



Effects of droughts on carbon allocation in plants

Angélica Alves GOMES¹, Andréa Carvalho da SILVA^{1*}

¹ Postgraduate Program in Agronomy, Federal University of Mato Grosso, Sinop, MT, Brazil.

*E-mail: andrea.silva@ufmt.br

(ORCID: 0000-0002-8966-2187; 0000-0003-2921-3379)

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ABSTRACT: The objective of this review was to gather information about the effects of droughts on the allocation of carbon in plants. Plants are sessile organisms; thus, they are continuously exposed to environmental changes, mainly, those related to climate. Water is the most important climate factor. Rainfall variations and poor rainfall distribution can result in drought conditions, affecting negatively essential processes in plants, such as photosynthesis. This review presents, in a summarized form, some responses of plants to drought conditions and the effects of droughts on the process of carbon allocation, which makes evident that the nature and intensity of its effects are variable and dependent on the species, ontogeny, and level of sensitivity of the plant to water stress.

Keywords: carbon balance; water deficit; photoassimilates; carbohydrates.

Efeitos da seca na alocação de carbono nos vegetais

RESUMO: Objetivou-se com esta revisão, levantar informações sobre os efeitos da “seca” no padrão de alocação de carbono nos vegetais. Por serem organismos sésseis, estão continuamente expostos as mudanças ambientais, principalmente a nível de clima. Dentre os fatores climáticos, a água é considerada o mais importante. As variações pluviométricas, e a má distribuição podem vir a ocasionar condições de seca, afetando negativamente processos essenciais como a fotossíntese. Nesta revisão, são apresentadas de forma resumida, algumas respostas dos vegetais frente as condições de seca, e a interferência desta no processo de alocação de carbono, ficando evidente que, a natureza e intensidade de interferência é variável, sendo determinada pela espécie, ontogenia e nível de sensibilidade ao estresse.

Palavras-chave: balanço de carbono; déficit hídrico; fotoassimilados; carboidratos.

1. INTRODUCTION

Plants are sessile organisms that are continuously exposed to environmental changes that threaten their survival, mainly those connected to climate. Water is among the most limiting climate factors to development and growth of plants.

Water availability can be limited by droughts, high salinity, and freezing; it is one of the main risk factors for plant production in natural and agricultural habitats. In this review, water availability is treated as result of conditions of drought, which refers to meteorological conditions commonly connected to periods of low or no rainfall that result in soil water deficit. In plants, droughts cause losses of water in their tissues and cells.

Considering the current situation of intense climatic variations over short periods, it is expected that extreme events, such as droughts, occur with high frequency and intensity, affecting the future climate and impacting the carbon (C) balance of ecosystems.

Considering the importance of water for agriculture, the effects of droughts on development of plants have been widely studied, focused on identifying physiological and molecular responses activated by plants under water limitations.

Some already identified responses include life cycle changes, phenotypic changes in leaf structure and development (REGIER et al., 2009), changes in root to shoot growth ratio (ANDEREGG, 2012), regulation of opening

and closure of stomata (RUEHR et al., 2009), accumulation of solutes (PEREIRA et al., 2012; MONTEIRO et al., 2014), strategies for detox of reactive oxygen species, and metabolic changes (CHAKRABORTY; PRADHAN, 2012; MAGALHÃES et al., 2016).

These responses are affected by C allocation, which refers to regulation of distribution of the assimilated C in the storage organ (leaf) for metabolism and transport as starch and sugars (HASIBEDER et al., 2015; TAIZ et al., 2017).

Therefore, predicting responses of plants to environmental changes and the consequences for the ecosystem functioning requires understanding the regulation of the C allocation process; thus, the objective of this work was to gather information on the effects of droughts on C allocation in plants.

2. LITERATURE REVIEW

2.1. Definition of drought and its implications

Drought is a meteorological term commonly connected to periods of low or no rainfall that result in water deficit. In the soil, drought is the result of several factors, such as strong evaporation resulting from a high evaporative demand of atmosphere caused by high radiation levels and high temperatures; Moreover, high salinity and freezing of soils reduce water availability, causing water stress in plants (Figure 1). In plants, droughts cause loss of water in tissues and cells (WOOD, 2005).

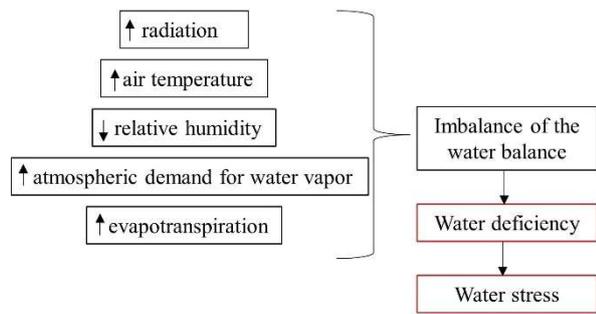


Figure 1. Water stress as result of interaction between climate factors.

Figura 1. Estresse hídrico como resultado da interação entre fatores climáticos.

A drought can be quantified, standardized, and compared through indicators. The Standardized Precipitation Index (SPI) developed by McKee; Doesken; Kleist, (1993) is among the indicators that have been increasingly used worldwide and is considered as one of the most updated for quantifying rainfall excess or water deficit in different time scales. SPI classifies droughts into classes, namely: light, moderate, severe, and extreme, which are also adopted for rainy periods (MCKEE et al., 1993).

In general, the water that enters and flows through a plant body is from the soil, and the force that drives this entry is dependent on the existence of a decreasing gradient of water potential (Ψ_w); in normal water availability conditions, the soil presents higher Ψ_w than the atmosphere, and the water exchange to the atmosphere is mediated by plants that work as a conductor.

Water deficit promoted by drought conditions prevents water exchanges in the soil-plant-atmosphere system, and it is considered as one of the most limiting abiotic factors to establishment, growth, and development of plants in most natural and agricultural habitats. The primary effects of this condition are expressed by decrease of Ψ_w in the soil, plant, and atmosphere, cell dehydration, and increase in water resistance (TAIZ et al, 2017).

There are several classifications for sensitivity to water stress, and the intensity of the effects caused by stress is connected to the sensitivity level and capacity of adaptation or acclimatization of plants, which enable them to survive and recover.

The adaptation to the environment is characterized by genetic changes in the whole population, fixed by natural selection during many generations, whereas acclimatization is a result of phenotypic plasticity, which corresponds to single and specific non-permanent changes in the plant physiology or morphology that result in ability to survive and develop in different environments and can be reverted in case of changes in the environmental conditions (VALLADARES et al., 2016).

Adaptation mechanisms and acclimatization of plants that allow them to thrive in drought conditions classify them into the categories: plants that delay, escape, or tolerate dehydration (BEWLEY, 1979). Plants that delay dehydration can keep their tissues hydrated by increasing their Ψ_w ; plants that escape from droughts can short their cycle, completing their vegetative and reproduction stages when water is still available in the environment; and plants that tolerate dehydration keep their metabolism even under conditions of low Ψ_w (WOOD, 2005; KOOYERS, 2015).

Mechanisms of delay, escape, and tolerance as response to soil water availability can be expressed through changes in the life cycle, phenotypic changes in the leaf structure and dynamics (REGIER et al., 2009), changes in the root to shoot growth ratio (ANDEREGG, 2012), regulation of stomatal opening and closure (RUEHR et al., 2009), accumulation of solutes (PEREIRA et al., 2012; MONTEIRO et al., 2014), strategies for detox of reactive oxygen species, and metabolic changes (CHAKRABORTY; PRADHAN, 2012; MAGALHÃES et al., 2016).

The amount of available water in the soil that is required for implementation, growth, development, and production of plants varies according to the species; the critical limit of available water is associated to the emergence of visible signs of injury and disturbances in a specific function in the plant. Soil water balance can be assessed through indicators, such as relative water content, water potential (Ψ_w), and osmotic potential (Ψ_s) (MONTEIRO et al., 2014; NASCIMENTO et al., 2019), which also indicate the plant water balance.

Ψ_w was used to represent the water balance of plants under drought conditions and its effects on physiological processes (Figure 2), and the soil Ψ_w was used to characterize the drought for some plant species under experimental conditions (Table 1). The Ψ_w results found denote a variation in sensitivity, according to the species and growing sites.

Table 1 shows that the species *Bowdichia virgilioides* tolerates a higher drought level than the others studied. The differences in Ψ_w between environments of open vegetation and Cerrado forest are mainly due to the type of vegetation. The highest Ψ_w found for the Cerrado forest is explained by a little presence of grass species and a high occurrence of shading, which decrease the water consumption and loss in the environment; this environmental condition is characteristic of a high sensitivity of the species, denoting an adaptation to the open vegetation environment, as the drought condition for the species in this environment expressed lower Ψ_w than that in the Cerrado forest.

Regarding the dynamics of plants in relation to water loss and the control mechanisms involved, the species are classified as isohydric and anisohydric. Maize is among the isohydric species that exhibit changes in stomatal conductance as a function of the soil water status before presenting any substantial change in leaf water potential, and the water loss is regulated by chemical products, such as abscisic acid (ABA) (hydro-active control) and water signaling (hydro-passive control). Sunflower is an example of anisohydric plant, presenting water loss control with lower contribution of hydro-passive signaling. Both water loss controls are mechanisms triggered by water deficit and are the first short-term feedback process in stress and high evaporative demand conditions (TARDIEU et al., 2018).

Five short-term feedback processes can be considered for control of water loss in plants: the first are hydro-active and hydro-passive; the second are changes in water conductance in tissues, attenuating fast changes in water potential, thus assisting to maintain water uptake in dry soils; the third is a fast osmotic adjustment (MONTEIRO et al., 2014); the fourth is a decrease in leaf area expansion, which decreases losses by evapotranspiration with effects on root growth, leading to an increase in the root to shoot ratio, stabilizing the leaf water status (ANDEREGG, 2012; DURAND et al., 2016); the fifth is the optimization of carbon to the water status, since in dry soil conditions, the expansive growth of plants is affected

earlier and more intensively than the photosynthesis due to a high resilience of the photosynthetic apparatus to water

deficit; therefore, plants under stress tend to present excess carbon in the source (SALMON et al., 2019).

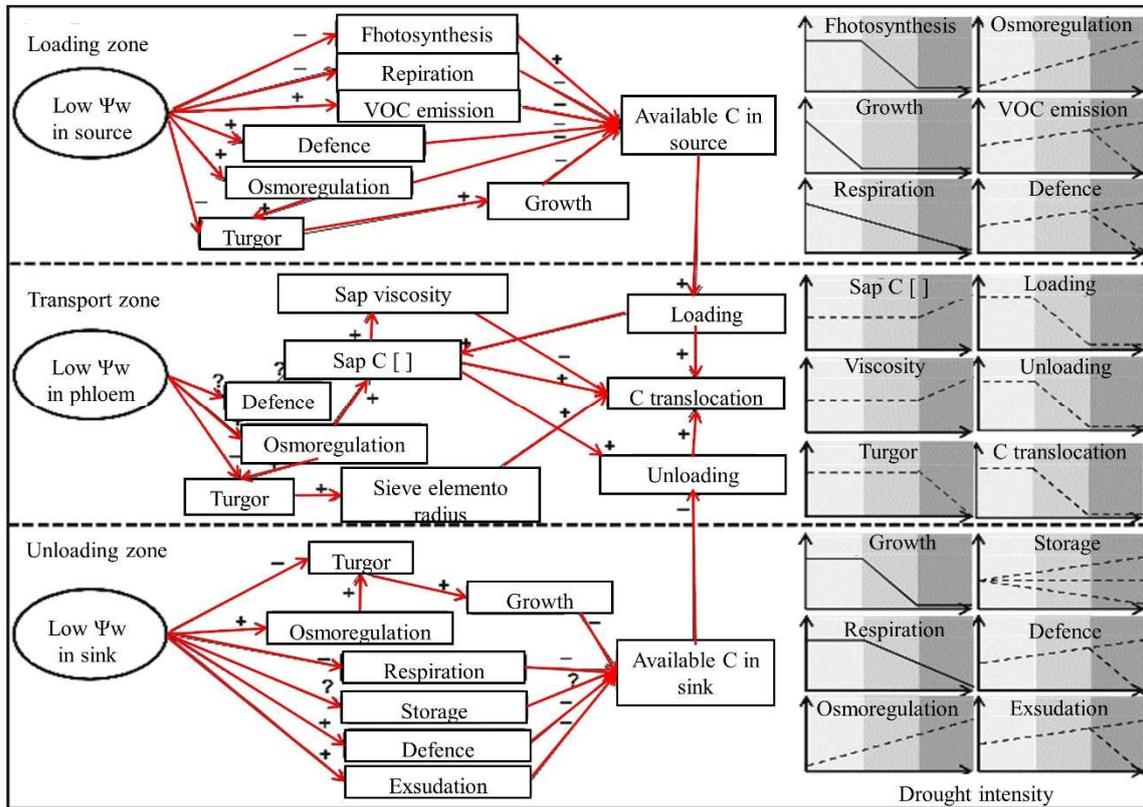


Figure 2. Simplified conceptual model of effects of drought in leaf, phloem, and root physiological processes, driven by reductions in water potential (left) and hypothetical physiological changes as the drought (right) progresses. (+) and (-) represent individual effect of each arrow; areas in light, medium, and dark gray represent light, moderate, and severe drought, respectively; continuous lines represent well-established relationships, and dashed lines represent speculative relationships. Source: Adapted from Salmon et al. (2019). Cerrado forest = forest formation, with tree cover of 50% to 90%; open vegetation = predominantly herbaceous-shrubby vegetation, occurring in shallow or deep soils with low fertility.

Figura 2. Modelo conceitual simplificado dos efeitos da seca em processo fisiológicos da folha, floema e raiz, impulsionados pela redução do potencial hídrico (esquerda) e mudanças fisiológicas hipotéticas com a progressão da seca (direita). Sinais de (+) e (-) simbolizam o efeito individual de cada seta, áreas em cinza claro, médio e escuro representam seca leve, moderada e severa respectivamente, linhas contínuas representam relações bem estabelecidas e linhas tracejadas relações especulativas, tons de cinza Fonte: Adaptado de Salmon et al. (2019). Cerradão = formação florestal, com cobertura arbórea variando de 50 a 90%; campo sujo = vegetação predominantemente herbácea-arbustiva, de ocorrência em solos rasos ou profundos de baixa fertilidade.

Table 1. Water potential (Ψ_w) in the soil, characterizing water stress conditions in experimental situations for different species and growing sites.

Tabela 1. Potencial hídrico (Ψ_w) do solo caracterizando condições de estresse hídrico em situações experimentais para diferentes espécies e locais de crescimento.

Species	Growing site	Experimental conditions	Soil Ψ_w (Mpa)	References
Sucupira-do-cerrado (<i>Bowdichia virgilioides</i>)	Cerrado biome, Brazil (tropical seasonal)	Open vegetation	-6.2	(KANEGAE et al., 2000)
Sucupira-do-cerrado (<i>Bowdichia virgilioides</i>)	Cerrado biome, Brazil (tropical seasonal)	Cerrado forest	-2.8	(KANEGAE et al., 2000)
Alamo negro (<i>Populus nigra</i> , Poli)	Southern Italy (hot and temperate)	Pots	-0.01	(REGIER et al., 2009)
Alamo negro (<i>Populus nigra</i> , 58-861)	Northern Italy (cold and temperate)	Pots	-0.02	(REGIER et al., 2009)
Autotetraploid rice (<i>Oryza sativa</i>)	Northern China (subtropical wet)	Pots	-0.02	(YANG et al., 2014)
Diploid rice (<i>Oryza sativa</i>)	Northern China (subtropical wet)	Pots	-0.04	(YANG et al., 2014)
Sorghum (<i>Sorghum bicolor</i>)	Central Minas Gerais state, Brazil (tropical)	Pots	-0.1	(MAGALHÃES et al., 2016)

Plants may also present long-term feedback processes, which include intrinsic properties for optimization of water resources over time, such as changes in cycle duration and phenology; abortion of grains, resulting in lower quantity, but more viable grains; root system architecture; deeper root systems with less lateral roots; leaves with the ability to maintain photosynthetic functions and delay senescence (Stay-Green phenotype) (TARDIEU et al., 2018).

2.2. Photosynthesis - primary process of survival

A large fraction of the planet's energy resources is a result of photosynthetic activity, from recent or past times. Photosynthesis is the process used by plants to convert solar energy into chemical compounds, which is responsible for the maintenance of life of heterotroph beings and involves photochemical processes (activated by the presence of light), enzymatic processes that require no light, and diffusion processes that are responsible for carbon dioxide and oxygen exchanges between chloroplasts and atmospheric air (STIRBET et al., 2020).

Photochemical processes occur in thylakoids inside chloroplasts, where oxidation process of water molecules occur, as well as reductions of NADP⁺ to NADPH, and synthesis of ATP, which are essential compounds for the enzymatic step which occurs in the stroma of chloroplasts. NADPH and ATP are used to reduce atmospheric CO₂,

incorporate CO₂ in organic molecules, the carbohydrates, which are the main sources of energy for growth and development of plants. The incorporation of C occurs through a cyclical sequence of reactions, termed pentose cycle or Calvin-Benson cycle (GEIGER; SERVAITES, 1994; TAIZ; ZEIGER, 2017).

Fixed C can be allocated from source tissues for storage (as starch in chloroplast or saccharose in the cytosol), or transported when the fixed C is incorporated into transport sugars that are taken to the different drain tissues; in addition, part of it can be temporarily stored in the vacuole and used for metabolic processes in source and drain tissues to meet energy demands and provide C skeletons for synthesis of other compounds needed by the cell (LAVIOLA et al., 2007; TAIZ et al., 2017).

Plants have leaf structures to capture CO₂, the stomata, which conduct gas exchanges with the atmosphere. Under ideal climate conditions of light, temperature, and water availability, stomata capture CO₂ and release water vapor to the atmosphere. Under prolonged drought conditions, decreases in Ψ_w in leaves result in decreases in photosynthesis, affected by decreases in stomatal conductance (Table 2). Therefore, the CO₂ availability for fixation process is limited and the carbohydrate production is reduced.

Table 2. Percentage of reduction in stomatal conductance (g_s) and CO₂ assimilation rate (A) in plant species under drought conditions. Tabela 2. Porcentagem de redução da condutância estomática (g_s) e taxa de assimilação de CO₂ (A) em espécies sob condições de seca.

Species	Stomatal conductance (g _s)	CO ₂ assimilation rate (A)	References
	Decrease (%)		
Faia europeia (<i>Fagus sylvatica</i> L.)	48	37	(RUEHR et al., 2009)
Sugarcane (<i>Saccharum officinarum</i>)	59.99	63.93	(GONÇALVES et al., 2010)
Conilon Coffee (<i>Coffea canephora</i>)	92.8	65	(SILVA et al., 2010)
Alamo tremedor (<i>Populus tremuloides</i> Michx.)	86.6	82	(GALVEZ et al., 2011)
Calendula (<i>Calendula officinalis</i> L.)	95.25	91.87	(PACHECO et al., 2011)
Mutambo (<i>Guazuma ulmifolia</i> Lam.)	57.27	72.55	(SCALON et al., 2011)
Mogno africano (<i>Khaya ivorensis</i>)	95	90	(ALBUQUERQUE et al., 2013)
Pata-de-elefante (<i>Beaucarnea recurvata</i>)	80	92	(BERTOLLI et al., 2015)
Maize (<i>Zea mays</i>)	12.8	26.57	(ANJUM et al., 2016)
Cowpea (<i>Vigna unguiculata</i>)	62.33	52.66	(SOUZA et al., 2020)

2.3. Drought as factor of regulation of C allocation in plants

2.3.1. Allocation, translocation, and partition of photosynthates

It is important to define the terms allocation, translocation, and photosynthate partition, as studies present different definitions for these terms, causing, in some cases, confusion between definitions or omissions.

Allocation refers to regulation of the distribution of the assimilated C in the source organ (leaf) for storage, metabolism, and transport as starch or sugars (HASIBEDER et al., 2015; TAIZ et al., 2017). The fixed C can be incorporated into transport sugars that are taken from the production areas to importing organs (drains), including short- and long-distance transports. This transport is termed translocation. Partition refers to the differential distribution of photosynthates among the different drains, which is a process that depends on the drain force of the assimilated C according to its size and activity (TAIZ et al., 2017).

Similar to photosynthesis, these processes are affected by water deficit, since they are connected to photosynthetic metabolism products. However, the present review is focused on a more investigative form of C allocation, which can vary over the plant life cycle, according to the age of different organs, and is affected by environmental conditions, such as droughts, high temperatures, and low rainfall and relative air humidity (OLIVEIRA et al., 2019).

All organic compounds inside the plant that can be reintroduced or recycled in the primary metabolism can serve as C reserves when C requirement exceeds the C supply by the photosynthesis. Most of these compounds are used for other functions and storage. For example, sugars of low molecular weight can be used as intermediate metabolites, C transport compounds, osmolytes, and C sources for structural growth or respiration. The multifunctional nature of many compounds denotes that they cannot be completely degraded in live tissues, even when the plant is passing through strong stressful conditions (HOCH, 2015).

Despite the large number of compounds that can be used as reserve, only two classes are synthesized exclusively as storage compounds, which are polysaccharides (starch and fructan) and neutral lipids (triacylglycerols), the latter is important, quantitatively, in only a small number of species (HOCH, 2015). Studies that show C reserves term compounds such as starch plus sugars of low molecular weight as non-structural carbohydrates (NSC) (WOODRUFF; MEINZER, 2011; HOCH, 2015).

Growth and other physiological functions of plants depend on momentaneous photosynthetic rates and NSC reserves. When the photosynthesis produces more C than that required by the plant, part of the C is stored as NSC, whose concentrations determine the balance between fixed C and demanded C for growth, respiration, defense metabolism, reproduction, and exudates (WOODRUFF; MEINZER, 2011).

NSC accumulation is affected by water availability; a low water availability affects cell expansion rates driven by the turgor. Decreases in turgor of tissues decrease the translocation from source to drain, and the assimilated C is incorporated as sugars or converted into starch for storage, resulting in accumulation of C allocated as NSC, providing energy for metabolic processes for plant survival.

Under water stress conditions, plant growth rates are lowered before the photosynthesis and respiration, resulting in a more intense decrease in aerial growth than that in the root system growth (Figure 2). More significant decreases in aerial growth result in intense accumulation of NSC, with high amounts of sugars. Roots depend exclusively on fixed C in leaves, which is exported in high amounts for maintenance of roots, despite the export speed be reduced.

Maintenance of root system to the detriment of shoot growth was reported for *Arabidopsis thaliana*. The water deficit decreased the shoot growth, but increased NSC accumulation and resulted in a higher C allocation in roots. The root system growth was little affected, with different intensities of decrease between the growths of lateral roots and main root, thus presenting little interference (DURAND et al., 2016). The decreases in growth found for lateral and main roots indicate that the plant may have undergone an acclimatization process, prioritizing the growth of the main root, since it can reach greater depths, thus increasing water absorption, as deeper regions are less prone to water loss than soil surface layers where lateral root grow.

NSC accumulation in drought conditions was previously identified by Woodruff; Meinzer (2011), who analyzed the seasonal course of NSC in *Pseudotsuga menziesii* with heights of 2 to 57 m. Higher NSC accumulations were found in leaves, followed by branches and shoots; starch was the main component, followed by saccharose. The greater NSC accumulation in the leaf is because it is the organ responsible for C assimilation and synthesis of sugar and has larger number of live cells that can convert and store NSC, resulting in decrease of photosynthetic rates and in maintenance of cell turgor.

The positive correlation between plant height and NCS accumulation and the negative correlation between plant heights and water and osmotic potentials are also important, as proved for *A. thaliana*: regardless of the higher C accumulation, the C allocated for aerial growth was low. The highest heights found for *P. menziesii* plants were because tall trees are subject to greater gravitational effects and greater hydraulic resistance as the soil moisture decreases, therefore,

the stress increases and taller trees present higher stress levels (WOODRUFF; MEINZER, 2011).

Therefore, a low Ψ_w reduces the plant growth, resulting in lower biomass accumulation, which is connected to the plant production. Thus, plant growth and biomass production present the same dynamics, favoring root growth, as found for *A. thaliana*, which, although presented decreases in dry weight for both organs, it was less significant for roots when compared to the control (DURAND et al., 2016), again denoting the greater impact of water deficit on the plant aerial part, which results in lower grain yield (SANTOS et al., 2012; ARRUDA et al., 2015).

In addition to stress caused by drought, the factors species and ontogeny also affect C allocation, and different strategies of allocation can be found for a same genotype, as they show variations in sensitivity to stress.

The growth of a same plant species in different regions is possible due to the plant phenotypic capacity for acclimatization, which can result in different levels of sensitivity to stress in different environments. Regier et al. (2009) induced to drought conditions two clones of *Populus nigra* (Alamo negro) from contrasting climatic origins, one of them adapted to drought (Poli) and other sensitive to drought (58-861). The responses presented for accumulations of total NSC (starch, saccharose, glucose, and fructose) and soluble sugars (saccharose, glucose, and fructose) were different between the clones. Sensitive plants presented decreases in total NSC contents in leaves and roots, and the opposite was found for adapted plants. Soluble sugar contents decreased only in leaves of sensitive plants with accumulation in roots, whereas adapted plants had decreases in leaves and roots.

Roots are the main reserve organ in the plant, and decreases in starch contents in roots observed in plants sensitive to stress can be connected to a high activity of the enzymes that perform the hydrolysis of this compound to provide substrate for the respiration process for growth or maintenance. Whereas the accumulation of starch in roots of plants adapted to drought conditions indicates that even under stress conditions they prioritize growth and storage and can allocate higher amounts of compounds for roots, favoring their development and increasing their capacity to absorb water and minerals.

The same result found for plants adapted to drought conditions was found for seedlings of *Populus tremuloides* (Alamo tremedor) subjected to drought under protected environment conditions. In general, total NSC concentrations in roots were 73.7% higher than those found in seedling roots used as control (GALVEZ et al., 2011). Similar results were found for plants of the same species under mountain pasture conditions and subjected to drought in the field.

The examples presented referring to different species and studies showed that each species, under water deficit conditions, presents specific dynamics that are sometimes similar; however, their dynamics cannot be compared because of the different experimental conditions and growth stages. Moreover, the definition of drought effects cannot be treated in a general approach, but with a distinction between the investigations adopted to clearly assess the reaction of each species separately.

2.3.2. Root exudates

Plants release exudates through the root system, which are complex and soluble mixtures of C compounds, such as

sugars, amino acids, organic acids, and secondary metabolites, reaching up to 10% of the plant photosynthates, composing a dynamic source of C to the soil and promoting maintenance of ecosystems (FELLBAUM et al., 2012; LU et al., 2018).

An intriguing question about exudates is: why plants release significant quantities of a resource that is essential for them? The answer is given by the interaction between plants and soil microorganisms, known as symbiosis (FELLBAUM et al., 2012).

Symbiosis has a cost-benefit relation in which plants regulate the C allocation for microorganisms in response to changes in environmental conditions, making C availability to promote microbial growth in the soil, and microorganisms provide significant quantities of nutrients to plants, such as nitrogen, affecting plant phenology, triggering flowering, stimulating growth, and increasing reproduction. Therefore, exudates are important for the communication between plant and microorganisms (FELLBAUM et al., 2012; LU et al., 2018).

Droughts have a potential to change the soil microorganism community and C availability through the production of exudates by plants. The response of a community to a stressful environment depends on the physiological tolerance and metabolic flexibility of the microorganisms; therefore, droughts affect the selection of resistant or tolerant microorganisms, and the C availability promotes organic matter decomposition through them and, consequently, availability of nutrients for both symbiotic microorganisms and plants.

The use of ^{13}C isotope tracer is an important methodology for studies evaluating C allocation, exudates, respiration, and community of microorganisms in underground systems. For example, decreases in respiration and allocation of momentarily assimilated ^{13}C to the soil microbial mass was found for plants of *Fagus sylvatica* (RUEHR et al., 2009). Decreases in the respiration process was also found by Hasibeder et al. (2015) in mountain pastures, resulting in lower soil C availability.

Mountain pastures were also evaluated by Fuchslueger et al. (2013), who assessed changes in the microbial communities and amount of available ^{13}C to them and found significant increases in fungal and bacterial biomasses in treatments under drought conditions, with lower recently-assimilated ^{13}C availability in bacteria, but not for fungi, when the transfer of ^{13}C was not affected by drought.

The association of fungi with plant roots can increase nutrient and water availability to the root system, as a higher soil volume is explored, reaching depths inaccessible by roots (FUCHSLUEGER et al., 2014; CHITARRA et al., 2016). Therefore, this lack of changes in ^{13}C allocated to soil fungi may compose a strategy of plants to survive under water deficit conditions. Another possible survival strategy in pastures was the great capacity of plants to stimulate the microbial activity and mineralization of nutrients, even when the quantities of exudates were significantly reduced by the drought (VRIES et al., 2019).

Droughts not only reduce the amount of exudates and C allocated in them, but their quality. For example, Gargallo-Garriga et al. (2018) evaluated plants of *Quercus ilex* and found release of exudates consisted mainly of secondary compounds (flavonoids, terpenoids, and phenols), corresponding to approximately 71% of the total metabolites, whereas 81% of exudates corresponded to

primary metabolites (saccharides, amino acids, and organic acids) under recovery conditions (after a drought period).

Secondary organic compounds are highly specific and important for the species evolution and interaction between organisms, which are connected to plant defense mechanisms against biotic and abiotic stresses, as primary compounds are connected to plant growth and development. This explains the dominance of secondary compounds in exudates of *Quercus ilex* found by Gargallo-Garriga et al. (2018) under drought conditions; the plants activated their defense metabolism against the abiotic stress and produced more primary compounds in rehydration condition as a strategy for fast recovery of their functions and growth.

2.3.4. Phloem and metabolism of defense

The connection and transport of C from the shoot to the root system occurs through the phloem tissue, which is in the center of structural functions of the plant, transporting C as NSC, nutrients, defense compounds, and all types of information throughout the plant body. The capacity of the phloem to transport compounds is controlled by the balance of C and water flows inside the plant. Therefore, it is expected that droughts affect the phloem function, as the amount of available water and the photosynthate production are reduced (SALMON et al., 2019).

Water is the main substance for dilution of organic and mineral solutes. Water enters the root system and is redistributed to all plant tissues through the xylem, which is also responsible for supplying the phloem. When the soil presents low Ψ_w , the amount of water transported through the xylem and made available to the phloem is reduced, leaving a more viscose solution. In addition to the phloem texture, droughts can modify the anatomy of conducting elements, decreasing their radius and the speed of recently assimilated C (SALMON et al., 2019; DANNOURA et al., 2019).

The increase in viscosity and decrease in radii of phloem elements were reported by Dannoura et al. (2019), who investigated effects of droughts on phloem anatomy and transport in *Fagus sylvatica* and found that plants treated with droughts had an increase of 0.41 mPa in viscosity as response to a high carbohydrate accumulation in the phloem, and a decrease of 3 μm in the radius of phloem elements, with a decrease of 70% in the phloem hydraulic conductivity.

The effects of the decrease in radii of conducting elements result in lower C allocation rates to the different organs and metabolic pathways, thus increasing the time of permanence of temporarily assimilated C in the leaf biomass of *F. sylvatica* L. and mountain pastures (RUEHR et al., 2009; FUCHSLUEGER et al., 2014).

Investigation in mountain pastures was more detailed by Hasibeder et al. (2015), who made distinction between the ^{13}C allocated and the speed of allocation in compounds such as starch, saccharose, glucose, and fructose in shoots and roots. They found no effect of the drought treatment on the shoot, but found a decrease in the amount of C allocated, and delay in the speed of allocation to roots, which was five days for starch, 20 hours for saccharose, and 10 days for glucose and fructose. The authors also investigated the speed of ^{13}C allocated to the respiration and found significant decreases in the treatments, with concentrations of breathed ^{13}C reaching peaks of 8 and 24 hours after marking for control plants and 24 hours for plants under stress.

Hasibeder et al. (2015) also found a significant increase in saccharose, glucose, and fructose concentrations in the root system, approximately 41% for saccharose over two weeks after marking with ^{13}C , and glucose and fructose concentrations more than doubled during one and two weeks of treatment.

The results indicate that drought conditions modulate the allocation of recent assimilates to favor reservoirs of carbohydrates as soluble organic compounds, mainly saccharose. These syntheses of soluble organic compounds are due to a defense strategy defense of osmotic adjustment, which allows the plant to keep the integrity of its cells and membranes by maintaining cell turgor; however, this accumulation of osmolytes is the main process that competes with the loading of phloem, decreasing the amount of C for exports.

The osmotic adjustment is a physiological/molecular response to water deficit by two ways: production of soluble organic compounds and absorption of ions from the soil or other organs. However, the use of ions in the osmotic potential regulation can cause harmful effects to cell metabolism when at high concentrations (SILVENTE et al., 2012).

However, the production of osmolytes, or compatible solutes, does not destabilize the membrane or affect enzymatic functions, acting as protectors for them (KRASENSKY; JONAK, 2012; SILVENTE et al., 2012).

The most common compatible solutes are amino acids, such as proline, mannitol (sugar alcohols), and betaine glycine (ammonium quaternary compound) (ALBUQUERQUE et al., 2013; MONTEIRO et al., 2014). The synthesis of these solutes is an active metabolic process that requires a large amount of energy, and the amount of C used in this process can be high.

Considering these compounds, proline is very important for plants under water stress, and presented increases in several studies (Table 3), in which the highest increases were found for plants of *Lippia sidoides* Cham. and *Khaya ivorensis*: approximately 13 and 16.5-fold, respectively.

Table 3. Studies that found increases in proline levels in plants under drought conditions.

Tabela 3. Estudos que identificaram aumento nos teores de prolina em plantas sob condições de seca.

Species	Increase		Authors
	μmol	g	
Coffee	4.12		(SILVA et al., 2010)
Peanuts	0.47		(PEREIRA et al., 2012)
Tomato	15.59-28.3		(CHITARRA et al., 2016)
Lemon	65.04		
Orange	51.69		
Alemow	60.51		
Bael	66.71		
Lemon	13.54		(ZAHER-ARA et al., 2016)
Red Blush	16.24		
Orange	2.33		
Pineapple	83		
Shel	3.86		
	μmol	g	
Rosemary	0.94		(ALVARENGA et al., 2011)
Papaya	13.93		(SILVA et al., 2012)
Mogno	42.28		(ALBUQUERQUE et al., 2013)

The proline accumulated during water stress conditions does not act only as an osmolyte, but as a signaling and defense molecule against oxidative damages. In the cytoplasm, it promotes stabilization of protein structure, assists in the maintenance of pH and redox status, decreasing the amount of oxygen radicals responsible for thylakoid membrane lipid peroxidation (KHAN et al., 2018).

The synthesis and accumulation of this amino acid are found usually higher in leaves because of a need for regulation of cell osmotic pressure to increase their water retention capacity, thus limiting losses by transpiration. The proline content in leaves can continue to increase even after the beginning of irrigation, which can contribute to a fast recovery of the plant water status (SILVA et al., 2012; ALBUQUERQUE et al., 2013).

The proline content varies according to the plant sensitivity level to water stress; however, it increases in all cases under deficit water conditions (Table 4), as resistant plants express greater capacity to synthesize this compound, increasing its concentration.

As proline, other compounds are responsible for osmotic adjustment, decreasing cell dehydration and protecting membranes. These compounds include saccharose and glycine betaine, which also present expressive accumulation in leaves when compared to that in the root system (SILVA et al., 2012; ZAHER-ARA et al., 2016)

These higher concentrations in leaves are connected to the transpiration process, which is more intense in these organs, and the increase of resistance to water loss promoted by the osmotic adjustment makes the plant more resistant to drought conditions. However, osmotic adjustment does not occur only in leaves, the root system also has such capacity, as this plant structure is in direct contact with the low Ψ_w of soil and cannot easily regulate water loss.

The water stress caused by drought is usually combined with other environmental factors, such as high temperatures, which are intensifiers of the drought effect by increasing evapotranspiration, affecting fluidity of lipids in cell membranes, which can compromise their integrity and inactivate enzymes in chloroplasts and mitochondria.

However, stressful processes can activate and increase the activity of antioxidant enzymes, decreasing the amount of reactive oxygen species (ROS) originated from the incorporation of electrons to molecular oxygen that would be used to reduce NADP⁺ into NADPH in chloroplasts (CARVALHO; CARVALHO NETO, 2016).

ROS are highly oxidizing substances, and the most known and studied are the triplet state of chlorophyll (3Chl*), single oxygen ($^1\text{O}_2$), superoxide (O_2^-), hydroxyl (OH^-), and hydrogen peroxide (H_2O_2), which can damage cell structures through the removal of electrons from several molecules, including proteins, lipids, DNA, and carbohydrates (CARVALHO; CARVALHO NETO, 2016).

Plants have two defense lines against ROS. The first involves the xanthophyll cycle, which acts in the following steps: chlorophyll absorbs energy from photons and reaches an excited state, this excitation energy can be rapidly photochemically dissipated (photochemical quenching); if this dissipation is not rapid, a super photosystem excitation occurs and the excited chlorophyll can react with molecular oxygen forming reactive oxygen species. The xanthophyll cycle prevents the super photosystem excitation, releasing excess energy as heat (non-photochemical quenching), thus preventing ROS formation (TAIZ et al., 2017).

The second defense line consists of production of enzymatic components (superoxide dismutase, catalase, peroxidases, and glutathione reductase) to neutralize oxidative damages and protect cell membranes (BITTENCOURT; SILVA; 2018).

Considering these enzymes, superoxide dismutase is the only responsible for the reaction against high O₂⁻ toxicity, and peroxidases and catalase are responsible for removing H₂O₂ radicals. Several studies have shown that the activity of these enzymes increases under drought conditions. Increase of the three enzymes were found in wheat and peanut plants (CHAKRABORTY; PRADHAN, 2012; PEREIRA et al.,

2012), increase of catalase was found in sorghum (MAGALHÃES et al., 2016), and increase of superoxide dismutase and catalase was found in *Populus nigra* (REGIER et al., 2009).

In these studies, increases in antioxidant enzyme activity were connected to resistance to drought and can be used to identify the plant sensitivity to water stress, as species tolerant to stress express increasing antioxidant activity even under severe stress conditions, and sensitive species also express increase in enzymatic activity, but it decreases as the drought becomes more severe as a response to high ROS concentrations (CHAKRABORTY; PRADHAN, 2012).

Table 4. Average proline values in different plant genotypes subjected to water stress by suspension of irrigation.

Tabela 4. Valores médios de prolina em diferentes genótipos submetidos à estresse hídrico por suspensão de rega.

Crop	Genotypes	Control	Stress	Authors
		µmol g MS ⁻¹		
Wheat	Anahuac	24.64	94.54	(FUMIS; PEDRAS, 2002)
	IAC-24	19.09	80.63	
	55 437	0.65	1.33	
Peanut	BR 1	0.88	1.31	(PEREIRA et al., 2012)
	LBM Branco	1.00	1.29	
	LBR Branco	1.20	1.74	
	LViPE-06	1.23	1.67	
Sugarcane	RB867616	0.16	0.86	(MEDEIROS et al., 2013)
	RB962962	0.21	0.76	
Potato	Euro bravo	1	130	(BÜNDIG et al., 2016)
	Maxi	1	140	

Most responses of plants to drought occurs as a function of hormonal signaling, through a positive regulation of abscisic acid (ABA), which is the stress hormone (TARDIEU et al., 2018) and acts as main sign involved in the processes of adaptation to droughts, including stomatal closure, which is the first response of plants to water loss caused by water stress (GONÇALVES et al., 2010; ALBUQUERQUE et al., 2013; BERTOLLI et al., 2015).

Roots use the stored C to promote metabolism of ABA under drought conditions, which is exported to leaves, where the transpiration is more intense, causing stomatal closure and decreasing photosynthesis in a short time. The function of this hormone is to control the ionic balance in guard cells through the regulation of influx and efflux of K⁺, Cl⁻, and organic acids (CARVALHO; CARVALHO NETO, 2016).

The synthesis of ABA in roots can stimulate their growth and, when translocated to the shoot, it can cause stomatal closure and decreased leaf growth with subsequent abscission (TARDIEU et al., 2018).

Leaf abscission and decreases in leaf area caused by ABA are visible responses to water stress, through which the plant reduces C and energy consumptions, allowing a higher amount of assimilates to be directed to the root system, prioritizing their growth to favor water absorption by increasing the soil volume explored, also composing a strategy to maintain the growth after the stress.

A. thaliana plants showed approximately four-fold decreases in leaf area, culminating with a 30% decrease in number of leaves and 80% in biomass accumulation (DURAND et al., 2016). This result shows the pros and cons of decreasing in leaf area; it allows an economy of the energy demanded for the expansion process, but results in lower photosynthetic area and consequent lower C assimilation and

carbohydrate formation, making NSC the main source of energy.

Leaf abscission and decreases in leaf area are acclimatization strategies of plants to environmental variations; another important leaf tissue specialization is the decrease in stomatal density, increase in opening of ostioles (REGIER et al., 2009; SCALON et al., 2011), thickening of leaves (REGIER et al., 2009), and decrease in stomata opening time (GALVEZ et al., 2011; SCALON et al., 2011).

3. DISCUSSION

The plant environment may present several stressful agents. Plants are subjected to several environmental factors over time, such as high and low temperatures, high and low solar irradiance, high salinity, nutritional deficiency, toxicity by elements, droughts, and floods (ALVARENGA et al., 2011; ARRUDA et al., 2015); they are sessile organisms, thus they must thrive under these challenges that are imposed by the environment (SOUZA; LÜTTGE, 2015).

Water is the main essential factor for survival of biological life as we know it, without it no life exists. The importance of water to plants can be evaluated by assessing the constitution of plant tissues, which consist, on average, of 85% to 90% water (WOOD, 2005).

From the agriculture point of view, water is the most limiting factor for agricultural production in the world. Despite some plants are in regions with high water availability, a holistic view should be presented, considering that the world water availability level is a great problem, and depending on the evolution of climate changes, it can be aggravated due to the occurrence of more frequent and intense droughts during plant development stages, which can cause plant death (SCALON et al., 2011).

The occurrence of droughts alone is a great problem for the maintenance of native and agricultural vegetations and can be aggravated, considering the vegetation variability in the environments. Drought situations diverge between species (Table 1) and are dependent on their tolerance to stress.

Severe water stress caused by drought conditions is responsible for significant physiological and metabolic changes in plants. Several responses to water scarcity have been observed, and decreased growth is by far the most significant (HASIBEDER et al., 2014; MONTEIRO et al., 2014; ARRUDA et al., 2015).

The main growth promoting agent is water, which, through the turgor pressure, promotes irreversible expansion of cell wall. Thus, droughts affect the plant growth, mainly by limiting water availability for cell expansion and decreasing the amount of energy available for this process by decreasing photosynthesis and carbohydrate production (PACHECO et al., 2011; MEDEIROS et al., 2013).

Decreases in photosynthetic process occur because of different reasons and are intensified by water scarcity due to stomatal limitations for influx of CO₂; damages to the photosynthetic apparatus, mainly to the photochemical step; reductions in energy production (ATP); and decreases in the Rubisco enzyme activity or regeneration (MARENCO et al., 2014). This enzyme is responsible for catalyzing C fixation reaction.

A reduced Rubisco activity and regeneration decreases the production of glyceraldehyde-3-phosphate (PGAL) molecules used for synthesis of starch, sugars, and many cell components. That means decreases in compounds used as source of energy for the metabolic processes, inducing the different uses of carbohydrates and their different allocations (organs) (FUCHSLUEGER et al., 2014; BERTOLLI et al., 2015; SOUZA; LU, 2015).

Percentages of decrease in the photosynthetic process resulting from limitations in stomatal conductance are presented in Table 2. The comparison between species shows those with greater capacity to thrive in hostile environments regarding water availability. Therefore, the plants that are more able to survive in such conditions, present lower percentages of decrease in stomatal activity and photosynthesis. Considering the species presented here which were evaluated under drought conditions, maize presented the greatest capacity to maintain its metabolism with no significant changes; this is because maize plants present a C₄ metabolism, which enables them to explore drier environments using water more efficiently, in addition to being an isohydric species which controls water loss through chemical and hydraulic signs (TARDIEU et al., 2018).

Water shortage conditions result in low amounts of C allocated to respiration (RUEHR et al., 2009; HASIBEDER et al., 2015); increases in C allocation for defense metabolism, with higher synthesis of ABA, osmoprotectant compounds and antioxidants (ALBUQUERQUE et al., 2013; MAGALHÃES et al., 2016); reduction in the radius of phloem conducting elements; increase in phloem viscosity; increase in C concentration in phloem; reduction of C loading, discharge, and translocation and in the speed of these processes (DANNOURA et al., 2019; SALMON, 2019); and decrease of leaf area, density and size of stomata, number of structures, and crop yield (REGIER et al., 2009; ARRUDA et al., 2015; DURAND et al., 2016).

The high production of osmoprotectant compounds, such as proline which is widely studied in drought conditions, can be used to identify tolerant species to water stress. Tables 3 and 4 show species/genotypes that grow low and high amounts of this amino acid; those with higher production are more tolerant to water scarcity. The fast increase in proline content can also be a signaling denoting that the plant is under a water stress condition (KHAN et al., 2018).

Therefore, the response of plants to lack of water depends on the species; *Bowdichia virgilioides*, for example, tolerate a higher stress level than the other species presented in Table 1, which are more sensitive to water stress, according to the definition of drought for them.

The species factor, which is specific for the definition of climatic stress conditions, and the soil characteristics determine the characteristics of the vegetation of each region. For example, regions that have greater water availability, such as the Amazon, tend to present taller plants, and regions with lower water availability, such as the Cerrado and Caatinga biomes, tend to present smaller plants, i.e., water availability determines the genetic codes and metabolisms of plants that developed in the environment (KRASENSKY; JONAK, 2012; SOUZA; LÜTTGE, 2015).

Plant species can be categorized according to their dynamics under water scarcity into species that delay, escape, or tolerate dehydration (BEWLEY, 1979). These categories are determined according to plant acclimatization or adaptation capacity, which includes different responses to stress conditions.

Water stress affects the plant C balance, directly effecting the crop yield; thus, it is an interesting factor for farmers. Low crops yields can decrease food reserves, increase prices of agricultural products, and decrease irrigation levels, impacting the production chain of the agribusiness (FAO, 2004).

According to the United Nations Convention to Combat Desertification (UNCCD, 2016), a proactive approach to increase the resistance to drought is composed by three bases: monitoring of droughts and use of early warning systems that integrate different variables, such as rainfall depths, stream flows, snow, underground water levels, reservoir and lakes levels, and soil moisture; vulnerability and risk evaluation, which adopt important resources, such as record of impacts of droughts on economic sectors, vulnerability reasons, and conditions that impact the resistance of a system to drought, resilience of affected communities, and assessment of sector, populational groups, and ecosystems under high risk; and measures to mitigate the risks of drought, which include capture of water, protection of water sources, construction of dams, restoration of pastures areas, planting of trees, improvement and adequation of irrigation systems, and growth of crops tolerant to drought.

Considering the three bases described by the UNCCD, measures for mitigation can be the most used in rural properties; the use of genetic resources is the main measure used to reduce impacts of droughts on the production. An example is the growing of species with different tolerance levels to water stress, maintaining the production during gradual or moderate soil water deficit. However, the choice of species may consider the plant tolerance level to stress and its dynamics when associated with the different environmental factors and the interaction between them.

Plants that present right tolerance level to stress usually have morphophysiological characteristics that enable their implementation, growth, and development, such as a leaf orientation that avoids excessive warming and a consequent transpiration; more developed and efficient root systems that explore greater soil volume when searching for moisture; presence of structures that reduce leaf water loss, such as trichomes, thick cuticles, and lower leaf area; and protection mechanisms, such as tolerance to desiccation, detox, and recovery from emboli in the xylem (TARDIEU et al., 2018).

In addition to the use of tolerant species, farmers can use no-tillage system; according to the Food and Agriculture Organization (FAO, 2004) of the United Nations, it is characterized by the maintenance of straw on the soil, which is a practice used for conservation of soil moisture and improvement of soil conditions.

4. CONCLUSIONS

The responses of plants to water stress conditions include greater allocation of carbon for formation of non-structural carbohydrates (energy source of metabolic processes for plant survival); maintenance of root system growth for production of volatile organic compounds (osmoregulation) and antioxidant enzymes (defense metabolism); and decreases of the carbon allocated for maintenance of aerial growth and for root exudates, and decreases in speed of carbon allocation caused by increases in viscosity of phloem. However, these responses may present variations because the origin and intensity of the effects are determined by the species, ontogeny, and level of sensitivity of the plant to stress.

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