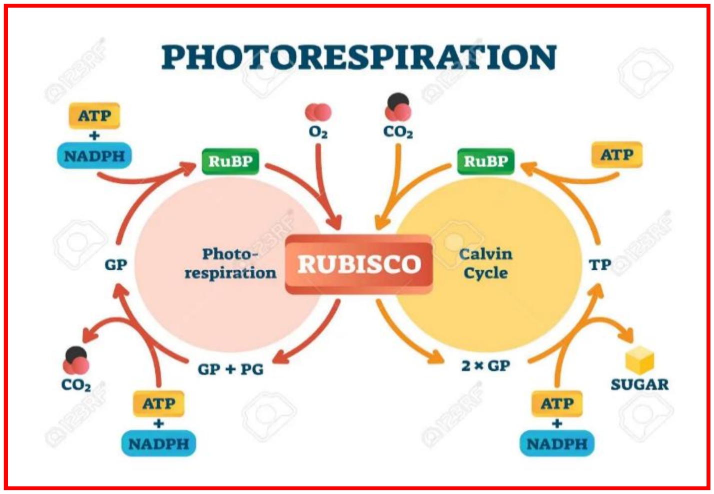


Fig. 15: Illustrates the key enzyme of Ribulose-1, 5-bisphosphate carboxylase/oxygenase, known by the name Rubisco, which responsible for photosynthetic and chemoautotrophic carbon fixation and oxygen metabolism.

Plants under thermal acclimation, can adapting through shifting their photosynthetic temperature optimum and maximizing photosynthesis at higher growth temperatures, but increasing temperature may damage the photosynthetic apparatus Flexas *et al*. (2014), or increase transpiration to an extent where it leads to drier soils in already water-limited habitats Gunderson *et al*. (2010) Fig. (16).

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is Earth’s most abundant enzyme, used by autotrophic organisms to convert CO_2 into organic compounds via the Calvin-Benson pathway Andersson and Backlund, (2008). Rubisco catalyzes photosynthetic carbon reduction and photo respiratory carbon oxidation upon reaction with its substrates riboluse-1,5-bisphosphate, and CO_2 or O2, respectively. The poor catalytic properties of Rubisco CO_2 fixation necessitate a high abundance of this enzyme. Hence, Rubisco constitutes ~30–50% of the soluble protein in C3 plant leaves Feller *et al*., (2008); Phillips and Milo, (2009) Fig. (17).

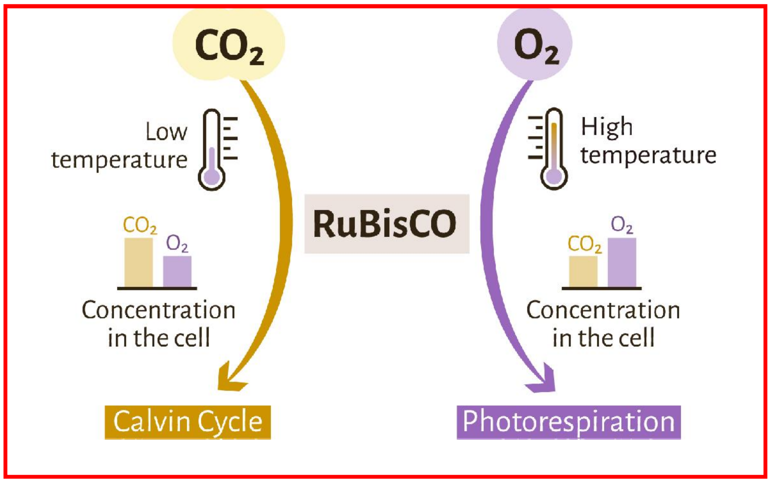


Fig. 16: Illustrates air temperature, that affect the photosynthesis through altering either the catalytic properties of Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) or the ratio between CO_2 and O_2

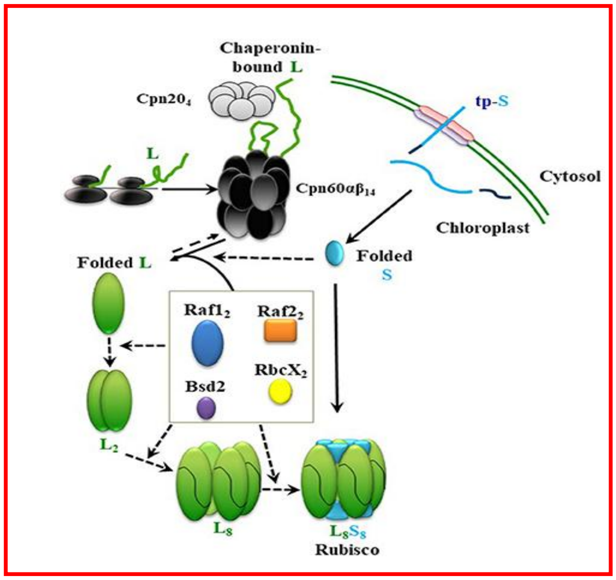


Fig. 17: Model summarizing the roles of different chaperones in Rubisco assembly. From top; Newly-synthesized RbcL (L) interacts with the chaperon in complex, which leads to correct folding (Native L). After import into chloroplast and cleavage of its transit peptide, RbcS (S) folds spontaneously, or with the help of a chaperone. Raf1, Raf2, RbcX, and Bsd2 form dynamic intermediates with the folded RbcL. RbcS subunits could either displace the chaperones in a final chaperone-RbcL intermediate to form the holoenzyme (L8S8), or interact with chaperones and RbcL in earlier stages of the assembly. Continuous and dashed arrows indicate certain and speculative nature of each step, respectively.

This enormous investment of energy, water and nitrogen limits biomass and crop yields Since all biomass results from the act of Rubisco in photosynthesis, increasing crop yields ultimately depends on improving the efficiency of carbon fixation. Although the catalytic performance of bacterial and archaeal Rubisco was successfully enhanced Durão *et al*., (2015), Wilson *et al*., (2016), efforts to engineer a more catalytically efficient plant Rubisco remain unsuccessful Parry *et al*., (2013). Consequently, not only has Rubisco become an intriguing model for studying protein folding and assembly, but also, elucidating the process of its biogenesis should allow researchers to improve its efficiency. In order to engineer plant Rubisco or transplant a more productive version into hosts of agricultural or biotechnological interest, this protein should be viewed as a multi enzyme complex, in which all the parts work together and cannot be excluded John Andrews and Whitney, (2003); Erb and

Zarzycki, (2018). This review focused on what is known about the folding and assembly of plant Rubisco. The chloroplast system supporting Rubisco biogenesis is unique in its complexity and only the precise orchestration of folding and assembly leads to functional protein.

Yamori *et al*. (2012) stated that plants acclimation resulted in increased stability of photosystem membrane, expression of heat-stable Rubisco enzymes, and production of heat-shock proteins. Flexas *et al*. (2014) reported that decreasing in both respiration and stomatal conductance were noticed by a decline in intercellular CO_2 .Increasing temperatures are expected to increase respiration and photorespiration, but minimized through acclimation or even down-regulation of photosynthetic capacity Flexas *et al*. (2014). Buckley (2015) stated that high temperature gradually increasing both outside-xylem hydraulic conductance and mesophyll conductance Flexas *et al*. (2014), increasing gas-phase conductance Buckley (2015), that can sustain turgor pressure within guard cells and increasing the transpiration rates Buckley *et al*. (2015). Dhirendra Singh *et al*. (2011) , Swidrak *et al*. (2014) Begum *et al*. (2013), Prislan *et al*. (2013) reported that in seasonal climates, temperature may play an essential role in vascular development of woody plants through stimulation of cambial activity, as earlier warming of temperature induces an earlier onset of the growth season . Cufar *et al*. (2011) reported that increasing temperature of at least 6–8^{-0C} at the onset of the growing season stimulates xylogenesis, however formation of phloem, requires lower temperature as compared to xylem cells, Swidrak *et al*. (2014), Prislan *et al*. (2013). Dhirendra Singh *et al*. (2011), Begum *et al*. (2012) stated that In woody plants, higher temperature can increase Khasi pine or decrease Momifir tracheid diameter, depending on the species . Increasing diameter of xylem vessel or tracheid gradually increases and stimulate the efficiency of water transport Pittermann (2010). Begum *et al*. (2012) reported that earlier cambial activity, at temperature warming, may be positive and results in increased wood biomass production and water transport efficiency, and also be at greater risk from frost damage if there are any sudden drops in temperature after the initial early spring warming . In herbaceous plants, such as potato, increasing temperature lead to enlarge and deform vessel cells and improper phloem division. These changes can reduce crop yields due to enlarged xylem negatively affects the phloem by putting mechanical pressure on its cells, resulting in decreasing the translocation of sugar Paul *et al*. (2017), De Schepper *et al*. (2013). Plants under extreme heat stress can be susceptible to vascular damage. Typically, plant cells have a threshold temperature, after which vascular cell death is observed; however, cell death can also occur due to prolonged heat stress at a level below the threshold Dickinson *et al*. (2004). Heat stress can increase vulnerability to cavitation by changing sap surface tension and deforming conduit cell walls Michaletz *et al*. (2012). Qaderi *et al*. (2006) reported that plants with thicker epidermis or stem diameter could be protected from damage to their vascular bundles under high temperature conditions Fig. (18).

3.2. Carbon dioxides, their effect on plant physiology

Several researchers Pittermann (2010). Qaderi and Reid, (2008), Qaderi *et al*. (2013), Perry, *et al*. (2013), Abrams (2011), reported that carbon dioxides (CO_2) stimulates plant growth, and protects the negative effects of environmental stressors. Elevated CO_2 can gradually decreases stomatal conductance, alters capacity for carboxylation. Buckley (2015), Medeiros *et al*. (2013), Perry, *et al*. (2013),they reported that CO_2 resulted in accumulation of photo assimilates Reddy *et al*. (2011), Abrams (2011), it also increased water potential and reducing the transpiration stream, higher WUE, and increased the resistance to cavitation Fig. (19).

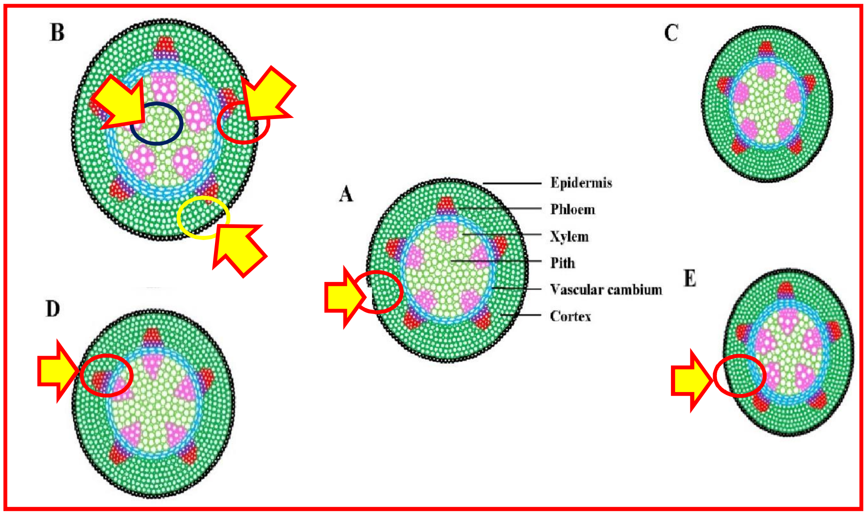


Fig. 18: Predicted interactive effects of higher temperature, elevated CO_2, and drought stress on plant vascular system. (**A**) Control (lower temperature, ambient CO_2, no drought), (**B**) higher temperature with elevated CO_2, (**C**) higher temperature with drought stress, (**D**) elevated CO2 with drought stress, and (**E**) higher temperature with elevated CO_2 and drought stress. For higher temperature with elevated CO_2, increased xylem diameter and density, increased cell wall thickness and cambial thickness, and increased stem diameter are expected. For higher temperature with drought stress, decreased xylem diameter and density, maintained cambial thickness, increased cell wall thickness, and decreased stem diameter are anticipated. For elevated CO_2 with drought stress, decreased xylem diameter and density, maintained cambial thickness, increased cell wall thickness, and stable stem diameter are expected, unless DS becomes extreme, in which case it may decrease. In the instance of higher temperature with elevated CO_2 and drought stress, increased vessel wall thickness, increased cambial thickness, and decreased stem diameter are expected, illustration is based on data from the literature. After Qaderi *et al*. (2019)

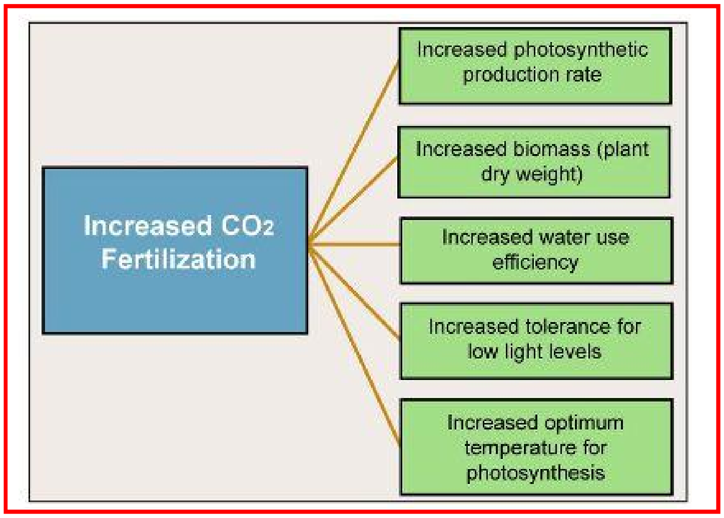


Fig. 19: Conceptual diagram outlining important plant responses to higher concentrations of CO_2 in the atmosphere.

Plants grown under elevated CO_2 have a higher transpirational demand and reduction of prediction into plant cell walls Medeiros *et al*. (2013). Overall, carbon dioxides (CO_2) assimilation is expected to increase to a certain extent because of increased atmospheric CO_2 concentration. Increasing will occurred either as a result of increased CO_2 available for the Rubisco active site or decreasing the transpiration Pérez-López *et al*. (2012). In response to increasing atmospheric CO_2, stomatal conductance, is often reduced which increases water use efficiency WUE, Flexas *et al*. (2014), casing an increase of leaf temperature, furthermore increasing water transport through the transpiration stream. Elevation of CO_2 stimulate root architecture the belowground biomass, allowing for greater water uptake, in addition to a reduction in stomatal density in plants with passive stomatal control Haworth *et al*. (2013), Medeiros *et al*. (2013), Reddy *et al*. (2011). In short term experiments, it was noticed that elevated of CO_2 generally increases photosynthesis and decreases transpiration, however long term exposure of CO_2, photosynthetic processes were acclimate. Carbon dioxides CO_2 can offset the negative effects of decreased Rubisco activity; as such, photosynthetic acclimation typically that leads to a decrease photosynthetic capacity as opposed to activity Pérez-López *et al*. (2012)]., Alfonso *et al*. (2012) Fig.(20),(21).

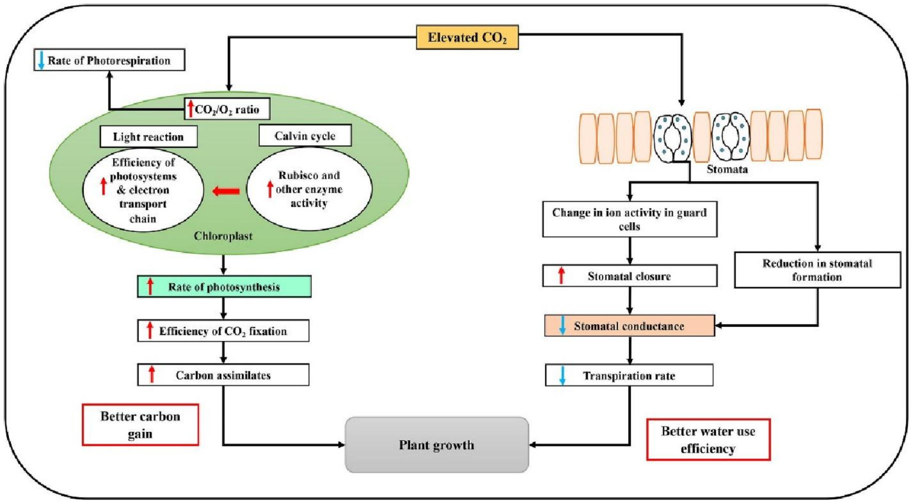


Fig. 20: Illustrates the effects of CO_2-induced photosynthesis and stomatal conductance on plant growth responses (Green circle = chloroplast; orange squares = epidermal cells; half circles = stomata; red arrow denotes an increase; and blue arrow denotes a decrease).After Dananjali Gamage *et al*. (2018).

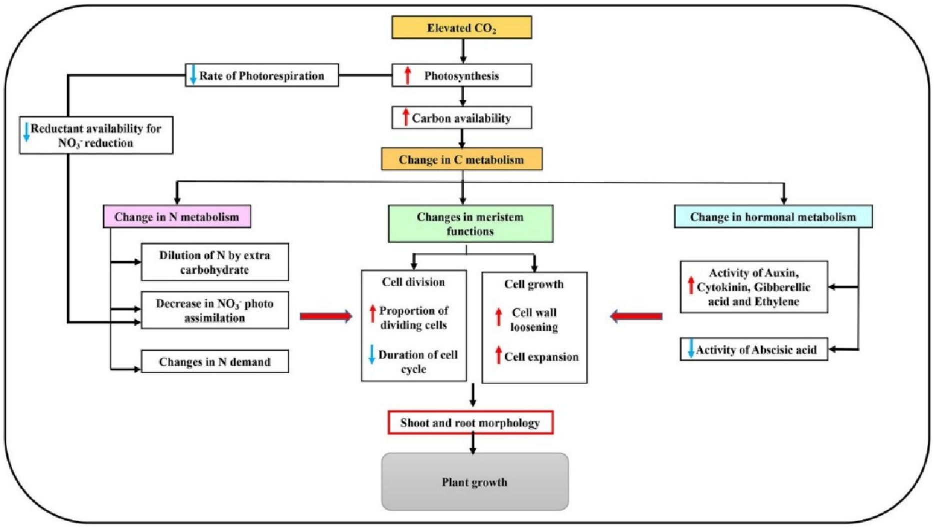


Fig. 21: Effect of increased carbon supply at elevated [CO_2] on other cellular processes and plant growth responses (C = Carbon; N = Nitrogen; NO3 − = Nitrate; red arrow denotes an increase; and blue arrow denotes a decrease). Dananjali Gamage et al. (2018).

Dananjali Gamage *et al.* (2018) stated that elevated [CO_2] directly and/or indirectly affects plant growth and development by modifying a range of physiological processes. Plant growth at e [CO_2] changes due to the immediate effects of e [CO_2] on photosynthesis and stomatal conductance Ainsworth *et al*., (2008); Drake *et al*., (1997); Seneweera & Conroy, (2005); Fig. (20). On the other hand, plant growth at e [CO_2] also depends on the post-photosynthetic process that may lead to changes in carbon and nitrogen metabolism, changes in cell cycle properties, and hormonal metabolism as a result of increased supply of carbon to the growing shoots and roots under e[CO_2] Fig.(21). Increasing in photosynthetic carbon assimilation could be offset by changes in investment in photosynthetic proteins because of foliar adjustments to plant carbon and nitrogen metabolism at e [CO_2]. Most of the research has tended to focus on changes in photosynthesis and stomatal conductance in response to e [CO_2] whereas very less attention has been paid to variations in other cellular mechanisms that may moderate plant growth response to e [CO_2]. Changes in carbon and nitrogen metabolism, cell cycle properties, and hormonal metabolism together with source-sink optimization at e [CO_2] are significant and largely determine the growth responses of plants to e [CO_2] Seneweera *et al.* (2003); Taylor *et al.* (1994). Holistic changes of these processes are complex, closely interrelated, and determine the growth responses by differential allocation of resources to shoot and root depending on the environmental conditions. A thorough understanding of these processes and their association with high carbon input will advance our knowledge of the mechanistic basis of differential plant phenology observed at e [CO_2]. They reported that stomatal conductance is mainly controlled by the size of the stomatal aperture Ainsworth and Rogers, (2007); number of stomata per unit of leaf area Casson and Gray, (2008); Casson and Hetherington, 2010); and water transport capacity of the guard cell Leakey *et al*., (2009). Stomatal conductance is decreased in crops exposed to e [CO_2] Ainsworth and Long, (2005); Leakey *et al*., (2009); Fig. (21), the size of the stomatal aperture is mainly determined by the turgor pressure of guard cells, which is mediated through ion concentration Araújo *et al*. (2011). It is reported that e[CO_2] increases the activity of outward rectifying K^+ channels relative to that of inward rectifying K^+ channels, causing stomatal closure Brearley *et al.* (1997). Elevated [CO_2] also stimulates Cl^- release from guard cells and increases Ca^{2+} concentration within them Brearley *et al*., (1997); Webb *et al.* (1996). These changes help to depolarize the membrane potential of guard cells causing stomatal closure Hanstein and Felle, (2002), which is very common under e [CO_2]. It has also been demonstrated that e [CO_2] increases the concentration of malate, the effector mediating flux flow between CO_2 and these anion channels Hedrich *et al*., (1994). Modified malate concentrations under e [CO_2] enhance the activation potential of anion channels, thus indirectly influencing stomatal closure. Because e [CO_2] is known to promote anion channels, attempts have been made to identify genes encoding guard cell anion channels. Stomatal guard cell responses to e [CO_2] are also driven by multiple signalling components associated with guard cell activity. Because e [CO_2] is known to promote anion channels, attempts have been made to identify genes encoding guard cell anion channels. As a result, SLAC1 (Slow Anion Channel Associated 1) was identified in Arabidopsis thaliana that encodes a protein mediating CO_2 induced stomatal closure through regulating S-type anion channels Laanemets *et al*., (2013); Negi *et al*., (2008); Vahisalu *et al*., (2008). The gene OST1 activates SLAC1 (open stomata 1) that is a SNF-1 related protein kinase 2, a positive regulator of CO_2-induced stomatal closure Lind *et al*., (2015); Merilo *et al*., (2013). Activation of OST1 is triggered by abscisic acid (ABA) signalling at e[CO_2] involving PYR/RCAR family of ABA receptors Chater *et al*., (2015); Merilo *et al*., (2013); Merilo *et al.* (2015). In another study, Yamamoto *et al.* (2016) showed that SLAC1 channel perceives CO_2 signals by an ABA-independent pathway in a transmembrane region of the guard cells. In addition, it has been reported that other phytohormones such as jasmonic acids are altered at e [CO_2]. Jasmonic acid is known to play a significant role in mediating stomatal closure at e [CO_2] Geng *et al*., (2016). A very recent study by He *et al.* (2018) revealed that a novel allele of the Arabidopsis BIG locus named cis1 is involved as a signalling component responsible for controlling stomatal aperture at e [CO_2]. Further, they indicated that loss of BIG function compromises activation of guard cell S-type anion channels by bicarbonate at e [CO_2].

Therefore, plants grown at elevated CO_2 have a decreased ability to meet water demand through xylem water transport Medeiros *et al.* (2013). Haworth *et al.* (2013), they stated that high concentrations of CO_2 (1500 µmol mol^{-1}), decreased the stomatal aperture and stomatal conductance particularly in royal fern (Osmunda regalis L.). However did not show in other species due to some of these response, may have different levels of acclimation Flexas *et al.* (2014) in FACE (free-air CO_2 enrichment) experiments using soybean (Glycine max (L.) Merr.) . Some evidence suggests that woody plants may have reached a saturation level of CO_2 Körner (2003), whereas other studies have predicted a positive effect of CO_2 on plant growth and development Flexas *et al*. (2014)], Haworth *et al*. (2013), Medeiros *et al*. (2013), Abrams (2011). Increased hydraulic demand may result in larger conduits, higher conduit density, or greater xylem size in reference to stem cross-sectional area. When grown at elevated CO_2, plants have been shown to have larger xylem conduits than those grown at ambient CO_2, with a reduced ratio of conduit wall thickness to diameter Medeiros *et al*. (2013). This may be beneficial because increased conduit diameter results in a four-fold increase in leaf transpiration and water supply. On the other hand, larger leaf area with thinner leaves and larger stomata Medeiros *et al*. (2013) could increase vulnerability to cavitation, as insufficient carbon supply may lead to increased conduit membrane porosity and likelihood of air entry Rico *et al*. (2013). Elevated CO_2 is likely to result in greater fortification of xylem conduits via an increase in double wall thickness Domec *et al*. (2017), and, in order to reduce sensitivity to other environmental stress factors, plants can develop more robust pit membranes to reduce vulnerability to embolism Rico *et al*. (2013). In woody plants (e.g., Norway spruce), elevated CO_2 decreases the concentrations of soluble sugar, acid-soluble lignin, and nitrogen Kostiainen *et al*. (2004).

Drought their effect on plant physiology

Alfonso *et al*. (2012) stated that drought phenomena might inhibited photosynthetic through leaf senescence, reduced growth, and feedback inhibition of photosynthetic enzymes. Besides along with initial processes, such as stomatal closure, which occurs as one the earliest responses to drought, reported by Flexas *et al*. (2002). because of drought stress, water associated with carbon fixation have a negative tradeoff of plants either dehydrate or reduced the rate of carbon fixation, creating carbon starvation Zwieniecki, and Secchi (2015). Plants can be considered under drought stress when the soil water content is not replenished by either rainfall or irrigation Aroca *et al*. (2012). Under circumstances drought stress, stem hydraulic capacitance, transpiration and root water uptake begin to decline Aroca *et al*. (2012), Salomón *et al*. (2017). Conductance will declines of root hydraulic as soil water content diminishes, roots lack sufficient water supply. Moreover, root hydraulic conductance decreases, and the Casparian band potentially reduce the backflow of water from root to soil Aroca *et al*. (2012). Under such condition photosynthesis will reducing rapidly when stomatal is closed subsequently a reduction of carbon fixation and supply of carbon to chloroplasts and Rubisco active sites Qaderi *et al*. (2006) Centritto *et al*. (2011) and Alfonso *et al*. (2012). Drought stress can accelerates the loss of hydraulic conductance and, in turn, to the desiccation of aboveground tissues and plant mortality Martínez-Vilalta *et al*. (2014). Drought stress also may reduce vessel diameter while maintaining vessel density, hydraulic conductance, and conductive area Pinto *et al*. (2012). Precipitation is one of the essential factors for the formation of late wood in many ring-porous trees Cufar *et al*. (2011). During the dry periods a study showed that in Ivory Coast there were no developing cambium cells in teak tree (Tectona grandis (L.f.) Kuntze).However at the beginning of the rainy season, cambial cells began to swell ,and phloem cells was started to division before xylem cells, after that xylem cells stating for expand and differentiated Dié *et al*. (2012). Cufar *et al*. (2011), reported that study on chestnut (Castanea sp.) indicated that production of new xylem and phloem still happened, regardless of an extremely hot and dry month, suggesting there are differences among species. Variation of climatic responses may cause shifting in cambial activity. Therefore drought can suppress cambial cell division and inhibits turgor-driven cell enlargement Swidrak *et al*. (2014). Under dry conditions, plants increase suberization of root apoplastic, which is important for water retention, increased in the endodermis whereas decreasing in the sclerenchyma, cells as observed in rice plant Henry *et al*. (2012). Increasing suberization is observed under a number of stress conditions Lynch *et al*. (2014). In the drought-sensitive cultivars of grapevine, more rapid root suberization occurs even under control conditions, as opposed to root suberization in drought-insensitive cultivars of grapevine Fig. (22).

Barrios-Masias *et al*. (2015) stated that suberization could occurred closer to the root tip in both cultivars, particularly under drought stress, indicating that a faster maturation of root tissue. Hydrotropism phenomena resulted in deeper roots, with access to deep water Eapen *et al*. (2005). Under deep water when it is available, plants make adaptation for longer root systems with increasing root and their density network in order to increase the capacity for water transport from soil to shoot Pinto *et al*. (2012) Fig. (22). Drought can also affected other vascular characteristics of trees, such as pit membrane structure, conduit size, and wood density Zwieniecki, and Secchi (2015). Under dry condition plant can adapt by create smaller pits with thicker and less porous membranes Zwieniecki, and Secchi (2015).

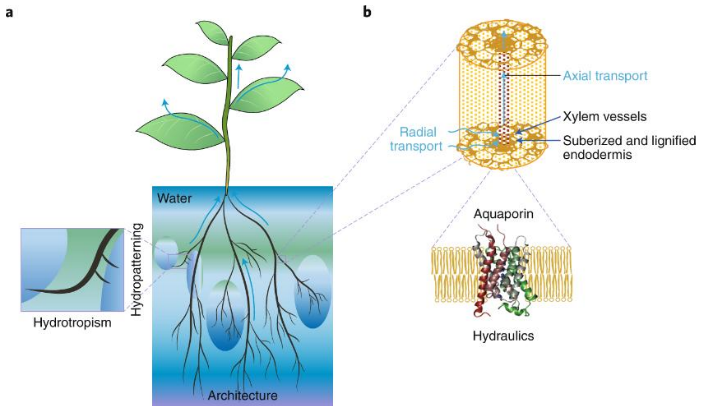


Fig. 22: Illustrates the water uptake capacity of a root system is determined by both its architecture and hydraulics. **(a)** The root system architecture is determined in part by soil water availability, which can be highly heterogeneous depending on soil layers. As shown in the inset, these local heterogeneities can orientate root tip growth (hydrotropism) and lateral root formation (hydro patterning). Dark blue colouring indicates water-rich soil zones, whereas light blue/green colouring indicates water-deprived soil zones**. (b)** Water uptake can be decomposed in radial water transport, from the soil to the root stele, and axial transport along the xylem vessels. Aquaporins, which contribute to transcellular water flows during radial transport, determine largely the root hydraulic conductivity. Suberized and lignified endodermis or exodermis (not shown) can also affect radial transport .After Christophe Maurel and Philippe Nacry (2020)

Christophe Maurel and Philippe Nacry (2020) stated that roots fulfil their anchoring and foraging functions through continuous growth and branching, thereby producing a highly complex and specialized network: the so-called root system architecture (RSA) Fig.(22 1a). Experimentally, RSA can be defined by length (depth) of the main root(s), the density and elongation of lower order roots, their gravitropic set-point angle and the possible presence of crown roots or adventitious roots. A large body of research has addressed the elementary mechanisms that determine each of these individual traits and emphasized the role of hormones, including auxin, abscisic acid (ABA), cytokinins and ethylene Jung, and McCouch (2013)– Lavenus (2013). Other studies have addressed the adaptive significance of varying RSA. In a search for root ideotypes that could provide cereal crops with an adaptive advantage under drought, deep rooting has been proposed as a key trait as it permits access to unexploited water resources when the soil surface desiccates Lynch (2013). Yet this ideotypes may not be optimal for quick recovery after drought in seasonal precipitation regimes16 or for acquisition of nutrients, such as phosphate Shahzad and Amtmann (2017). One initial approach to investigate the role of roots during drought consisted of searching for correspondences between quantitative trait loci (QTLs) for specific root morphological traits and whole-plant performance under water deficit Tuberosa, (2002), Ruta, *et al*. (2010). In grasses, for instance, suppression of crown roots was found to promote drought tolerance Gao, and Lynch (2016), Sebastian (2016). In addition, plant geneticists have recently succeeded in cloning such critical genes as rice *DEEPER ROOTING 1* (*DRO1*), which determines root growth angle and thereby enhances rice performance under drought by favouring deep rooting Uga,(2013). A natural variation approach, but in *Arabidopsis*, led to identification of EXOCYST70A3, an exocyst factor that also interferes with root growth orientation and root system depth by acting on expression of auxin efflux carriers in the root tip Ogura (2019). Although the two studies point to the central role of auxin in regulating RSA, they identify opposite and species-specific strategies for soil exploration under water deficit. More generally, much of the physiological and genetic components that shape the adaptive value of RSA under natural conditions are as yet unknown. To address these, elaborate time-lapse three-dimensional imaging and mathematical modelling approaches are under development to capture the great complexity of RSA as well as its intra- and interspecific variations Jiang, (2019), Rellan-Alvarez *et al.* (2016). Water uptake is not simply a matter of root growth: it is also critically determined by the intrinsic water transport capacity of the roots; that is, their hydraulics Fig.(22 1b). Water is first transported radially from the soil to the stele through concentric layers of root cells, loaded into xylem vessels and then transported axially up to the shoots. Our biophysical and physiological understanding of these processes has made significant progress in the last two decades Maurel, (2015), Bramley *et al.* (2009). Molecular physiological studies have shown that water channel proteins named aquaporins facilitate water diffusion across cell membranes and therefore contribute to cell-to-cell transport Maurel, (2015) Hachez *et al.* (2006). Yet many other components of root hydraulics are to be discovered. For instance, the crucial role of lignified and suberized barriers differentiated in the walls of exo-and endodermal cells has long remained elusive but can now be explored using genetic materials recently arising from sharp molecular dissection of these barriers Barberon, (2016).

Anatomical of xylem show that trees can adapted against drought stress. Drier conditions resulted in larger tracheid lumens, thicker cell walls, and a greater number of ray tracheid is, furthermore increasing efficiency of water transport Zwieniecki, and Secchi (2015), Martín *et al.* (2010).

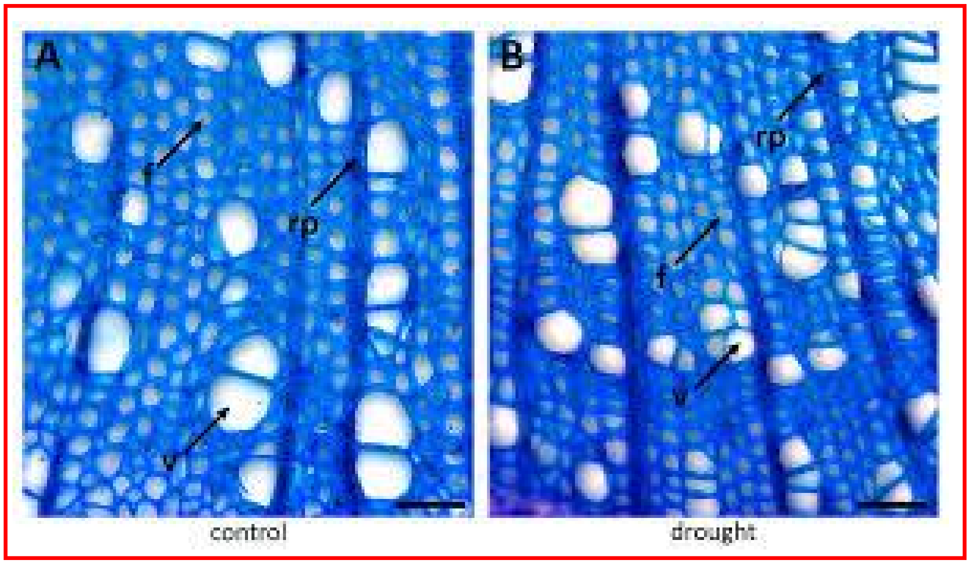


Fig. 23. Comparison of non-stressed (**A**) and drought-stressed (**B**) xylem tissue of Populus tremula x tremuloides. B shows vessels with reduced size but increased vessel frequency. **v**: vessel cells, **f**: fiber cells, rp: ray parenchyma. Bar = 50µm.After Christian Eckert *et al.* (2019)

Christian Eckert *et al.* (2019) reported that Drought has a major impact on wood and wood formation processes. Since the xylem is the tissue that enables water transport throughout the whole tree, it is pertinent to keep the xylem architecture intact and to acclimate it to changing water supply to prevent embolism Savi *et al.* (2015), Nardini *et al.* (2017). The effects of drought on xylogenesis have been studied on several angiosperm species over the last decade. Poplar, in particular, was intensely studied Fischer and Polle (2010), Polle *et al.* (2019). Cambial cell layers are reduced under drought compared to well-watered plants Wild Hagen *et al.* (2018) Arend (2007). When growth is still possible under water-limited conditions, poplars, regardless of whether they originate from dry or moist habitats, show reduced vessel lumina and an increased number of vessels compared to non-stressed plants (Populus x canescens, Beniwal *et al.* (2010); Populus euphratica, Bogeat-Triboulot *et al.* (2007); different Populus nigra genotypes originating from dry and moist areas, Wild Hagen *et al.* (2018), Figure (23). Moreover, Schreiber and colleagues reported a strong correlation between vessel diameter and cavitation resistance in five-hybrid poplar clones in Alberta, Canada Schreiber *et al.* (2016). However, these acclimatory anatomical changes are not only confined to water-spending trees species like poplar but also to more drought tolerant species such as oak depending on the level of acclimation

(Quercus pubescens > Quercus robur > Quercus petraea, Fonti *et al*. (2013). The importance of this safety strategy is further corroborated by a study on dead trees performed in Italian forests Colangelo *et al*. (2017). Here, the authors compared the wood anatomy of dead trees to that of surviving trees of the same age. They found that dead trees had formed wide early vessels and no vessels with reduced lumen during dry periods in contrast to trees that survived this period Colangelo *et al*. (2017). Taken together, these studies suggest that angiosperms have developed a common mechanism to acclimate their xylem to increasing drought. The xylem, as stated earlier, is formed by vessels and fibers, with the vessels forming the pipe system that facilitates water transport Schuetz *et al*. (2013) Under drought the plant has to fortify the vessels by thickening the secondary cell wall to prevent cavitation, which results in a reduced water transportation rate due to diminished vessel lumina Bogeat-Triboulot *et al*. (2007). To compensate the loss in vessel lumen, more vessels are formed to restore the water transportation rate that is necessary for tree growth Fig. (23). Improving the resistance against drought-induced xylem cavitation is a crucial acclimation mechanism of plants to dry environments Awad *et al*. (2010), Fichot *et al*. (2010). It is notable that these alterations resemble those of seasonal acclimation of wood to shorter day lengths and cold, which lead to the formation of tree rings. Tree rings are a result of changes in the activity of xylem building processes Rathgeber *et al*. (2016). Interestingly, Arend and Fromm (2007), observed that trees responded to drought with smaller vessel lumina only during the main growth season but not in fall, when late wood with small lumina was formed Arend and Fromm (2007). Still, controlled experiments to disentangle temperature and day lengths effects on wood anatomy and the impact of drought under these conditions are lacking Fig. (24).

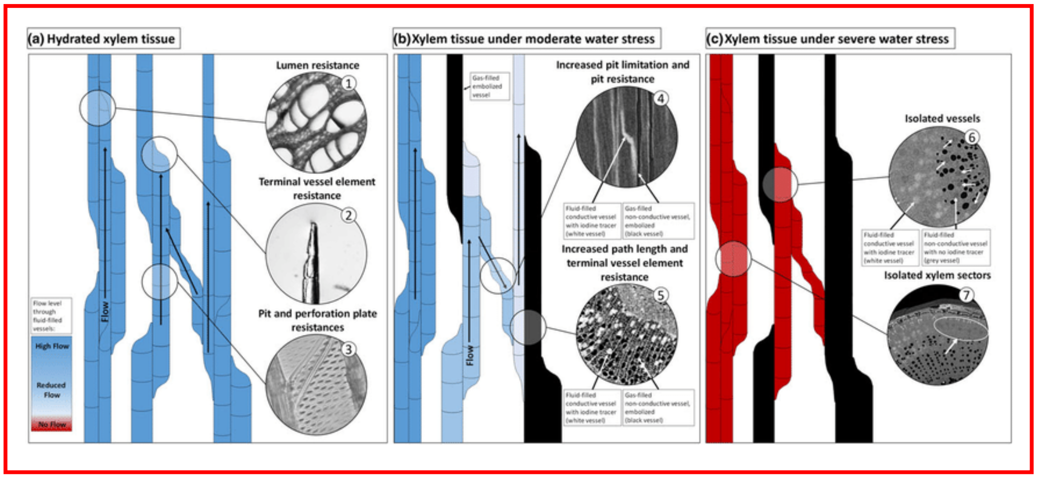


Fig. 24: Illustrates the estimating the hydraulic flow through vessels within the xylem tissue relies on knowledge of the resistances affecting flow. These resistances vary depending on the proportion of embolism within the vessel network. For hydrated xylem tissue **(a)**, flow through the tissue is determined by the lumen resistance of individual vessels (based on the Hagen–Poiseuille equation), resistance linked to vessel endings (terminal vessel element resistance) that require that flow be diverted to other conduits, pit and pit membrane resistances, and perforation plate resistances. As vessels within the network start to embolize **(b)**, flow is further reduced by increased pit limitation and path length. Embolism in a vessel reduces the flow through all vessels connected to it, because the number of pits that are available for water to flow into or out of a water-filled vessel is reduced (pit limitation). Additionally, fluid must flow through increasingly tortuous pathways of vessels, which increases the transport path length of fluid; in some cases, flow may even reverse direction within vessels in embolized networks after Lee *et al*., (2013). At more extreme water potentials **(c)**, propagation of embolism through the network results in vessels and xylem sectors becoming isolated leading to a conductivity of zero through these vessels, even though they remain water-filled. Inset photos: (**1**) vessel lumens from a xylem cross-section, (**2**) silicone cast of a terminal vessel element, (**3**) connections between vessel elements, including a perforation plate and many visible pits, (**4**) longitudinal section showing conductive vessels (white), with flow diverting around an embolized vessel (black) creating a very short and limited connection between two vessels, (**5**) cross section showing many embolized vessels (black) with dispersed conductive vessels (white), with flow likely having to considerably divert from the shorter pathways that would have connected vessels when most were fluid-filled, (**6**) several nonconductive fluid- filled vessels (grey; image modified from Pratt & Jacobsen, 2018), and (**7**) a sector of xylem

containing many nonconductive fluid-filled vessels (after Pratt & Jacobsen, 2018). Images 4–7 are high resolution computed tomography scans (micro CT, photos 4 and 5 Pratt unpublished data) of xylem that has been feed iodine tracer to identify conductive fluid-filled vessels. See method of Pratt and Jacobsen, (2018).After Jacobsen, and Pratt (2018).

Jacobsen and Pratt (2018), reported that to understand how conductivity declines as vessels in a network due to embolize is very important for biological and methodological reasons Choat *et al*., (2016). Some methods rely on evaluation of visual data such as micro CT and optical methods, and image-based estimates of hydraulic function have assumed that water-filled vessels always maintain the optimum values of hydraulic conductivity under drought condition. Therefore, image-based studies have used Hagen–Poiseuille based flow estimates for xylem vessel conductivity across all water potentials and levels of network embolism. Mrad *et al*. (2018) stated that assumption has not been carefully tested, suggesting that there is potential for considerable divergence between visual estimates of conductivity and the actual conductivity. Data from visual methods assumed maintenance of optimal flow would not be expected to agree with methods that directly measure hydraulic conductivity. Developing visual methods that can account for the importance of network properties in determining tissue function, particularly in the networks that contain embolism, and it is an important research priority. For hydrated xylem tissue samples, theoretical conductivity (Kt) estimates based only on Hagen–Poiseuille calculations overestimate conductivity. Tyree and Ewers, (1991), stated that due to vessels are not perfect cylinders and vary in diameter longitudinally, Ellerby and Ennos, (1998) neither perforation plate resistance nor pit membrane resistance as reported by Sperry *et al*. (2005) is accounted for Figure (24 1a). Embolization of vessels, water-conductivity will decline relative to Hagen–Poiseuille based on the Kt estimates the vessel become limited. Fig. (24-1b) illustrates the, path length increased due to divert the flow particularly around blocked conduits. According to the air-seeding model of cavitation, the most vulnerable conduits with the most conductive pit membranes particularly the larger diameter pores, embolized, and limiting transport to more resistant and less conductive vessels within the tissue. At more extreme water potentials, propagation of embolism through the network results in vessels and xylem sectors becoming isolated leading to minimum the conductivity up to zero and remaining sap-filled as illustrated in Fig. (24-1c). Mrad *et al*., (2018); Venturas *et al*., (2016), they stated that degree of vessel isolation is affected the connectivity and the distribution of vessels of differing vulnerabilities within the network. Estimation of Kt will based on Hagen–Poiseuille based calculations and the estimation become error and increasingly susceptible to overestimation as dehydrated the samples and embolize. Using method of Mrad *et al*.'s on xylem anatomy and network structure could be used for estimation of conductivity

Zwieniecki and Secchi (2015) reported that in dry weather promotes a narrow vessel element particularly in, angiosperms that reducing the occurrence of embolism, and it could be a tradeoff through decreased xylem transport capacity. Moreover, drought may decreasing the diameter of xylem vessel , for adapting and increasing water transport through radius of xylem, particularly in early season plant can use less water for conserving the physiological processes, such as grain filling Lynch *et al*. (2014). Lynch *et al*. (2014). Twumasi *et al*. (2005), Li *et al*. (2013) reported that increasing xylem diameter can be considered as desirable characteristic, and is target in selective breeding processes. Drought condition decreases vessel diameter in herbaceous plants, similar to woody plants. Also in common zinnia observed that , thickening of cell wall is induced by increasing in lignin polymerization in response to drought Twumasi *et al*. (2005), sugarcane Dos Santos *et al*. (2015) and white clover Li *et al*. (2013). Since most current research focuses on woody plants, there is a need for more studies with focus on herbaceous plants Lens *et al*. (2016), Sevanto (2018).

Climates, their effect on crops

Climate change is a long-term challenge, requiring un urgent action given the pace and the scale by which greenhouse CO_2 , O_3 , and CH_4 gases are accumulating in the atmosphere stimulates environmental risks and increasing high temperature more than 20C global temperature rise. IPCC, (2014) reported that greenhouse gases directly affecting on crop productivity. However high concentrations of CO_2 are expected to act as a fertilizer by improving net photosynthesis rates and increasing water use efficiency Long *et al*., (2004); Long *et al*., (2004); Deryng *et al*., (2016). Such phenomena may be a positive effect for C_3 plants such as wheat, rice and soybean, due to the limited photosynthetic output of photo respiratory carbon losses Fig. (25), (26).

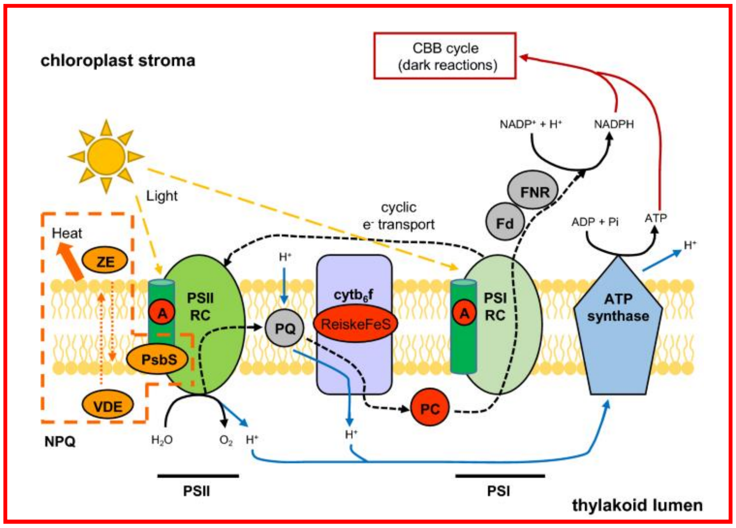


Fig. 25: Illustrates schematic diagram of photosynthetic light reactions and non-photochemical quenching in C3 plants. Blue lines denote proton movement, black discontinuous lines denote movement of electrons, and red lines denote movement to the Calvin–Benson–Bassham cycle. Thermal dissipation of excess light energy via non-photochemical quenching (NPQ) is boxed in orange. Components of the light reactions and NPQ that have been modulated (either directly or indirectly) for improvement of photosynthetic efficiency are shown in red and orange, respectively. A light-harvesting antennae complexes, CBB Calvin–Benson–Bassham, cytb6f cytochrome b6f complex, Fd ferredoxin, FNR ferredoxin:NADP+ reductase, NPQ non-photochemical quenching, PC plastocyanin, PQ plastoquinone, PSI photosystem I, PSII photosystem II, PsbS photosystem II subunit protein, RC reaction centre, RieskeFeS component of the cytb6f complex encoded by Pet C, VDE violaxanthin de-epoxidase, ZE zeaxanthin epoxidase. After Singer *et al*. (2020).

Singer *et al*. (2020) stated that photosynthesis could be divided into two sets of reactions, which are often termed the light reactions Fig. (25), and the Calvin–Benson–Bassham cycle (or dark reactions). The light reactions involve the capture of light energy by chlorophyll and associated pigments, the splitting of water, and electron transport, which reduces nicotinamine adenine dinucleotide phosphate (NADP) to NADPH and provides a proton gradient to fuel the phosphorylation of adenosine diphosphate (ADP) to produce adenosine triphosphate (ATP). The Calvin–Benson–Bassham cycle utilizes the resulting NAPDH and ATP to power the assimilation of CO_2 and its reduction to carbohydrate Long *et al*. (2015). During C3 photosynthesis,CO2 fixation begins with the carboxylation of ribulose 1,5-bisphosphate (RuBP) in a reaction catalyzed by ribulose 1,5-bisphosphate carboxylase-oxygenase (RuBisCo), leading to the production of two molecules of 3-phosphoglycerate (3PGA). At current atmospheric concentrations, O2 competes with CO_2 at RuBisCo active sites resulting in the oxygenation of RuBP and the ensuing photo respiratory pathway Fig. (26), that recycles the products of oxygenation, which can substantially reduce the efficiency of the photosynthetic process Atkinson *et al*. (2016).

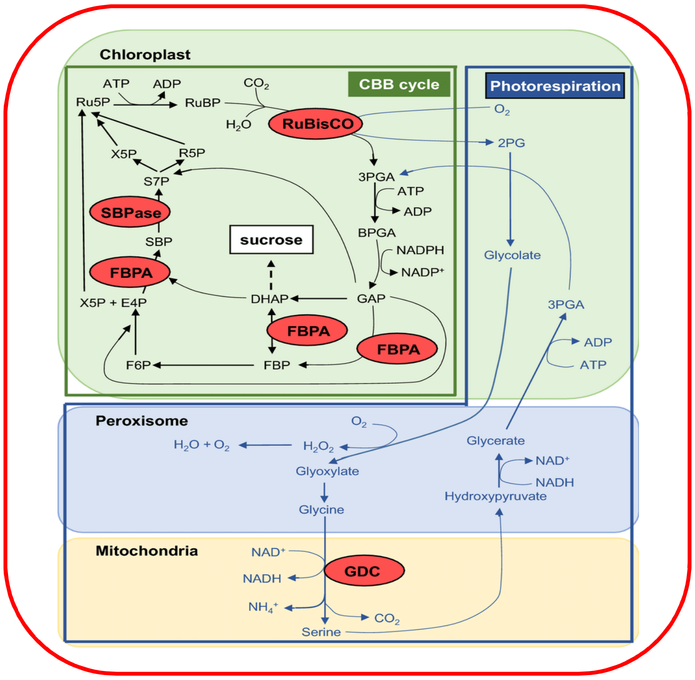


Fig. 26: Illustrates schematic representation of Calvin–Benson–Bassham and photo respiratory cycles in C3 plants. Calvin–Benson– Bassham cycle reactions are boxed in green, while photo respiratory cycle reactions are boxed in blue with blue type. Modifying the expression of genes encoding enzymes shown in red ovals has been demonstrated to enhance photosynthetic rates and/ or biomass production. 2PG 2-phosphoglycolate, 3PGA 3-phosphoglycerate, BPGA 1,3-bisphosphoglycerate, CBB Calvin–Benson–Bassham, DHAP dihydroxyacetone phosphate, E4P erythrose 4-phosphate, FBP fructose 1,6-bisphosphate, FBPA fructose 1,6-bisphosphate aldolase, F6P fructose 6-phosphate, GAP glyceraldehyde 3-phosphate, GDC glycine decarboxylase, R5P ribose 5-phosphate, Ru5P ribulose 5-phosphate, RuBP ribulose 1,5-bisphosphate, S7P sedoheptulose 7-phosphate, SBP sedoheptulose 1,7-bisphosphate, SBPase sedoheptulose 1,7-bisphosphatase, X5P xylulose 5-phosphate

They also reported that increasing atmospheric [CO_2] enhances C3 photosynthesis in saturating light conditions through the presence of elevated substrate for carboxylation, which boosts the rate of carboxylation by RuBisCo Leakey *et al*. (2009). Concomitantly, it reduces the incidence of photorespiration by decreasing the ability of O_2 to compete with CO_2 $_2$at the active site of RuBisCo Drake *et al*. (1997); Long *et al*. (2004), which also increases the efficiency of photosynthesis. Since εc depends on a combination of the efficacy of the photosynthetic process itself and the amount of net losses from photorespiration Long *et al*. (2015), it makes sense that e[CO_2] would provide overall benefits in relation to both. However, in actuality, this enhancement in εc is not necessarily durable, and after long-term exposure of plants to e[CO_2] (a minimum of 3–4 weeks to months), photosynthetic benefits can decline in a process termed acclimation Peet *et al*. (1986); Sage *et al*. (1989); Rogers and Ellsworth (2002). Indeed, in free-air CO_2 enrichment (FACE) experiments with C3 plants, there has been an immense amount of variation in terms of photosynthetic responses to e [CO_2] over the long term, with acclimation being associated with both a decrease in maximum carboxylation rate (Vcmax) and (in some instances) reductions in maximum rates of electron transport (Jmax) Ainsworth and Long (2005); Ainsworth and Rogers (2007); Warren *et al*. (2015). These differences in photosynthetic responses to e [CO_2] have been attributed to many factors, including plant functional group and interacting environmental conditions Wang *et al*. (2012). Reduced stomatal conductance, which tends to occur under e[CO_2] via multiple CO_2 sensing signals such as changes in guard cell cytosolic pH and Ca^{2+} levels Assmann (1999); Ainsworth and Rogers (2007), may play a role in this phenomenon. However, it is generally accepted that non-stomatal limitations such as those related to sink capacity and/or nitrogen utilization efficiency (NUE) are more likely to be the cause Tausz *et al*. (2013); Kromdijk and Long (2016). The sink limitation theory assumes that increased rates of carbon assimilation under e[CO_2] leads to an accumulation of non-structural carbohydrates in leaf tissues due to a lack of sufficient sink capacity (i.e. the ability to develop new sinks or to expand the storage capacity or growth rate of existing sinks) Lewis *et al*. (2002); Erice *et al*. (2011). The resulting carbohydrate saturation exerts negative feedback on the photosynthetic process by down regulating the expression of genes encoding photosynthetic enzymes such as RuBisCo Sheen (1994); Moore *et al*. (1999); Erice *et al*. (2011). The nitrogen limitation hypothesis, on the other hand, is based on the finding that acclimation to e[CO_2] is typically associated with reduced nitrogen levels in leaves Leakey *et al*. (2009). It has been suggested that this results from the increase in biomass production often seen initially under e[CO_2], which is not accompanied by an increase in nitrogen uptake and, therefore, limits the amount of available nitrogen for distribution over a greater amount of plant tissue Tausz *et al*. (2013). In at least certain cases, nitrogen uptake may even decrease under long-term exposure to e[CO_2] due to reduced mass flow resulting from decreased stomatal conductance and associated declines in transpiration Stitt and Krapp (1999), further exacerbating deficiencies. In addition, plants appear to allocate less of their existing nitrogen to leaves Seneweera (2011) and RuBisCo under e[CO_2], allowing more resources to be accessible for other metabolic processes Sage *et al*. (1989); Drake *et al*. (1997) and hindering further improvements in photosynthetic capacity. Although it remains to be determined with any certainty whether the observed reductions in leaf nitrogen and RuBisCo levels are a causative factor for photosynthetic acclimation or whether they are simply a symptom, it is clear that sustaining an elevation of photosynthesis under e[CO_2] will almost certainly demand increased sink capacity and/or NUE to keep up with enhancements in plant growth West *et al*. (2005).

Increment of CO_2 concentration will have a negative impact in the climate, thus counterbalancing the increase in crop yield Specht *et al*., (1999); Long *et al*., (2004); Dong *et al*., (2018), Senapati *et al*., (2019); Wei *et al*., 2019). Ozone-O_3 have significant negative effects on the yield of major agricultural crops Abou seeda *et al*. (2021). O_3 is one of the most highly reactive oxidants, provoking damage in plant tissues, which includes visible leaf injuries, decreased photosynthesis and accelerated senescence and cell death Vandermeiren *et al*., (2009), Abou seeda et al. (2021) Fig. (27).

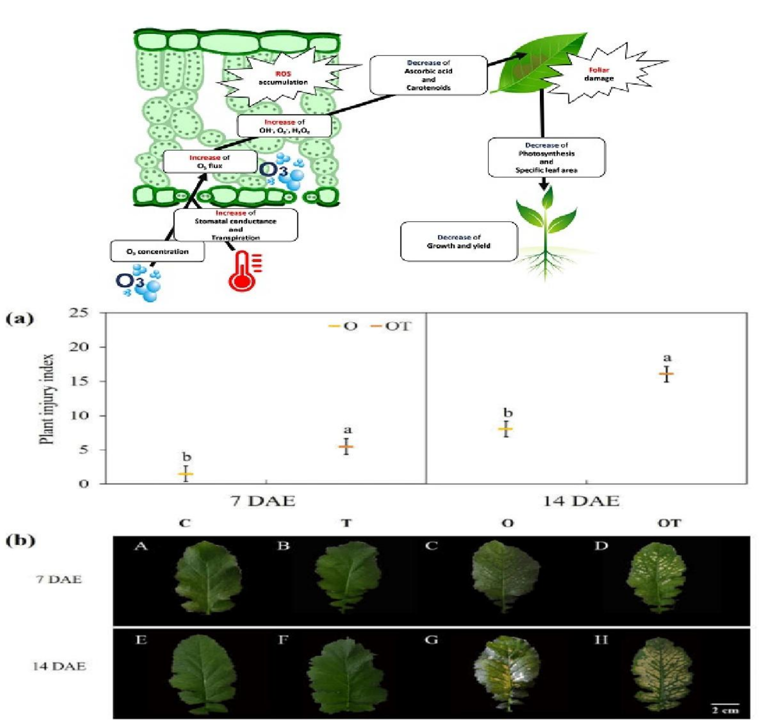
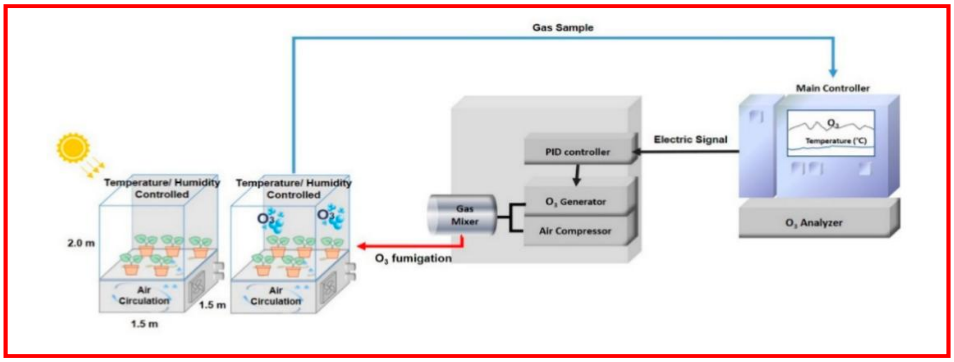


Fig. 27: Illustrates (**a**) Plant injury index and (**b**) visible symptom of *Brassica juncea* L. under different ambient and elevated temperature and O3 treatments at 7 (A–D) and 14 (E–F) DAE. Data are plotted as means ± standard error (SE) ($n = 5$). Different letters indicate significant differences between treatments at $p < 0.05$ according to

Tukey's HSD test. O: optimal temperatures and elevated O3; OT: elevated temperature and elevated O3; DAE: Days after exposure. (A, E) Leaf appearance under control conditions at 7 and 14 DAE; (B, F) leaf appearance at elevated temperature and ambient O3 at 7 and 14 DAE; (C, G) leaf appearance at optimal temperatures and elevated O3 at 7 DAE and 14 DAE; and (D, H) leaf appearance under elevated temperature and O3 conditions at 7 and 14 DAE. (C, D, G, H) Chlorosis was observed on the adaxial side of the leaf. After Jong Kyu Lee et al. (2020).

Jong Kyu Lee et al. (2020) stated that global warming and ozone (O_3) pose serious threats to crop yield and ecosystem health. Although neither of these factors will act individually in reality, most studies have focused on the responses of plants to air pollution or climate change. Interactive effects of these remain poorly studied. Therefore, this study was conducted to assess the effects of optimal (22/20 ^{0}C day/night) and elevated temperature (27/25 ^{0}C) and/or ambient (10 ± 10 nL.L^{-1}) and elevated O_3 concentrations (100 ± 10 nL.L^{-1}) on the growth, physiology, and reactive oxygen species (ROS) accumulation of leaf mustard (*Brassica juncea* L.) under the phytotron on growth chamber and its environmental control system as follow:



The aim of this study is to examine the elevated of high temperature and the Ozone O_3 damage due to increasing stomatal conductance, and thus, O_3 flux into the leaf. Significant reductions in photosynthetic rates occurred under O (elevated O_3 with optimal temperatures) and OT (elevated O_3 and temperature) conditions compared to C (controls). Stomatal conductance was significantly higher under T than in the C at 7 DAE. Under OT conditions, O_3 flux significantly increased compared to that in O (elevated O_3 with optimal temperatures) conditions at 7 days after exposure (DAE). Significant reductions in total fresh and dry weight were observed under OT conditions compared to those under O. Furthermore, significant reductions in levels of carotenoids and ascorbic acid were observed under OT (elevated O_3 and temperature) conditions compared to (elevated O_3 with optimal temperatures). Lipid peroxidation and accumulation of ROS such as hydroxyl radical, hydrogen peroxide, and superoxide radical were higher under (elevated O_3 with optimal temperatures) and OT(elevated O_3 and temperature) conditions than in C conditions at 7 and 14 DAE. Because of O_3 stress, the results of the present study indicated that the plant injury index significantly increased under OT (elevated O_3 and temperature) compared to O conditions. This result suggested that elevated temperature (+5°C) might enhance O_3 damage to B. juncea by increasing stomatal conductance and O_3 flux into leaves.

There are pronounced differences in O_3 sensitivity between plant species Mills *et al*., (2007). Ozone causing a reduction in crop biomass particularly in wheat and soybean and more specifically in root biomass, during reproductive and grain filling stages leading to a reduction of overall crop yield. As the results, Ozone may reduce global production losses of these crops than rice and maize Van Dingenen *et al*., (2009); Avnery *et al*., (2011); Tang *et al*., (2013); Feng *et al*., (2019); Wang *et al*., (2019). Lobell and Burke, (2008).

Sharif *et al*., (2017) stated that intense rainfall during autumn and winter periods may boost the appearance of diseases particularly in cultivation of oil seed rape. However, in maize and soybean plants, heavily precipitations of rain in caused damage in young plants Urban *et al*., (2015) Fig. (28).

Fig. 28: Illustrates agriculture disaster, field of flooded soybean crops

Moreover, extreme rainfall casing intensification of flooding events. Monirul Qader Mirza, (2002); Xu *et al*., (2013); Iizumi and Ramankutty, (2015), reported that floods put in danger the food security may destroying cropping areas or delaying crop planting. However, in coming years flooding risk of coastal regions will increase due to the rising of sea level and alteration of the climatology. Seawater flooding of coastal area is becoming more frequent due to waves and storm surges are getting stronger Vitousek *et al*., (2017). Hanley *et al*., (2019) stated that Osmotic and anionic stress due to high salinity of seawater will become an additional problem to crops besides the low both O_2 and CO_2 levels which caused by anoxia. It has been shown that oilseed rape plants exposed to seawater flooding conditions suffering a reduction of plant biomass as well as their productivity. because of longer periods without rain added to warmer temperatures ,more frequent drought events are also expected .Several researchers, Saadi *et al*., (2015); Lesk *et al*., (2016); Zipper *et al*., (2016) reported that droughts restrict cropping areas, decreasing agricultural productivity due to a direct effect on crop yield. Boyer and Westgate, (2004) stated that most damaging of drought stress on crop productivity occurred at reproductive or growing stages, such as pollen sterility as observed in barley plant or ovary abortion in maize and the latter a reduction in kernel number and biomass. Drought period generally caused a reduction of water consumption by the plant, leading to a stomatal closure and lower CO_2 intake. Following decrease in photosynthesis ratio provokes a final reduction of crop biomass Garofalo *et al*., (2019). Water scarcity imposed by drought is frequently accompanied by salinity stress. The ion toxicity and the reduction of soil water potential contribute to a severe reduction of plant growth. Soil salinity reduces yield in highly tolerant crops as cotton, barley and sugar beet as well as in crops with high salinity sensitivity as sweet potato, wheat or maize Zörb *et al*., (2019). Climate effects together with elevated temperature will increase agriculture losses. Fuhrer, (2003); Lobell and Burke, (2008); Ainsworth, (2017); Tai and Val Martin, (2017). Battisti and Naylor, (2009) several reports suggesting that warming will lead to substantial declines in mean crop yields in the next future, and tropic areas are the most serious agricultural impacts Furthermore, the crop yield will decline and their variability will gradually increase even under unchanged climatic, Tigchelaar *et al*., (2018). Guarino and Lobell, (2011) reported that under such situation show possible yield losses of 6–10% per 10C of warming in the average temperature of the growing season. In addition, climate variation is already causing a major effect on the stability of crop production. Since yields of barley, cassava, maize, oil palm, rapeseed, rice, sorghum, soybean, sugarcane and wheat are considers as the top ten global crops has been affected significantly in different regions all over the world Ray *et al*., (2019). Focusing on the effect and consequences of one of the major components of climate change, increased temperature and, in particular, its effect on crop and their parts.

Temperature and their effect on crops

Because of global warming, the yield increment that started in the last century is stagnant and even decreasing in some areas Lobell and Field, (2007). High temperature response has been studied at extreme conditions characterized by the heat shock esponse. However, even small differences in ambient growth temperature can have profound effects on crop growth and yield. Although abundant literature is available on how plants tolerate extreme damaging heat less is known on how crops adapt to moderately increased or warmer temperatures Quint *et al*., (2016); Vu *et al*., (2019b). Prediction models reveal that the continuous increment in temperature would result in heavy losses in crop yield at medium latitudes Liu *et al*., (2016), Fig. (29),

Fig. 29: Illustrates higher global warming, would result in heavy losses in crop yield

whereas less fertile soil areas located at extreme latitudes are getting a more appropriate climate for agriculture Long and Ort, (2010); Lobell *et al*., (2011); Iizumi and Ramankutty, (2015); Sharif *et al*., (2017). Thus, warmer temperature could expand the areas potentially suitable for cropping, increase the length of the growing period, and crop yields may rise in these areas (How to Feed the World in 2050, Rome; FAO, (2009b). However, globally higher temperatures shorten the growth season, letting the crops with a much shorter period to perform photosynthesis even in the case of well-irrigated and tolerant crops. Moreover, heat stress directly affects photosynthetic rate accentuating the effect of this shorter growth period. As a result, crops have less biomass to face the anthesis and the consequent grain filling Fig. (30).

Akanksha Sehgal *et al*. (2018) reported that drought (water deficits) and heat (high temperatures) stress are the prime abiotic constraints, under the current and climate change scenario in future. Any further increase in the occurrence, and extremity of these stresses, either individually or in combination, would severely reduce the crop productivity and food security, globally. Although, they obstruct productivity at all crop growth stages, the extent of damage at reproductive phase of crop growth, mainly the seed-filling phase, is critical and causes considerable yield losses. The findings in various food crops showing how their seed composition is drastically impacted at various cellular levels due to drought and heat stresses, applied separately, or in combination. The combined stresses are extremely detrimental for seed yield and its quality, and thus need more attention. Understanding the precise target sites regulating seed filling events in leaves and seeds, and how they are affected by abiotic stresses, is imperative to enhance the seed quality. It is vital to know the physiological, biochemical and genetic mechanisms, which govern the various seed filling events under stress environments, to devise strategies to improve stress tolerance. Converging modern advances in physiology, biochemistry and biotechnology, especially the "omics" technologies might provide a strong impetus to research on this aspect. Such application, along with effective agronomic management system would pave the way in developing crop genotypes/varieties with improved productivity under drought and/or heat stresses.

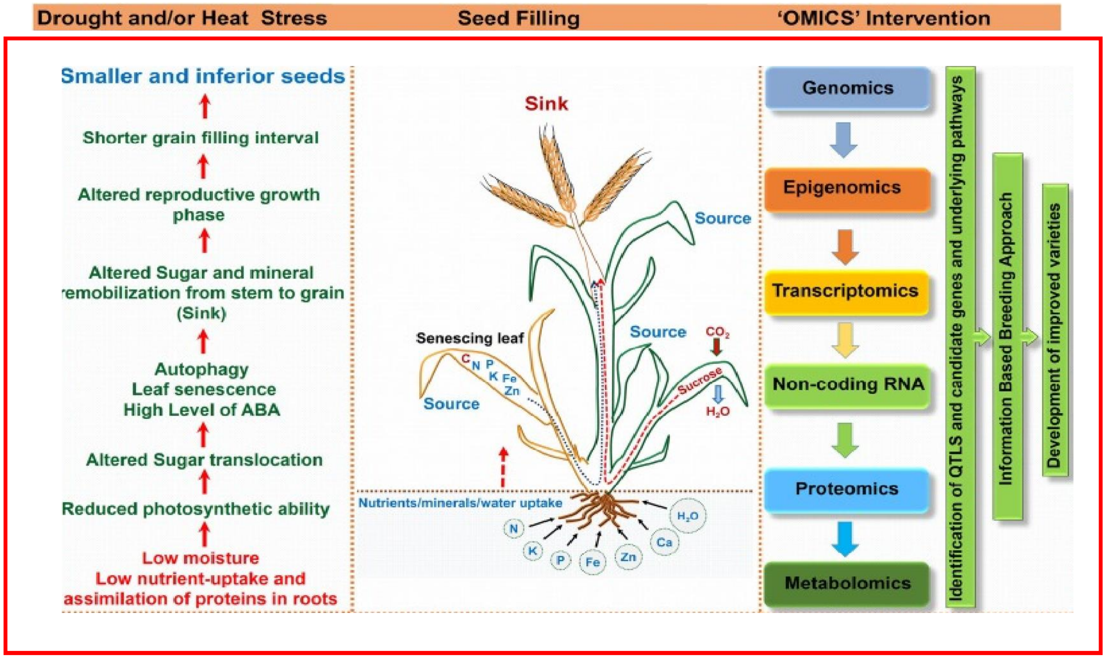


Fig. 30: Illustrates the schematic representation highlighting consequences of drought and/or heat stress on seed filling and 'omics' approach for crop improvement After Akanksha Sehgal *et al*. (2018).

They also concluded that seed-filling processes are adversely affected by heat and drought stress in all crop species, resulting in poor-quality seeds and reduced seed yields. The frequency of these two stresses occurring at the same time is increasing, for both for summer and cool-season crops, which is highly detrimental to the qualitative and quantitative aspects of yield. Hence, future research should focus on investigating the dual effects of drought and heat, involving various physiological, biochemical and molecular approaches. Future endeavors should also pay attention on screening the existing germplasm of various crops under combined stress environment to identify tolerant genotypes and their subsequent incorporation into breeding programs. It is vital to understand and dissect various components influencing seed-filling processes under separate and combined stress environments to unveil varying responses of different crops to these two stresses. Identification of sensitive sites (embryonic stages, hormonal changes and biochemical pathways for seed reserves, signaling molecules, proteins and genes) related to seed-filling processes in stressed plants, especially under the combined stress, would provide useful cues in developing strategies to improve seed quality. As photosynthetic activity mainly determines crop productivity, the breeding for 'stay-green' trait is essential to combat drought as well as heat stress. 'Omics' studies are in progress that will be useful for identifying the genes, proteins, and metabolites in developing seeds that are, impacted by heat or drought stress. Modeling the stages of development, growth, grain productivity, grain quality and sink-source relations will enable better insights on the physiological and genetic nature of stress tolerance, ultimately resulting in enhanced grain yields and quality in crops. Improved models can enhance the likelihood of predicting crop performance in future challenging climates, which will largely help to identify traits that can be exploited through breeding to produce sustainable climate-resilient genotypes with acceptable yield under stressed environments

Warmer environments also affect post-anthesis stages reducing grain growth and promoting fruit senescence. Additionally, the increase in temperature promotes a higher evapotranspiration rate that, ultimately reduce soil moisture and the available water needed for grain filling. When plants suffer extreme temperatures of short duration these processes are even more severely affected Asseng *et al*., (2011), (2015), (2019); Liu *et al*., (2014), (2019); Lesk *et al*., (2016). Accordingly, it has been reported that in wheat, rice and sorghum heat causes loss of grain yield by shortening its growth period, altering spikelet's development (number of spikes per plant and spikes size), grains per spike and reducing grain size Prasad *et al*., (2006); Jagadish *et al*., (2010); Fahad *et al*., (2017). Similarly, in oilseed rape, *Brassica rapa and Brassica juncea* yield losses are produced by a decrease in seeds per Siliques and number of Siliques per plant as well as defects in pod formation Angadi *et al*., (2000); Morrison and Stewart, (2002). High temperatures also lead to a decrease in crop quality by changing seed composition Fig. (31).

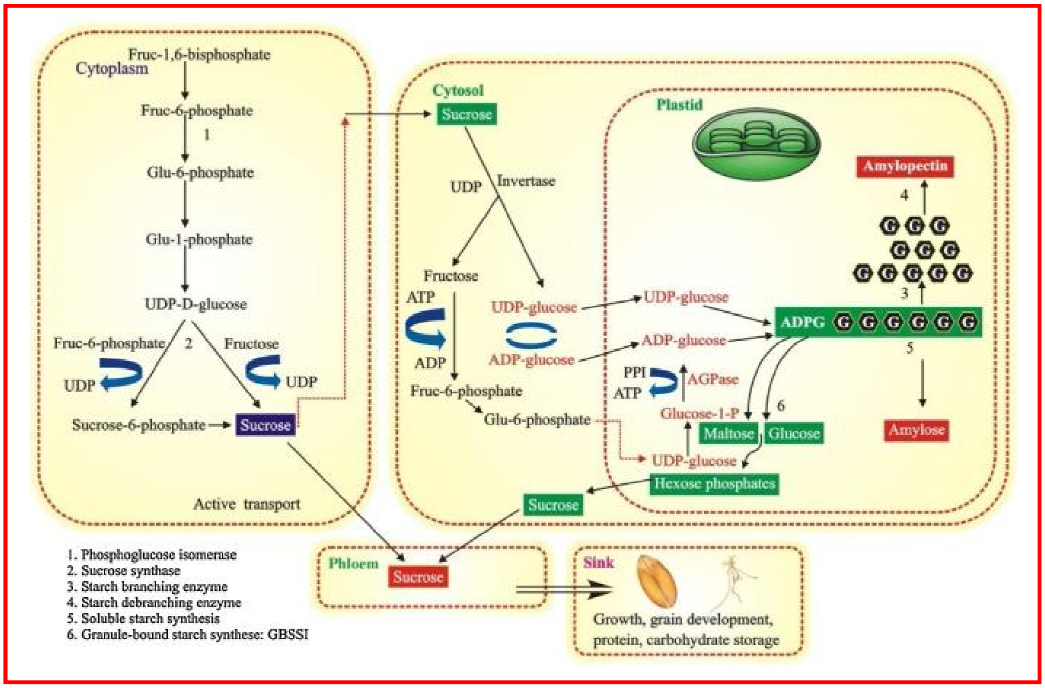


Fig. 31: Illustrates schematic diagram of grain development in wheat under combine effects of heat and drought stress.

Thus, in cereals and oilseed crops heat stress reduces the oil, starch, and protein contents of seeds Jagadish *et al*., (2015); Fahad *et al*., (2017). It has been shown that in wheat, increased temperatures reduce the levels of valuable protein whereas it causes the accumulation of proline and soluble carbohydrates Qaseem *et al*., (2019). On the other hand, higher temperature also reduces oilseed rapeseeds quality by reducing the amounts of oil and increasing the levels of proteins and glucosinolates Aksouh *et al*., (2001). In rice, high temperatures during ripening led to the deterioration of grain quality including starch accumulation Morita *et al*., (2016); Chen *et al*., (2017). In brief, crops are substantially but heterogeneously affected by temperature variability Thiault *et al*., (2019). To remedy this effect, we need to evaluate and understand further the changes that crops undergo under the future climatic scenario.

Temperature and their effect on root network

Crops face rising temperatures by triggering a heat response, whose timing and effectiveness will determine if the plants overcome the stress. The effect of increased temperatures on aerial parts of the plants and their responses has been well studied, whereas their influence and response on roots (and root-to-shoot signaling) has been less explored Wahid *et al*., (2007). If we attempt to enhance adaptation of crops to severer environments triggered by climate change, we need to take into account below ground traits. For that, first, we need to improve our understanding of the processes regulating the root response to increased temperature. Plants have a greater water demand in warmer environments due to increased water loss by evapotranspiration and decreased water uptake by the root, causing an overall water deficit situation Heckathorn *et al*., (2013). Water uptake takes place in the root either through aquaporins, membrane channels that facilitates water transport inside the cells, or by diffusion through plasmatic membrane Maurel *et al*., (2015) Fig. (32).

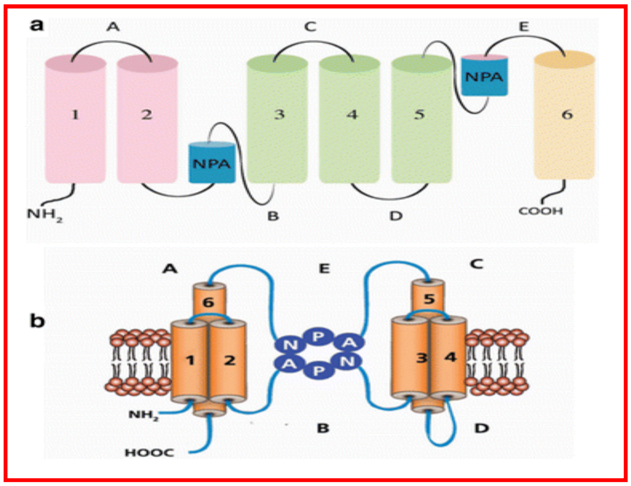


Fig. 32: (a) Protein arrangement showing how the two regions of helical domains interact to form the three dimensional structure of the protein. Pore of the AQP is composed of two halves called as hemipores. MIPs consist of six transmembrane domains connected by five loops (A–E), with cytoplasmic N- and C-termini. Locations of NPA (Asn-Pro-Ala) motifs are at the loops B and E. **(b)** Functional AQP formed by the interaction of the two hemipores (Siefritz *et al*. (2001), Santoni and Maurel (2014)). After Kapilan *et al.* (2018)

Kapilan, *et al*. (2018) Aquaporins (AQP) are channel proteins belonging to the Major Intrinsic Protein (MIP) superfamily that play an important role in plant water relations. The main role of aquaporins in plants is transport of water and other small neutral molecules across cellular biological membranes. AQPs have remarkable features to provide an efficient and often, specific water flow and enable them to transport water into and out of the cells along the water potential gradient. Plant AQPs are classified into five main subfamilies including the plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), nodulin 26 like intrinsic proteins (NIPs), small basic intrinsic proteins (SIPs) and X intrinsic proteins (XIPs). AQPs are localized in the cell membranes and are found in all living cells. However, most of the AQPs that have been described in plants are localized to the tonoplast and plasma membranes. Regulation of AQP activity and gene expression, are also considered as a part of the adaptation mechanisms to stress conditions and rely on complex processes and signaling pathways as well as complex transcriptional, translational and posttranscriptional factors. Gating of AQPs through different mechanisms, such as phosphorylation, tetramerization, pH, cations, reactive oxygen species, phytohormones and other chemical agents, may play a key role in plant responses to environmental stresses by maintaining the uptake and movement of water in the plant body.

Studies with several crops have shown different response of aquaporins and plasmatic membrane fluidity to higher temperatures in roots. Thus, in pepper and wheat, water uptake in warmer soil seems to positively correlate with aquaporin activity Carvajal *et al*., (1996); Cabañero *et al*., (2004), whereas in broccoli (Brassica oleracea var. italica) and maize, warmer temperatures decrease aquaporin quantity and activity but increase membrane fluidity. When temperature is extreme, the membrane starts to rigidify heavily decreasing even more water uptake Iglesias-Acosta *et al*., (2010); Ionenko *et al*., (2010) Fig. (33). Nutrient balance is also altered by changes in temperature. Similarly, to water, temperature effect on nutrient uptake varies depending on the crop. In tomato, warmer soils limit root growth and decrease nutrient uptake causing a reduction in macro and micronutrient levels Tindall *et al*., (1990); Giri *et al*., (2017).

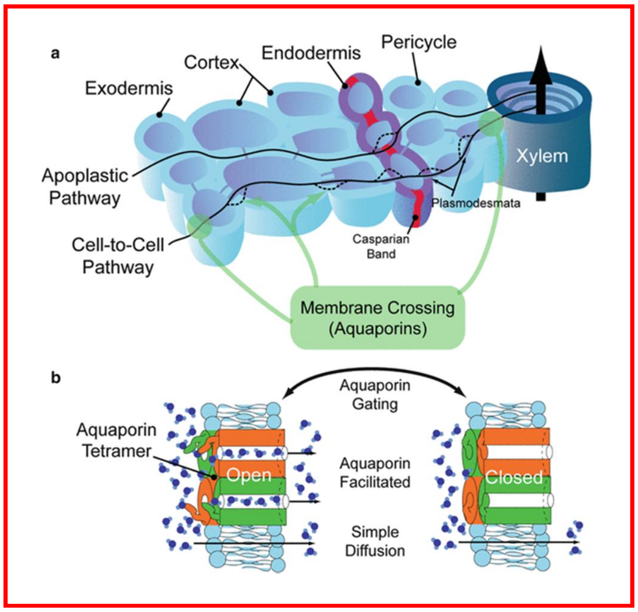


Fig. 33: Illustrates **(a)** the composite model of water transport proposes that water can flow from the soil to the root xylem along two parallel pathways. One pathway is the apoplastic pathway (through the cell walls) and the other is the cell-to-cell pathway. Water flow through the apoplast can encounter a hydraulic barrier at the endodermis (Casparian band in red) which can force water flow across endodermal cell membranes if suberized (dotted line). The cell-to-cell pathway involves the flow of water through plasmodesmata and/or across membranes (dotted lines; i.e., the transcellular pathway). **(b)** Water crosses cell membranes by simple diffusion and/or by facilitated diffusion through aquaporins. Aquaporins function as homo- and heterotetramers, and their contribution to water transport can be regulated by their abundance, location, and interaction between different aquaporin isoforms. In addition, aquaporin proteins undergo gating, where various stimuli (e.g., pH, reactive oxygen species) can modulate the proteins between open and closed configurations, thus rapidly controlling their activity.

Steudle and Peterson (1998); Steudle (2000), stated that absorption by the root, water first crosses the epidermis and then moves toward the center of the root crossing the cortex and endodermis before arriving at the xylem Fig. (33). Based on the composite model of water transport across roots water can flow along two pathways in parallel between the soil and the root, i.e., along the apoplast and/or from cell-to-cell encountering a major hydraulic barrier at the endodermis. The apoplastic path involves a substantial movement of water through the cell wall up to the endodermis, where water either is forced through endodermal cell membranes (if Casparian bands containing hydrophobic suberin depositions are present) or continues to move along the radial walls of endodermal cells. The cell-to-cell path involves mainly a flow of water across membranes (transcellular), which can occur by simple diffusion through the lipid bilayer and by facilitated diffusion through aquaporins and/or transport across plasmodesmata (symplastic). The actual pathway of water transport across the root is extremely complex, and the relative contribution of each pathway likely varies with species, plant development, and growth conditions. It should be noted that aquaporins can only make a significant contribution to root water uptake when the dominating flow path through the root cylinder is from cell to-cell Knipfer and Fricke (2010), (2011)

In Agrostis stolonifera, a grass species used as fodder for livestock, the application of high temperature to roots results in a lower number of roots and an increase in the uptake and partitioning of nitrogen, phosphorous and potassium Huang and Xu, (2000). In Andropogon gerardii, another plant used as fodder, supra-optimal root temperatures cause a decrease in root and shoot growth. Further higher temperatures moderately affects nitrogen uptake but its efficiency use is severely perturbed DeLucia *et al*., (1992). In contrast, warm temperature does not alter nitrogen, phosphorus and potassium uptake in maize, but higher temperatures seem to only slightly decrease phosphorus and potassium uptake Bravo-F and Uribe, (1981); Hussain *et al*., (2019). All these negative root responses to increase temperature severely compromise water and nutrient uptake and the consequence is a dramatic reduction on crop yield. Cultivars better adapted to temperature will have to shape their roots to improve their water and nutrient efficiency if they aim to secure yield stability under this challenging environment. As we will ascertain during this review, root organization shows a high plasticity in response to soil changes providing high opportunities for improvement. Better comprehension of the physiological, genetic and molecular mechanisms regulating this plasticity will allow us to develop better-adapted crops.

4. Plant responses to multiple environmental factors

In natural habitats, plants experience multiple factors; earlier findings have considered the effects of environmental factors on plant growth and physiological activities. Natural plant communities are normally composed of several species, each with slightly different physiological characteristics and requirements. Consequently, each species in a community may be limited by a slightly different combination of resources. When light, nutrients, and temperature were altered in two tundra communities, each species showed a different pattern of response Chapin and Shaver (1985). Similarly, each species responds differently to annual variations in environment. Years that are favorable for growth of some species reduce the growth of other species, both because of direct plant responses and competitive interactions. Consequently, community productivity is much more stable in the face of environmental variation than is the productivity of any individual species Chapin and Shaver (1985). Interspecific variation in resource requirements almost certainly plays a role in community population dynamics comparable in importance to its role in community productivity. Collaborations between physiological ecologists and ecosystem and community ecologists will be a key for developing a mechanistic understanding of the dynamics of complex natural communities.

4.1. Combined effects of temperature and carbon dioxide on plants

Increasing temperature alone is expected to only marginally increase photosynthesis as described through using mathematical model, whereas when combined the two factors such as higher temperature with elevated CO_2, larger net of photosynthesis is expected by up to 50%. Due to this model, plant species that do not acclimate to elevated CO_2 will experience a greater enhancement of photosynthesis Tamanqueiro Faucet *et al*. (2019); therefore, a greater volume of water will be lost to the atmosphere and requiring water for root uptake, which may be problematic particularly in water-limited environments. Plants have been shown to exhibit plastic responses to a number of environmental factors, but many mathematical models fail to consider these, likely because they remain poorly understood. Photosynthesis and respiration can acclimate in response to temperature and CO_2, depending on the length and intensity of the stimuli Reducing transpiration can occurred particularly at very high temperatures because of Rubisco is temperature-sensitive, slowing down carbon fixation and reducing need for water transport, Smith and Dukes (2013). Kurepin *et al*. (2018) , Tamanqueiro Faucet, *et al*. (2019) they reported that combination of higher temperature and elevated CO_2 observed that either increasing or decreasing the net of CO_2 assimilation, stomatal conductance, and growth particularly In woody plants. However in herbaceous plants, these two factors together will decreased the net CO_2 assimilation and stomatal conductance, increasing or decreasing transpiration, whereas water use efficiency (WUE) will increase the effects varied with species Medeiros, and Ward, (2013), Qaderi and Reid (2008) Fig. (34).

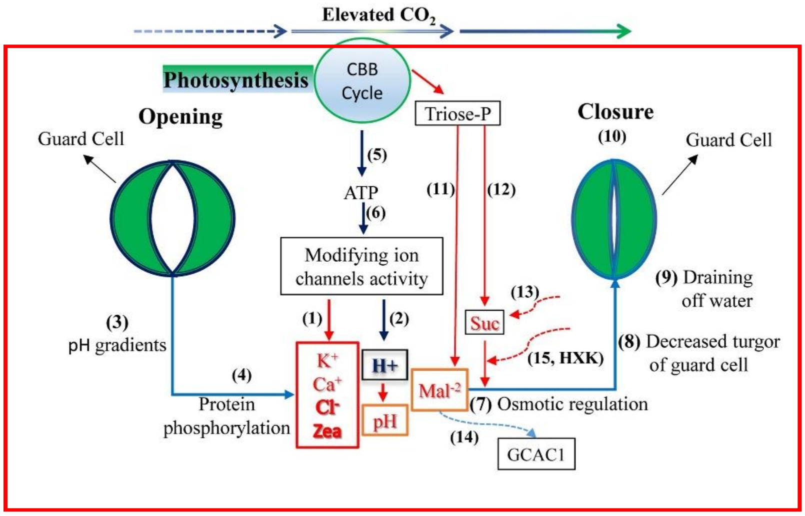


Fig. 34: Possible stomatal response mechanisms controlling guard cells (GC) under elevated CO_2. With rising CO_2, a depolarization in GCs appears: the levels of K+, Ca2+, Cl−, and zeaxanthin (Zea) may decrease **(1)**, whereas the H+ concentration may remain at a high level **(2)** leading to a lower pH value. The pH gradient **(3),** protein phosphorylation **(4),** and photosynthesis-derived ATP **(5, 6)** are involved in the regulation process by modifying channel activities; together, they promote osmotic regulation **(7)** and decrease GC turgor **(8)** consequently causing the GCs to drain water **(9)** leading to stomatal closure to some extent **(10).** Meanwhile, Calvin–Benson–Basshan (CBB) cycle and sugar metabolism in GC may produce less malate (Mal2−), **(11)** and sucrose (Suc) **(12)** with triose phosphate (triose-P) at eCO_2, which also affects osmotic regulation. Furthermore, elevated CO_2 may reduce Suc accumulation in the vicinity of the GC wall from the mesophyll due to the limitation of some apoplastic Suc in the transpiration stream toward GC **(13)** and enhance Mal2− transport from GCs into mesophyll cells by stimulating anion efflux through channels such as GCAG1 and the potential involvement of the AtABCB14 gene **(14),** also resulting in stomatal closure. Finally, hexokinase (HXK) involvement may limit sugar synthesis and its entrance into GCs from mesophyll cells **(15)** and then inducing stomatal closure. Webb *et al*., (1996); Assmann, (1999); Schroeder *et al*., (2001); Kang *et al*., (2007); Lee *et al*., (2008); Kim *et al*., (2010); Fujita *et al*., (2013); Kelly *et al*., (2013); Lawson *et al*., (2014); Negi *et al*., (2014). After Xu *et al*. (2016)

Xu *et al*. (2016), reported that molecular Mechanisms Controlling Guard Cell in Response to Elevated CO_2 General Molecular Mechanism Guard cell (GC) metabolism and the signal transduction network have been reviewed in several reports , Lawson *et al*., (2014); Negi *et al*., (2014). Here, we succinctly present the findings of these reports, particularly the explanations concerning the regulation of CO_2 concentration Fig. (34). Generally, ion and organic solute concentration levels determine the turgor pressure of guard cells and subsequently affect stomatal aperture. Under elevated CO_2, stomata tend to close because a greater depolarization seems to appear in GCs. The process may be controlled by (a) a decrease in K+ concentration, with enhanced activity in outward rectifying K+ channels and decreased inward activity, (b) decreased cytosolic Ca^{2+} in GCs, (c) decreased Cl^{-} and malate ($Mal2^{-}$) concentrations by stimulating the release of Cl^{-} and $Mal2^{-}$ from GCs resulting from the activation of S-type anion channels, and (d) by decreases in the cytosolic zeaxanthin level and the pH value in GCs. Together, these factors lead to a decline in GC turgor, causing the GCs to shrink and the stomatal aperture to close Webb *et al*., (1996); Zhu *et al*., (1998); Assmann, (1999); Schroeder *et al*., (2001); Fujita *et al*., (2013); Lawson *et al*., (2014). The potential messengers in the stomatal response to CO_2 concentrations mainly include ion channel activity, cytosolic free calcium, ABA, malate levels, membrane potential, pH gradients, zeaxanthin content in chloroplasts, photosynthesis-derived ATP content, protein phosphorylation, and dephosphorylation processes (McAinsh *et al*., 1990; Schroeder *et al*., 2001; Ainsworth and Rogers, 2007; Kim *et al*., 2010; Wang *et al*., 2013; Lawson *et al*., 2014). For instance, the experiments have shown that elevated CO_2 can enhance anion channel activity in GCs to induce stomatal closure. In this event, the SLAC1 protein provides or regulates a gate for anion transport

(Raschke *et al*., 2003; Marten *et al*., 2008; Vahisalu *et al*., 2008; Negi *et al*., 2014; Yamamoto *et al*., 2016).

Temperature and CO_2 greatly affected photosynthesis in night-flowering catchfly (Silene noctiflora L.). Higher temperature will gradually increase transpiration, but did not increase either net CO_2 assimilation or WUE, whereas elevated CO_2 increased net CO_2 assimilation and WUE, but decreased transpiration. Multi environmental factors combined together such as high temperature and elevated CO_2, the highest transpiration rate will occurred in plants and these plants were of comparable size to those of control Qaderi and Reid (2008). Results on alfalfa showed that elevated of CO_2 in combination with high temperature were decreased the crude protein but increasing plant growth, whereas elevated CO_2 under ambient temperature or under partial irrigation has no effect on plant growth Irigoyen *et al*. (2014). We need more studies to examine the effects of interaction between carbon dioxides and temperature on vascular cambium; however, since plants were of similar size when under higher temperature and elevated CO_2, this may indicate that vascular cambium may be unaffected, but more in-depth morphological studies are required.

4.2. Combined effects of temperature and drought on plants.

Combination effects of, higher temperature and drought stress lead to reduce the crop yield production Lobell and Gourdji, (2012), Yamori *et al*. 2012). It is projected that negative climatic changes, such as higher temperature and drought stress, which associated with high atmospheric CO2, may eventually outweigh the beneficial effects of CO_2 to plant. Lobell and Gourdji, (2012). Higher temperature in combination with drought stress, the carbon balance of leaves may be offset, due to an imbalance of photosynthesis and respiration as will. Fixed carbon will lost in the respiration, resulting that the net photosynthesis and respiration may decline. Moreover, full photosynthetic capacity can potentially be restored following restoration of water supply in the absence of irreversible damage Centritto *et al*. (2011). Higher temperature and precipitation may act synergistically on the reactivation of cambial cells and the subsequent the formation and differentiation of both xylem and phloem cells Dhirendra Singh *et al*. (2011), Cufar *et al*. (2011) Fig. (35).

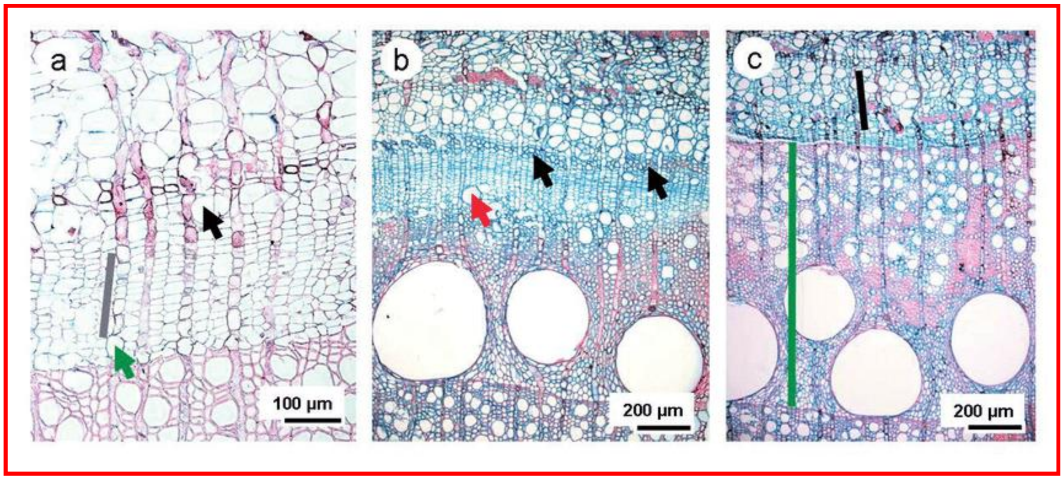


Fig. 35: Illustrates **(a)** Newly formed phloem (black line) and xylem (green arrow) cells and active cambium (gray line) at the beginning of April; **(b)** late wood formation (red line) and development of phloem fibers (black line); **(c)** phloem (black line) and xylem (green line) increment in 2007. After Jožica Gričar (2010).

Jožica Gričar (2010) stated that cell divisions in the cambium had already started on 30 March 2007; the number of cambial cells had increased to 9-11 layers and the walls of cells were very thin Fig. (35- 2a). Observing that 1-2 layers of sieve tubes in the early phloem adjacent to the cambium at that time. At the beginning of April, newly formed xylem (early wood vessels and fibers) and phloem cells (early phloem sieve tubes) adjacent to the cambium slowly began to expand, this proses would indicated that development of vascular cambium could not occur without both available water and higher temperature. However, the combination effects between high temperatures, water deficit may change the timing of cambial cell initiation. Temperature has the potential effects of water deficit, that creating the earlier suberization Barrios-Masias *et al*. (2015), under such condition vascular tissue may become narrower, resulting in a reduced capacity for xylem-driven water transport Zwieniecki and Secchi, (2015) In woody plants (e.g., black poplar), extreme drought stress led to metabolic impairment of photosynthesis. A combination of higher temperature and drought stress decreased net CO_2 assimilation and stomatal conductance. Drought stress had greater effects on plant metabolic activities particularly at low temperature (25^{oC}) than at high temperature (35^{oC}), because maximum photosynthesis was about four fold lower and the maximum rate of Rubisco carboxylation and the apparent maximum rate of electron transport at saturating irradiance were two fold lower at lower temperature than at higher temperature. Moreover, plants recovery under low temperature was more slowly than those under high temperature Centritto *et al*. (2011). In herbaceous plants (e.g., spring wheat), high temperature combined with drought stress gradually decreased the net CO_2 assimilation, stomatal conductance, transpiration, and growth, but water use efficiency were increased (WUE) Zhang *et al*. (2010). In canola (Brassica napus L.), plants grown under high temperatures and drought stress had a lower biomass than plants grown under control conditions lower temperatures and watering to field capacity. The canola seedlings also had a reduced stem mass Qaderi *et al*. (2012), which could indicate a reduction of vascular tissues, as they are responsible for the majority of stem girth Milhinhos and Miguel, (2013) Fig. (36).

Fig. 36: Illustrates canola starts to move from flowering and into pod formation, due to the combination of heat, drought that the reasons for missing pods

Increases in temperature may exacerbate the magnitude of water-stress effect, but this depends, in part, on species and geographical location Irigoyen *et al*. (2014.

4.3. Combined effects of carbon dioxide and drought stress on plants.

Elevated of atmospheric CO_2 may lead to improved drought tolerance in plants Swann *et al*. (2016). However, another studies suggesting that drought may minimized the positive effects regardless of increased water use efficiency (WUE) Olano *et al*. 2014). In addition, C3 plants, the elevated of atmospheric CO_2 enhanced carbon gain and decreasing stomatal conductance Milhinhos and Miguel (2013). Elevated of CO_2 has a direct effect which increasing photosynthetic activities, that contributing to increased growth even under deficit water status improvements Perry *et al*. (2013). Increased photosynthetic rates at elevated CO_2 have the most prominent particularly under drought stress, indicating that elevated CO_2 could mitigate the negative effects of drought stress Fig. (37).

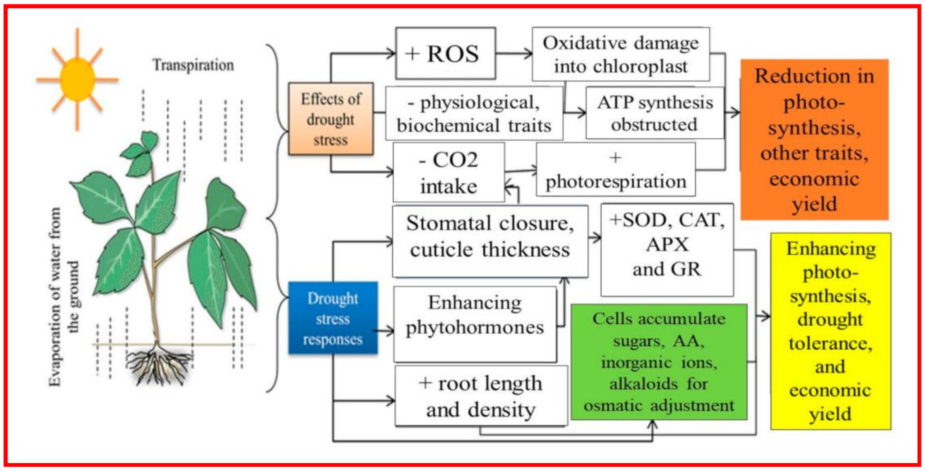


Fig. 37: Illustrates the adverse effects and adaptations of plants to drought stress, modified from Ullah *et al*. (2017) (- means reduce; + means increase). After Seleiman *et al*. (2021)

Seleiman *et al*. (2021) reported that drought stress, being the inevitable factor that exists in various environments without recognizing borders and no clear warning thereby hampering plant biomass production, quality, and energy. The key important environmental stress occurs due to temperature dynamics, light intensity, and low rainfall. Despite this, its cumulative, not obvious impact and multidimensional nature severely affects the plant morphological, physiological, biochemical and molecular attributes with adverse impact on photosynthetic capacity. Coping with water scarcity, plants evolve various complex resistance and adaptation mechanisms including physiological and biochemical responses, which differ with species level. The sophisticated adaptation mechanisms and regularity network that improves the water stress tolerance and adaptation in plants were discussed. Growth pattern and structural dynamics, reduction in transpiration loss through altering stomatal conductance and distribution, leaf rolling, root to shoot ratio dynamics, root length increment, accumulation of compatible solutes, and enhancement in transpiration efficiency, osmotic and hormonal regulation, and delayed senescence are the strategies that are adopted by plants under water deficit. Approaches for drought stress alleviations are breeding strategies, molecular and genomics perspectives with special emphasis on the omics technology alteration i.e., metabolomics, proteomics, genomics, transcriptomics, glyomics and phenomics that improve the stress tolerance in plants.

Many of these measurements, however, have been conducted at the leaf level instead of the whole plant level, which yields less clear-cut results Milhinhos and Miguel (2013). In another studies, results noticed that, elevated of CO_2 biomass of plants were increased by about 15% under water-stressed Perry *et al*. (2013). Under drought conditions elevated of CO_2 can increase water use efficiency WUE, however biomass decreased comparing to normal conditions in several riparian tree species Perry *et al*. (2013).; indicating that variation of plant species is response. In most plants, elevated of CO_2 decreases the stomatal conductance but increases of water use efficiency (WUE), these effects are increased under drier conditions, which may lead to a reduction in plant water demand. In semi-arid region, transpiration is reduced under elevated CO_2; increasing plant growth under dry periods and counteract the negative effects of warming on the supply of available water to plant roots Perry *et al*. (2013). Partial closure of stomata particularly under both drought stress and elevated CO_2, because of increasing sub-stomatal CO_2 concentration Reddy *et al*. (2010). In woody plants (e.g., lemon tree), combined effects decreased both stomatal conductance and transpiration, however plant biomass had no significant effects Paudel, *et al*. (2018). In addition, drought stress reduces suberin by up to 70% Song *et al*. (2011) Fig. (38),

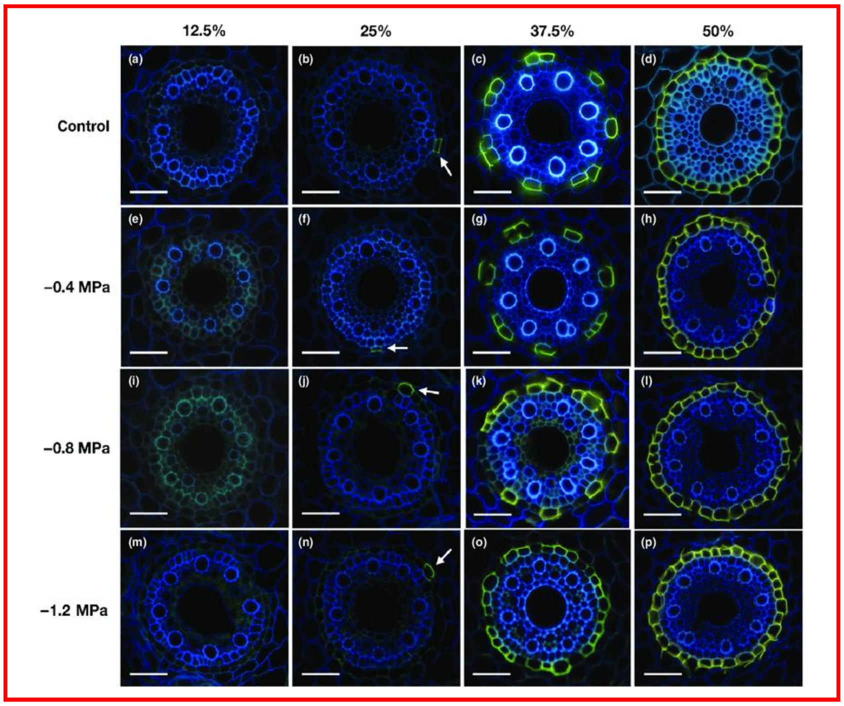


Fig. 38: Illustrates the development of suberin lamellae in the endodermis of barley seminal roots. Suberin lamellae in different zones of roots grown under different water potentials were stained with fluorol yellow 088. The presence of suberin lamellae is indicated by a bright yellow fluorescence. At a distance of 12.5%, no suberin lamellae are visible (a, e, i, m). At 25% of relative root length, the first single, only partially suberized, cells (arrows) are visible (b, f, j, n). At 37.5% of relative root length, a patchy suberization is visible, which is stronger in roots grown in the presence of (k, o) À0.8 MPa and À1.2 MPa compared with (c) control and (g) À0.4 MPa. At a distance of 50%, the endodermis is complete suberized in all growth conditions (d, h, l, and p). Bars, 50 lm. After Kreszies *et al*. (2018).

Kreszies *et al*. (2018) reported that barley (*Hordeum vulgare*) is more drought tolerant than other cereals, thus making it an excellent model for the study of the chemical, transcriptomic and physiological effects of water deficit. Roots are the first organ to sense soil water deficit. They studied the response of barley seminal roots to different water potentials induced by polyethylene glycol (PEG) 8000. We investigated changes in anatomical parameters by histochemistry and microscopy, quantitative and qualitative changes in suberin composition by analytical chemistry, transcript changes by RNA-sequencing (RNA-Seq), and the radial water and solute movement of roots using a root pressure probe. In response to osmotic stress, genes in the suberin biosynthesis pathway were upregulated that correlated with increased suberin amounts in the endodermis and an overall reduction in hydraulic conductivity (Lpr). In parallel, transcriptomic data indicated no or only weak effects of osmotic stress on aquaporin expression. These results indicate that osmotic stress enhances cell wall suberization and markedly reduces (Lpr) of the apoplastic pathway, whereas (Lpr) of the cell-to-cell pathway is not altered. Thus, the sealed apoplast markedly reduces the uncontrolled backflow of water from the root to the medium, whilst keeping constant water flow through the highly regulated cell-to-cell path.

They also concluded that In conclusion, this multifaceted study showed that water deficit, mimicked by different osmotic potentials through PEG 8000 treatment, markedly upregulated the suberin biosynthesis genes in barley seminal roots. By contrast, there was no or minimal effect on the expression of aquaporin genes, which are the regulatory components of water transport through the plasma membrane. The upregulation of suberin biosynthesis genes resulted in an increased endodermal suberization, thus reducing water movements through the apoplastic cell walls to prevent uncontrolled water losses from the root to the dry soil/medium. By contrast, water transport through the cell-to-cell path remained unaffected, and thus maintained further efficient water uptake from the soil into the central cylinder of the root. In the future, barley mutants might help to identify further suberin genes and to verify their functions. This could help us to better understand how altered suberin compositions and amounts in roots affect/regulate water and solute transport, and will aid in the improvement of future breeding programs to develop drought-tolerant barley cultivars.

Wang *et al*. (2019) stated that the endodermis is a key cell layer in plant roots that contributes to the controlled uptake of water and mineral nutrients into plants. In order to provide such functionality the endodermal cell wall has specifc chemical modifications consisting of lignin bands (Casparian strips) that encircle each cell, and deposition of a waxy-like substance (suberin) between the wall and the plasma membrane Fig (39). These two extracellular deposits provide control of diffusion enabling the endodermis to direct the movement of water and solutes into and out of the vascular system in roots. Loss of integrity of the Casparian strip based apoplastic barrier is sensed by the leakage of a small peptide from the stele into the cortex. Here, we report that such sensing of barrier integrity leads to the rebalancing of water and mineral nutrient uptake, compensating for breakage of Casparian strips. This rebalancing involves both a reduction in root hydraulic conductivity driven by deactivation of aquaporins, and downstream limitation of ion leakage through deposition of suberin. These responses in the root are also coupled to a reduction in water demand in the shoot mediated by ABA-dependent stomatal closure.

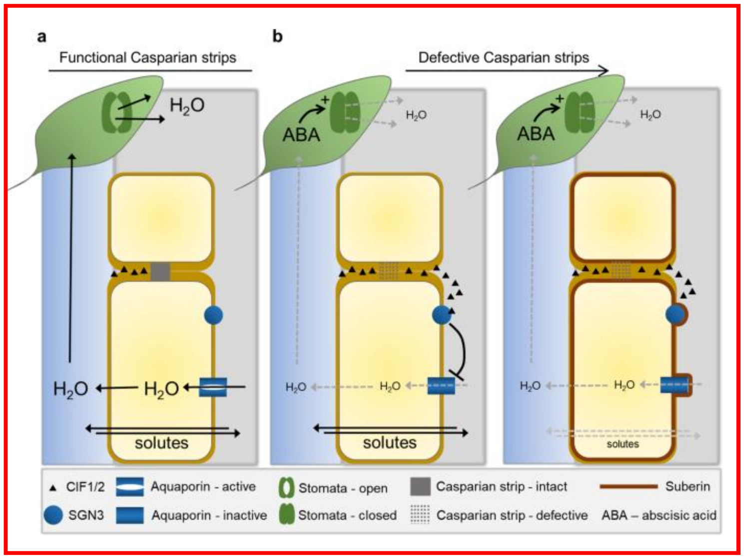


Fig. 39: Illustrates the integration between apoplastic endodermal diffusion barriers, hydraulic conductivity, solute permeability and stomatal conductance. (a) Functioning Casparian strips at the endodermis prevent the apoplastically localized peptide CIF1& 2 from diffusing from the stele, across the endodermis, and into the cortex. (b) Defective Casparian strips are detected by leakage of CIF1& 2 into the cortical apoplast where the peptides are sensed by binding to SGN3, signalling inactivation of aquaporins. This leads to reduced hydraulic conductivity and closure of stomates in leaves through a process mediated locally by ABA. Inactivation of aquaporins leads to the enhanced deposition of suberin that reduces solute conductivity across the root into and out of the xylem. After Wang *et al*. (2019)

If CO_2 does not increase suberin biosynthesis, and plants may suffer from water loss. The beneficial effects of CO_2 have been shown to vanish particularly under extreme drought stress, CO_2 fertilization may be unable to compensate for the negative effects of drought stress Zwieniecki, and Secchi (2015). In herbaceous plants (e.g., soybean), combination of elevated CO_2 and drought stress decreased the net of CO_2 assimilation, stomatal conductance, transpiration and biomass, but increasing water use efficiency (WUE) Milhinhos and Miguel (2013). In a study, the common bean (Phaseolus vulgaris L.) grown under pre-industrial CO_2 had a higher transpiration rate under moderate drought, and maintained normal net photosynthesis more than plants that were grown under ambient or elevated CO_2, which had increased WUE and water potential has not changed Milhinhos and Miguel (2013).. High atmospheric of CO_2, the bean plants were decreased the capacity of xylem, water transport in order to meet water demand, besides inducing transpiration limitations under stronger drought stress Milhinhos and Miguel (2013). Elevated of atmospheric CO_2 increased the diameter of xylem vessel .However no significant effect due to the interaction between them. Moreover, elevated CO_2 increases the chance of embolism due to increased vessel diameter Milhinhos and Miguel (2013).. In rice plants results showed that drought-tolerant rice grown at elevated CO_2, were able to maintain their stomatal conductance under drought conditions through reducing stomatal density Caine *et al*. (2019).

Temperature and their effects on root

Thermo morphogenesis signaling could differs between roots and shoots, a common set of mechanisms of temperature sensing mediate organ response Frontiers in at a molecular and cellular level Bellstaedt *et al*., (2019). Plants can sense small variations in temperature, and this sensing can be translated into activation of several physiological processes that are considered the primary temperature-sensing events Penfield, (2008); McClung and Davis, (2010). Roots sense these thermal changes directly or indirectly, indirect sensing is triggered either by the shoot demand of water and nutrient or by the supply of carbon from the shoot to root (Plieth *et al*., 1999; Heckathorn *et al*., 2013). Warmer temperatures, and more sharply, high temperature, alter the stability of membranes and cytoskeleton components, as well as proteins and nucleic acids Vu *et al*., (2019a).

Membranes serve as a selectively permeable barrier, and they are primarily composed of proteins and lipids in moving mosaics. Lipids with a polar head group and diverse types of long hydrophobic tails spontaneously form two leaflets in aqueous environments due to their amphipathic properties. Lipid species can be divided into three primary classes by chemical structure, namely, glycerolipids, sphingolipids and sterols Enrique Gomez *et al*., (2017). Among the abundant glycerolipids, phospholipids predominantly occur in the PM and mitochondrial envelope, while galactolipids primarily constitute the thylakoid membrane Dubots *et al*., (2012). Phospholipids contain two fatty acyl chains and a variable polar head group assembled to the glycerol backbone. Although their polar head groups usually sort phospholipids, the fatty acid moieties greatly control their physicochemical properties Escribá *et al*., (2008). The number and position of C–C bonds within hydrophobic acyl tails and the length of the carbon chains are thought to be key factors in determining the membrane fluidity Fujimoto and Parmryd, (2017). Moreover, the lipid composition of each leaflet reflects another membrane property (asymmetry). Lipids are selectively embedded in membrane bilayers; phosphatidylcholine (PC), glycolipids and sphingomyelin are predominantly enriched on the exoplasmic face of the PM and the lumenal side of internal organelles, while phosphatidylserine (PS), phosphatidylethanolamine (PE), and phosphatidylinositol (PI) are primarily found on the cytoplasmic side; cholesterol shows preferential accumulation on the exoplasmic leaflet, although it can move freely between the two leaflets Lenoir *et al*., (2007); Andersen *et al*., (2016). Additionally, some minor phospholipids, such as phosphatidic acid (PA), phosphatidylinositol-4-monophosphate (PIP) and phosphatidylinositol-4,5-biphosphate (PIP2), are also enriched on the cytoplasmic leaflet Gascard *et al*., (1991).

The fluid mosaic hypothesis proposed by Singer and Nicolson (1972) indicated that lipids formed a discontinuous, fluid bilayer in which proteins were embedded via specific interactions with lipids. Today, evidence regarding the structure and function of membranes inspires us to consider the bio membrane as a more complex and exquisite device Vereb *et al*., (2003); Cacas *et al*., (2012); Konrad and Ott, (2015). Different regions of membranes with defined lipids and clusters of proteins are not always equal, forming discrete platforms with varying sizes and traits in the plane of the membrane (which are denominated as membrane microdomains) Karnovsky *et al*., (1982); Thompson and Tillack, (1985); Simons and Ikonen, (1997); Simons and Toomre, 2000; Lillemeier *et al*., (2006); Fig. (40).

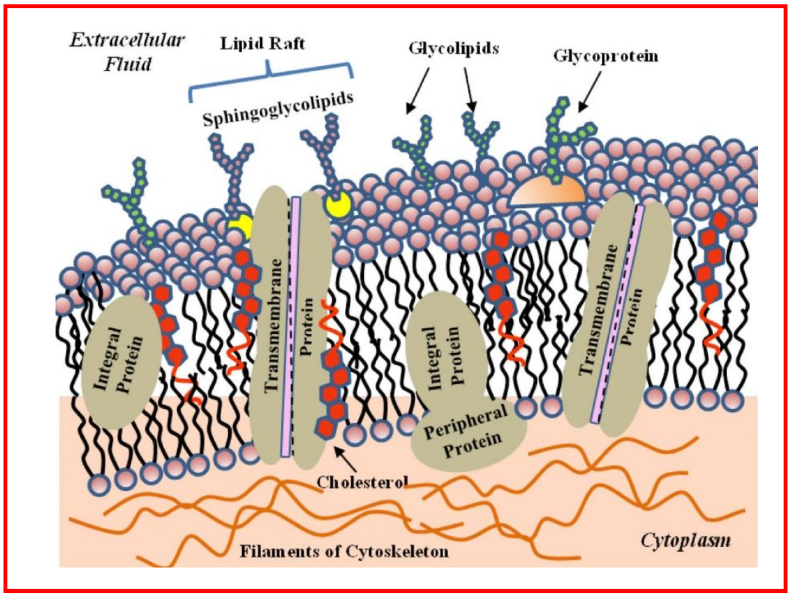


Fig. 40: Illustrates diagram of the fluid bilayer model of biological membranes in living Organism (fluid mosaic model). After Lombardo *et al*. (2020)

Historically, lipid rafts enriched in sphingolipids, sterols and glycosylphosphatidylinositol (GPI)-anchored proteins were thought to be equivalent to membrane microdomains or detergent-insoluble membranes (treated with 1% Triton X-100 at 4◦C; Brown and Rose, (1992); Cacas *et al*., (2012); Malinsky *et al*., (2013). Fig. (41).

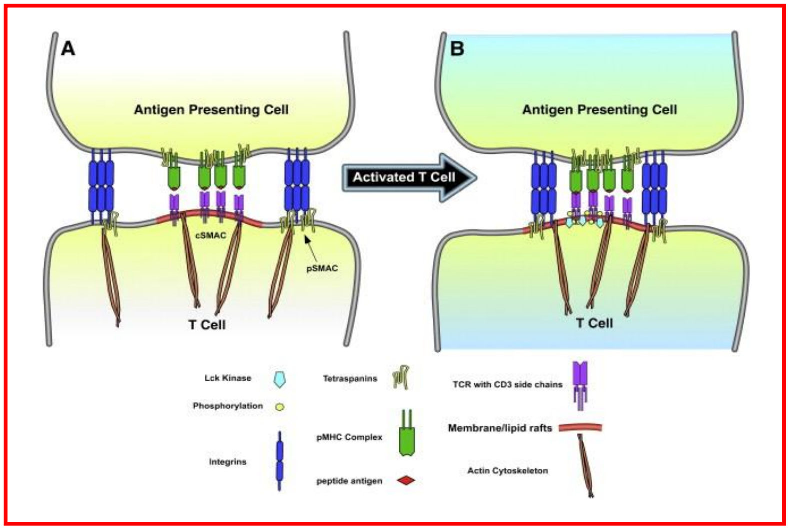


Fig. 41: Illustrates the interaction of membrane /lipid rafts with the cytoskeleton impact on signalling and function membrane lipid /rafts

Over the past decade, this idea has come to be considered controversial, if all of the above concepts reflect the authentic membrane substructure Malinsky *et al*., (2013). With the development of experimental approaches, the microdomains of membranes can now be distinguished at multiple scales Konrad and Ott, (2015). Nanoscale domains based on lipid rafts (2–100 nm) are incorporated into larger microdomains (e.g., raft platforms) via the interactions between specific lipids and proteins; both cytoskeleton and cell wall components prop up the largest units, which are denominated as the membrane compartments (40–300 nm), depending on the cytoskeletal and cell wall restriction of the lateral diffusion of membrane proteins Kusumi *et al*., (2005), (2011), (2012); Jacobson *et al*., (2007); Martinière *et al*., (2012). In contrast to lipid rafts with a highly dynamic nature in mammalian cells, special lateral membrane compartments in plant cells are more stable Cacas *et al*., (2012); Malinsky *et al*., (2013). Substantial evidence supports the notion that the microdomain acts as a harbor in which cellular signaling is clustered by the interactions between membrane components (including previously isolated channels, receptors, other signaling complexes and specific lipids) during many physiological processes, such as biotic and abiotic stress responses, membrane transport and polarized plant growth Laude and Prior, (2004); Lingwood and Simons, (2010); Malinsky *et al*., (2013); Jarsch *et al*., (2014); Wang *et al*.,(2018). An ROS-generating enzyme known as respiratory burst oxidase homolog D (RBOHD) has been suggested to localize to membrane microdomains Hao *et al*., (2014); Fig. (42)

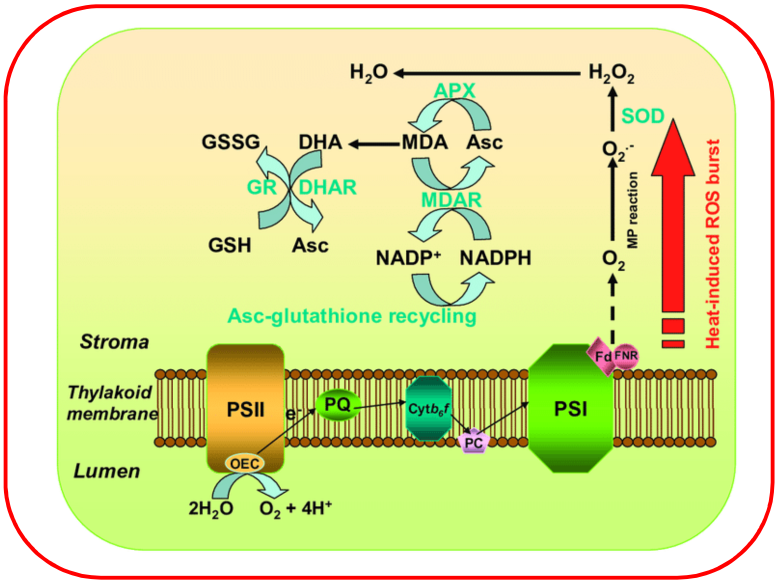


Fig. (42): A representative scheme of reactive oxygen species (ROS) generation and scavenging in chloroplasts under heat stress. High temperature stress triggers oxidative bursts of superoxide and/or hydrogen peroxide in plants. The transfer of excitation energy in the photosystem II (PSII) antenna complex and the electron transport in the PSII reaction center can be inhibited by heat stress. It has been established that ROS are generated on both the electron acceptor and the electron donor side of PSII under heat stress during which electron transport from the manganese complex to plastoquinone (PQ) is limited. The leakage of electrons to molecular oxygen on the electron acceptor side of PSII forms O2 •–, inducing initiation of a cascade reaction leading to the formation of H2O2. A diversified ROS-scavenging network functions in concert in chloroplasts, mainly including antioxidants and APX-glutathione cycle, to keep the equilibrium between ROS production and scavenging. The efficient enzymatic scavenging systems are composed of several key enzymes, including superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), Dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX) and glutathione-S-transferase (GST) and non-enzymatic systems contain antioxidants such as ascorbic acid (Asc) and glutathione (GSH). After Wang *et al.* (2018)

Wang *et al.* (2018) stated that increases in ambient temperatures have been a severe threat to crop production in many countries. Chloroplasts serve as metabolic centers and play a key role in physiological adaptive processes to heat stress. Heat shock proteins that protect proteins from heat-induced damage, metabolic reprogramming occurs during adaptive physiological processes in chloroplasts. Heat stress leads to inhibition of plant photosynthetic activity by damaging key components functioning in a variety of metabolic processes, with concomitant reductions in biomass production and crop yield. In this review article, we will focus on events through extensive and transient metabolic reprogramming in response to heat stress, which included chlorophyll breakdown, generation of reactive oxygen species (ROS), antioxidant defense, protein turnover, and metabolic alterations with carbon assimilation. Such diverse metabolic reprogramming in chloroplasts is required for systemic acquired acclimation to heat stress in plants. They also concluded that high temperature stress is one of the most important constraints to plant growth and productivity, especially for crop plants. The mechanism underlying the development of heat-tolerance for important agricultural crops as well as plant responses and adaptation to elevated temperatures needs to be better understood. Metabolic regulation of adaptation processes during heat stress is not only an important developmental process, but also allows for flexibility of physiological responses to heat stress. In photosynthetic organisms, heat stress can affect photosynthesis through altered carbon assimilation metabolism in chloroplasts with remobilizing their starch reserve to release energy, sugars and derived metabolites in order to help mitigate the stress. This is thought to be an essential process for plant fitness with important implications for plant productivity under high temperature stress. One future challenges is to dissect the complex interaction networks between heat stress sensing, signal transduction and activations of key genes involved in metabolic reprogramming in coordination with developmental programmes. Accumulation and modification of metabolites in chloroplasts under heat stress may play a key role in the regulation of adaptation processes at cellular levels in plants, allowing plants to interact with their environment and to activate cellular heat stress responses at the optimal time in order to maintain photosynthesis. This kind of metabolic reprogramming is critical for plants to survive stress periods, and to prevent further damage to the whole plant. The role of chloroplast in the metabolic regulation of heat stress responses has attracted increasing attention and extensive investigations from an organellar perspective have provided insights into better understanding the hypothesis stated that the heat stress-induced reprogramming, including decline in photosynthesis and alterations in photosynthetic metabolites which, in turn, could act as signal(s) or trigger the initial signal cascades to activate cellular heat stress responses. The present knowledge concerning the interplay between the chloroplast and nucleus in heat stress signal perception and activation of cellular heat stress responses is emerging, but more efforts are needed to reach a detailed overview. It can be predicted that uncovering the molecular mechanisms of heat sensing will pave the way to engineering plants capable of tolerating heat stress. It is well known that the ability of plants adapting to different climate regimes vary dramatically across and within species. Identification and functional analysis of the valuable heat-tolerant genetic resources will bring about a further significant improvement in manipulation of photosynthesis to increase crop yield based on a direct comparative analysis between the different manipulations with all the transgenic and wild type plants grown and assessed in parallel under filed growth conditions. Thus, in-depth analyses of the interactions between the chloroplast and nucleus in heat stress responses are likely to be in focus during forthcoming years. On the other hand, Rubisco activase and enzymes functioning in the detoxification of reactive oxygen species are thought to be critical targets for breeding heat-tolerant crop plants with high yields under high temperature stress.

Heat induced cytosolic calcium increase to immediately produce an oxidative burst Suzuki *et al*., (2011) Fig. (43). However, numerous microdomain-associated proteins remain to be elucidated in plants. Notably, increasing evidence from mammals has illustrated that several HSPs localize to PM rafts via interactions with specific lipids Escribá *et al*., (2008). These HSPs include abundant HSP70, HSP90 and other small HSPs (e.g., HSP27), the functions of which have been suggested to include the recruitment of signaling proteins to the PM, the folding of membrane proteins, assisting polypeptides in translocation across the membrane bilayer, and rapidly remodeling and protecting the PM under cellular stresses Arispe *et al*., (2002); Shah *et al*., (2002); Vega and De Maio, (2005); Vigh *et al*., (2005), (2007b). Although the mechanism controlling the interactions between HSPs and membrane lipids and proteins is less well known, it is speculated that the structure of lipid rafts is crucial for HSPs to perform their individual functions in cell responses Escribá *et al*., (2008). Whether HSPs in plants exhibit similar behaviors at PM microdomains has not yet been explored.

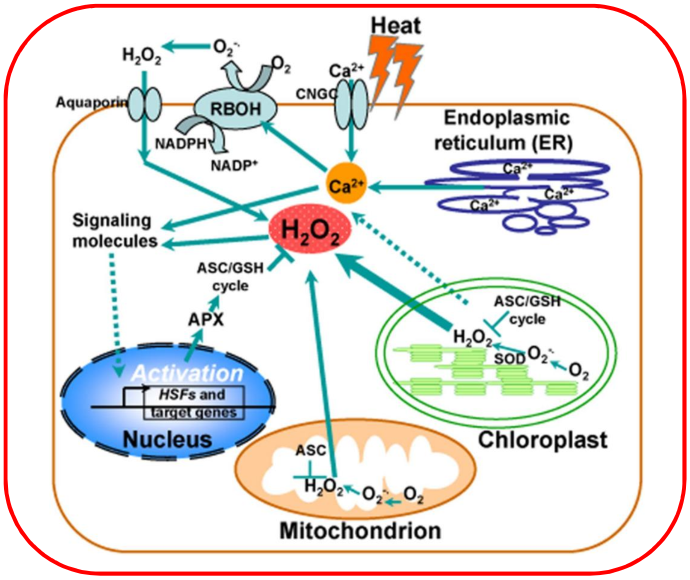


Fig. 43: Schematic representation of the major generation sites of ROS and transient calcium increase from different intracellular stores and the influx of extracellular calcium into the cell induced by the opening of cyclic nucleotide gated channels (CNGC) in the plasma membrane in response to heat stress. Heat stress induces activation of calcium channels in ER membranes, leading to the release of calcium in to the cytosol. Chloroplast is a major producer of ROS during photosynthesis under heat stress and contains a large array of ROS-scavenging mechanisms. ROS production also occurs in mitochondria. Hydrogen peroxide (H_2O_2) and Ca_2+ serve as second messengers involved in heat-responsive activation of genes with heat shock elements in their promoters, such as heat shock transcription factors (HSFs), heat shock proteins (HSPs), and cytosolic ascorbate peroxidase (APX). Under heat stress, the maintenance of ROS homeostasis is involved in redox enzymes and metabolites, such as superoxide dismutase (SOD) and the ascorbate–glutathione (ASC–GSH) cycle, functioning in different cell compartments. A NADPH oxidase (respiratory burst oxidase homolog RBOH) in the plasma membrane becomes activated by heat stress via an increased membrane fluidity and/or via a consequent increase in cytosolic levels of Ca_2+ controlled by a Ca_2+ permeable channel (CNGC). Ca_2+ influx activates RBOH by promoting its phosphorylation, leading to the increase of ROS. After Sun and Guo (2016).

Sun and Guo (2016) reported that intracellular signaling from chloroplast to nucleus plays a vital role in stress responses to survive environmental perturbations. Chloroplasts proposed as sensors to heat stress since components of the photosynthetic apparatus housed in the chloroplast are the major targets of thermal damage in plants. Thus, communicating subcellular perturbations to the nucleus is critical during exposure to extreme environmental conditions such as heat stress. By coordinating expression of stress specific nuclear genes essential for adaptive responses to hostile environment, plants optimize different cell functions and activate acclimation responses through retrograde signaling pathways. The efficient communication between plastids and the nucleus is highly required for such diverse metabolic and biosynthetic functions during adaptation processes to environmental stresses. In recent years, several putative retrograde signals released from plastids that regulate nuclear genes have been identified and signaling pathways have been proposed. In this review, we provide an update on retrograde signals derived from tetrapyrrole, carotenoids, reactive oxygen species (ROS) and organellar gene expression (OGE) in the context of heat stress responses and address their roles in retrograde regulation of heat-responsive gene expression, systemic acquired acclimation, and cellular coordination in plants.

Temperature changes alter membrane fluidity and composition causing the activation of calcium (Ca_2C) channels. Increased intracellular Ca2C triggers the lipid signaling through the lipid-modifying enzymes PLD and PIPK. Subsequent accumulation of PIP2 and IP3; in turn, enhances Ca2C entry in the cell Mittler *et al*., (2012). The Ca2C influx can activate several heat shock transcription factors (HSFs) and calcium-dependent protein kinases (CDPKs and MAPKs) that control heat stress responses. The ROS/redox signaling network is also mediating plant sensing to high temperature due to direct activation of HSFs and heat related MAPKs. ROS accumulation may produce as unwanted products of several metabolic pathways due to heat mediated changes in the stability and activity of their enzymes or by calcium activation of ROS-producing enzyme RBOHD Suzuki *et al*., (2011); Rasul *et al*., (2017). Heat stress causes accumulation of unfolded proteins in the endoplasmic reticulum (ER) that are potentially toxic leading to what is known as ER stress. ER stress elicits the unfolded protein response (UPR), a cytoprotective response to mitigate and to protect from this damage Howell, (2013). The UPR is signaled through two pathways: one involving the proteolytic processing transcription factor bZIP28, and the other involving the ribonuclease IRE1, which mediates the splicing of the bZIP60 transcription factor mRNA Neill *et al*., (2019). Both UPR pathways induce the expression of Heat Shock Proteins (HSPs) and activation of brassinosteroids (BRs) signaling Che *et al*., (2010). These two pathways seems to be less sensitive than Ca2C channels because only high temperatures are able to provoke a global unfolding of proteins Liu and Howell, (2016). HSPs are actively translated during the onset of temperature stress response to protect proteins from misfolding and subsequent loss of functionality. Nevertheless, HSPs also improves membrane stability and detoxification of ROS by regulating several antioxidant enzymes therefore attenuating stress response Ul Haq *et al*., (2019). ARP6, a subunit of SWR1 complex, has been proposed as a histone them sensor. ARP6 mediates the insertion of the variant histone H2A.Z in the nucleosome. H2A.Z nucleosomes wrap DNA more tightly, which affects the ability of RNA polymerase (Pol) II to initiate transcription. At warmer temperatures, H2A.Z is evicted from the nucleosomes located at the transcriptional start of heat response genes Kumar and Wigge, (2010). This process also required the recruitment of HSFA1 to the promoters of these genes to activate their transcription Cortijo *et al*., (2017). Therefore, the antagonistic roles of H2A.Z and HSF1 seems to be require to activate gene expression rapidly and precisely in response to elevated temperature Wigge, (2013). Lastly, warmer temperature could alter RNA unfolding, metabolism and structure Su *et al*., (2018) as well as changes in small RNA expression Liu *et al*., (2017). It also causes a recruit of alternative splicing (AS) machinery that will allow the rapid adjustment of the abundance and function of key stress-response components Laloum *et al*., (2018). All these pathways trigger different sensing events that contribute to the activation of the overall heat response. This heat response includes a large number of morphological, physiological, metabolic and molecular changes altering root growth that we will describe in more detail. Morphological and Physiological Response Roots need an optimal temperature range to have a proper growth rate and function. In general, optimal root temperature tends to be lower than optimal shoot temperature. Crop roots have different optimal root temperature depending on the species. Within this range, a higher temperature is usually associated to altered root:shoot ratio, and a further increase in temperature would limit root development and alter root system architecture (RSA) reducing root:shoot ratio Ribeiro *et al*., (2014); Koevoets *et al*., (2016). RSA is defined as the organization of the primary, lateral, adventitious and accessory roots. Each RSA is determined by parameters such as length, number and angle of these root components. RSA is the main factor that controls nutrient and water uptake efficiency since it determines the soil volume that roots are able to explore at different environmental situations Lynch, (1995) Fig. (44).

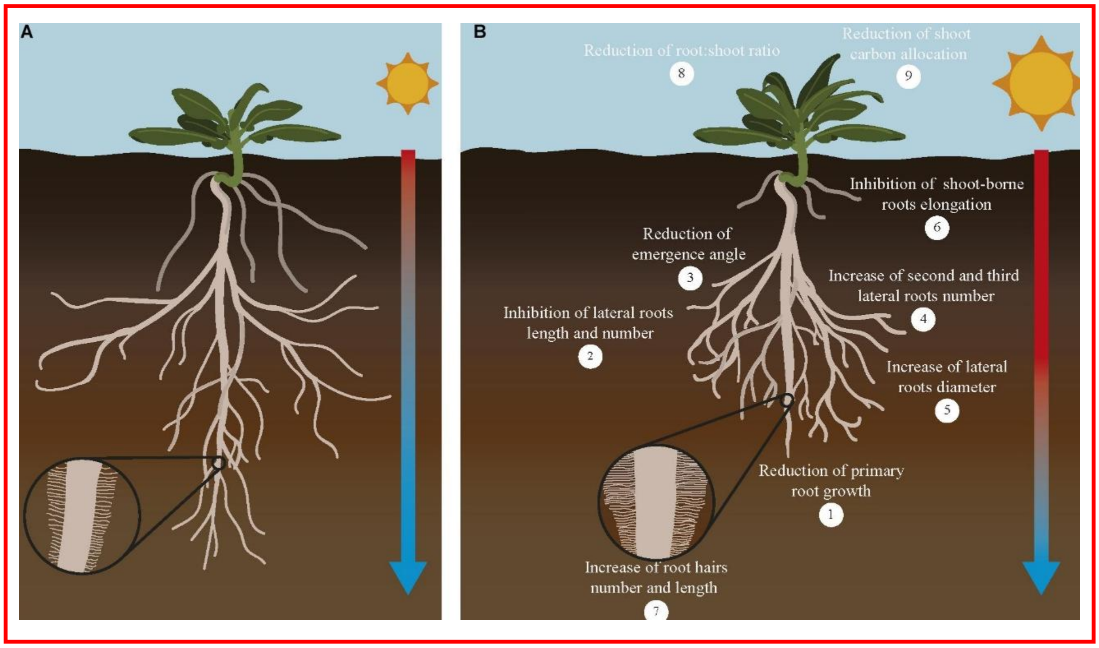


Fig. 44: Illustrates the response of major root traits to increasing temperatures in crops. Increasing temperature of the soil affects root traits related with its organization, growth and function. Root system architecture defined as the organization of the primary, lateral, shoot-borne and lateral roots is drastically altered in response to increased temperature in the soil (B) compared to plants growing in optimal conditions (A). Crops growing under higher temperatures show shorter primary roots (1), reduction of lateral roots growth and number (2) and their angle of emergence (3), higher number of second and third order roots (4) with larger diameter (5), inhibition of shoot-borne roots (adventitious and nodal roots) elongation and number (6) and increase of root hairs number and length (7). In addition, this overall reduction on root system growth causes a reduction of root:shoot ratio (8) and reduction of root carbon allocation (9). Because of all these changes, nutrient and water uptake conducted by the roots for the whole plant is compromised and crop yield is severely affected. Although most of these effects are detrimental to root growth, some responses alleviate this situation by increasing root:soil surface [increase in number of second to third roots number (4) and number and length of root hairs (7)], improving water efficiency uptake [increase in diameter of roots (5)], or increase in root depth (lower root angle). Interestingly, these root responses coincide with root traits associated with cultivars more tolerant to high temperatures. A comprehensive evaluation of these traits and their impact on crops productivity will help to decide which root traits are more valuable to be incorporated to breeding programs designed to improved crop yield under climate change conditions. After Calleja-Cabrera *et al*. (2020).

Generally, the exposure of roots to temperatures higher than the optimal causes a decrease in the primary root length, number of lateral roots and their angle of emergence. Moreover, the increase in temperature causes the initiation of second and third order lateral roots that are characterized by a larger diameter Fig. (43). The negative effect of increasing temperatures usually reduces the surface between root and soil, therefore decreasing nutrient and water uptake Nagel *et al*., (2009). In cassava and sweet potato, high root zone temperature significantly decreases the total length of the adventitious roots and the number and total length of the first order lateral roots Pardales *et al*., (1999) Fig. (45 a&b).

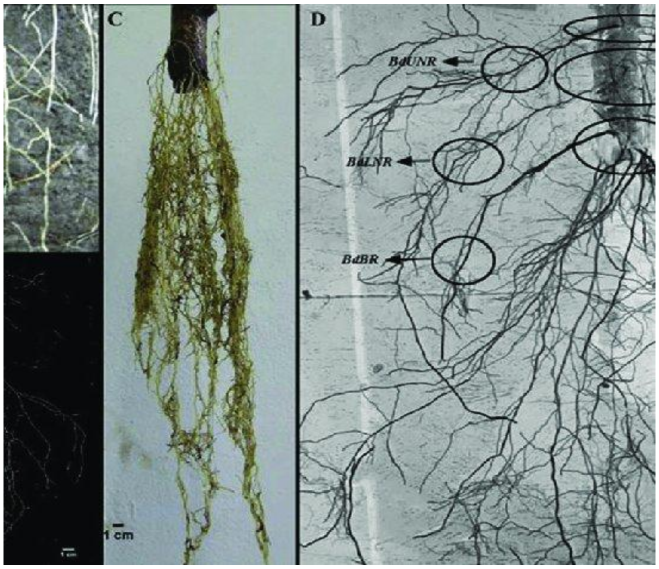


Fig. 45a: Illustrates **(A)** image of cassava plant growing in polyethylene pot. **(B)** Image showing a cross-section of a 30 d old cassava plant root system growing in a soil-filled polyethylene pot. **(C)** Image illustrating a washed root system of a juvenile (45 DAP) cassava plant. **(D)** Category of adventitious roots used in this study: upper nodal roots: emerged from the topmost nodes within the top 7 cm below the soil surface; lower nodal roots: emerged from the nodes on the stem cutting with 7e13 cm below the soil surface; basal roots: emerged from the callus at the base of the stem cutting. Ten traits were assessed visually on the washed root system: number of upper nodal roots (NUNR), diameter of upper nodal roots (DUNR), branching density of upper nodal roots (BdUNR), number of lower nodal roots (NLNR), diameter of lower nodal roots (DLNR), branching density of lower nodal roots (BdLNR), total number of nodal roots (TNR), number of basal roots (NBR), diameter of basal roots (DBR) and branching density of basal roots (BdBR); **(E)** Sample image of a cassava root system showing skeletonized root image for measuring total root length. After Michael *et al*. (2018).

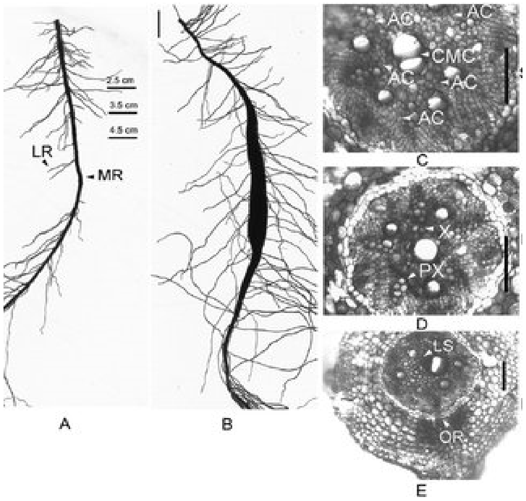


Fig.45b: Illustrates root samples harvested at 20 (A) and 40 (B) d after transplanting and representative micrographs used to classify 20-d-old adventitious roots into various stages in ‘Beauregard’ sweet potato: initiated storage root (C), pencil root (D), and lignified root (E). Adventitious roots (A–B) were floated on waterproof trays and images were acquired using a scanner equipped with the WinRhizo positioning system. (A) Location of tissue sections used for anatomical examination for each 20-d-old adventitious root sample. Samples C–E were derived

from the 4.5-cm section of the respective 20-dold adventitious root specimens. LR = lateral root; MR = main root; SR = initiated storage root; PR = pencil root; LG = lignified root; AC = anomalous cambium; PX = protoxylem; CMC = central metaxylem cell; X = protoxylem element remains connected to CMC; LS = lignified stele; OR = origin of lateral root. Scale bars for A–B = 1 cm. Scale bars for C–E = 0.15 mm. After Villordon (2012).

Seminal and crown roots retarded their emergence and elongation when wheat seedlings are grown at high temperature Huang *et al*., (1991a). In maize adult plants, the increase in temperature slows down lateral root growth to promote the development of long axile roots to reach the water of the deeper soil layers Hund *et al*., (2008). Nevertheless, in potato, the increase in temperature causes the inhibition of adventitious and lateral roots initiation and elongation. Other effects of the warmer soil in potato are the swelling of the root cap meristem and bending of the root tip. Alteration of root growth in these crops seems to be caused by a decrease in the cell division rate Sattelmacher *et al*., (1990); Joshi *et al*., (2016). Similarly, in sorghum, high root zone temperature reduces the elongation and cell production rate in seminal roots Pardales *et al*., (1992). Interestingly, in wheat the increase in temperature causes a decrease in the length and number of central late metaxylem in the root tip. This change has been interpreted as an adaptation to limit damage in the root by the changes in water viscosity and root hydraulic conductance produced by heat Huang *et al*., (1991b); Morales *et al*., (2003). Another strategy used by roots to cope with changing environmental conditions that affect water and nutrient availability is increasing the number of root hairs and their length. This increase enhances root surface area that in turn will improve soil exploration, and therefore, water and nutrient uptake Pregitzer *et al*., (2000). Hence, the contribution of root hairs to total root surface area in two crops, oilseed rape and barley increases with temperature. This increase provides their roots with a greater surface area for absorption per unit root weight or length Macduff *et al*., (1986). In Arabidopsis and soybean, the lack of root hairs produces reduction in heat adaptation competence suggesting a key role of root hairs in short-term adaptation to high temperatures Tanaka *et al*., (2014); Valdés-López *et al*., (2016). Moreover, since genes that participate in early sensing and adaptation to high temperature are switched off in barley root-hairless mutant plants, it has been suggested a role of root hairs as sensors of environmental soil condition Kwasniewski *et al*., (2016). Communication between aerial and belowground organs seems to underlie heat tolerance and root response in some crops. Several studies made with tomato have shown that the more heat tolerant varieties are those that have a higher root activity or a larger RSA. Wider root system can access to more water and nutrient sources, increasing the water uptake and letting the leaves to increase its evapotranspiration rate, cooling their canopy temperature and improving the photosynthetic rate. This in turn allows that larger quantity of assimilates can be used to boost root growth Shaheen *et al*., (2016); Zhou *et al*., (2019). On the other hand, it has also been observed that carbon translocation from shoots to roots is inhibited at high soil temperatures. Under high temperature field conditions, wheat root growth is diminished due to a reduction in the carbon partitioned belowground, and the number, length and diameter of roots are especially affected Batts *et al*., 1998). Similarly, in grape, an increase in the temperature reduces root growth rate whereas shoot growth increases due to alteration of assimilate partition (Mahmud *et al*., (2018). This sink effect of the aerial part of the plants is mostly observed during the reproductive stage, when the carbon partitioning to the root decreases to help flowering and seed development. In summary, warmer soils cause alteration in RSA and root functionality triggering numerous changes in the whole plant in order to adapt to this climatic variance. One more aspect of root adaptation that is being increasingly explored is the effect of gradient temperature on root architecture. Parts *et al*., (2019). Füllner *et al*., (2012).. Pfeifer *et al*., (2014); Hecht *et al*., (2016).

Role of hormones in plant adaptation to heat Stress

Plant growth and development are precisely regulated by coordination of both exogenous (environmental) and endogenous signals Peleg and Blumwald (2011), Santner *et al*. (2009). External environmental factors such as light, temperature, moisture, and atmospheric carbon dioxide at optimum levels are essential for normal metabolic processes in plants. Among those various environmental factors, temperature is of great significance in the regulation of plant phonological development Bahuguna and Jagadish (2015). A temperature beyond the “physiological optimum” that disturbs normal growth and development of a plant is generally considered as “high temperature” for that plant. Extremely high temperatures have the potential to cause “heat stress” in plants. However, the physiological threshold for the highest temperature that causes irreversible damage varies significantly across the plant kingdom even within genotypes. Heat-induced damages include changes in stability of proteins, enzymes, nucleic acids, bio membranes, and cytoskeletal structures Asthir (2015) Fig. (46).

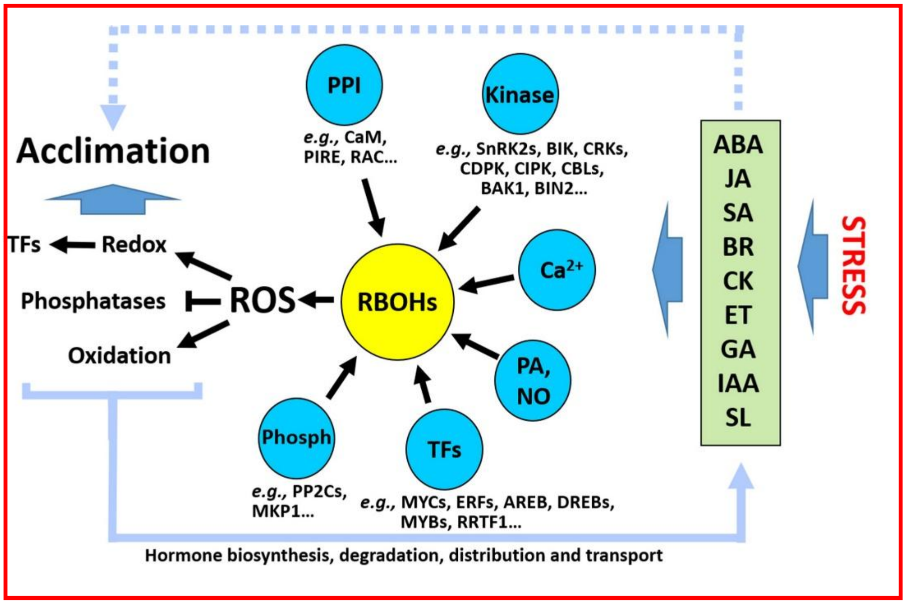


Fig. 46: Illustrates the respiratory burst oxidase homolog (RBOH) proteins play a key role in the integration of reactive oxygen species (ROS) and hormone signaling in plants. Stress is shown to alter the levels of different hormones that in turn regulate RBOHs activity and ROS production via many different mechanisms. These include, but are not limited to, phosphorylation/dephosphorylation, calcium binding, nitrosylation, binding of phosphatidic acid (PA) and changes in the level of RBOH proteins via enhanced transcription mediated by different transcription factors (TFs). Enhanced ROS levels in turn alter different redox reactions and impact transcription, inhibit phosphatases and/or cause direct hormone oxidation, altering the overall level of different hormones and regulate acclimation. ABA, abscisic acid; AREB/ABF, ABA-responsive promoter elements binding factors; BAK1, brassinosteroid insensitive 1-associated kinase 1; BIK, Botrytis-induced kinase 1; BIN2, brassinosteroid insensitive 2; BR, brassinosteroid; Ca2+ , calcium; CaM, calmodulin; CBLs, calcineurin B-like proteins; CDPK, calcium-dependent protein kinase; CIPK, calcineurin B-like interacting protein kinase; CK, cytokinin; CRKs, cysteine-rich kinases; DREBs, dehydration response element binding factors; ERFs, ethylene response factors; ET, ethylene; GA, gibberellin; IAA, indole-3-acetic acid; JA, jasmonic acid; MKP1, mitogen-activated protein kinase phosphatase 1; NO, nitric oxide; PIRE, PBL13 interacting RING domain E3 ligase; PP2Cs, protein phosphatase 2Cs; PPI, protein–protein interactions; RAC, Rac-like GTP-binding protein; RBOHs, respiratory burst oxidase homologs; RRTF1,redox responsive transcription factor 1;SA, salicylic acid; SL, strigolactone; SnRK2s, SNF1-related protein kinase 2. After Devireddy *et al*. (2021).

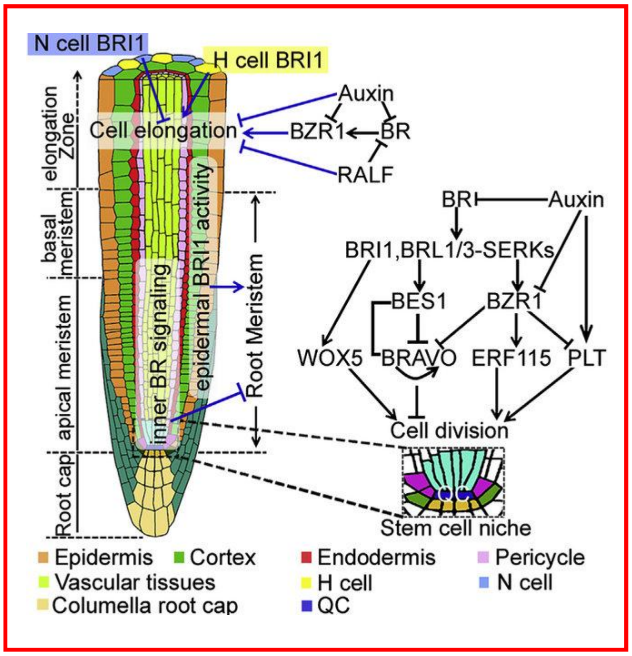
Devireddy *et al*. (2021) reported that abiotic stress conditions such as drought, heat, salinity, cold and particularly their different combinations inflict a heavy toll on crop productivity worldwide. The effects of these adverse conditions on plant productivity are becoming ever more alarming in recent years in light of the increased rate and intensity of global climatic changes. Improving crop tolerance to abiotic stress conditions requires a deep understanding of the response of plants to changes in their environment. This response is dependent on early and late signal transduction events that involve important signaling molecules such as reactive oxygen species (ROS), different plant hormones and other signaling molecules. It is the integration of these signaling events, mediated by an interplay between ROS and different plant hormones that orchestrates the plant response to abiotic stress and drive changes in transcriptomic, metabolic and proteomic networks that lead to plant acclimation and survival. Some of the different studies that address hormone and ROS integration during the response of plants to abiotic stress, further highlight the integration of ROS and hormone signaling during early and late phases of the plant response to abiotic stress, the key role of respiratory burst oxidase homologs in the integration of ROS and hormone signaling during these phases, and the involvement of hormone and ROS in systemic signaling events that lead to systemic acquired acclimation. Lastly, we underscore the need to understand the complex interactions that occur between ROS and different plant hormones during stress combinations.

In order to maintain appropriate balance in metabolic processes, plants thoroughly or partially reprogram its transcriptome, proteome, metabolome, and lipidome Mittler *et al*. (2012). The frequency and magnitude of temperature extremes are being increased due to global climate change. Extreme seasonal heat that is considered as an important attribute of climate change could have detrimental impacts on agricultural productivity and food security by directly affecting crop growth and yield. In the tropics and subtropics, growing season temperatures will exceed the recorded highest seasonal temperatures of the last century by the end of the twenty-first century. Empirical data show that every 1 °C increase in seasonal temperature will likely to cause 2.5 to 16 % direct yield losses Battisti and Naylor (2009), Lesk *et al*. (2016).

Estimating that a 1°C increase in seasonal mean weather associated with extreme heat disasters results in a yield sensitivity of 6–7 %. Thus, rising temperature represents severe risks of food insecurity. It is anticipated that increasing heat stress will cause complete extinction of many species Field *et al*. (2014). A better understanding of this complex heat response mechanism is important for future genetic manipulation of crops to ensure food security in the face of climate change Hasanuzzaman *et al*. (2013); Kazan (2015). Phytohormones are the endogenous messenger molecules that play a critical role in plant growth, development, and responses to various stresses. A number of previous reports provided solid evidence that phytohormones are actively involved in the response of plants to heat stress Ahammed *et al*. (2014); Peleg and Blumwald (2011) ; Xia *et al*. (2015). Moreover, majority of the phytohormones provide physiological protection against heat stress. In addition to the individual role of a plant hormone, cross talk between multiple hormones precisely coordinates plant defense response to heat stress. Although significant advancement has been achieved in the molecular mechanisms of heat perception, the mechanisms that control phytohormones mediated responses to heat stress remain largely unknown.

Plant hormones for root development and growth

Several plant hormones that take part in root development and growth have been described to mediate temperature stress response in this organ. In particular, a role of BRs Bajguz and Hayat, (2009); Anwar *et al*., (2018), salicylic acid (SA) Dat *et al*., (1998), ethylene (ET) Lin *et al*., (2009), abscisic acid (ABA) and cytokinin (CK) Vishwakarma *et al*., (2017) has been reported in several crops. Temperature-mediated alteration of these hormone levels trigger signal transduction pathways that prepare plants to overcome the stress situation. Key phytohormones including ABA, SA, and ET increase their levels under heat stress, while others such as CK, auxin (AUX), and gibberellins (GAs), decrease Talanova *et al*., (2003); Larkindale and Huang, (2004); Larkindale *et al*., (2005); Nolan *et al*., (2017), (2019). Regulation of root response to temperature is mediated by BRs signaling in Arabidopsis Fig. (47).



Fig, 47: Illustrates BRs Play Important Roles in Regulating Root Meristem Maintenance and Root Elongation. The anatomy of an Arabidopsis root is shown. While BR signaling in the epidermis promotes stem cell proliferation to regulate root meristem size, BR signaling in the inner cells attenuates the effect of BRI1 in epidermal cells (left). In addition, BRs control root meristem size by directly regulating QC cell division (right). The functions of BRs in regulating root cell elongation are shown in the left panel. The expression of BRI1 in hair cells or no hair cells promotes or inhibits root elongation, respectively. BR and auxin antagonistically regulate the expression of BZR1-target genes to control root elongation. RALF antagonizes the action of BR in regulating root cell elongation. Arrows and bar ends indicate activation and inhibitory effects, respectively. After Wei and Li (2016).

The Arabidopsis primary root is also patterned longitudinally along its apical-basal axis, including the root cap, meristematic zone, elongation zone, and differentiation zone. Stem cells in the meristematic zone at the root tip divide multiple times to generate a pool of cells that will elongate and differentiate. Shoot ward of the meristematic zone is the elongation zone where cells lose their ability to divide but increase in length by many times their width. In the differentiation zone, cells exhibit their mature characteristics and functions, for instance, the formation of root hairs from epidermal cells. The differentiation zone is also the site of emergence of lateral roots. Growth and development of a plant root system needs coordinated regulation of endogenous cues as well as environmental signals. Previous studies demonstrated that plant root growth and development are inextricably linked with phytohormones Pacifici *et al*., (2015). Brassinosteroids (BRs) are a class of polyhydroxylated steroidal hormones playing pivotal roles during many aspects of plant growth and development, such as cell elongation, cell division, senescence, vascular differentiation, reproduction, photo morphogenesis, and responses to various stresses Clouse and Sasse, (1998); Divi and Krishna, (2009). A variety of BRs were identified in the roots of different plant species, such as maize and Arabidopsis Yokota *et al*., (2001); Shimada *et al*., (2003); Kim *et al*., (2005b). Mutants impaired in BR biosynthesis or signal transduction display a short-root phenotype Li *et al*., (1996); Mussig *et al*.,(2003). Physiological analyses indicated that supplementation of low concentrations of BRs can promote root growth, whereas application of high concentrations of BRs can inhibit root growth Roddick *et al*., (1993); Clouse *et al*., (1996); Mussig *et al*.,(2003). Recent studies suggested that BRs play important roles during root growth and development. Here we briefly summarize our current understanding of BR signal transduction and homeostasis, and discuss the roles of BRs and their interplays with other signaling pathways in regulating root growth and development.

Increasing temperature reduces the level of the BR receptor BRI1 to down regulate BR signaling and increases root elongation independently of auxin Martins *et al.*, (2017). Interestingly, it has been proposed that down regulation of BR signaling by temperature elevation could promote GA-dependent root growth. In contrast, in crops, different behavior of BRs has been reported. The application of 24-epibrassinolid (24-EBR), a functional BR, to tomato and oilseed rape seedlings inhibits root elongation in both species but increase their acquired thermatolerance. Molecular analyses of 24-EBR treated and untreated seedlings show that this thermatolerance is a result of increased levels of HSPs Dhaubhadel *et al.*, (1999), (2002). On the contrary, transgenic lines of oilseed rape overexpressing AtDWF4, an Arabidopsis gene encoding an enzyme that catalyzes a bottleneck step in BR biosynthesis, shows an increased root length and fresh and dry root weight. However, the transgenic plants show an increased thermatolerance, and consistent with the results in tomato and oilseed rape, the level of different HSPs gene family members were increased Sahni *et al.*, (2016). Improved plant tolerance to heat stress mediated by SA has also been reported in crops Khan *et al.*, (2015); Nazar *et al.*, (2017). In soybean, wheat, maize and chamomile, this tolerance seems to be mediated by the growth-stimulating effects of SA Rivas- San Vicente and Palencia, (2011). Additionally, exogenous SA has a protective role in mitigating extreme temperature-induced damages in different crops Hasanuzzaman *et al.*, (2017). In grape cultivars root-derived SA have a role in the response to aboveground high temperature. The increase in temperature did not affect free SA content in roots but reduced the levels of conjugated SA, a storage form of this hormone. It is proposed that the sensing of warmer temperatures causes roots to send its conjugated SA reserves to the aboveground parts of the plant where is transformed into free SA to promote the adaptation and resistance to heat stress Liu *et al.*, (2008). Elevated temperature (ET) also takes part in root adaptation to increased temperatures. ET production is increased under heat stress, although exogenous ET application cannot confer heat tolerance Müller and Munné-Bosch, (2015). Nevertheless, thermatolerance is enhanced in rice seedlings under heat stress by an increase in the levels of ET Wu and Yang, (2019). In sorghum, heat induced inhibition of root elongation and cell production rate is affected by ET levels Prasad *et al.*, (2008). Likewise, in lettuce, temperature promotes the synthesis of ET. Moreover, exogenous ET application to the root causes heat stress symptoms including reduced root length and surface area and increased root diameter. Application of ET biosynthesis inhibitors to plants exposed to heat alleviates the root growth inhibition. Interestingly, ET effect in this crop has been linked to a similar root-to-shoot communication mechanisms described for SA signaling. Higher ET biosynthesis produced by increased temperatures causes an efflux of ACC, the ET precursor, to the shoot via xylem. ACC then promotes thermatolerance in aboveground tissues by the reduction of oxidative damage and maintenance of chlorophyll content Qin *et al.*, (2007). ABA is one of the main hormones to control tolerance to abiotic stress and its biosynthesis is promoted by these stresses in roots. In cucumber, the application of higher temperature to the whole seedling increases the levels of ABA in both leaves and roots Talanova *et al.*, (2003). ABA seems to improve heat tolerance through exogenous application or by manipulation of ABA-related genes in some crops. This tolerance is achieved by increasing leaf photochemical efficiency and membrane stability or by induction of HSF Abass and Rajashekar, (1991); Zhou *et al.*, (2014); Wang *et al.*, (2017). ABA also seems to increase root hydraulic conductance and promote root hair development during adverse environmental situations Vishwakarma *et al.*, (2017) and it has been suggested as a potential candidate of root-to-shoot communication Talanova *et al.*, (2003). CKs are one of the key regulators of root system architecture and they have been implicated in heat stress. In contrast to their role in promoting growth in the shoot, CKs reduce root growth, by inhibiting primary root elongation and promoting cell differentiation in the root apical meristem Dello Ioio *et al.*, (2008). They are also regulators of root branching Chang *et al.*, 2015). A decrease in CK levels or a reduction in CK signaling can lead to an enlarged root system improving temperature root response Bielach *et al.*, (2017); Kieber and Schaller, (2018). Contrarily, stress driven alteration of CKX1 levels in roots, a CK oxidase/dehydrogenase (CKX) enzyme that regulates CK degradation, results in enhanced drought and heat tolerance in tobacco. The enhanced stress tolerance of these plants has been correlated with raised bioactive CK levels during the early phase of the stress response Macková *et al.*, (2013). In summary, several hormones are known to control root growth and are in charge of controlling this process during high temperature stress. Modulation of hormonal signaling in roots in response to heat not only prepares this belowground organ to respond to this stress but also the whole plant since some hormones like SA, ET and ABA could act as intercommunication signals between the root and the aboveground organs.

Hormones response to root under heat Stress

Several researchers Ribeiro *et al*., (2014); Aidoo *et al*., (2016); Sun *et al*., (2016), reported that during heat stress, plant roots suffer large quantity of metabolic changes to maintain homeostasis and allow the plant to survive. It has been suggested that overall alteration of metabolic pathways probably depend on the sensitivity to high temperature of key metabolic regulatory enzymes. Different studies carried out in crops and fodder species shows a common pattern in the response of primary and secondary metabolism to heat stress in roots. Main carbohydrates such as glucose, fructose, galactose, sucrose or xylose are usually lower after the root experience high temperatures, as well as the levels of several glycolytic cycle enzymes. In, cassava, warmer soils inhibit starch biosynthesis through the direct decrease of enzymatic activity or down regulation of transcriptional levels of the main starch biosynthesis enzyme Ma *et al*., (2018) Fig. (48).

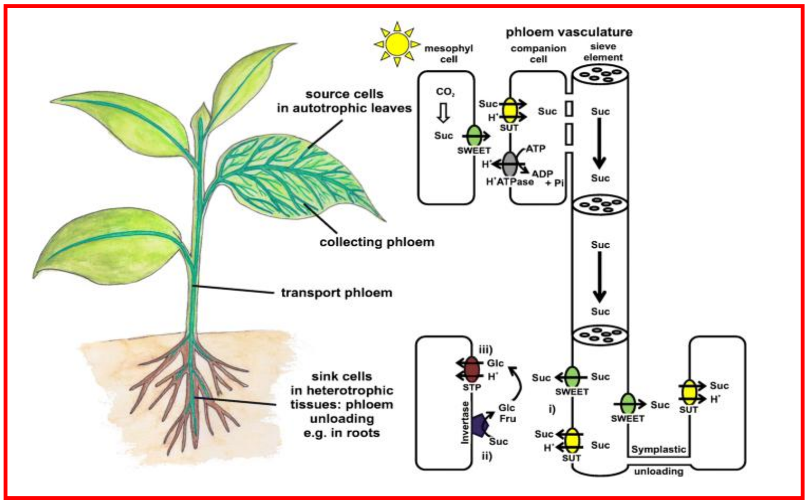


Fig. 48: Illustrates long-distance transport of sucrose from source to sink tissues in apoplastically loading plants and the involvement of STPs in loading of sink cells with monosaccharide's. Left: cartoon of a plant showing the phloem vasculature in dark green. The branched collecting phloem is illustrated only in the right fully developed leaf. Right: Illustration of the loading, the long-distance transport and the unloading of photoassimilate. In plants, photosynthetically synthesized sucrose is released from mesophyll cells to the apoplast (extracellular cell wall space) via SWEET type facilitators. At the source site of the phloem vasculature, H+ -coupled sucrose transporters (SUTs) accumulate sucrose in the SE/CC (sieve element/companion cell complex—phloem tissue) complex for long-distance distribution throughout the plant body. H+ -ATPase provide the proton motive force for sucrose loading energized by ATP hydrolysis. To provide heterotrophic sink cells with photoassimilate, sucrose is either imported symplasmically via plasmodesmata or via a three-step apoplastic sugar import: (i) sucrose is released from the phloem cells into the apoplasm, (ii) cell wall-bound invertases hydrolyse sucrose to fructose and glucose, (iii) followed by the uptake of the breakdown products into sink cells via STP-type proton-coupled monosaccharide transporters. After Geiger (2020).

Geiger (2020), reported that The carbohydrate D-glucose is the main source of energy in living organisms. In contrast to animals, as well as most fungi, bacteria, and archaea, plants are capable to synthesize a surplus of sugars characterizing them as autotrophic organisms. Thus, plants are de facto the source of all food on earth, either directly or indirectly via feed to livestock. Glucose is stored as polymeric glucans, in animals as glycogen and in plants as starch. Despite serving a general source for metabolic energy and energy storage, glucose is the main building block for cellulose synthesis and represents the metabolic starting point of carboxylate- and amino acid synthesis. Finally yet importantly, glucose functions as signalling molecule conveying the plant metabolic status for adjustment of growth, development, and survival. Therefore, cell-to-cell and long-distance transport of photoassimilate/ sugars throughout the plant body require the fine-tuned activity of sugar transporters facilitating the transport across membranes. The functional plant counterparts of the animal sodium/glucose transporters (SGLTs) are represented by the proton-coupled sugar transport proteins

(STPs) of the plant monosaccharide transporter (-like) family (MST). In the framework of this special issue on "Glucose Transporters in Health and Disease," this review gives an overview of the function and structure of plant STPs in comparison to the respective knowledge obtained with the animal Na+ - coupled glucose transporters (SGLTs).

Other sugars and polyols such as raffinose, galactinol, and glycerol that has been described as stress tolerance compounds increase its content during stress conditions El Sayed *et al*., (2014); Salvi *et al*., (2018). In contraposition of down accumulation of carbohydrates, some amino acids seem to be accumulated during heat stress. This negative correlation between sugars and amino acid appears to be provoked by the inhibition of carbon assimilates supply to the roots during heat stress. One of the accumulated amino acid is proline, an osmoprotective compound, used to avoid molecular and cellular damage during stress situations Szabados and Savoure, (2010). Increase temperature also regulates significantly lipid metabolism probably associated to the cell membrane rigidity needed to counteract the fluidity provoked by warmer soils. Thus, fatty acids, phospholipids and glycerolipids shows a reduction in their accumulation after exposing the plant to heat stress together with TCA cycle intermediaries and related enzymes Ribeiro *et al*., (2014). There is fewer and fragmentary data concerning secondary metabolism response to rising temperatures in roots. In maize, increase in temperature causes a decrease in the level of secondary metabolism compounds such as fitosterols and terpenoids Sun *et al*., (2016), but in castor bean, although b-sitosterol levels decrease, ampesterol storage is increased. The levels of other metabolites like tocopherol, squalene and ricinine, also change in response to heat. During heat stress, as with other stresses, the intracellular levels of ROS increase sharply. Although it could act as a signaling molecule, higher levels of ROS cause damage at cellular level and interfere with protein and enzymatic activities and gene expression. It has been reported in several crops that the high temperatures promote the expression of ROS scavenging enzymes such as catalases (CAT), peroxidases, superoxide dismutase (SOD) and ascorbate peroxidase to counteract ROS damage Gill and Tuteja, (2010). Glutathione (GSH) has been described to take part in thermatolerance in eukaryotic organisms by scavenging ROS Colville and Kranner, (2010). Under heat stress, roots use cysteine to synthesize GSH that could increase the thermatolerance of these organs Nieto-Sotelo and Ho, (1986). NO and H2S are two gaseous molecules that act as signaling compounds during different developmental processes, including root morphogenesis, and stress situations, like heat stress. It has been described for both molecules that its external application confers thermatolerance in both shoot and roots Li *et al*., (2013); Singh *et al*., (2019). Altogether, significant changes in metabolism in response to high temperature have been reported in different crops directed to alleviate the damage triggered by this stress. Although significant information in this process has been conveyed from several groups, the complete picture of how temperature regulates metabolism in roots is far from been complete. A substantial effort in the study of this regulation will be needed to understand how metabolic changes are integrated in the overall response of roots to this stress.

Conclusions and perspectives

Because of global climate change, the deleterious effects of heat stress on crop yield are expected to be increased in the future. Thus, a better understanding of the mechanisms involved in plant tolerance to heat stress is of vital significance. The deleterious effects of heat stress can be ameliorated through developing new varieties with improved thermatolerance. Manipulation of phytohormones through breeding or exogenous application of various phytohormones at optimal dose may help to manage heat stress and thereby sustaining crop production in the face of climate change. It is worth mentioning that activation of hormone-responsive genes in a specific tissue is crucial for the induction of stress tolerance and thus targeted manipulation of the plant hormone pool offers better efficacy for modulating the response of plants to heat stress.

In order to predict how plant hydraulics will respond to a changing climate, both structural and functional components, such as plant metabolism, xylem properties, vascular architecture, and leaf size are needed for incorporation into a functional model. Responses to climatic conditions are species-dependent and, therefore, there may be a genetic component to climatic responses, with plant species having differential physiological responses to similar stimuli. In addition, studies have shown that the formation of xylem is more sensitive to environmental factors than the formation of phloem. This emphasizes the need for research into the development of vascular tissues, including xylem, phloem, parenchyma and fibers, from the base of plant to shoot apex. The general approach to study plant response to high temperature is by exposing plants to either short-term heat stress or extended high-temperature stress or heat acclimation and heat stress recurrence. Although the purpose of studying high-temperature stress is to understand plant response, it often does not mimic the real-world situation even considering a single stress. For example, on a hot day temperature may vary a lot during hours of the day. Certainly, it declines at night providing the plants an opportunity to recover. However, the next day the plant may have to face another episode of abnormal high temperature regimes. Many heat acclimation studies could explain plant response to heat stress; however, to a various extent, those conditions often cannot mimic the real-world temperature regimes. Nonetheless, multiple abiotic and/or biotic hazards may coexist in the natural ecosystem.

A current challenge in plant physiology is to associate particular structural characteristics of the vascular bundle to specific functions regarding efficiency of water transport. Studies that examine vascular tissue differentiation are rare, and the majority of existing studies look at woody species. More work is needed in determining the effects of environmental factors on vascular development, especially in herbaceous plants. Our lack of understanding makes it difficult to predict how climate change will affect vascular development and the transpiration stream in plants; however, decreased shoot biomass under stress conditions may be indicative of a reduction in vascular tissue. It is essential to understand how plant forms (e.g., vascular tissues) and functions (e.g., photosynthesis and transpiration) will respond to climate change. Optimization of hydraulic efficiency is the first step in ensuring that plants may be better equipped to cope with future climate change. Therefore, it is of great significance to study plant response to high temperature getting close to the real-world temperature hazard, which may provide a better understanding of the mechanisms of plant tolerance to various high-temperature stresses. As phytohormones play a crucial role in imparting thermatolerance, establishing a role for a hormone in protection of crop yield from heat stress may have significant implications in breeding programs as well as field application of plant hormones.

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