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Review article

Ecophysiological response of tropical trees to climate change: drought and temperature

Respuesta ecofisiológica de árboles tropicales ante el cambio climático: sequía y temperatura

Resposta ecofisiológica das árvores tropicais às alterações climáticas: seca e temperatura

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ABSTRACT

This review organizes the existing and current knowledge of the ecophysiology of tropical trees, related to the processes of response to global climate change, with emphasis on water relations, due to the increase in temperature and droughts. The intertropical zone is characterized by a strip with an exuberant biodiversity. Given the current scenario of climate change, the conservation of tropical forests is of vital importance for its intervention in the global carbon cycle, in addition to providing guidelines for carrying out the necessary restoration actions in areas degraded by deforestation, being a source of carbon capture and, in turn, one of the components that will help in mitigating climate change. The methodology of information search was made because of the relevance of the topic, in pertinence with previous and current researches, which contributed solid arguments to the basic understanding of tropical trees ecophysiology. This is a very complex subject and, although there are advances, it is necessary to know the answers and adaptations that trees have developed throughout time. It was inquired to possess in context, the panorama of some species of the tropic, with respect to the mechanisms of survival and the capacity to support drastic changes in its area of distribution. From the review analysis, it can conclude that the knowledge and importance of these studies in the tropical zone is not null. However, more research are needed to know and to understand the behavior of some tropical trees of economic and ecological importance for the society and that, they will be affected by own environmental factors of their geographic region bordering on the extinction.

Keywords: Water deficit; Water stress; Stomas; Transpiration.

RESUMEN

Esta revisión ordena los conocimientos precursores y vigentes de la ecofisiología de árboles tropicales, relacionados con los procesos de respuesta ante el cambio climático global, con énfasis en las relaciones hídricas, por el aumento de la temperatura y sequías. La zona intertropical se caracteriza por ser una franja con una exuberante biodiversidad. Ante el escenario actual de cambio climático, el conservar los bosques tropicales resulta de vital importancia por su intervención en el ciclo global del carbono, además de dar las pautas para llevar a cabo las acciones necesarias de restauración en las zonas degradadas por la deforestación, al ser una fuente de captura de carbono y, a su vez, uno de los componentes que ayudarán en la mitigación del cambio climático. La metodología de búsqueda de información se efectuó por relevancia del tema, en pertinencia con investigaciones precedentes y actuales, las que aportaron sólidos argumentos al entendimiento básico de la ecofisiología de árboles tropicales. Es este un tema muy complejo y, aunque se tienen avances, es necesario conocer las respuestas y adaptaciones que han ido desarrollaron los árboles a través del tiempo. Se inquirió poseer en contexto, el panorama de algunas especies del trópico, respecto a los mecanismos de supervivencia y la capacidad de soportar cambios drásticos en su área de distribución. Del análisis de revisión, se concluyó que el juicio e importancia que se advierte de la zona tropical, no es nulo, aunque se necesitan más investigaciones para conocer e interpretar el comportamiento de algunos árboles tropicales de valor económico y ecológico para la sociedad, que serán afectados por agentes ambientales propios de su región geográfica, orillándolos a la extinción.

Palabras clave: Déficit hídrico; Estrés hídrico; Estomas; transpiración.

RESUMO

Esta revisão organiza o precursor e os conhecimentos atuais da ecofisiologia das árvores tropicais, relacionados com os processos de resposta às alterações climáticas globais, com ênfase nas relações de água, aumento da temperatura e secas. A zona intertropical é caracterizada como uma faixa com uma biodiversidade exuberante. Dado o atual cenário de alterações climáticas, a conservação das florestas tropicais é de importância vital para a sua intervenção no ciclo global do carbono, além de fornecer orientações para a realização das ações de restauração necessárias em áreas degradadas pela deflorestação, sendo uma fonte de sequestro de carbono e, por sua vez, um dos componentes que ajudará a mitigar as alterações climáticas. A metodologia de pesquisa de informação foi baseada na relevância do tema, de acordo com pesquisas anteriores e atuais, que contribuíram com argumentos sólidos para a compreensão básica da ecofisiologia das árvores tropicais. Este é um assunto muito complexo e, embora tenham sido feitos progressos, é necessário conhecer as respostas e adaptações que as árvores têm desenvolvido ao longo do tempo. Foi inquirido para possuir em contexto, o panorama de algumas espécies dos trópicos, no que diz respeito aos mecanismos de sobrevivência e à capacidade de apoiar mudanças drásticas na sua área de distribuição. Da análise da revisão concluiu-se que o juízo e a importância da zona tropical não é nulo, embora seja necessária mais investigação para conhecer e interpretar o comportamento de algumas árvores tropicais de valor económico e ecológico para a sociedade, que serão afetadas por agentes ambientais típicos da sua região geográfica, levando-as à extinção.

Palavras chave: Défice hídrico; Stress hídrico; Estômatos; Transpiração.

INTRODUCTION

Climate change itself is complicated, and not because of the social or economic consequences that may result in the coming decades, but because of the increase in temperature in many regions of the planet, a phenomenon that is beginning to be distinguished. This is going to cause one of the most worrying environmental complications that human beings will face. In contrast, it is essential to reflect on the importance of forests, and even more so if most of them are located in the tropics (45 %) (FAO 2012; Esquivel *et al*., 2018 Buchhorn *et al*., 2019).

The agreements and decrees signed in world conventions still do not compensate for the alterations caused over the last 30 years; by causing numerous, unequal transformations in the distribution and abundance of species, in addition to the non-legal exploitation of wood, agricultural expansion and forest fires (natural and prescribed) (Potapov *et al*., 2017; Fremout *et al*., 2019; Sage 2019).

At present, because of these changes, some tropical species are in serious danger of extinction; only in the last two decades about 19 % of these forests have been lost; if this situation is not reversed, a more severe reduction is expected by 2040, and with it, the loss of many tropical forest species (Rodríguez *et al*., 2010; del-Val and Sáenz 2017). Thomas *et al*., (2004) mentioned that, with a minimum change in climate, 18 % of known species (animals and plants) will be lost, while with a much greater change, 35 % of these species will disappear; a critical figure for the subsistence of organisms present in these ecosystems (McDowell *et al*., 2018). For its part, the IPCC (2007) announced in its report IV that if the temperature increases by approximately 1.5 to 2.5°C, 20 to 30 % of plant and animal species will be at risk of extinction.

Most tropical forest species, from primary forest, do not present dominance within the characteristic forest canopy, growing in a limited geographical area. However, since it hosts a great diversity of species, as well as incomparable architecture and morphology, a wide physiological diversity can be found. The challenge of climate change in the tropics is enormous, especially because of the high level of deforestation that persists in regions not protected by the corresponding governments, followed by temperature changes (Andrade 2005).

The latter led to direct research and approaches towards the response in transpiration, photosynthesis and physiological development of trees, in relation to climate and water deficit. Therefore, there is still much to be researched and done, due to the great diversity of species found in these ecosystems. Finally, it is not intended to present an in-depth review of the main mechanisms of response of tropical trees to climate change. Rather, to define and reveal an issue based on basic and current research information that has been experienced in water relations, to tropical species.

DEVELOPMENT

Climate change and tropical species

In the last 34 years, greenhouse gases increased by approximately 70 % due to human activities. At the Intergovernmental Panel on Climate Change (IPCC) (2007), they reported that by 2050, the temperature is expected to increase by 1.5 to 2.5° C (Locatelli *et al*., 2008). Aragão *et al*. (2009) mentioned a possible increase in temperature in the tropical regions of the Amazon; 0.25°C every decade for a period of 30 years. The effect of climate change in the tropics will definitely affect different scales: spatial and temporal. In this context, not only are increases in temperature expected and predicted, but also changes in the distribution of rainfall during low water (Aragão *et al*., 2009), even prolonging the risk of drought (Allen *et al*., 2010) with a high possibility of forest fires (Nepstad *et al*., 2004), hurricanes and cyclones, among others. Similarly, there will be risks of damage to ecological processes related to the floristic and phenological structure of tropical species, due to the effects mentioned above (Fischlin *et al*., 2009, Gutiérrez and Silver 2018).

Drought: water relations and conductance

In recent years, the study of the physiology of tropical trees focused on understanding water relationships, recorded a growth and development of techniques to study the processes of water deficit. Among the techniques used in this type of research are the use of stable isotopes, as well as probes to measure sap flow (Andrade 2005). It is important to know the water relationships that occur in the tree, because the sprouting, growth (primary and secondary) and flowering, involve cell expansion, and this can be inhibited with moderate water deficits (Borchert 1998), resulting in drought stress and inhibiting photosynthesis, causing oxidative cell damage (Lukic *et al*., 2020).

Plants survive water deficit conditions in the urgency to evolve, allowing them to develop response and adaptation mechanisms that continue in constant ecophysiological adjustment with temperature changes, high CO_2 concentrations and water deficit (Nilsen and Orcutt 1996). The adaptations that they present, often, go from the capacity to be able to absorb and to transport water, in a morphological, anatomical and cellular level; including, the efficient use of the hydric resource, when looking for to be more tolerant to the stress by drought. Other adaptations are focused on the development of metabolisms that allow them to grow in different environments, generally arid; depending on the species, they can present C4 or CAM metabolism (Lüttge 2004). Low temperatures and high soil salinity are also factors that lead to water deficit. Under these conditions, cells experience osmotic stress, i.e., water availability in the cytoplasm decreases (Levitt 1980). Gómez *et al*., (2020), modeled climate niches for two temperate species, *Pinus devoniana* and *Abies religiosa*. The results they reported suggest that by 2060, climate niches for both species will be at elevations that are 300-500 m higher than they are today. Similarly, the loss of range, for both species, could disappear at 46 % to 77 %, affecting the limits of distribution of these trees. The conditions of habitat loss in the temperate zones are worrisome, talking about a third of the loss in this region, leads to the reflection of the area that will be lost in the tropical regions. Taking into consideration that the loss will be in a staggered way and in an inverted way with a regional displacement of species that support the changes that are approaching with the increase of the temperature and decrease of the precipitation. As with conifers, human assistance will eventually be required to migrate at altitude in search of the climates to which tropical and temperate forest species are adapted (Gómez *et al*., 2020).

Water, as a vital resource, is one of the basic factors in the growth of every individual in the development of plants and, the lack of the liquid, represents a stress. Most plants have developed responses that allow them to tolerate and survive in different climates, these range from a mild water stress, with the decrease of water potential during midday, to those that survive in desert areas (Moreno, 1998); the soil, moisture and the amount of water available to the root system is also essential to calculate the water balance and its state in the forests (Slatyer 1967). An important aspect to consider is the capacity of the roots to explore the depths of the soil as well as the form of distribution; depending on the species, they will have different forms and capacity of exploration.

For example, Nepstad *et al.*, (2004) investigated the depth of roots of some tropical species in an evergreen and deciduous forest in Brazil, and found that the "evergreen-ness" properties were related to the depth of roots and access to water stored in the soil during the wet season; which allows species to buffer the dry season thanks to the extension of roots in the soil. Similarly, Borchert (1998) concluded that the availability of water in the soil in tropical tree areas in two consecutive dry seasons shows that the water status of trees will vary with the availability of water from the ground and a variety of biotic factors, such as leaf structure and life, leaf shedding time, wood density and stem water storage capacity, and the depth and density of root systems. Therefore, the water storage capacity of the stem (400 - 20 % of the dry mass) is highly correlated with the degree of drying during the drought.

Córdoba *et al*., (2011) evaluated three-year-old plants under greenhouse conditions, the interesting thing was to know the distribution of roots when subjecting different levels of water deficit in the soil. As expected, they found that soil moisture determines the number of roots that will be formed and that, in the absence of water, plants will show mechanisms that will allow them to reduce the effects of that shortage and, in general, show a tendency to reduce the accumulation of biomass and the ratio of air to root, with a greater amount of resources allocated to the latter (Doi *et al*., 2008); this is particularly common when plants face water stress, as reported in some species (Martínez *et al*., 2002; Baquedano and Castillo 2007).

Even in drought conditions, there is a significant reduction in the air/root ratio. It is a physiological mechanism that ensures a balance between the water absorption capacity and the transpiration demand of the foliage (Costa *et al*., 2004). However, with a water deficit in the soil, the species can also respond at the cellular and molecular level, this response occurs around the modification of gene expression, presence of proteins with protective function, participation of osmolites in the osmotic adjustment, closure of stomas, cavitation of the xylem, among other responses that are involved in the response to water stress (Cushman 2001; Shinozaki and Yamaguchi 2007, Scoffoni *et al*., 2018; Knipfer *et al*., 2020).

In the species of *Tectona grandis* (Singh and Srivastava, 1985) and *Eucalyptus globulus* (Kätterer *et al.,* 1995), they obtained results that do not coincide with the authors mentioned above. Singh and Srivastava (1985) and Kätterer *et al*., (1995) found that the amount of roots increased after a period of drought, suggesting that this event managed to stimulate root formation. Consequently, root formation is going to be regulated by the tropical species and the development conditions under which it is, as well as by the response mechanisms to the water deficit in the soil and, of course, the type of soil. Finally, according to the requirement of the plant, it will be classified in three types: hydrophytes, adapted to live totally or partially in water; mesophytes, which grow in environments with a moderate water supply; and xerophytes, adapted to arid environments (Nilsen and Orcutt 1996).

One of the tools that are being used to understand in a practical way the effects of climate change on tropical species and that can support political and ecological conservation decision making is climate niche modeling, which seeks to understand the potential distribution of trees of interest. Garza *et al.,* (2018) determined the potential distribution of contemporary and future climate habitat (decade centered on 2030) of *Lysiloma latisiliquum* (L.) Benth. in the Yucatan Peninsula, Mexico. It is projected that by 2030, a 43 % loss of climate habitat relative to contemporary habitat will be redistributed towards the center of the Yucatan Peninsula due to the modification of sea breeze patterns as they become more intense and far-reaching due to a warmer climate.

For their part, Navarro *et al*., (2020) used bioclimatic variables to model the effects of climate change on a smaller scale of *Buddleja coriacea, Carica candicans, Haplorhus peruviana, Kageneckia lanceolata* and *Weberbauerella brongniartioides* in their current and projected ecological niches at four future emissions scenarios (2050 and 2070). They demonstrated with this hypothesis that there will be a possible reduction of the population of *B. coriacea* by 80 % due to variations in temperature and precipitation, while for *Carica candicans, Haplorhus peruviana, Kageneckia lanceolata* and *Weberbauerella brongniartioides*, they deduced that the effects on these species will be due to anthropogenic activity, but that they will be able to maintain and increase their dispersion.

Adsorption and transport of water

Adsorption and transport of water is related to the storage of water in the tree or its tissues; roots, stems, branches or foliage. In this way, the capacitance, will allow to analyze the movement of water inside and outside the tissues of the tree, determining the change of the water content of the tissue with the change in the water potential (Scholz *et al*., 2011).

The xylem is the most efficient tissue of water conduction in its transport, is the means by which vascular plants make the water movement. The movement is through a network of specialized ducts along the tree. The transport is done through a tension in the xylem and is known as the cohesion-tension theory in a metastable state (Tyree and Zimmermann 2002).

For this reason, the water in the xylem is prone to cavitation, resulting in a subsequent embolism (Nardini *et al*., 2011). That is, the consequence of seasonal drought and freezing stress in the xylem, detected even in plants with constant watering (Choat *et al*., 2012). For this reason, the immediate effect observed in xylem cavitation is the total or partial closure of the stoma depending on the intensity and duration of cavitation, as well as the reduction in the hydraulic conductance in the xylem and the reduction of the photosynthetic rate (Brodribb 2009) in periods of intense drought (McDowell 2011).

Scholz *et al*., (2011) combined different studies related to water absorption and transport, showed that tree size and daily use of stored water have a positive linear relationship. In addition, they found that the specific capacities of both angiosperms and conifers have a similar value, contrary to a marked difference in wood anatomy. Despite this, in different ecosystems and species, there is a positive relationship between air biomass production and water use in the tree (Meinzer *et al*., 2001), according to their studies. They also evaluated 20 tropical species with taxonomic and architectural differences, and found good correlations between trunk diameter or sapwood area and water use (Meinzer et *al*., 2001).

One of the advantages in the distribution of the tree root system is the ability to redistribute water from the depths of the soil profile to the surface or catchment area of the trees, this distribution is also lateral and downward (Scholz *et al*., 2004). The researcher Dawson (1993), was a pioneer in demonstrating this hydraulic mechanism. In addition, the process of transporting water from one area to another helps neighboring plants with shallow roots survive and prevent salt accumulation on the soil surface (Landsberg *et al.,* 2017).

In tropical species, the type of forest will determine the maximum depth to which the root system can reach, generally on the order of 2 to 5 m (Canadell *et al*., 1996), however, in Amazon forests depths of up to 18 m were reported (Nepstad *et al*., 1994). However, the fact that the distribution of the roots in the soil is known does not mean that such an area is usable in the adsorption of water and nutrients. For this reason, in recent years, work is still being done on the depth at which the root extracts water (Andrade *et al*., 2005; Romero *et al*., 2005).

But, the absorption and transport of water in tropical trees are also affected by the flooding, causing the stomata to close and reducing the photosynthetic rate. Consequently, the movement of water through the conductive spaces in the tree is limited by the availability of water in the soil and the season of the year in the tropics. Rojas and Gutiérrez (2011) investigated the water relations of *Enterolobium cyclocarpum* at different times during the night and along two phenological cycles. With the data they observed that the water potential of stems and thick roots decreased during early foliage growth, from -0.3 MPa to -0.55 MPa, which shows the use of internal water reserves to support this process. The authors determined that the young leaves are the main responsible for avoiding water loss and maintaining water balance during the dry season, due to the low stomatic conductivity and stability of its water potential (g_s de 50 mmol m^{-2} s^{-1}; Î¨H$_H$ de -0.75 mPa).

Temperature: effects on growth and development

At present, investigations by groups of scientists have been presented that are really not very encouraging regarding climate change (Trugman *et al*., 2018; Pesendorfer *et al*., 2019; Navarro *et al*., 2020). The levels of increase in surface temperature on our planet are becoming increasingly alarming, due to greenhouse gas (GHG) emissions (Warrick *et al.,* 1996) and the difficulties in reducing them immediately (IPCC, 1992).

In some tropical species, the methods that show response: direct or indirect, to minimize damage to biological processes by changes in temperature, are a function of the optimal levels at which they develop, through mechanisms of tolerance or avoidance (Levitt 1980). Two decades of research have shown that temperature is one of the main environmental factors that control the development and productivity of trees, by affecting physiological processes in a temporary or spatial way (Sage and Kubien 2007).

In the same way, the loss of turgor in broadleaf and coniferous trees is a product of water stress due to the lack of water movement caused by environmental factors in the growing region. In Australia, the seasonal environments that occur have developed in species such as eucalyptus, the shedding of leaves as a response to water stress, reducing their water potential, and the stomatal activity is a characteristic adaptation of that species. Therefore, these ecosystems allow the study of the processes and behaviors that are involved in the tree-environment interaction during the loss of turgor (Landsberg *et al*., 2017).

In the Yucatan Peninsula, Mexico, it is common for tropical forest species to be exposed to recurring periods of water stress due to local environmental conditions (Hasselquist *et al*., 2010). So the species that predominate in these forests are deciduous, for their efficiency in saving water in times of low water availability (Murphy and Lugo 1986); the adaptations they developed are; foliar abscission, decrease in water potential and water storage in the organs (Tyree *et al*., 2002). Solar radiation is one of the most important environmental components influencing temperature and humidity in ecosystems (Romo 2005) and therefore, in the development and growth of plants. The excess or absence of solar radiation directly affects morphological changes in leaf structure, especially leaf thickness and area (Close *et al*., 2009; Cruz and López 2010). It can be observed in continuous and seasonal periods, depending on the light intensity to which the plants are exposed, affecting their growth (Puntieri 2005).

Tropical species adapted to shade are not capable of regulating physiological processes to such drastic changes as changing from shade trees to sun trees. Since shade-adapted plants show low plasticity, which limits them to direct exposure to the sun without having to reduce their photosynthetic response to prevent leaf death, they exhibit a greater tendency to photoinhibition than intolerant species and are likely to present greater damage when exposed to higher than usual levels of solar radiation (Salisbury and Ross 1992).

Salisbury and Ross (1992) conducted studies with an herbaceous species to document the response in an open zone environment (high radiation) and under canopy (low radiation). They evaluated two clones of *Solidago virgaurea*; results indicated that the shadow clone maintained a lower photosynthetic rate, growing at high radiation than the same clone growing at low illumination, due to the inability of the chloroplasts of these species to dissipate the excitation energy to the absorbed radiation (Fitter 2012 and Hale 1987). As expected, clones of the sun perform photosynthesis with greater speed at high radiation. Thus, the response to avoid photoinhibition is related to reducing light absorption through para-heliotrophic foliar movements and withering (Kozlowski *et al.*, 1991).

CONCLUSIONS

Finally, the challenges presented by climate change in tropical ecosystems are great, and it is one of the challenges that we face as a society in a race to reverse the actions that have been generated in the last couple of decades by polluting and overexploiting the environment. It is clear that tropical resources are fundamental as important components in the adaptation and conservation of biological diversity.

The knowledge and importance that is known of these regions is not null, but more research is still needed to know and understand the behavior of tropical species in the face of environmental factors in which they are growing. Knowing the response mechanisms and the capacity to adapt will help to measure the survival of tropical species and, if they are able to withstand drastic changes in temperature. That is to say, the plasticity that the species of the tropics present to resist and maintain their development before the scenario in which they are found, will determine their permanence.

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Alexis Domínguez Liévano: Conception of the idea, literature search and review, instrument application, literature search and review, general advice on the topic addressed, statistic analysis, preparation of tables, graphs and images, database preparation, drafting of the original (first version), review and final version of the article, article correction, general advice on the topic addressed, translation of terms or information obtained, review of the application of the applied bibliographic standard.