Chapter 2

# Drought and Its Consequences to Plants – From Individual to Ecosystem

Elizamar Ciríaco da Silva,
Manoel Bandeira de Albuquerque,
André Dias de Azevedo Neto and
Carlos Dias da Silva Junior

Additional information is available at the end of the chapter

http://dx.doi.org/10.5772/53833

## 1. Introduction

Climate-change scenarios around the world indicate that many areas of the globe will increase in aridity. Thus, all living organisms will suffer from a water scarcity, especially plants, which do not have locomotive structures that allow them to move elsewhere when water and food becomes scarce. As a result, different terrestrial ecosystems (natural and agricultural) will be severely affected and some may even collapse due to the extinction of plant species.

It is therefore important to gain a better understanding regarding the effect of frequent drought stress on biochemical and physiological processes in plants as well as on the plant population and/or community in a particular ecosystem. Despite the negative aspects of such changes, severe environmental conditions can induce interesting adaptations in plants that allow them to survive and reproduce. These adaptations can lead to the emergence of new functional groups in a given ecosystem or serve as an important tool for improving agricultural practices and plant breeding programs.

In recent decades, a large number of investigations have addressed strategies used by plants to control water status, avoid oxidative stress and maintain vital functions in an attempt to understand the morphological and physiological changes plants undergo to ensure their survival under different environmental conditions. Special attention has been given to molecular processes involved in drought tolerance and resistance. While some advances have

been made, we still do not fully understand the underlying survival mechanisms in plants due the complex interaction of different forms of stress in natural habitats.

On the ecosystem level, drought induces changes in different processes and frequently demands functional plant responses. Some ecosystems, such as savannas, steppes and scrublands, have intermittent low annual precipitation. In these water-limited ecosystems, drought can seasonally modify carbon and nitrogen cycles, resulting in poor water and mineral uptake by roots, lesser plant growth, a reduction in litter decomposition and the biogenic emission of $CO_2$ from the soil. Severe drought can also induce a higher vegetation mortality rate due to cavitation and/or carbon starvation (reduced photosynthesis and enhanced autotrophic respiration). Thus, more frequent and intense drought periods (and the consequent death of plant species) can alter the phytosociology of entire plant communities over time.

Reductions in aboveground net primary productivity and alterations in functional plant groups are observed in places subjected to prolonged, severe drought. This chapter offers an overview of the effect of drought on individual plants and ecosystems, emphasising aspects of growth, water relations and photosynthesis, especially the electron transport chain, as well as radical oxygen species (ROS) scavenging and its role in avoiding oxidative stress. On the ecosystem level, functional traits commonly associated to water stress tolerance and changes in ecological processes and functional responses in plants will be also discussed.

## 2. Drought as a stress factor to the plants

In recent decades, a large number of models have been developed to estimate climate changes around the world. Climate change is defined as a significant difference between two mean climatic states, with substantial impact on the ecosystem [1]. Extreme climatic events, such higher temperatures, more intense precipitation, increased drought risk and duration as well as cyclones and flooding in coastal areas, are expected to increase in both frequency and intensity [2, 3]. In some countries, large arid and semiarid areas are expected to increase in size, leading to desertification. Currently, the consequences of global warming are widely discussed, especially regarding plant productivity and the increase in areas subject to desertification.

According to Assad et al. [4], the average temperature of the planet will increase by 1.4 to 5.8 °C by the end of the century, with drought being one of the consequences of this warming. Thus, one may deduce that the planet is heading toward a serious water crisis. Desertification corresponds to a reduction in the productive capacity of arid, semiarid and sub-humid lands as a result of climatic and edaphic factors. This growing, worldwide phenomenon has been causing both social and environmental problems, including the disappearance of animal and plant species [5].

In semiarid regions of Brazil, for example, inappropriate cultivation techniques resulting in soil erosion and a loss of water retention capacity in the soil as well as the expansion of live-

stock farming and the indiscriminate extraction of firewood deplete the nutritional content of the soil, thereby contributing toward the process of desertification. These activities lead to progressive degradation that results in the loss of soil cover [6, 7].

Plants need a large amount of water and nutrients throughout their life cycle and all aspects of plant development are affected by a reduction in water content in the soil. This reduction in soil moisture leads to changes in the physical environment, which subsequently affect physiological and biochemical processes in plants [8-10]. Drought can cause nutrient deficiencies, even in fertilised soils, due the reduced mobility and absorbance of individual nutrients, leading to a lower rate of mineral diffusion from the soil matrix to the roots [3]. Thus, drought is doubtlessly the most important stress factor limiting plant life.

Water is required for processes such as germination, cell division and elongation for the promotion of plant growth in height and width and metabolic activities, such as the synthesis of organic compounds, photosynthesis, respiration and a number of other physiological and biochemical processes [11]. Thus, when water availability decreases, changes occur in all molecular, biochemical, physiological and morphological aspects of plants.

Drought triggers a wide variety of plant responses [12]. Plant growth is altered, with changes in the architecture of individuals, which are translated into lower height, reduced leaf size, a smaller number of leaves, less fruit production and changes in the reproductive phase. Osmoregulatory processes generally occurs to protect membrane integrity and maintain the inflow of water to the cell as well as the accumulation of organic solutes as sugars, quaternary ammonium compounds (glycine betaine and alanine betaine) [13, 14], hydrophilic proteins (late embryogenesis abundant proteins) [15], soluble proteins and amino acids (proline) [10, 14]. Water is the most important substance in the initial phase of plant development from germination and seedling formation to establishment in the field [16] and a reduction in the water supply in this stage can lead to dehydration and even death.

In agricultural ecosystems, drought has a detrimental effect on crop production, affecting the growth rate and development of the economically important portions of the plant, such as fruits, grains and leaves. Without irrigation, production in crops such as coffee can be reduced by as much as 80% in dry years [17]. In Mexico, 80% of the problems caused by drought are related to losses in agricultural systems [18]. During a 45-day drought in the state of Paraná, Brazil, the 2008/2009 soybean harvest was reduced by 80% in areas without dry cover [19]. The same can be estimated for important crops such as sugarcane, corn, wheat and a number of others. The tragic effect on productivity is explained by the vital importance of water in living cells, which affects all biochemical and metabolic processes.

### 2.1. Water relations and influence on plant growth and development

Water is attracted to soil pores predominantly due to its attraction to other surfaces (adhesion) and capillarity. Its movement in the soil occurs mainly through mass flow: water fills micropores in the soil, which are interconnected and allow water movement. Contact between the surface of the roots (mainly in the root hair zone) and soil provide the sur-

face area necessary for water uptake. The growth of the roots into the soil maximises water absorption [11].

Water flow from the soil to the roots depends on the water potential gradient between the soil and plant, which is affected by the water needs of the plant, the hydraulic conductivity of the soil, soil type, moisture content in the soil [20] and the atmospheric demand, which directly affects water loss through transpiration, generating considerable tension in the xylem and contributing to the creation of this potential gradient. Water potential ($\Psi w$) is an expression of the energy status of water in any system, such as soil, tissues, the whole plant or the atmosphere, and its energy is influenced by four components: surface force or matrix potential ($\Psi m$), gravitational potential ($\Psi g$), hydrostatic pressure or pressure potential ($\Psi p$) and solutes or osmotic potential ($\Psi s$), which, in most cases, exert a negative effect on total water potential ($\Psi w$), reducing water energy and consequently water capacity for moving into a system. Thus, water flow in the soil-plant-atmosphere system always follows a downhill direction from higher to lower, which is the driving force of water transport [11, 20]. Water potential is always represented by negative values. The reference is pure water under normal conditions of temperature and pressure assumed to be equal to zero ($\Psi w = 0$), which denotes maximum energy status.

In wet soil, the hydrostatic pressure is closer to zero and $\Psi w$ is about -0.03 MPa [11]. A reduction in the water supply when the soil becomes dry leads to a decrease in hydrostatic pressure ($\Psi p$), which becomes quite negative. Thus, due to the high surface tension that tends to minimise the air-water interface, water becomes strongly adsorbed by the electrical charges of the soil particles (adhesion) [11, 20]. Under this condition, the plant absorption process requires a reduction in $\Psi w$ in the roots cells in relation to the rhizosphere. Moreover, the constant absorption of water by the plant leads to a reduction in the moisture content of the neighbouring soil.

The coordination of water flow from the soil to the roots, xylem, leaf apoplast and bulk air follows a decreasing status of water energy. This water gradient established between the rhizosphere through the plant and atmosphere favours the inflow of water in well-watered plants. In dry soil, however, the flow is interrupted due to barriers in the soil, such as increased surface forces, as well as in the plant, such as resistance offered by stomatal closure [20, 21]. When moisture availability in the soil decreases and there is continuity in the loss of water through transpiration, cavitation can occur, causing the interruption of water flow through the xylem due to the formation of air bubbles.

The continued inflow of water contributes to growth processes, as turgor pressure is responsible for cell elongation. Plant growth is the result of daughter-cell production by meristematic cell divisions in the shoot and root and the subsequent massive expansion of the young cells [12]. The constant inflow of water exerts pressure within the cell, causing the cell wall to stretch and inducing the elongation or growth of the cell in both size and volume. This physical process is repeated until the cell becomes mature, at which point cell size is no longer significantly altered [11]. These two processes (cell division and expansion) are important to the growth and development of tissues and organs.

http://dx.doi.org/10.5772/53833

Dry soil and the loss of water through a high transpiration rate makes the plant experience drought stress [12], which leads to the loss of turgor. As a result, the development of some structures is compromised and the growth rate slows. Thus, plants are generally shorter in dry environments. Although the formation of the organs is genetically defined, environmental conditions exert an influence on this process. Once formed, the cells of the leaves and fruit rarely undergo cell division and their growth relies on cell expansion. If the water pressure is insufficient to promote elongation, these organs will be small in relation with the those formed in a well-hydrated environment [22].

Plants also need carbon dioxide and light to produce organic matter throughout the process of photosynthesis. Carbon dioxide enters the leaves through the stomata and the turgor of the guard cells is the regulatory mechanism for maintaining the stomata opened [11]. Plants differ morphologically and/or physiologically under drought conditions. Different mechanisms allow plants to survive and even produce with a limited water supply, such as the maximisation of water uptake by deep, dense root systems, the minimisation of water loss by stomatal closure and a reduction in leaf area, osmotic adjustment or changes in cell wall elasticity as well as other essential processes for maintaining physiological activities throughout extended periods of drought [23].

Deciduous species have an efficient mechanism for coping with drought, which involves stomatal closure, changes in the orientation of the leaf and the reduction in leaf area by shedding leaves to minimise water loss through transpiration [24]. In the dry season, the leaves that remain on the plant can strongly influence the water balance by adjusting transpiration as a function of hydraulic limitation due to an increase in atmospheric vapor pressure deficit and surface soil desiccation [25].

Cell turgor is maintained by the accumulation of organic substances and inorganic ions in a stress response mechanism denominated osmotic adjustment [26, 27]. Organic solutes, also referred to as compatible solutes, are highly soluble compounds of low molecular weight that have no toxicity at high concentrations within the cells [14]. When plants are exposed to water deficit, changes occur in biochemical substances, such as the conversion of starch to soluble sugars (sucrose, glucose, fructose, etc.) [9, 27,28]. Nitrogenous compounds, such as proteins, amino acids (arginine, proline, lysine, histidine, glycine, etc.) and polyamines, are another group of compounds affected by water deficit that participate in osmotic adjustment [29]. In response to drought, there is an increase in the levels of free amino acids [9] and a reduction in the rate of synthesis or a decrease in proteins [29]. The increase in proline content is of considerable importance to plant adaptation during stress [8] and its accumulation usually occurs in large amounts in higher plants in response to environmental stress [14]. Proline is an amino acid resulting from the hydrolysis of proteins and plays an important role as an osmoprotectant in many cultivated species [27, 28, 30]. The increase of proline has also been linked to the reduction in leaf water potential [30]. In addition to its role as an osmoregulator, proline stabilises membranes and proteins and contributes to the removal of free radicals [14].

## 3. Drought and phothosynthesis

Drought is arguably the most important factor limiting plant yields throughout the world. Climate change and global warming in the tropical zone is expected to affect the photosynthesis, development and biomass production of plants in many regions as a result of the significant rise in temperature and concentration of atmospheric $CO_2$, which will also lead to a reduction in water availability in the soil, with a consequent effect on carbon assimilation and plant growth [31]. Semiarid regions are subject to water shortages and soil degradation in such places is likely to increase with climate change. The response of photosynthesis to drought merits special attention, as water is an electron donor that allows the maintenance of this process and biomass productivity [32, 33].

Under conditions of low water availability, a reduction in stomatal conductance constitutes one of the first strategies used by plants to diminish the transpiration rate and maintain turgescence [34]. Accordingly, stomatal behaviour in response to situations of drought stress may be indicative of water use efficiency for the production of photosynthates. Exposure to stress may induce alterations in photobiological processes, resulting in stomatal restrictions regarding the supply of carbon dioxide, the loss of water vapour and limitations to non-stomatal components, with harm to the reaction centres of photosystems I and II (PSI and PSII), thereby compromising photosynthesis efficiency [32]. According to Bolhàr-Nordenkampf et al. [35], Bolhàr-Nordenkampf and Öquist [36] and Baker [37], changes in the photochemical efficiency of plants under drought conditions may be assessed through an analysis of chlorophyll *a* fluorescence efficiency associated with PSII.

The chlorophyll fluorescence of water-stressed barley plants is characterised by a mild decrease in Fv/Fm (Fv is the variable part of Chl fluorescence and Fm is Chl fluorescence intensity at the peak of the continuous fluorescence inductive curve) and significant increase in F0 (Chl fluorescence with all PSII reaction centres open), together with a slight decrease in Fm [38]. The optimal temperature for most species ranges from 25 to 35 $^{o}$C, above which a decline in the rate of photosynthesis is observed [39, 40]. Under natural conditions, momentary water deficit is observed during warm hours of the day, which promotes stomatal closure. Consequently, the temperature of leaves exposed to direct sunlight can be equal to or higher than the air temperature. This rise in leaf temperature results in biochemical and biophysical disturbances in the mesophyll, which may or may not be reversible [39].

The main effects of high temperature on photosynthesis result from alterations in thylakoid physical-chemical properties [41], besides inducing an increase in lipid matrix fluidity [42], with the consequent formation of a single-layer structure. High temperature causes the following disturbances to the organisation of the photosynthetic apparatus: a) destruction of the oxygen evolution complex; b) dissociation of the light harvesting complex of PSII accompanied by variations in energy distribution between PSII and PSI; and c) inactivation of the PSII reaction centre (P680), which disturbs grana stacking [43]. All these events result in the loss of photochemical and carboxylation efficiency as well as serious metabolic restrictions in the Calvin cycle, such as the inactivation of ribulose-1,5-bisphosphate carboxylase/oxygenase and variations in the metabolic pool, especially ATP and NADPH availability

[44]. In some situations, F0 can be used as an indicator of irreversible damage to PSII [45] associated with LHCII dissociation [43, 46] and the blocking of the electron transference on the reductant side of PSII. In wheat and barley plants, high temperature tolerance is positively correlated with maximum F0 [47]. However, Yamane et al. [48] suggest that the inactivation of the PSII reaction centre caused by the denaturation of chlorophyll-protein complexes in response to high temperature correlates with a decay in Fm values. Changes in these fluorescence variables cause alterations in the Fv/Fm ratio, indicating a disturbance in the photochemical activity of photosynthesis. The Fv/Fm ratio has been inferred as an indicator of environmental stress, such as high temperature, drought and excess light, as it is easy and fast to measure [49].

### 3.1. Aspects of chlorophyll *a* florescence transient: *Kielmeyera rugosa* Choisy as case study

The genus Kielmeyera belongs to the family Clusiaceae (Guttiferae), subfamily Kielmeyeroideae, and is endemic to South America. The vast majority of these species occur exclusively in Brazil, where nearly 50 species are found chiefly in the *restinga* (sand dune), rocky savannah and the savannah-like *cerrado* vegetation south of the Amazon [50]. Some species are traditionally used in Brazilian folk medicine to treat tropical diseases, such as schistosomiasis, leishmaniasis and malaria, as well as fungal and bacterial infections [51].

A case study was performed with a population of 10 adult plants of *Kielmeyera rugosa* Choisy (Clusiaceae) in a *restinga* ecosystem in the municipality of Pirambu, state of Sergipe (northeastern Brazil), where the climate is characterised by irregular rainfall, with a wet season from April to September. Leaf water potential ($\Psi w$) was determined between 9:00 and 11:00 am and the chlorophyll and chlorophyll *a* fluorescence indexes were determined between 12:00 and 1:00 pm in March 2011 (dry season) and July 2011 (wet season). The mean air temperature in the rainy and dry seasons was 26.8 and 39 ºC, respectively.

Chlorophyll transient florescence (JIP-test): Polyphasic Chl *a* florescence transient (OJIP) was measured in healthy, completely expanded leaves using a hand-held fluorometer (Handy-PEA, Hansatech, King Lynn, UK). The selected leaves were subjected to a 30-min dark adaptation period, which is enough time for all reaction PSII centres to open [52]. The leaves were then immediately exposed to a pulse of saturating light at an intensity of 3000 $\mu mol.m\text{-}2s^{-1}$ provided by an array of three high-intensity light-emitting diodes. The JIP-test [53] was used to analyse each Chl *a* fluorescence transient. This test is based on the energy flux from bio-membranes [54]. The performance index (PIABS) [55] was employed as a parameter to quantify the effects of environmental factors on photosynthesis in several studies.

Figure (1A) shows that *K. rugosa* underwent a significant decrease of 120 and 38% in leaf water potential and the chlorophyll index (1B), respectively, in the dry season. Mean leaf $\Psi w$ was -0.34 MPa in the wet season and -0.75 MPa in dry season.

An analysis of florescence transients in *K. rugosa* under the two distinct water availability conditions (wet and dry season) may provide information on changes taking place in the structure, conformation and function of the photosynthetic apparatus, especially in PSII. Ini-

tial florescence (F0) represents the basal emission of Chl florescence when redox components of photosystems are fully oxidised. This requires appropriate dark adaptation. The results reveal an increase in F0 in the dry season, which may be explained by the initial damage occurring in PSII, likely due to the high temperatures and low water availability (Table 1). This increase in F0 is dependent on structural conditions affecting the probability of the energy transference within the pigments of the light harvesting complex to the PSII reaction centre [56]. According to Bolhàr-Noderkampf et al. [35], the increase in F0 increase in the dry season may indicate a reduction in energy transference to the PSII reaction centre or a partially-reversible inactivation [48].

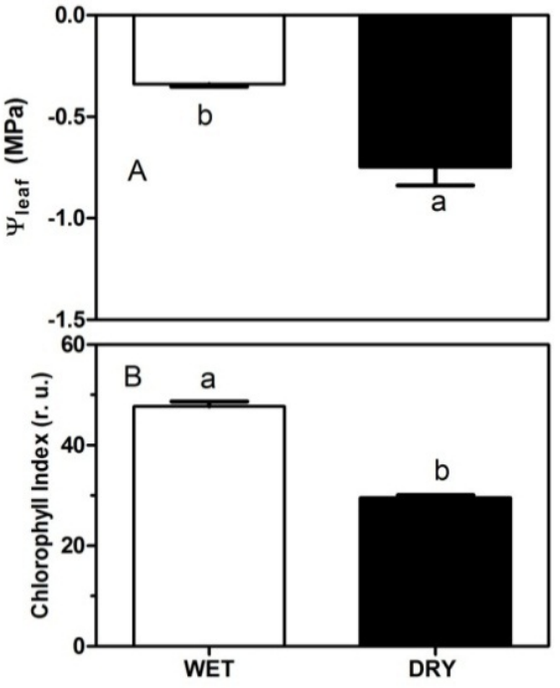


**Figure 1.** Mean values of leaf water potential (A) and Chlorophyll index (B) on wet and dry season in *Kielmeyera rugosa* Choisy growing under field conditions at 'restinga' in the Municipality of Pirambu, Sergipe State, Brazil. Each value represents a means of 10 replicates and bars indicate standard deviations. Mean values followed by the same small letters for the seasons are not significantly different (*P>0.05*; t-test). (Silva Junior CD, unpublished data).

The strong decrease in Fm in the dry season was likely associated with the higher temperatures (Table 1). This decrease in *K. rugosa* may be related to the loss of PSII activity due to conformational changes in the D1 protein [57], causing alterations in the properties of PSII electron acceptors [58]. Other factors may be associated with the heat-related decrease in Fm, such as the migration of damaged PSII reaction centres to non-stacked thylacoid regions and accelerated energy transference to non-fluorescent PSI [48]. The decrease in Fm may also be due to the disruption of electron donation from water to PSII due to the loss of the manganese atom and extrinsic proteins from the oxygen evolution complex [59]. Such events may be related to susceptibility to high temperatures.

| | Seasons | |
|---|---|---|
| **Variable** | **Wet** | **Dry** |
| F0 | 513 ± 7b | 627 ± 26a |
| F50μs (O) | 570.5 ± 9b | 692.8 ± 27a |
| 100 μs | 622.3 ± 12b | 760.5 ± 30a |
| F300μs | 840.4 ± 19b | 966.2 ± 41a |
| F2ms (J) | 1434 ± 32a | 1299 ± 53b |
| F30ms (I) | 2394 ± 67a | 1575 ± 88b |
| Fv | 2425 ± 59a | 1352 ± 123b |
| Fm (P) | 2938 ± 65a | 1979 ± 110b |
| tFm | 370.0 ± 26a | 248,0 ± 12b |
| **Area** | **67636 ± 2308a** | **35236 ± 2657b** |

**Table 1.** Initial florescence (F0), florescence intensity at 50 μs ($O=F_{50\mu s}$), 100 μs ($F_{100\,\mu s}$), 300 μs ($F_{300\mu s}$), 2 ms ("$J"_{F2ms}$), and 30ms ("$I"_{F30ms}$), variable florescence ($F_v$) maximum florescence ($F_m$=P) time to reach Fm ($t_{Fm}$) and area beneath the florescence in *Kielmeyera rugosa* Choisy on wet and dry season. Mean values (*n*=10) ±SE are show. Mean values followed by the same small letters for the seasons are not significantly different (*P>0.05*; t test). (Silva Junior CD, unpublished data).

The area over the fluorescence curve between F0 and Fm was lower in dry season than in the wet season, suggesting a decrease in the electron pool size of PSII, including QA, QB and PQ (Table 1) [60]. If the electron transfer from the reaction centre (RC) to the quinone pool is blocked, this area is dramatically reduced [61]. In comparison to the wet season, the area over the florescence curve was significantly decreased with the increase in drought and temperature. This inhibition is more accentuated by the interaction between high temperatures and light intensity, which leads to the blockage of electron transfers from the RC to the quinone pool. These results are in agreement with those described by Metha et al. [62], who found an inhibition in the electron transfer rates on the donor side of PSII in *Triticum aestivum* leaves treated with 0.5 M NaCl.

The results of flux ratio (yields) in *K. rugosa* revealed a decrease in TRO/ABS ($\varphi_{Po}$), ETO/TRO ($\psi_o$) and, consequently, ETO/ABS ($\varphi_{Eo}$) in the dry season (Figure 2 A, E and B). The decrease in $\varphi_{Po}$ (18%) under water stress indicates a loss of the maximum quantum efficiency of primary photochemistry due to photoinhibition caused by excess energy. Moreover, this excess induced the inactivation of 31% of active RCs per cross-section in the dry season, causing increased energy dissipation as well as lower $\varphi_{Po}$ values (Figure 2C). Under water stress, *K. rugosa* also exhibited a 35% decrease in $\varphi_{Eo}$ in comparison to the wet season.

The performance index (PIABS) combines three independent functional steps of photosynthesis (the density of RCs in the chlorophyll bed, excitation energy trapping and conversion of excitation energy to electron transport) in a single multi-parametric expression [55], which is a function of $\psi_0$, $\varphi_{Po}$ and RC/ABS [63, 64]. The results revealed much higher PIABS

values in the wet season than in the dry season, possibly due to the photoinhibition caused by excess of light energy and lower water potential (Figure 1).

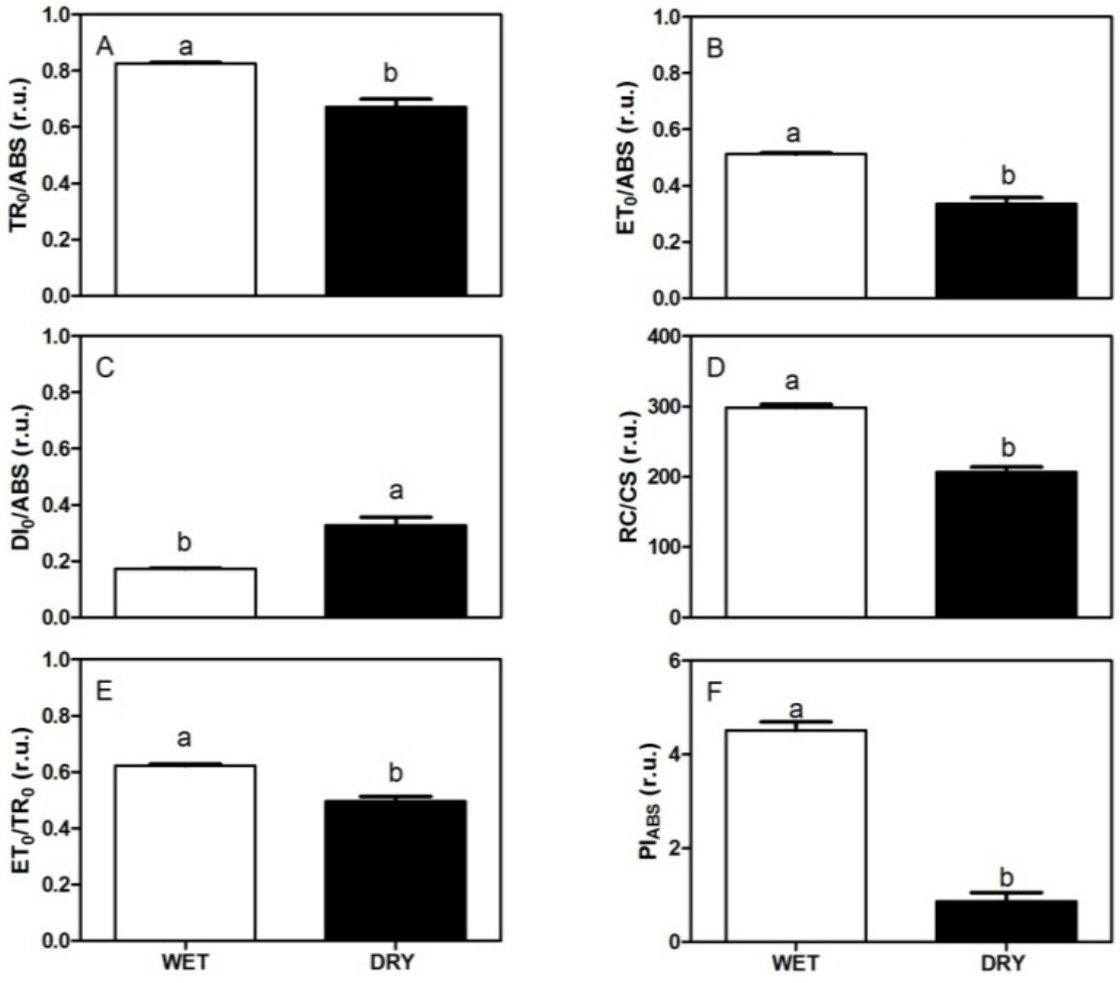


**Figure 2.** Maximum efficiency of PSII ($\varphi_{Po}$= $TR_O$/ABS), maximum efficiency of non-photochemical de-excitation ($\varphi_{Do}$= $DI_O$/ABS), probability that a trapped exciton ($\psi_o$= $ET_O/TR_O$) or that an absorbed photon ($\varphi_{Eo}$= $ET_O$/ABS) can move an electron further from QA, density of active reaction centers per cross section (RC/CS), and performance index (PIABS) in *Kielmeyera rugosa* Choisy under wet and dry season. Mean values followed by the same small letters for the seasons are not significantly different (*P>0.05*; t test). Mean values (*n*=10) ±SE. (Silva Junior CD, unpublished data).

$\varphi_{Po}$ (Fv/Fm = TRO/ABS) is a parameter that expresses maximal PSII efficiency, which is controlled by the primary photochemistry of PSII (charge separation, recombination and stabilisation), the non-radiative loss of excited states in light-harvesting antennae and excited states quenched by oxidised PQ molecules from the PQ pool [65]. The low $\varphi_{Po}$ values in *K. rugosa* under drought conditions could have resulted from the inactivity of the RCs, which may favour greater energy dissipation in the form of heat and fluorescence, as deduced from the high $\varphi_{Do}$values. This may be associated with increased heat sinks (heat-sink centres or silent centres), which may absorb light in a similar manner as that of active RCs, but are unable to store the excitation energy as redox energy and dissipate their total energy as heat

[66]. Moreover, due to excess irradiance, the transfer of energy to other systems could also take place, such as the energy-dependent formation of ROS [61].

Analysing $\Psi_0$, the lowest $\varphi_{Po}$ values in *K. rugosa* were found under drought conditions. $\Psi_0$ values decreased to a remarkably greater extent in the dry season in comparison to wet season. This result reflects a reduction in the pool of plastoquinone (PQ) in an oxidised state and the reoxidation inhibition of QA- and demonstrates that, besides the loss of energy to QA, the loss of excitation energy further from QA was significant [67]. The $\varphi_{Po}$, $\Psi_0$ and $\varphi_{Eo}$ results allow one to deduce that *K. rugosa* may use light energy more efficiently in the wet season due to the greater amount of chlorophyll and higher leaf water potential (Figure 1A,B).

The performance index (PIABS) is a consistent parameter for the evaluation of plant performance regarding light energy absorption, excitation energy trapping and the conversion of excitation energy to electron transport by photosynthesis under different stress conditions [55, 68]. The PIABS expresses both a function of the fluorescence extreme F0 and Fm as well as the intermediate J-step and the slope at the origin of the fluorescence rise, whereas $\varphi_{Po}$ expresses a function of only $F_0$ and Fm, independently of how the trajectory of the fluorescence intensity reaches its maximal value [68]. Furthermore, the PIABS allows a broader analysis of photosynthetic performance, such as the relationship between photon absorption efficiency and the capture of excited energy in PSII, as well as an analysis of the density of active RCs and the probability that excited energy moves an electron further than QA-. Therefore, the PIABS is a better parameter for evaluating the responses of PSII to stressful conditions than $\varphi_{Po}$ alone. In the present case study, the PIABS in *K. rugosa* was much lower in the dry season.

## 4. Oxidative stress and its effect to plants

### 4.1. Living with oxygen

The production of reactive oxygen species (ROS) is an unavoidable consequence of life with oxygen. The introduction of molecular oxygen ($O_2$) in the atmosphere during the Paleoproterozoic era (between 2.7 billion and 1.6 billion years ago) by the emergence of photosynthetic blue-green algae and later by higher plants led to the accumulation of $O_2$ in the atmosphere and oceans, inducing substantial changes in the living conditions of the earth. The atmosphere gradually changed from a reducing to an oxidising environment, thereby altering the pace and direction of evolution [69]. Ever since, ROS have been the unwelcome companions of aerobic life. Unlike of $O_2$, these partially reduced or activated derivatives of oxygen [singlet oxygen ($^1O_2$), superoxide radical ($^{\bullet}O2^-$), hydrogen peroxide ($H_2O_2$) and hydroxyl radical ($^{\bullet}OH$)] are highly reactive and toxic and can cause oxidative damage to carbohydrates, lipids, amino acids, proteins and nucleic acids [70]. Consequently, the evolution of all aerobic organisms has been dependent on the development of efficient ROS-scavenging mechanisms.

Under normal plant growth conditions, ROS are continuously produced and scavenged in organelles, such as chloroplasts, mitochondria and peroxisomes. However, the balance between ROS-producing pathways and ROS-scavenging mechanisms may be disrupted when plants experience environmental stress, such as drought, flooding, salt, heat, chill, heavy

metals, nutrient deficiencies, UV radiation, intense light, air pollutants, herbicides, mechanical stress and attacks from pathogens [71].

The excessive production of ROS is responsible for secondary stress known as oxidative stress. Therefore, plant tolerance to drought and other forms of abiotic stress that induce an increase in the generation of ROS depends on the development of efficient ROS-scavenging mechanisms.

### 4.2. Chemistry of ROS

Much of the behaviour of molecular oxygen (or dioxygen) and its partially reduced species derive from their reduction potentials and molecular orbital structures. The dioxygen molecule is a highly unusual, stable diradical with a pair of electrons with parallel spins. To oxidise a non-radical atom or molecule, dioxygen would need to react with a chemical species that provides a pair of electrons with parallel spins that fit into its free electron orbitals. Fortunately, pairs of electrons typically have opposite spins, which imposes a restriction on the reaction of molecular oxygen with most organic molecules, such as amino acids and nucleic acids [70].

However, dioxygen may be converted into ROS either by energy transfer or monovalent reduction. If oxygen absorbs enough energy to reverse the spin of one of its unpaired electrons, it forms singlet oxygen ($^1O_2$), in which the two electrons have opposite spins. Since paired electrons are common in organic molecules, singlet oxygen is much more reactive toward organic molecules than dioxygen in its ground state. The second mechanism of oxygen activation is stepwise monovalent reduction through electron transfer reactions with the unpaired electrons of transition metals and organic radicals, resulting in the sequential formation of superoxide anion ($^{\bullet}O2^-$), hydrogen peroxide ($H_2O_2$), hydroxyl radical ($^{\bullet}OH$) and, finally, water (Figure 3). The first reduction step is free energy dependent (endergonic) and requires electron donation, but the following one-electron reduction steps are exergonic and can occur spontaneously, using transition metal ions ($Fe^{2+}$ and $Cu^+$) and semiquinones as electron donors [70].

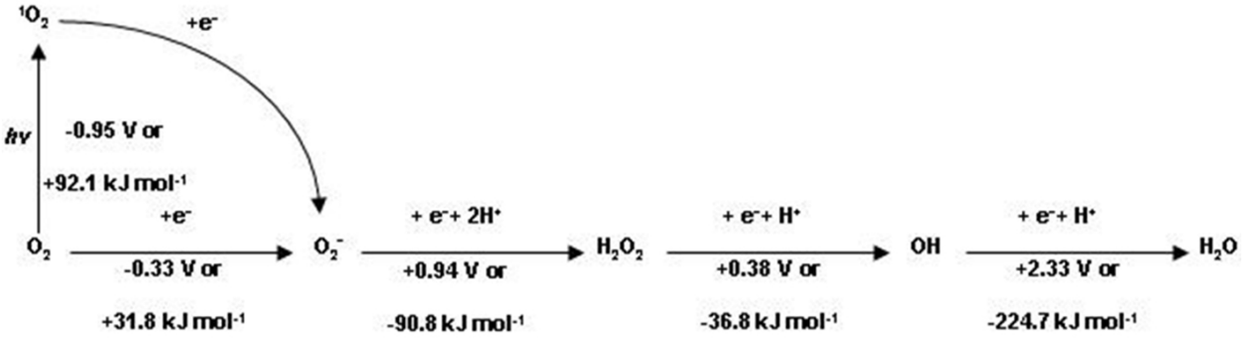


**Figure 3.** Pathways in the univalent reduction of oxygen to water leading for the formation of various intermediate reactive oxygen species (ROS). Numbers give approximate redox potentials (in volts) or the standard free energy of the reaction (in kJ $mol^{-1}$).

http://dx.doi.org/10.5772/53833

The superoxide ($^{\bullet}O_2^-$) produced during the first reaction is a short-lived ROS (approximately 2 to 4 μs) and not readily diffusible [72]. In the cellular environment, $^{\bullet}O_2^-$ may cause lipid peroxidation, thereby weakening cell membranes. The second reduction is an exergonic reaction that generates hydrogen peroxide ($H_2O_2$), a relatively long-lived (1 ms) and stable form of ROS that can diffuse through membranes and therefore reach cellular components distant from its site of synthesis [73]. The last ROS generated by this series of reductions is also exergonic and produces the highly reactive hydroxyl radical ($^{\bullet}OH$), which is the most harmful form of ROS in plant tissues, has a half-life of 1 ρs and has a very high affinity for biological molecules [74]. The hydroxyl radical is generated from the reaction between $^{\bullet}O_2^-$ and $H_2O_2$ either spontaneously through the Haber-Weiss reaction or in the presence of reduced transition metals through the Fenton reaction.

Under normal cell conditions, the Haber-Weiss reaction (1) occurs very slowly and very low amounts of $^{\bullet}OH$ are formed:

$$H_2O_2 + {}^{\bullet}O_2^- \rightarrow {}^{\bullet}OH + OH_2 \quad (1)$$

The hydroxyl radical is also formed in very low amounts in the Fenton reaction (2), which is common in biological systems, with its transition metals $Fe^{2+}$ and $Cu^{+}$ in a chelated form:

$$H_2O_2 + Fe^{2+} \rightarrow Fe^{3+} + {}^{\bullet}OH + OH \quad (2)$$

The availability of $Fe^{2+}$ limits the reaction rate, but $Fe^{3+}$ can be efficiently reduced by superoxide, thereby maintaining the Fenton reaction ongoing and leading to the generation of $^{\bullet}OH$, as shown in the two half reactions (3) and (4):

$$H_2O_2 + Fe^{2+}\left(Cu^{+}\right) \rightarrow Fe^{3+}\left(Cu^{2+}\right) + {}^{\bullet}OH + OH \quad (3)$$

$$^{\bullet}O_2^- + Fe^{3+}\left(Cu^{2+}\right) \rightarrow Fe^{2+}\left(Cu^{+}\right) + O_2 \quad (4)$$

The prevention of the Haber-Weiss and Fenton reactions is achieved when $H_2O_2$ and $^{\bullet}O_2^-$ are eliminated prior to these molecules entering into contact with each other.

Due to the high reactivity of $^{\bullet}OH$ radicals, which is the main cause of cell damage under oxidative stress, it is difficult to control their concentration enzymatically. Therefore, plants reduce the presence of this radical by controlling the upstream reactions of $^{\bullet}OH$ formation via Haber-Weiss/Fenton reactions through the elimination of $H_2O_2$ and $^{\bullet}O_2^-$ prior to their contact with each other. The efficient destruction of $^{\bullet}O_2^-$ and $H_2O_2$ requires the coordinated action of several antioxidative enzymes and a network of low molecular mass antioxidants.

### 4.3. Antioxidative system

To mitigate oxidative harm from ROS, plants possess a complex antioxidative system that involves both non-enzymatic and enzymatic antioxidant defences. Non-enzymatic defences include hydrophilic compounds, such as ascorbate and reduced glutathione, and lipophilic compounds, such as tocopherols and carotenoids, which are capable of quenching ROS. Enzymatic defences include superoxide dismutase, catalase and peroxidase. Moreover, an entire array of enzymes is needed for the regeneration of the active forms of antioxidants (glutathione reductase, monodehydroascorbate reductase and dehydroascorbate reductase) [70, 75].

#### *4.3.1. Superoxide Dismutases (SOD)*

Superoxide dismutases (EC 1.15.1.1) catalyse the dismutation of superoxide into hydrogen peroxide and water. SOD activity modulates the relative amounts of $^{\bullet}O_2^-$ and $H_2O_2$ (the two Haber-Weiss reaction substrates) and decreases the risk of the formation of the $^{\bullet}OH$ radical. Since SOD is one of the ubiquitous enzymes in aerobic organisms and is present in most subcellular compartments that generate ROS, this enzyme is considered to play a key role in cell defence mechanisms against ROS [76, 77]. The product of SOD activity is $H_2O_2$, which is toxic and must be eliminated by conversion into $H_2O$ in subsequent reactions. Although a number of enzymes regulate the intracellular levels of $H_2O_2$ in plants, catalases and peroxidases are considered to be the most important.

#### *4.3.2. Catalases (CAT)*

Catalases (EC 1.11.1.6) are tetrameric heme-containing enzymes that catalyse the dismutation of hydrogen peroxide into water and molecular oxygen, thereby protecting the cell from the harmful effects of $H_2O_2$ accumulation. CAT is found in all aerobic eukaryotes and is associated with the removal of $H_2O_2$ generated in biochemical processes, such as the β-oxidation of fatty acids, the glyoxylate cycle (photorespiration) and purine catabolism. CAT activity may decrease under salt stress, heat shock or cold stress, which may be related to plant tolerance to the secondary oxidative stress induced by these forms of environmental stress.

#### *4.3.3. Peroxidases and enzymes regenerating active forms of ascorbate and glutathione*

Peroxidases constitute a class of enzymes in the tissues of animals, plants and microorganisms and catalyse the oxidoreduction between hydrogen peroxide and different reductants. There are three classes of plant peroxidases, but ascorbate peroxidase (APX), class III plant peroxidases [or non-specific peroxidases or guaiacol-type peroxidase (POX)] and glutathione peroxidase (GPX) are considered to be the most important plant peroxidases related to the antioxidative system.

Ascorbate peroxidase (EC 1.11.1.11) catalyses the reduction of $H_2O_2$ to $H_2O$ and has high specificity and affinity for ascorbate (ASC) as a reductant. Its sequence is distinct from other peroxidases and different forms of APX are found in the chloroplasts, cytosol, mitochondria,

peroxisomes and glyoxysomes [78]. APX seems to play a key role as a scavenger of $H_2O_2$ that could leak from these cell organelles.

APX uses two ASC molecules to reduce $H_2O_2$ to water and produce two monodehydroascorbate (MDHA) molecules (Figure 2). MDHA is a short-lived radical that can either spontaneously dismutate to ascorbate and dehydroascorbate (DHA) (Figure 2) or be reduced to ascorbate by NAD(P)H via monodehydroascorbate reductase (MDHAR; EC 1.6.5.4) (Figure 2), which is found in different cell compartments [16] (Asada, 1997). DHA is reduced to ascorbate by the action of dehydroascorbate reductase (DHAR; EC 1.8.5.1), using reduced glutathione (GSH) as the reducing substrate. This reaction generates reduced glutathione (GSSG), which is, in turn, re-reduced to GSH by NADPH, a reaction catalysed by glutathione reductase (GR; EC 1.6.4.2). The removal of $H_2O_2$ through this series of reactions is known as the ascorbate-glutathione cycle or the Halliwell-Asada pathway (Figure 2) [75]. Ascorbate and glutathione are not consumed in this pathway, but participate in the cyclic transfer of reducing equivalents, which allows the reduction of $H_2O_2$ to $H_2O$, with NADPH as the reducing equivalent donor.

Class III plant peroxidase (EC 1.11.1.7) is a plant-specific oxidoreductase, the activity of which was described as early as 1855. This enzyme is a heme-containing glycoprotein encoded by a large multigene family in plants. POX, which is found in the cytosol, vacuole and cell wall, is less specific to the electron donor substrate than APX and decomposes $H_2O_2$ through the oxidation of co-substrates, such as phenolic compounds and/or ascorbate [79]. This enzyme is relatively stable at high temperatures and its activity is easily measured using simple chromogenic reactions.

The different types of GPX (EC 1.11.1.9) form a large family of diverse isozymes that reduce $H_2O_2$ and organic and lipid hydroperoxides using GSH as a reducing agent. In plants, however, it has been suggested that GPX preferably uses thioredoxin as a reductant [80, 81]. Most cellular GPXs are tetrameric enzymes with four identical 22 kDa subunits, each containing a selenocysteine residue in the active site [82]. Selenocysteine participates directly in electron donation to the peroxide substrate and becomes oxidised in the process. The enzyme then uses reduced glutathione as a hydrogen donor to regenerate selenocysteine. GPX uses two GSH molecules to reduce $H_2O_2$ to water and produce a GSSG molecule (Figure 4).

Taken together, the major ROS-scavenging pathways in plants include SOD, found in almost all cell compartments, CAT in peroxisomes, POX in the cytosol, vacuole and cell wall and the ascorbate-glutathione cycle in the chloroplasts, cytosol, mitochondria, apoplast and peroxisomes. As mentioned above, CAT has extremely high maximal catalytic rates, but low substrate affinities, while APX has a much higher affinity for $H_2O_2$ than CAT. The high affinity of APX for $H_2O_2$, in conjunction with the finding of the ascorbate-glutathione cycle in nearly all cell compartments, suggests that this cycle plays a crucial role in controlling the level of ROS in these compartments. Moreover, APX might also be responsible for the fine modulation of $H_2O_2$ for signalling. In contrast, CAT, which is only present in peroxisomes, is indispensable to $H_2O_2$ detoxification during stress, when high levels of ROS are produced.

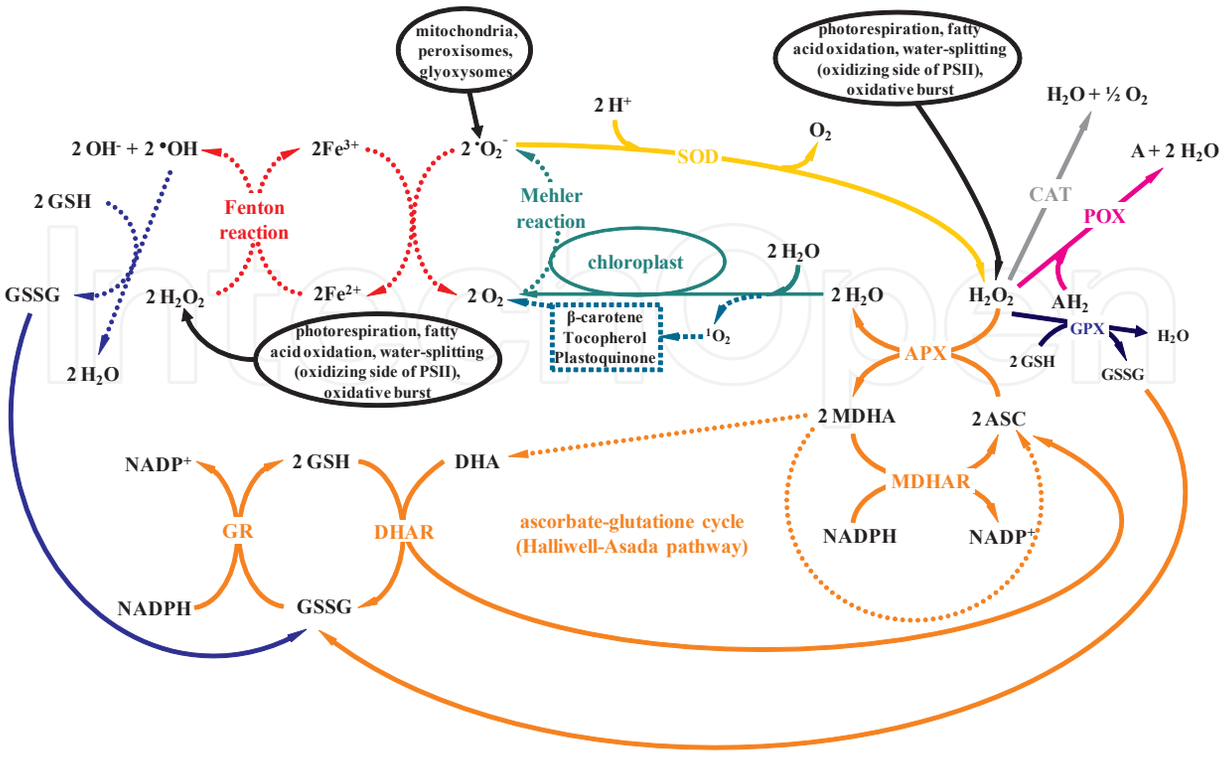


**Figure 4.** Generation of •OH by Fenton reaction (in red); $^{\bullet}O_2^-$ in the mitochondria, peroxisomes and glyoxysomes and by Mehler reaction in chloroplast (in green), singlet oxygen in chloroplast (in dark green), and $H_2O_2$ by SOD, photorespiration, fatty acid oxidation or other reactions. SOD acts as the first line of defense converting $^{\bullet}O_2^-$ into $H_2O_2$ (in yellow). CAT (in grey), POX (in pink), GPX (in dark blue), and APX (in orange) then detoxify $H_2O_2$. In contrast to CAT, APX requires ASC, POX requires phenolic compounds and/or ASC, and GPX requires GSH as electron donor substrate. In the removal of $H_2O_2$ through the ascorbate-glutathione cycle (in orange), ASC and GSH participate of the cyclic transfer of reducing equivalents. This cycle uses NADPH as reducing power. •OH may be removed by GSH (in blue), and the GSSG formed is regenerated via GR. Although the pathways of generation and scavenging in the different cell compartments are separate, $H_2O_2$ can easily diffuse through membranes and antioxidants such as GSH and ASC can be transported between the different compartments. Non-enzymatic pathways are indicated by dotted lines. Abbreviations: APX, ascorbate peroxidase; ASC, ascorbate; AH2, oxidizable substrate; DHA, dehydroascorbate; DHAR, dehydroascorbate reductase; GPX, glutathione peroxidase; POX, non-specific peroxidase; GR, glutathione reductase; GSH, reduced glutathione; GSSG, oxidized glutathione; hydrogen peroxide ($H_2O_2$); hydroxyl radical (•OH); MDHA, monodehydroascorbate; MDHAR, monodehydroascorbate reductase SOD, superoxide dismutase; superoxide radical ($^{\bullet}O_2^-$).

## 4.4. ROS production and scavenging in drought-stressed plants

The root system is the first plant organ to detect a reduction in the water supply. Besides water and minerals, the roots send signals to the shoots through the xylem sap and the phytohormone abscisic acid is considered to be one of the major root-to-shoot stress signals [83]. In leaves, abscisic acid triggers stomatal closure and the plant shifts to a water-saving behaviour. By controlling the stomatal opening, plants reduce water loss by decreasing the transpiration flux. However, the entrance of carbon dioxide ($CO_2$) is also reduced simultaneously. This plant response has direct and indirect effects on the net photosynthesis and overall production of ROS under water deficit conditions [84]. A number of studies report increased ROS accumulation and oxidative stress in plants under drought stress [85, 86]. When stomata close in order to limit water loss, there is the occurrence of either a re-

http://dx.doi.org/10.5772/53833

stricted $CO_2$ supply or $CO_2$-limited carbon fixation and reduced $NADP^+$ regeneration through the Calvin cycle. Photosynthetic electron transport is, however, maintained at a relatively higher rate in the stressed leaves in comparison to the accentuated reduction in the $CO_2$ fixation rate [87]. This imbalance between the electron transport and $CO_2$ fixation rates results in an accentuated reduction of the electron transport chain and the transfer of electrons to $O_2$ through the Mehler reaction [88]. One study estimated a 50% increase in the leakage of photosynthetic electrons through the Mehler reaction in drought-stressed wheat plants in comparison to non-stressed plants [89].

The photorespiratory pathway is also enhanced under drought stress, especially when the oxygenation of ribulose-1,5-bisphosphate is maximal due to limited $CO_2$ fixation [90]. Thus, $O_2$-dependent electron flow and photorespiration can be considered common mechanisms that plants employ to protect the photosynthetic electron transport chain components from photodamage during water deficit. Although it is very difficult to discriminate the amount of ROS generated by the Mehler reaction from that generated by photorespiration, it has been estimated that photorespiration is likely to account for over 70% of total $H_2O_2$ production under drought stress conditions [90]. In such a scenario, there is considerable potential for the increased accumulation of $^{\bullet}O_2^-$ and $H_2O_2$ in plants [91]. In a number of plant species, an increased formation of ROS, lipid peroxidation and protein modification have been observed under water deficit conditions [92-94]. The following the sequence of events occurs in plant tissues subjected to such conditions: 1) increased production of ROS and oxidised target molecules; 2) increased expression of genes for antioxidant functions; and 3) increased the levels of non-enzymatic and enzymatic antioxidants, resulting in tolerance to drought stress [95].

Drought stress enhances the *de novo* synthesis of some antioxidative enzymes to overcome the increase in oxidative stress. In rice plants, the *de novo* synthesis of MDHAR, DHAR and GR increases the capacity for ASC and GSH regeneration, which is considered to be one of the primary responses to water deficit so as to mitigate oxidative stress [92, 93]. An increase in the activity of antioxidative enzymes has been reported in a number of plant species submitted to drought stress, enhancing the capacity of the antioxidative system to scavenge ROS and thereby suppressing the level of lipid peroxidation under drought conditions [93, 96, 97].

Additionally, the increase in the activity of antioxidative enzymes and antioxidant content under water deficit conditions appears to be extremely variable among different plant species and even cultivars of the same species. Thus, comparative studies using drought-tolerant and drought-sensitive genotypes demonstrate greater antioxidant capacity in tolerant genotypes. In one study, among five mulberry cultivars subjected to drought, two had efficient antioxidative characteristics that could provide better protection against oxidative stress in leaves under water-limited conditions [98]. Under water stress, a drought-tolerant maize genotype exhibited lower MDA and $H_2O_2$ contents and an increase in the SOD, CAT, and POX activities in comparison to a drought-sensitive maize genotype [99]. A drought-tolerant wheat genotype exhibited greater APX and CAT activities, higher ASC content and lower $H_2O_2$ and MDA contents in comparison to a drought-susceptible wheat genotype

[100]. In response to water deficit, the drought-sensitive apple rootstock *Malus hupehensis* exhibited greater increases in $H_2O_2$, $^{\bullet}O_2^-$ and MDA levels than the drought-tolerant *M. prunifolia*. In contrast, SOD, POX, APX, GR and DHAR activities and ASC and GSH contents increased to a greater extent in *M. prunifolia* than *M. hupehensis* [101]. It has also been reported that the drought-acclimated leaves of wheat plants exhibited a systematic increase in the APX and CAT activities and the maintenance of an adequate ascorbate redox pool through the efficient functioning of the APX enzyme. As a result, lesser membrane damage was found in the drought-acclimated plants [94, 102].

The drought response of a plant species also depends on the duration and severity of the drought period. SOD and CAT activities are reported to have increased in response to severe water deficit in mature leaves of two clones of *Populus deltoids* x *nigra* [103]. For both clones, Mn-SOD, Fe-SOD, and Cu/Zn-SOD isoforms were detected in varying amounts, depending on drought intensity.

Taken together, these findings provide additional evidence that the antioxidative system plays a key role in the process of plant acclimation to drought stress. Thus, greater protection from drought-induced oxidative damage may, at least in part, be involved in tolerance to water deficit.

## 5. Drought and ecosystems: changes in natural cycles and functional groups

According to Chapman [104], there are an estimated 390,800 plant species worldwide (Magnoliophyta, gymnosperms, ferns, allies and Bryophyta). Despite their occurrence on all continents, biodiversity and distribution is quite variable even within a few kilometres. From an ecologic standpoint, the occurrence of a specific plant species in an area depends on the combination of three factors:

**a.** **Chance** – the possibility of a propagule reaching and establishing itself in a certain location;

**b.** **History** – the current abundance of a species is probably correlated with its abundance in the near past;

**c.** **Necessity** – demands for growth, competence for competition and interactions with other organisms; Coexistence with other plants depends on the complexity of the environment in terms of fertility, sunlight and water availability and on how strongly the plant can withstand the action of competitors, herbivores, parasites, etc.

Among these needs, water availability can be considered the most influential and even shapes the phytophysiognomy of some ecosystems. According to Puig [105], while drought has little influence in a tropical rain forest (where precipitation surpasses evapotranspiration more than ten months per year), water regime variability in a tropical dry forest is the major

environmental factor exerting an influence on the ecological processes that regulate its vegetation maintenance and distribution [106].

On the ecosystem level, a drought event can be (i) **permanent –** in regions where a desert climate predominates; (ii) **seasonal** – as observed in semi-arid regions; (iii) **irregular or variable** – as occurs in regions with humid or sub-humid climates (this normally takes place in limited areas and the return of drought is unpredictable); or (iv) **invisible or green drought** – as occurs when precipitation is not interrupted, but lesser than evapotranspiration, causing a regional moisture imbalance. In the latter case, there is a drop in relative air humidity, leading to a reduction in moisture content in the soil. Moisture is evaporated into the atmosphere and comes back as rainfall, but not enough to increase the moisture content in the soil. This is considered the worst kind of drought due to the fact that is difficult to perceive.

### 5.1. Formation of functional groups under natural cycles

Excessive insolation, fire, shade, wind, herbivory, nutrient availability and water availability are factors that force plants to exhibit different kinds of adaptation to overcome the constraints to their survival and establishment. In some cases, plant species from unrelated taxonomical groups use very similar strategies, resulting in a phenomenon denominated convergent evolution.

Cummins [107] proposed a plant classification system based on similar roles or analogous processes in the ecosystem. This classification allows us to simplify the biodiversity in a given location and correlate it with that of another location, even without taxonomic relatedness among the species found [108]. A number of papers have since been published revealing the existence of vegetation patterns as responses to the influence of biotic and/or abiotic factors in different ecosystems. Consequently, knowledge on how an assemblage of plants organises itself to occupy all available niches under given environmental conditions has continually increased. The three general mechanisms used by plants to cope with drought [**avoidance** (dormancy in the dry season), **delay** (through increased water uptake and reduced water loss) and **physiological tolerance** (maintenance of plant functioning with low cell water content)] are closely linked to the functional traits of the species [109] (Table 2).

| Functional trait | Role | Some co-existing species | Source |
|---|---|---|---|
| Life form | Species can avoid drought remaining as seed during dry season (Therophytes) | *Gomphrena* aff. *leucocarpa* Mart (Amaranthaceae)<br>*Taccarum peregrinum* L (Araceae)<br>*Pithecoseris pacourinoides* Mart (Asteraceae)<br>*Cleome guianensis* Aublet (Capparaceae)<br>*Euphorbia comosa* Vell. (Euphorbiaceae)<br>*Cuphea ericoides* Cham. & Schlech (Lythraceae)<br>*Richardia scabra* L. (Rubiaceae)<br>*Amasonia campestris* L. (Verbenaceae) | Mendes [110] |

| Functional trait | Role | Some co-existing species | Source |
|---|---|---|---|
| Specific leaf area | This is an index of sclerophylly. | *Prunus ilicifolia* (Nutt. ex Hook. & Arn.) Walp. (Rosaceae)<br>*Ceanothus oliganthus* var. *sorediatus* (Rhamnaceae )<br>*Mimulus aurantiacus* Curtis (Phrymaceae)<br>*Baccharis pilularis* DC. (Asteraceae) | Ackerly et al. [111] |
| Leaf size | Influences leaf cooling and light capture efficiency (self-shading) | *Cercocarpus betuloides* Nutt. (Rosaceae)<br>*Comarostaphylis diversifolia* (Parry) Greene (Ericaceae)<br>*Quercus agrifolia* Née (Fagaceae) | Scoffoni et al. [112] |
| Leaf phenology | Plays an important role in drought resistance, as deciduous trees are able to reduce water loss by dropping leaves, while evergreen trees must resist drought. | EVERGREEN<br>*Capparis flexuosa* L. (Capparaceae)<br>*Maytenus rigida* Mart. (Celastraceae)<br>*Licania rigida* Benth. (Chysobalanaceae)<br>*Ximenia americana* L. (Olacaceae)<br>DECIDUOUS<br>*Amburana cearensis* (Allemão)AC Smith (Faboideae)<br>*Jatropha mollissima*(Pohl) Baill.(Euphorbiaceae)<br>*Combretum leprosum* Mart. (Combretaceae)<br>Pseudobombax marginatum (A. St. –Hil.,Juss&Camb.) A. Robyns (Bombacaceae) | Barbosa et al. [113] |
| Stem / Wood density (WD) | This is negatively correlated with cavitation resistance and negatively correlated with water storage. | *Anogeissus latifolia* (Roxb. Ex DC) Wall. ex Bedd. (Combretaceae)<br>*Soymida febrifuga* (Roxb.) A. Juss. (Meliaceae)<br>*Acacia catechu* (L. f.) Willd. (Fabaceae)<br>*Shorea robusta* Roth (Dipterocarpaceae)<br>*Chloroxylon swietenia* DC. (Rutaceae) | Kushwaha et al. [114] |
| Root deep | Allows an exploration of the moister deeper soil layers | SHALLOW<br>*Schefflera macrocarpa* (Seem.) D. C. Frodin (Araliaceae)<br>*Miconia ferruginata* DC. (Melastomataceae)<br>*Roupala Montana* Aubl. (Proteaceae)<br>*Ouratea hexasperma* (St. Hil.) Baill. (Ochnaceae)<br>DEEP<br>*Vochysia elliptica* Mart. (Vochysiaceae)<br>*Dalbergia miscolobium* Benth. (Fabaceae)<br>*Kielmeyera coriacea* Mart. (Clusiaceae) | Franco et al. [115] |

**Table 2.** Some functional traits associated to drought tolerance in plants under dry conditions.

http://dx.doi.org/10.5772/53833

### 5.2. Climate change: New challenge for plants

Drought is a deviation from normal climatic conditions in which there is a lack of precipitation over an extended period and the resulting water shortage has negative implications [116]. Drought differs from aridity, which is a normal condition of a severe lack of water availability in a specific region.

In recent decades, the planet has witnessed intense climate changes due to global warming. Extreme climatic events, such as tornados, hurricanes, floods, blizzards and drought, have become more frequent and intense. Some annual plant events, such as flowering, fruiting and re-sprouting, follow a specific timing, which is denominated phenology. Global warming can affect this timing and its consequences can affect water supplies, pollination and the overall functioning of natural and agricultural ecosystems. This situation suggests a bleak future for mankind and nature, as all organisms will face substantial disturbances in their environment, possibly beyond their capacity for resistance and resilience. Resistance is the ability of a system to maintain its structure and functioning after a disturbance and resilience is the ability to re-establish equilibrium after it has been disrupted [117].

A given plant species can either escape from or acclimate to adverse environmental conditions, which can change in space and time. When a specific genotype exteriorises different phenotypes under different conditions, it is considered to have adequate phenotypic plasticity. Changes in the partitioning of resources can be the result of different strategies under different selection pressures. However, this phenotypic plasticity is quite limited due both the physiological costs and ontogenetic drift [118, 119].

The following are the most detectable features of global warming: 1) its influence on the perception of plants regarding the seasons (the advance of biological spring and the delay in biological winter have been observed and such changes have a direct effect on the reproductive events of flowering and fructification, which can affect the dynamics of plant populations and communities) [120-122]; 2) alterations in the floristic composition and phytosociology of plant communities due to changes in the seedling mortality rate; 3) the occurrence of a climate-induced shift in the range of species, which can force the interaction of plants with those from which they were formerly spatially separated [123]; and 4) increased biological plant invasions, as global warming can modify the dynamics and climate of new environments, making them suitable for invasion [124, 125].

Despite the volume of studies on plant responses to global warming, a great deal of uncertainty remains. After an extensive survey of plant phenology databases for long-term observations and short-term warming experiments involving 1634 species, Wolkovich et al. [126] concluded that such experimental studies underpredict plant phenological responses to global warming. Thus, more in-depth studies are needed to help predict the effects of global warming on plant communities in the near future and develop strategies to mitigate these effects.

## Author details

Elizamar Ciríaco da Silva[1*], Manoel Bandeira de Albuquerque[2], André Dias de Azevedo Neto[3] and Carlos Dias da Silva Junior[1]

*Address all correspondence to: elizaciriaco@gmail.com

1 Laboratory of Applied Botany, Department of Biology, Federal University of Sergipe, Brazil

2 Laboratory of Plant Ecology, Department of Crop and Environmental Sciences, Federal University of Paraíba, Brazil

3 Laboratory of Biochemistry, Center of Exate and Technological Sciences, Federal University of Recôncavo da Bahia, Brazil

## References

[1] Agbola T, Ojeleye D. Climate change and food crop production in Ibadan, Nigeria. African Crop Science Conference Proceedings 2007; 8:1423-1433.

[2] Reynolds MP, Ortiz R. Adapting crops to climate changes: a summary. In: Reynolds MP (ed.) Climate Change and Crop Production. CABI series in climate change v.1. Chippenam: CPI; 2010. p1-8.

[3] Silva EC, Nogueira RJMC, Silva MA, Albuquerque MB. Drought stress and plant nutrition. Plant Stress 2011; 5(1): 32-41.

[4] Assad ED, Pinto HS, Zullo Junior J, Ávila AMH. Impacto das mudanças climáticas no zoneamento agroclimático do café no Brasil. Pesquisa Agropecuária Brasileira 2004; 39(11):1057-64.

[5] Abraham EM, Beekman GB. Indicadores de la desertificación para América Del Sur. Editorial Martin Fierro: Mendonza; 2006.

[6] Primack R, Rodrigues E. Biologia da conservação. Londrina: E. Rodrigues; 2001.

[7] Morales C. Pobreza, desertificación y degradación de tierras. In: Morales C, Parada S (eds.) Pobreza, desertificación y degradación de los recursos naturalis. CEPAL: Santiago de Chile; 2005. p.25-58.

[8] Sarker BC, Hara M, Uemura M. Proline synthesis, physiological responses and biomass yield of eggplants during and after repetitive soil moisture stress. Scientia Horticulturae 2005; 103:387-402.

[9] Sircelj H, Tausz M, Grill D, Batic F. Biochemical responses in leaves of two apple tree cultivars subjected to progressing drought. Journal of Plant Physiology 2005; 162:1308-18.

[10] Silva EC, Nogueira RJMC, Vale FHA, Melo NF, Araujo FP. Water relations and organic solutes production in four umbu tree (Spondias tuberosa) genotypes under intermittent drought. Brazilian Journal of Plant Physiology 2009; 21(1): 43-53.

[11] Taiz L, Zeiger E. Plant Physiology. Fourth Edition. Sinauer Associates: Los Angeles; 2006.

[12] Ajum SA, Xie XY, Wang LC, Saleem MF, Man C, Lei W. Morphological, physiological and biochemical responses of plants to drought stress. African Journal of Agricultural Research 2011; 6(9):2026-32.

[13] Sakamoto A, Murata N. The role of glycinebetaine in the protection of plants from stress: clues from transgenic plants. Plant Cell and Environment 2002; 25:163-171.

[14] Ashraf M, Foolad MR. Roles to glycine betaine and proline in improving plant abiotic stress resistance. Environmental and Experimental Botany 2007; 59: 206-216.

[15] Chaves MM, Maroco JP, Pereira JS. Understanding plant response to drought – from genes to the whole plant. Functional Plant Biology 2003; 30: 239-264.

[16] Jaleel CA, Manivannan P, Wahid A, Farooq M, Al-Juburi HJ, Somasundaram R, Vam RP. Drought stress in plants: a review on morphological characteristics and pigments composition. International Journal of Agriculture and Biology 2009; 11(1):100-105.

[17] DaMatta FM, Ramalho JDC. Impacts of drought and temperature stress on coffee physiology and production: a review. Brazilian Journal of Plant Physiology 2006; 18(1) 55-8.

[18] Saldaña-Zorrilla SO. Socioeconomic vulnerability to natural disasters in Mexico: rural poor, trade and public response. México: CEPAL; 2007.

[19] Franchini JC, Debiasi H, Nepomuceno AL, Farias RB. Manejo do solo para redução das perdas de produtividade por seca. Embrapa, 2009. http://bioinfo.cnpso.embrapa.br/seca/index.php/manejo-do-solo (acessed 10 August 2012).

[20] Chavarria G, Santos HP. Plant Water Relations: Absorption, Transport and Control Mechanisms. In: Montanaro G, Dichio B (eds.) Advances in Selected Plant Physiology Aspects. Rijeka: InTech; 2012. p105-132.

[21] Fitter AH, Hay RKM. Environmental physiology of plants. London: Academic Press; 2002.

[22] Miloud H, Ali G. Some aspects of leaf senescence. In: Nagata T. (ed.) Senescence. Rijeka: InThec; 2012. p107-116.

[23] Pinheiro HA, DaMatta FM, Chaves ARM, Loureiro ME. Drought tolerance is associated with rooting depth and stomatal control of water use in clones of Coffea canephora. Annals of Botany 2005; 96: 101–108.

[24] Gindaba J, Rozanov A, Negash L. Photosynthetic gas exchange, growth and biomass allocation of two Eucalyptus and indigenous tree species of Ethiopia under moisture deficit. Forest Ecology and Management 2005; 205:127-138.

[25] Prado CHBA, Wenhui Z, Rojas MHC, Souza GM. Seasonal leaf gas exchange and water potential in a woody cerrado species community. Brazilian Journal of Plant Physiology 2004; 16(1):7-16.

[26] Hare, PD, Cress WA, Van Staden J. Dissecting the roles of osmolyte accumulation during stress. Plant, Cell and Environment 1998; 21:535-553.

[27] Hong-Bo F, Xiao-Yan C, Li-Ye C, Xi-Ling Z, Gang W, Yong-Bing Y, Chang-Xing Z, Zan-Min H. Investigation on the relationship of proline with wheat anti-drought under soil water deficits. Colloids and Surfaces B 2006; 53:113-119.

[28] Sánchez FJ, Manzanares M, Andres EF, Tenorio JL, Ayerba L. Turgor maintenance, osmotic adjustment and soluble sugar and proline accumulation in 49 pea cultivars in response to water stress. Field Crops Research 1998; 59:225-235.

[29] Rabe ES. Stress physiology: the functional significance of the accumulation of nitrogen-containing compounds. Journal of Horticultural Science 1990; 65(3):231-243.

[30] Knipp G, Honermeier B. Effect of water stress on proline accumulation of genetically modified potatoes (Solanum tuberosum L.) generating fructans. Journal of Plant Physiology 2006; 163:392-397.

[31] Kellomäki S, Strandman H, Nuutinen T, Petola H, Kothonen KT, Väisänen H. Adaptation of forest ecosystems, Forest and Forestry to Climate Change. FINDAT Working Paper 4. Helsinki: Finnish Environment Institute Mimeographs. 2005. 44 p.

[32] Angelopoulos K, Dichio B, Xiloyannis C. Inhibition of photosynthesis in olive trees (Olea europaea L.) during water stress and rewatering. Journal of Experimental Botany 1996; 47:1093-1100.

[33] Nepomuceno AL, Oosterhuis DM, Stewart JM. Physiological responses of cotton leaves and roots to water deficit induced by polyethylene glycol. Environmental and Experimental Botany 1998; 40:29-41.

[34] Eckstein K, Robinson JC. Physiological responses of banana (Musa AAA; Cavendish sub-group) in the subtropics. VI. Seasonal responses of leaf gas exchange to short-term water stress. Journal of Horticultural Science 1996; 71:679-692.

[35] Bolhàr-Nordenkampf HR, Long SP, Baker NR, Öquist G, Schreiber U, Lechner EG. Chlorophyll fluorescence as a probe of the photosynthetic competence of leaves in the field: A review of current instrumentation. Functional Ecology 1989; 3:497-514

[36] Bolhàr-Nordenkampf HR, Öquist G. Chlorophyll fluorescence as a tool in photosynthesis research. In: Hall DO, Scurlock JMO, Bolhàr-Nordenkampf HR, Leegood RC, Long SP (eds) Photosynthesis and Production in a Changing Environment: a Field and Laboratory Manual. London: Chapman & Hall; 1993.

[37] Baker NR. Light-use efficiency and photoinhibition of photosynthesis in plants under environmental stress. In: Smith JAC, Griffiths H (eds) Water deficits plant responses from cell to community. Oxford: Bios Scientific Publisher; 1993. p221-235.

[38] Matoušková, M., Nauš, J., Flašarová, M., Fiala, J. Changes in curves of fast fluorescence induction caused by water stress of barley plants. – Acta Univ. Palacki. Olomouc, Fac. Rer. Nat. Physica 1996; 35:195-208.

[39] Berry J, Björkman O. Photosynthetic response and adaptation to temperature in higher plants. Annual Review of Plant Physiology 1980; 31:491-543.

[40] Pimentel C. Metabolismo de carbono na agricultura tropical. Seropédica:EDUR;1998.

[41] Gilmore AM, Govindjee. How higher plants respond to excess light: energy dissipation in photosystem II. In: Singhal Gs, Renger G, Sopory SK, Irrgang KD, Govindjee (eds), Concepts in photobiology: photosynthesis and photomorphogenesis. New Delhi: Narosa Publ.; 1999. p513-548.

[42] Raison JK, Roberts JKM, Berry JA. Correlations between thermal stability of chloroplast (thylakoid) membranes and the composition and fluidity of their polar lipids upon acclimation of the higher plant Nerium oleander, to growth temperature. Biochimica et Biophysica Acta 1982; 688:218-228.

[43] Yamane Y, Kashino Y, Koike H, Satoh K. Effects of high temperatures on the photosynthetic systems in spinach: oxygen-evolving activities, fluorescence characteristics and the denaturation process. Photosynthesis Research 1998; 57:51-59.

[44] Pastenes C, Horton P Effect of high temperature on photosynthesis in beans. II. $CO_2$ assimilation and metabolite contents. Plant Physiology 1996; 112:1253-1260.

[45] Pastenes C, Horton P. Resistance of photosynthesis to high temperature in two bean varieties ( Phaseolus vulgaris L.) Photosynthesis Research 1996; 62: 197-203.

[46] Briantais JM, Dacosta J, Goulas Y, Ducruet JM, Moya I, Heat stress induces in leaves an increase of the minimum level of chlorophyll fluorescence, F0 : a time-resolved analysis. Photosynthesis Research 1996; 48:189-196.

[47] Havaux M, Ernez M, Lannoye R. Correlation between heat tolerance and drought tolerance in cerals demonstrated by rapid chlorophyll fluorescence. Journal of Plant Physiology 1998; 133: 555-560.

[48] Yamane Y, Kashino Y, Koile H, Satoh K.Increase in the fluorescence F0 level reversible inhibition of Photosystem II reaction center by high-temperature treatments in higher plants. Photosynthesis Research 1997; 52:57-64.

[49] Maxwell K, Johnson GN. Chlorophyll fluorescence - A pratical guide. Journal of Experimental Botany 2000;51: 659-668.

[50] Saddi, N. A taxonomic revision of the genus Kielmeyera Mart. (Guttiferae). PhD thesis, University of Reading, UK; 1982.

[51] Alves TMA, Silva AF, Brandão M, Grandi, TSM, Smania, EF, Smania Junior, AS, Zani, CL. Biological screening of Brazilian medicinal plants. Memorial do Instituto Oswaldo Cruz 2000; 95: 367–373.

[52] Zouni A, Witt HT, Kern J, Fromme P, Kraub N, Saenger W, Orth P. Crystal structure of hotosystem II from Synecococcus elongatesat 3.8 A resolution. Nature 2001; 409:739-43.

[53] Strasser, RJ, Tsimilli-Michael M, Srivastava A. Analysis of the chlorophyll a fluorescence transient. In Papageorgiou GC, Govindjee (eds.) Chlorophyll a fluorescence: A signature of photosynthesis. Dordrecht: Springer; 2004. p321–62.

[54] Strasser RJ. The grouping model of plant photosynthesis: heterogeneity of photosynthetic units in thylakoids. In: Akoyunoglou G (ed.). Photosynthesis III. Structure and molecular organisation of the photosynthetic apparatus. Philadelphia: Balaban International Science Services; 1981. p727-737.

[55] Tsimilli-Michael M, Strasser R. In vivo assessment of stress impact on plants' vitality: applications in detecting and evaluating the beneficial role of Mycorrhization on host plants. In: Varma A (ed.) Mycorrhiza: State of the art, genetics and molecular biology, ecofunction, biotechnology, eco-physiology, structure and systematics. Berlin: Springer; 2008. p679-703.

[56] Krause GH, Weis E. Chlorophyll fluorescence as a tool in plant physiology. II. Interpretation of fluorescence signals. Photosynthesis Research 1984; 5:139-157.

[57] Bulkhov N, Wiese C, Neimanis S, Heber U. Heat sensitivity of chloroplasts and leaves: Leakage of protons from thylakoids and reversible activation of cyclic eletron transport. Photosynthesis Research 1999; 59:81-93.

[58] Andréasson LE, Vass I, Styring S. $Ca^{2+}$ depletion modifies the electron transfer on the both donor and acceptor sides in photosystem II from spinach. Biochimica et Biophysica Acta 1995; 1230:155-164.

[59] Enami I, Kitamura M, Tomo T, Isokawa Y, Ohta H, Katch S. Is the primary cause of thermal inactivation of oxygen evolution in spinach PS II membranes release of the extrinsic 33 kDa protein or of Mn? Biochimica et Biophysica Acta 1994; 1186:52-58.

[60] Joliot P, Joliot A. Cyclic electron transport in plant leaf. Proceedings of the National Academy of Sciences of the United States of America 2002; 99:10209-10214.

[61] Strasser RJ, Srivastava A, Tsimilli-Michael M. The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: Yunus M, Pathre U, Mohanty P

(eds), Probing Photosynthesis: Mechanisms, Regulation and Adaptation. London: Taylor & Francis; 2000. p445-483.

[62] Mehta P, Jajoo A, Mathur S, Bharti S. Chlorophyll a fluorescence study effects of high salt stress on photosystem II in wheat leaves. Plant Physiology and Biochemistry 2010; 48: 16-20.

[63] Srivastava A, Strasser RJ, Govindjee. Greening of peas: parallel measurements of 77 K emission spectra, O-J-I-P chlorophyll a fluorescence transient, period four oscillation of the initial fluorescence level, delayed light emission, and P700. Photosynthetica 1999; 37:365-392.

[64] Gonçalves, JFC, Silva, CEM, Guimarâes, DG. Fotossíntese e potencial hídrico foliar de plantas jovens de andiroba. Pesquisa Agropecuária Brasildeira 2009; 44(1):8-14.

[65] Lazar D. Chlorophyll a fluorescence rise induced by high light illumination of dark-adapted plant tissue studied by means of photosystem II and considering photosystem II heterogeneity. Journal of Theoretical Biology 2003; 220:469-503.

[66] Hermans C, Smeyers M, Rodriguez RM, Eyletters M, Strasser RJ, Delhaye JP. Quality assessment of urban trees: A comparative study of physiological characterization, airborne imaging and on site fluorescence monitoring by the O-J-I-P-test. Journal of Plant Physiology 2003. 160:81-90.

[67] Force L, Critchley C, Rensen JJS. New fluorescence parameters for monitoring photosynthesis in plants. Photosynthesis Research 2003; 78:17-33.

[68] Strauss AJ, Kruger GHJ, Strasser RJ, Van Heerden PDR. Ranking of dark chilling tolerance in soybean genotypes probed by chlorophyll a fluorescence transient O-J-I-P. Environmental and Experimental Botany 2006; 56:147-157.

[69] Scandalios J.G. The rise of ROS. Trends in Biochemical Science 2002; 27:483-486.

[70] Azevedo Neto AD, Gomes-Filho E, Prisco JT. Salinity and oxidative stress. In: Khan NA, Singh S (ed.) Abiotic stress and plant responses. New Delhi: I.K. International; 2008. p57-82.

[71] Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry 2010; 48(12):909-930.

[72] Smirnoff N. The role of active oxygen in the response of plants to water deficit and desiccation. New Phytologist 1993; 125:27-58.

[73] Willekens H, Chamnongpol S, Davey M, Schraudner M, Langebartels C, Van Montagu M, Inzé D, Van Camp W. Catalase is a sink for $H_2O_2$ and is indispensable for stress defense in C3 plants. EMBO Journal 1997;16:4806-4816.

[74] Dat J, Vandenabeele S, Vranová E, Van Montagu M, Inzé D, Van Breusegen F. Dual action of the active oxygen species during plant stress responses. Cellular and Molecular Life Sciences 2000; 57:779-795.

[75] McKersie BD. Oxidative stress. In: McKersie B.D., Leshem Y.Y. (eds.) Stress and stress coping in cultivated plants. Dordrecht: Kluwer Academic Publishes; 1994. p15-55.

[76] Bowler C, Van Montagu M, Inzé D. Superoxide dismutase and stress tolerance. Annual Review of Plant Physiology and Plant Molecular Biology 1992; 43:83-116.

[77] Scandalios JG. Oxygen stress and superoxide dismutase. Plant Physiology 1993;101:7-12.

[78] Shigeoka S, Ishikawa T, Tamoi M, Miyagawa Y, Takeda T, Yabuta Y, Yoshimura K. Regulation and function of ascorbate peroxidase isoenzymes. Journal of Experimental Botany 2002; 53:1305-1319.

[79] Hiraga S, Sasaki K, Ito H, Ohashi Y, Matsui H. A. large family of class III plant peroxidases. Plant and Cell Physiology 2001; 42:462-468.

[80] Herbette P, Lenne C, Leblanc N, Julien JL, JoeDrevet R, Roeckel-Drevet P. Two GPX-like proteins from Lycopersicon esculentum and Helianthus annuus are antioxidant enzymes with phospholipid hydroperoxide glutathione peroxidase and thioredoxin peroxidase activities. European Journal of Biological Chemistry 2002; 269:2414-2420.

[81] Jung BG, Lee KO, Lee SS, Chi YH, Jang HH, Kang SS, Lee K, Lim D, Yoon SC, Yun DJ, Inoue Y, Cho MJ, Lee SY. A chinese cabbage cDNA with high sequence identity to phospholipid hydroperoxide glutathione peroxidases encodes a novel isoform of thioredoxin-dependent peroxidase. The Journal of Biological Chemistry 2002; 277:12572-12578.

[82] Arthur JR. The glutathione peroxidases. CMLS, Cellular and Molecular Life Sciences 2000; 57:1825–1835.

[83] Davies W.J., Zhang J. Root signals and the regulation of growth and development of plants in drying soil. Annual Review of Plant Physiology and Plant Molecular Biology 1991;42 55-76.

[84] Mittler R. Oxidative stress, antioxidants and stress tolerance. Trends in Plant Science 2002; 7:405-410.

[85] Sgherri CLM, Pinzino C, Navari-Izzo F. Chemical changes and $O_2$- production in thylakoid membranes under water stress. Physiologia Plantarum 1993; 87:211-216.

[86] Beis A, Patakas A. Relative contribution of photoprotection and anti-oxidative mechanisms to differential drought adaptation ability in grapevines. Environmental and Experimental Botany 2012; 78:173-183.

[87] Foyer CH, Noctor G. Oxygen processing in photosynthesis: regulation and signaling. New Phytologist 2000; 146(3):359-388.

[88] Asada K. The water-water cycle in chloroplasts: scavenging of active oxygens and dissipation of excess photons. Annual Review of Plant Biology 1999; 50:601-639.

[89] Biehler K, Fock H. Evidence for the contribution of the Mehler-Peroxidase reaction in dissipating excess electrons in drought-stressed wheat. Plant Physiology 1996; 112:265-72.

[90] Noctor G, Veljovic-Jovanovic S, Driscoll S, Novitskaya L, Foyer C. Drought and oxidative load in the leaves of C3 plants: A predominant role for photorespiration? Annals of Botany 2002; 89:841-850.

[91] Robinson JM, Bunce J. A. Influence of drought-induced water stress on soybean and spinach leaf ascorbate-dehydroascorbate level and redox status. International Journal of Plant Sciences 2000; 161:271-279.

[92] Boo YC, Jung J. Water deficit-induced oxidative stress and antioxidant defenses in rice plants. Journal of Plant Physiology 1999; 155:255-261.

[93] Sharma P, Dubey RS. Drought induces oxidative stress and enhances the activities of antioxidant enzymes in growing rice seedlings. Plant Growth Regulation 2005; 46:209-221.

[94] Esfandiari E, Shakiba MR, Mahboob SA, Alyari H, Shahabivand S. The effect of water stress on the antioxidant content, protective enzyme activities, proline content and lipid peroxidation in wheat seedling. Pakistan Journal of Biological Sciences 2008; 11:1916-1922.

[95] Mano J, Torii Y, Hayashi S, Takimoto K, Matsui K, Nakamura K, Inzé I, Babiychuk E, Kushnir S, Asada A. The NADPH: Quinone oxidoreductase P1-ζ-crystallin in Arabidopsis catalyzesthe $\alpha$, $\beta$-hydrogenation of 2-alkenals: Detoxication of the lipid peroxide-derived reactive aldehydes. Plant and Cell Physiology 2002; 43(12):1445-1455.

[96] Azevedo Neto AD, Nogueira RJMC, Melo Filho PA, Santos R. Physiological and biochemical responses of peanut genotypes to water deficit. Journal of Plant Interactions 2010;5 1-10.

[97] Sayfzadeh S, Rashidi M. Response of antioxidant enzymes activities of sugar beet to drought stress. ARPN Journal of Agricultural and Biological Science 2011; 6(4):27-33.

[98] Reddy AR, Chaitanya KV, Jutur PP, Sumithra K. Differential antioxidative responses to water stress among five mulberry (Morusalba L.) cultivars. Environmental and Experimental Botany 2004; 52:33-42.

[99] Moussa HR, Abdel-Aziz SM. Comparative response of drought tolerant and drought sensitive maize genotypes to water stress. Australian Journal of Crop Science 2008; 1:31-36.

[100] Sairam RK, Deshmukh PS, Saxena DC. Role of antioxidant systems in wheat genotypes tolerance to water stress. Biologia Plantarum 1998; 41(3):387-394.

[101] Wang S, Liang D, Li C, Hao Y, Ma F, Shu H. Influence of drought stress on the cellular ultrastructure and antioxidant system in leaves of drought-tolerant and drought-sensitive apple rootstocks. Plant Physiology and Biochemistry 2012; 51:81-89.

[102] Al-Ghamdi AA. Evaluation of oxidative stress tolerance in two wheat (Triticum aestivum) cultivars in response to drought. International Journal of Agriculture and Biology 2009; 11:7-12.

[103] Marron N, Maury S, Rinaldi C, Brignolas F. Impact of drought and leaf development stage on enzymatic antioxidant system of two Populus deltoids x nigra clones. Annals of Forest Science 2006; 63:323-327.

[104] Chapman AD. Numbers of living species in Australia and the World. 2nd edition. Canberra: Australian Government, Department of the Environment, Water, Heritage and the Arts; 2009.

[105] Puig H. A floresta tropical úmida. São Paulo: Editora UNESP; 2008.

[106] Murphy PG, Lugo AE. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 1986; 17:67-88.

[107] Cummins K. Structure and function of stream ecosystems. Bioscience 1974; 24:631-641.

[108] Alvarez-Añorve M, Quesada M, De La Barrera E. Remote sensing and plant functional groups detection: physiology, ecology and spectroscopy in tropical systems. In: Kalacska M, Sánchez-Azofeifa GA (eds.) Hyperspectral Remote Sensing of Tropical and Sub-Tropical Forests. London:Taylor and Francis Group; 2008. p27–45.

[109] Poorter L, Markesteijn L. Seedling traits determine drought tolerance of tropical tree species. Biotropica 2008; 40:321–331.

[110] Mendes MRA. Florística e fitossociologia de um fragmento de caatinga arbórea, São José do Piauí, Piauí. MSc thesis. Universidade Federal de Pernambuco; 2003.

[111] Ackerly DD, Knight CA, Weiss SB, Barton K, Starmer KP. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses 2003. Oecologia; 130:449-457.

[112] Scoffoni C, Rawls M, McKown A, Cochard H, Sack L. Decline of leaf hydraulic conductance with dehydration: Relationship to leaf size and venation architecture. Plant Physiology 2011; 156:832–843.

[113] Barbosa DCA, Barbosa MCA, Lima LCM. Fenologia de espécies lenhosas da caatinga. In: Leal IR, Tabarelli M, Silva JMC (eds.) Ecologia e Conservação da Caatinga. Recife: Editora Universitária da UFPE; 2003. p657-693.

[114] Kushwaha CP, Tripathi SK, Singh GS, Singh KP. Diversity of deciduousness and phenological traits of key Indian dry tropical forest trees. Annals of Forest Science 2010; 67: Article 310. DOI: 10.1051/forest/2009116.

[115] Franco AC, Bustamante M, Caldas LS, Goldstein G, Meinzer FC, Kozovits AR, Rundel P, Coradin VTR. Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. Trees 2005; 19:326-335

[116] Wilhite DA, Glantz MH. Understanding the drought phenomenon: The role of definitions. Water International 1985; 10(3):111–120.

[117] Molles Junior MC. Ecology: Concepts and applications. Boston: McGraw-Hill. 2002.

[118] Valladares F, Gianoli E, Goéz JM. Ecological limits to plant phenotypic plasticity. New Phytologist 2007; 176:749-763.

[119] Weiner J. Allocation, plasticity and allometry in plants. Perspectives in Plant Ecology, Evolution and Systematics 2004. 6(4): 207-215.

[120] Intergovernmental Panel on Climate Change. IPCC. The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge university; 2007.

[121] Peñuelas J, Rutishauser T, Filella I. Phenology feedbacks on climate change. Science 2009; 324:887-888.

[122] Sherry RA, Zhou XH, Gu SL, Arnone JA, Schimel DS, Verburg PS, Wallace LL, Luo YQ. Divergence of reproductive phenology under climate warming. Proceedings of the National Academy of Sciences of the United States of America 2007; 104(1): 198-202.

[123] Walther GR. Community and ecosystem responses to recent climate change. Philosophical Transactions of Royal Society B 2010; 365:2019–2024

[124] Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH. Predicting plant invasions in an era of global change. Trends in Ecology and Evolution 2010; 25(5):310-318.

[125] Vila M, Corbin JD, Dukes JS, Pino J, Smith SD. Linking plant invasions to global environmental change. In: Canadell J, Pataki D, Pitelka L (Eds.) Terrestrial Ecosystems in a Changing World, New York: Springer; 2007. p.93-102.

[126] Wolkovich EM, Cook BI, Allen JM, Crimmins TM, Betancourt JL, Travers SE, Pau S, Regetz J, Davies TJ, Kraft NJB, Ault TR, Bolmgren K, Mazer SJ, McCabe GJ, McGill BJ, Parmesan C, Salamin N, Schwartz MD, Cleland EE. Warming experiments underpredict plant phenological responses to climate change. Nature 2012; 485:494-497.

IntechOpen