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Article

Mecanismos de respuesta al estrés abiótico: hacia una perspectiva de las especies forestales

Response mechanisms to abiotic stress: towards a forest species perspective

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Resumen

El estrés de origen abiótico tiene un importante impacto negativo para la productividad y supervivencia de los principales cultivos agrícolas y ecosistemas forestales del mundo. Las tendencias actuales del cambio climático pronostican un aumento en la severidad y frecuencia de fenómenos climáticos y condiciones ambientales adversas como la sequía, salinidad del agua y suelo, así como temperaturas extremas. A lo largo de la evolución, las plantas han desarrollado diversos mecanismos moleculares, morfológicos y fisiológicos para responder a las condiciones desfavorables del entorno. La comprensión de dichos mecanismos es esencial para implementar estrategias de conservación y mejoramiento genético de especies vegetales, a fin de proteger la biodiversidad y producir organismos tolerantes / resistentes al daño ocasionado por el estrés abiótico. Sin embargo, la mayoría de los estudios disponibles sobre identificación, transducción de señales y procesos de respuesta al estrés en plantas deriva de investigaciones en especies anuales. Aunque existen algunos trabajos realizados en taxones forestales de los géneros *Populus*, *Eucalyptus*, *Picea* y *Pinus*, se carece de estudios dedicados a especies mexicanas. Por su alta riqueza y diversidad biológica, México es un país privilegiado; no obstante, la falta de conocimiento sobre la susceptibilidad de sus recursos forestales es el principal obstáculo para diseñar planes de acción orientados a mitigar las consecuencias perjudiciales del estrés abiótico.

Palabras clave: Cambio climático, deficiencia hídrica, ecosistemas forestales, estrés abiótico, salinidad, transducción de señales.

Abstract

Abiotic stress is the leading threat to the productivity and survival of the most important crops and forest ecosystems worldwide, as current climate change patterns indicate likely increases in the severity and frequency of extreme weather events such as drought, water and soil salinity, and extreme temperatures. Through evolution, plants have developed diverse molecular, morphological and physiological mechanisms to respond to adverse environments. Understanding such mechanisms is essential to develop and apply conservation and breeding strategies for plant species, with the larger aim of protecting biodiversity and producing tolerant/resistant organisms capable of overcoming abiotic stress conditions. However, most of the available knowledge about stress recognition, signaling and response in plants come from the study of annual species. Even though there are some studies regarding forest taxa like *Populus*, *Eucalyptus*, *Picea*, or *Pinus*, Mexican species are absent from the literature. With its vast biological richness and diversity, Mexico is a privileged country; nevertheless, the lack of knowledge regarding the susceptibility of its forest resources is the main obstacle to enacting policies oriented towards mitigating the negative consequences of this type of stress.

Key Words: Climate change, drought, forest ecosystems, abiotic stress, salinity, signaling transduction.

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Introduction

Abiotic stress refers to the environmental factors that alter the physiological and metabolic processes of plants (Taiz and Zeiger, 2010). It is considered to be the central cause of the loss of over 50 % of the main crops of agricultural interest in the world (Boyer, 1982; Bray *et al.*, 2000), as well as the reduction of vegetal growth, development and yield (Sah *et al.*, 2016), which affects over 95 % of the agricultural surface (Cramer *et al.*, 2016). This situation is worsened by climate change, which impacts the frequency of fires, the rapid increase in the temperature, and disturbances in the rain precipitation patterns, among other factors (IPCC, 2007).

Consequently, the genotypes and species that are sensitive to these fluctuations may disappear and be replaced by other taxa (Alfaro *et al*., 2014). Such is the case of *Oreomunnea mexicana* (Standl.) J. F. Leroy, which is a relict species (Palacios-Chávez and Rzendowski, 1993) classified as threatened (González-Espinosa *et al*., 2011). Its potential distribution was predicted for several different climate change scenarios that suggested a reduction of 36 to 55 % of its habitat, as its ecological niche is highly specialized and sensitive to environmental changes (Alfonso-Corrado *et al.*, 2017).

The incidence of adverse environmental conditions involves significant changes in the net productivity of ecosystems (Thornley and Cannell, 1996; Wang *et al*., 2012). The forest biomes and their communities and dependent industries do not escape the effects of such disturbances (Hof *et al.*, 2017), as they influence the distribution and the growth rate of forest species (Hamann and Wang, 2006).

The forests provide timber and non-timber products, as well as an important diversity of environmental services, such as the regulation of the water cycle and the biochemical cycles, and the control of the soil erosion and soil formation, among others (Ninan and Inoue, 2013). As for the former, the total value of the global exportation of forest products has been estimated in 262 billion USD (FAOSTAT, 2018). Nevertheless, many of the ecosystem services do not have a market, and therefore their economic value cannot be estimated (Pearce, 2001).

Forest ecosystems occupy nearly 30 % of the earth's land surface, *i.e.* 42 million km^2 (Bonan, 2008); for this reason, their management and conservation is an essential strategy for mitigating the effects of climate change (Schimel *et al.*, 2001), as the trees and woody plants work as primary carbon (C) sequestration mechanisms (Thomas and Martin, 2012), capturing the atmospheric C and storing it in the trunk, branches and leaves, as part of their growth process (Justine *et al*., 2015). Water deficiency, salinity, and extreme temperatures are the main abiotic factors that limit the survival and productivity of tree species (Choat *et al*., 2012; Anderegg *et al*., 2013; Harfouche *et al*., 2014).

Furthermore, the negative consequences of abiotic stress are expected to worsen due to climate change (Fedoroff *et al.*, 2010). For example, one of the main causes of mortality and of reduced productivity is hydraulic failure during water deficiency, as gas embolisms are generated in the xylem, preventing the efficient flow of water to the leaves for photosynthesis (Choat *et al.*, 2012) and eventually causing death, as in the case of *Picea abies* (L.)H. Karst. (Solber, 2004), *Cedrus atlanticad* (Endl.)Manetti ex Carrière (Bentouati, 2008) and *Populus tremuloides* Michx. (Hogg *et al*., 2008). For a long list of forest species experiencing mortality due to drought, see Allen *et al.* (2010).

During the evolutionary process, the plants have developed mechanisms of tolerance and resistance to stress which allow regulatory responses to reestablish cellular homeostasis or act to reduce the harmful effects (Mickelbrat *et al*., 2015). Stress due to environmental conditions causes a series of reactions in the plants, such as the inhibition of the meristematic growth of aerial structures in order to favor root elongation, disturbances of carbon metabolism (Xiong and Zhu, 2002), detriment in the production of viable pollen (Alqudah *et al*., 2011), and even dysfunctions in the phenology that might cause asynchronism between the floral development and the availability of pollinizers (Dawson *et al.*, 2001). For example, *Cedrela odorata* L. is a native species of Mexico and one of the neotropical species with the highest economic importance (Patiño, 1997). Its pollination depends on insects (Cavers *et al.*, 2013), so that an asynchrony with these would result in a reduced production of seeds. However, there are no studies assessing the consequences of this type of alterations in *C. odorata*.

Knowledge of the effects of abiotic stress is based mainly on studies performed in model species and in agricultural species such as *Arabidopsis thaliana* (L.) Heynh. (arabidopsis), *Nicotiana tabacum* L. (tobacco), *Oryza sativa* L. (rice), *Triticum aestivum* L. (wheat), *Zea mays* L. (corn or maize), among others. However, the information about the molecular biology and physiology of forest species under conditions of stress is limited, even non-existent for a large number of species, as in the case of the forest resources of Mexico. In this regard, a small number of species has been the object of studies related to the response to abiotic stress. For example, sensitivity to hydric deficiency was assessed in *Pinus engelmannii* Carrière and *P. lumholtzii* Robinson and Fernald of northern Mexico in a range of altitudes through a dendrochronological study for the 1945-2004 period (Bickford *et al.*, 2011). The sensitivity of growth to the drought was determined, particularly at a low altitude, and *P. engelmannii* turned out to be the species with the least tolerance.

Due to its relevance in commercial forest plantations of the tropical and subtropical region of America, *Pinus oocarpa* Schiede ex Schltdl, *Pinus patula* Schiede ex Schltdl and *Pinus pseudostrobus* Lindl. were subjected to two contrasting hydric regimes in order to assess their tolerance to drought (Flores *et al.*, 2018). However, the three species exhibited a similar response mechanism, *i.e.* an allometric adjustment of the shoot/root biomass ratio; intraspecies variation was also identified in the phenotypic plasticity of growth in height, biomass of the needles and stem, and specific leaf area. Finally, the difference in the proportions of seedling survival was evidenced: 4 % for *P. pseudostrobus*, 12 % or *P. patula*, and 30 % for *P. oocarpa*.

These studies on Mexican species are valuable; however, they do not address the molecular and physiological origin of the response to stress. Therefore, the objective of this contribution is to present an overview of the signaling processes and the response mechanisms to three types of abiotic stress: water deficiency, high salinity and high temperatures. Emphasis is made on the available knowledge regarding the impact of each one of the types of stress mentioned on forest species.

General mechanisms of recognition, signal transduction, and response to stress in plants

The plants have developed adaptation, as well as defense mechanisms against the damage caused by the environmental conditions; this involves a large diversity of chemical compounds that regulate the transporters and the biochemical reactions, and modulate the gene expression (Tuteja and Sopory, 2008). These mechanisms comprise three phases (Figure 1): the recognition of the stress, the signal transduction, and the response (Biswal *et al.*, 2011).

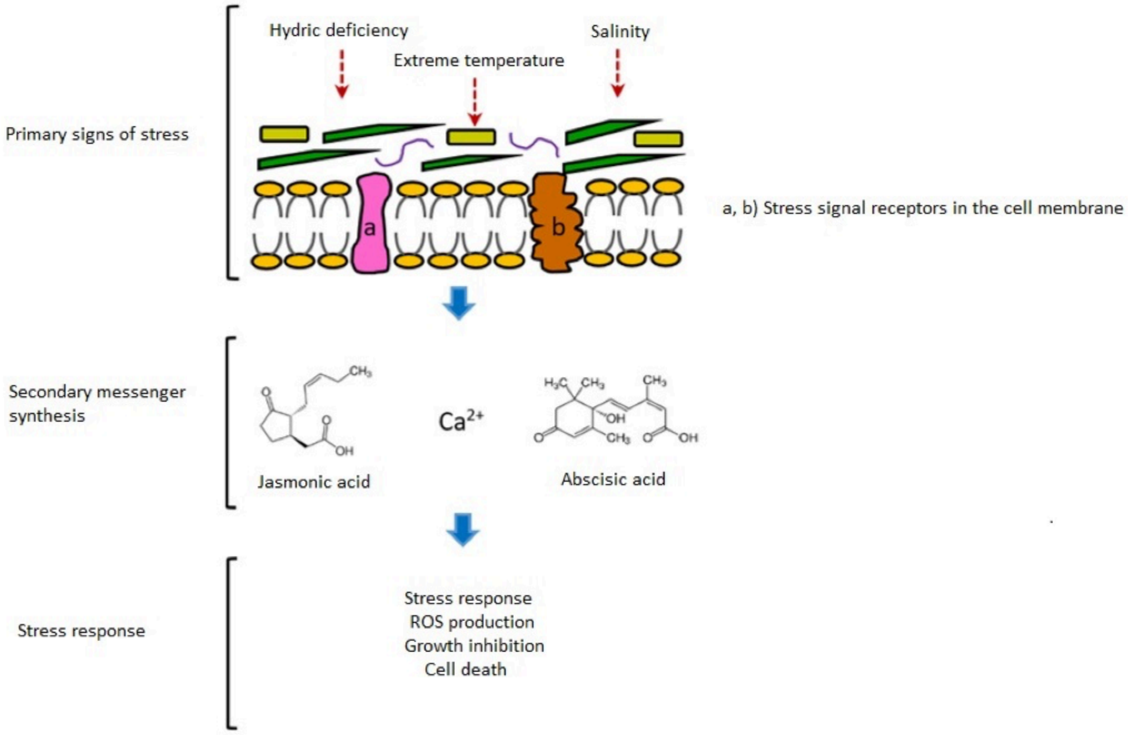

Figure 1. General mechanism of induction of response to abiotic stress in plants. The primary signs of stress are perceived by the receptors of the cell membrane that activate the production of second messengers. This signaling cascade results in the expression of response genes that induce a series of biochemical and physiological changes that will lead to tolerance, adaptation or death.

During the recognition phase, the primary signs of stress are processed via the receptors of the cell membrane (Tuteja *et al.*, 2011). For example, the primary sign for water deficiency is hyperosmolarity, while the primary signs for high salinity are altered osmotic pressure and ionic toxicity (Zhu, 2016). As for high temperature, four putative sensors have been proposed: a plasma membrane channel that triggers an influx of Ca^{2+}, a sensor histone sensor in the nucleus, and two protein sensors in the endoplasmic reticule and the cytosol (Mittler *et al.*, 2012). In general, despite all the resources allotted to the study of this topic, so far only a few potential receptors have been identified (Zhu, 2016), including G protein coupled receptors, ionic channels, kinase-type receptors or histidine kinase (Tuteja, 2007).

Signal transduction (also known as cell signaling or transmembrane signaling) is part of the process whereby the cells communicate with their environment and which allows them to respond to external stimuli through changes in the gene expression (Bradshaw and Dennis, 2010) that will eventually culminate in adaptation or in death (Tuteja, 2007). Thus, the reception of primary signals causes the production of second messengers (Dixit and Jayabaskaran, 2013), which are mainly non-protein molecules such as calcium, cyclic nucleotides, polyphosphoinositides, nitric oxide, sugars, abscisic acid, jasmonic acid, salicylic acid and polyamines (Tuteja and Sopory, 2008). The plants face various types of stress simultaneously, which suggests that the signaling routs interact with one another so that they may be additive, negative or compete for a target (Knight and Knight, 2001).

Vegetal hormones intervene not only in the regulation of vegetal growth and development, but also in signal transduction to respond to the environmental conditions (Sreenivasulu *et al*., 2012). In this sense, abscisic acid (ABA) is the most important (Hadiarto and Tran, 2011); Sreenivasulu *et al*., 2012; Sah *et al.*, 2016), and therefore it is also known as the stress hormone (Mehrotra *et al*., 2014). The relevance of this phytoregulator is such that the stress response mechanisms have been classified into two large groups: ABA-dependent and ABA-independent (Chinnusamy *et al*., 2004). In general, ABA regulates the increase of transcription factors, kinases and phosphatases that confer adaptation or tolerance to various types of abiotic stress (Tuteja, 2007; Sah *et al.*, 2016). Because the ABA is considered to be the main sign of stress response, it is suggested that it must be a central part of the strategies and programs oriented toward the generation of abiotic stress tolerant crops (Dar *et al.*, 2017).

Extensive publications describing in detail the importance of ABA in cell signaling may be consulted in Tuteja (2007), Kim (2014) Sah *et al*. (2016) and Dar *et al*. (2017).

Another one of the main secondary messengers of abiotic stress is calcium (Ca^{2+}) (Xiong and Zhu, 2002). Once the plant receives a stimulus, there is an immediate increase in the Ca^{2+} concentration in the cytosol, nucleus or mitochondria (Ranty *et al.*, 2016). The signs of Ca^{2+} are differentiated as to their spatial location, duration and frequency; therefore, each specific response is known as a signature of calcium; these are detected by means of various proteins, giving continuity to signaling cascades (Yuan *et al.*, 2017). Comprehensive reviews regarding the function of calcium in signal transduction can be consulted in Sanders *et al*. (2002), Kim *et al*. (2010), Dixit and Jayabaskaran (2013), and Ranty *et al*. (2016).

As for the response mechanisms to abiotic stress, these are based on genes grouped into three major categories: 1) genes involved in signaling cascades and transcription control; 2) genes with direct functions of protection of membranes and proteins, and 3) genes involved in ion transport and consumption (Wang *et al.*, 2003). The response depends on the type and duration of the stimulus. Table 1 shows the general mechanisms of response to water deficiency, salinity and high temperature.

Table 1. Main effects of abiotic stress in plants and general mechanisms of response.

Type of stress	Effects on the plant	Response mechanisms
Water deficiency	Reduction of the hydric potential, cell dehydration, reduction of cell expansion and of the metabolism, cavitation, ion cytotoxicity, cell death, inhibition of the photosynthesis (Taiz and Zeiger, 2010).	Accumulation of LEA proteins (Welin *et al*., 1994), especially of dehydrins (Arumingtyas *et al*., 2013), reduced root elongation, reduced leaf area (Hu and Xiong, 2014), stomatal closure (Froux *et al*., 2005).
High salinity	Reduction of the hydric potential, cell dehydration, ionic toxicity, inhibition of the photosynthesis (Taiz and Zeiger, 2010).	Ionic compartmentalization in vacuoles, reduction of shoot growth, limited ion flow from the roots to the shoots (Munns and Tester, 2008).
High temperature	Destabilization of the cell membrane and the cytoskeleton, various proteins and RNA, inhibition of the photosynthesis and of respiration, leaf senescence, fruit and flower abortion (Taiz and Zeiger, 2010; Mittler *et al.*, 2012).	Production of antioxidants, accumulation of solutes, induction of mitogen-activated kinase proteins (MAPK), induction of kinase protein cascades (CDPK), chaperone activation (Wahid *et al.*, 2007), accumulation of osmotic protectors, stomatal closure, synthesis of secondary metabolites (Mathur and Jajoo, 2014), thermal shock proteins (Iba, 2002) and salicylic acid (Nazar *et al*., 2017).

Water deficiency

Water is essential for the biochemical and molecular functioning of living organisms (Xiong and Zhu, 2002). Water deficiency triggers a series of ion, mechanical and osmotic signals recognized by various receptors (Hamisch *et al*., 2016). In general, cell dehydration, alteration of mitosis, and reduction of metabolism, of the cell volume and of turgidity are observed, and so is a negative hydric potential in the apoplast and a high ionic concentration that can turn out to be cytotoxic (Taiz and Zeiger, 2010; Farooq *et al*., 2009). One of the main processes affected by hydric stress is photosynthesis. A reduction in the production of biomass, reduced leaf expansion, inefficiency of the function of chloroplasts (Wahid *et al.*, 2007), a low diffusion of CO_2 (Pinheiro and Chaves, 2001), and a reduction of the net photosynthesis and of stomatal conductance have been observed (Mena-Petite *et al.*, 2000; Bigras, 2005). Furthermore, a reduction of the leaf area and the total number of leaves, of transpiration, of intercellular CO_2 concentration, and of the carboxylation efficiency are also observed in *Populus cathayana* Rehder (Xu *et al.*, 2008).

Two of the main molecule groups involved in water deficiency resistance and response are LEA (late-embryogenesis abundant) proteins and the growth hormone, abscisic acid (ABA). LEA proteins were discovered in terrestrial plants (Hand *et al.*, 2010) and owe their name to having been identified during the last stages of development of the seeds (Pedrosa *et al*., 2015). Their main functions are tolerance to dehydration and protection of seminal viability during *ex situ* storage, as well as resistance to stress due to drought, salinity and cold, as they stabilize other proteins and cell membranes and prevent protein aggregation during stress periods (Close, 1996; Goyal *et al*., 2005; Hong-Bo *et al*., 2005).

The genes codifying for the synthesis of LEA proteins are a broad family that has been extensively studied in angiosperms, particularly in those of agricultural interest, of which the only evaluated forest species is *Populus trichocarpa* Torr. & A.Gray ex Hook. (Lan *et al*., 2013). However, in relation to gimnosperms, only a few partial studies have been carried out on groups of proteins of this family in *Picea glauca* (Moench) Voss (Jin-Zhuo and David, 1998; Sena *et al*., 2017); *Pseudotsuga menziessi*

(Mir.)Franco (Jarvis *et al*., 1996), *Pinus pinaster* Aiton (Perdiguero *et al*., 2014) and *Pinus tabuliformis* Carrière (Gao and Ting, 2016).

Dehydrins belong to the LEA protein group and accumulate in various ways, according to the type and intensity of the stress in ripe seeds or vegetal vegetative tissues in response to dehydration, salinity, cold and freezing (Close, 1996; Tunnacliffe and Wise, 2007). 41 complete dehydrin codifying sequences were identified in *Picea glauca* by Sena *et al*. (2017); these represent more than four times the number of sequences found in angiosperms, and even more times than those found in the species of the genus *Pinus* studied so far.

The morphological responses to hydric deficiency include the following: leaf cuticular waxes occur on the surface of all terrestrial plants (Jetter *et al.*, 2006) and is one of the first protective barriers against various biotic and abiotic factors (Shepherd and Griffiths, 2006). The increase and change of composition of the cuticular wax under adverse environmental circumstances has been evident in several edible species like wheat, alfalfa and sweet peas (Sánchez *et al*., 2001; Aharoni *et al*., 2004; Zhang *et al*., 2005; Kosma *et al*., 2009; Seo *et al*., 2011; Lee and Suh, 2015; Zhang *et al*., 2013; Zhang *et al*., 2015). As for forest species, the comparative study of six conifer species —*Picea engelmannii* Engelm., *Abies lasiocarpa* (Hook.) Nutt., *Pinus contorta* Douglas ex Loudon, *Pseudotsuga menziesii*, *Pinus ponderosa* Douglas ex Lawson and *Pinus flexilis* E.James— is prominent, and although this study does not identify the relationship between the hardness and the composition of the cuticle with resistance to dehydration, it does determine the level of tolerance to drought of each of these taxa (Hadley and Smith, 1990).

Radicular system also responds to hydric stress; for example, in *Pinus pinaster*, two provenances with differential tolerance to hydric stress were subjected to a high osmotic potential (0.8 MPa) that resulted in a quicker and longer root elongation in the drought-tolerant population than in the susceptible population (Nguyen and Lamant, 1989). This response mechanism is induced by ABA and allows exploring adjoining sites in search of water, as has been observed in corn (Spollen *et al*., 2000; Sharp *et al*., 2002).

ABA is the most important plant hormone in signal transduction related to drought stress (Harfouche *et al*., 2014). One of its functions is the stimulation of stomatal closure in order to reduce water loss due to transpiration (Kim *et al.*, 2010). Stomata consist of two guard cells that detect high levels of ABA, and which therefore reduce their volume and turgidity by eliminating potassium ions and anions (MacRobbie, 1998). In addition, ABA induces the overexpression of nearly 50 % genes associated with the cuticle (Jenks *et al.,* 2007). However, the relationship between the molecular mechanisms of cuticular wax and ABA is yet to be clarified (Xue *et al.*, 2017).

Ionic stress and hyperosmolarity due to hydric deficiency also cause oxidative damage as a result of the excess of reactive oxygen species (ROS) (Xiong and Zhu, 2002). ROS play an important role in plant signaling and are involved in growth, development and response to biotic and abiotic stress, as well as in programmed cell death (Bailey-Serres and Mittler, 2006). Nevertheless, in high concentrations, ROS damage the cell lipids, carbohydrates, proteins and DNA (Das and Roychoudhury, 2014). In most cases, defense against ROS depends on antioxidants such as ascorbic acid, glutathione, thioredoxin and carotenoids, as well as on enzymes like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), and guaiacol peroxidase (GPX) (Xiong and Zhu, 2002; Das and Roychoudhury, 2014).

Salinity

Soil salinity is a growing problem for crops across the world, especially on irrigated land (Negrão *et al*., 2017). The main consequence is yield reduction, as salt alters osmolarity or promotes ion toxicity within vegetal tissues. In such circumstances, plants respond quickly, by readjusting the osmotic potential, or slowly, by reducing salt toxic concentrations in their cells (Munns and Tester, 2008). Adaptation mechanisms in response to salinity have three purposes: to produce tolerance to osmotic stress, to avoid ion excess (particularly Na^+) in plant tissues, and to increase tissues tolerance to ion accumulation (Munns and Tester, 2008). These can complement one another and vary the responses, depending on stress severity and on the affected species.

Due to its ability to survive high concentrations of NaCl, *Populus euphratica* Oliv. has served as a model for studies to elucidate the physiological and molecular mechanisms involved in tree species tolerance to saline stress. Cl^- compartmentalization in the vacuoles of the root tissue cells or Na^+ in the leaf apoplast; diminution of the NaCl levels in the xylem, and prevention of K^+ loss through ion channels in order to maintain the ion balance are examples of the physiological mechanisms of this species (Chen and Polle, 2010). Genomic studies suggest that *P. euphratica* tolerance to salinity is the result of duplication and/or positive regulation of several families of genes involved in ion transport and maintenance of the homeostasis (Ma *et al.*, 2013).

The best studied example is the HKT1 gene family, whose proteins participate in Na^+ transport in different species, functioning as Na^+/K^+ cotransporters and as high- and low-affinity selective Na^+ transporters (Davenport *et al.*, 2007). *P. euphratica* has four HKT1 paralogues within its genome, unlike *P. trichocarpa*, which has only one (Ma *et al*., 2013).

Many of the genes related to saline stress include different proteins that participate in the uptake and transport of salts. However, some genes have an osmoprotective function and antioxidant enzymes, while others are involved in growth and development, including transcription factors, kinase proteins, phosphatase proteins or signaling molecules, such as calmodulin-binding proteins and certain ABA-induced proteins (Munns, 2005).

The technology of recombinant DNA allows evaluating the potential utility of certain genes to confer tolerance to salinity in forest species; an example of these is *Pinus taeda* L., in which the overexpression of osmoregulatory enzymes increases the survival rate under high salinity conditions (Tang *et al.*, 2005). Tolerance to saline stress has been successfully increased in *Populus* through the transfer of a transcription factor in this species’ response to ethylene, which plays a role in growth and development of the plant (Li *et al.*, 2009).

Thermal stress (high temperature)

An increase of 0.85 °C in the combined global mean temperature of the land and ocean surfaces was registered between 1880 and 2012 (IPCC, 2014), and an increase of 0.2 to 0.3 °C per decade has been predicted for the next years (Jones *et al*., 1999; Fahad *et al*., 2017). Increases of 10-15 °C in the ambient temperature are regarded as thermal stress or shock, generally causing the denaturalization and aggregation of proteins and an increased fluidity of membrane lipids (Wahid *et al*., 2007), as well as a disturbance in the organization of the microtubules and in cell division (Smertenko *et al.*, 1997), alterations in photosynthesis and in the primary and secondary metabolism of lipids (Xu *et al.*, 2006), and, therefore, delayed development and growth, or death (Mathur and Jajoo, 2014). For a comprehensive review of signaling and response to high temperatures, we recommend consulting Wahid *et al*. (2007), Mittler *et al*. (2012) and Wang *et al*. (2017).

Although accurate mechanisms for heat detection and signaling in plants are still unknown, molecules such as proteins bound to guanosine triphosphate, nucleoside diphosphate kinase, annexin and brassinosteroid kinases are known to participate in signal transduction (Wang *et al.*, 2017).

Photosynthesis is one of the main metabolic processes affected by high temperatures (Farooq *et al*., 2009), as these alter photosystem II and the electron transport chains, disrupt the tilacoidal membrane, and inhibit the b6/f cytochrome complex, ribulose-1,5-biphosphate carboxylase/oxygenase, ATP synthesis, and carbon fixation (Biswal *et al*., 2011; Ashraf and Harris 2013; Mathur and Jajoo, 2014). This may account for limited growth of various species and for early senescence, as has been observed in sugar cane (*Saccharum officinarum* L.) (Ebrahim *et al.*, 1998). In *Picea glauca*, temperatures of 42-43 °C impede photophosphorylation by tilacoids and to supply water to photosystem II, while even higher temperatures (44-46 °C) drastically reduce the use of NADPH and ATP in the Calvin cycle (Bigras, 2005).

Root system is more sensitive to heat than certain aerial parts, as its optimal level of growth is 5 to 6 degrees lower (DiPaola, 1992; Paulsen, 1994). For this reason, heat negatively affects the hydraulic conductivity of the root system (Morales *et al.*, 2003), as well as the capacity to uptake and assimilate nutrients (Giri *et al*., 2017), especially nitrogen, phosphorus and potassium (Fahad *et al.*, 2017). Balance, stability, concentration, biosynthesis and compartmentalization of plant growth hormones are altered under high heat conditions (Maestri *et al.*, 2002). As in the case of water deficiency, extreme temperature results in ROS release (*Wang et al*., 2017), and the previously mentioned enzyme and non-enzyme mechanisms act in response to damage caused by these free radicals.

In response to high temperature, the main strategy of plants is the synthesis of heat shock proteins (HSP) (Iba, 2002) that confer membrane stability, efficiency in water and nutrients use efficiency, and protect of the photosynthetic apparatus (Camejo *et al*., 2005; Ahn and Zimmerman, 2006; Momcilovic and Ristic, 2007; Horváth *et al*., 2008). The HSPs were identified in heat stress conditions; however, today they are known to participate in response to biotic stress (Yu *et al.*, 2016), cold, dehydration, UV light, salinity, heavy metals, and mechanic damage (Swindell *et al.*, 2007). In addition to HSPs, there are other groups of compounds that intervene in the response to heat shock and which have very diverse origins, such as cytokinins, fatty acids, terpenoids, and flavonoids —the metabolic routes that most influence the response to high temperature in *Pinus radiata* (Escandón *et al.*, 2018)—, as well as giberelines, ethylene and brassinosteroids (Clarke *et al*., 2009; Zhang and Wang, 2011; Dubois *et al.,* 2018).

Final considerations

Adaptation to abiotic stress is controlled by molecular networks that trigger a series of morphological and physiological responses. Research on the processes involved in the adaptation and resistance to adverse conditions in forests species advances slowly, as they are highly complex and involve the long life cycles and large genomes. Given the scarcity of information about tree species, it is impossible to formulate a complete overview of the above processes in this group of organisms. However, the constant development of *omic* tools provides an opportunity to study the functioning of these living beings in an integrative way for the purpose of describing, elucidating, and understanding such processes.

Several authors consider that the mechanisms of response, tolerance and resistance to abiotic stress are difficult to control and utilize in genetic improvement programs, as the response processes are genetically complex. Nevertheless, characterization and understanding of molecular mechanisms and stress physiology will make it possible to explore strategies for achieving genetic improvement through the use of characteristics and organisms with an ecological and productive value, which must necessarily include the main Mexican forest species.

Conflict of interests

The authors declare no conflict of interests.

Contribution by author

Claudia Méndez-Espinoza: drafting of the abstract, introduction, development, and conclusions sections, and design of the figure and table; Miguel Ángel Vallejo Reyna: drafting of the section on salinity and general review of the manuscript.

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