COCOS, 2023 ***24:*** *55 - 73*
Printed in Sri Lanka

https://doi.org/10.4038/cocos.v24i1.5828

RESEARCH ARTICLE

Fighting Drought: A Mini Review with Special Reference to Tropical Palms

P. R. Weerasinghe[1*], H. D. M. A. C. Dissanayaka[1], C. R. K. Samarasinghe[1],
M. G. O. S. Thilakarathne[1] and M. K. Meegahakumbura[2*]

[1]Genetics and Plant Breeding Division, Coconut Research Institute, Lunuwila, Sri Lanka,

[2]Department of Export Agriculture, Faculty of Animal Science and Export Agriculture, Uva Wellassa University, Badulla, 90000, Sri Lanka

[*]Corresponding Author : P. R. Weerasinghe, Email: pabasaraweerasinghe@yahoo.com

ABSTRACT

Drought stress is the most important environmental stress which affects negatively on plant growth and productivity. With the climate change and the scarcity of water, drought conditions have become frequent and prominent, affecting the agricultural production worldwide. Therefore, breeding crops for drought tolerance has gained significant attention at present. To cope with drought, plants possess different mechanisms and understanding their biological significance would enable the utilization of these mechanisms in crop improvement for drought tolerance. Therefore, in the current review an effort has been made to compile the information related to drought tolerance mechanisms and drought resistant/tolerant crop improvement with special reference to tropical palm tree species.

Keywords: Drought, Drought tolerance, Palms

1. INTRODUCTION

Among the negative impacts of severe environment on plants, drought can be considered as one of the most significant environmental stresses that affects the plant growth and performance. Drought stress occurs as a result of an imbalance between the evapotranspiration flux and water intake from the soil (Lipiec et al., 2013) where the soil and atmospheric humidity becomes lower than the ambient air temperature. The adverse effects of drought stress involve mainly the reduction of crop productivity and yield. For instance, 21% and 40% of yield reduction has been observed in wheat and maize crops respectively due to drought stress caused by approximately a 40% reduction of water (Daryanto et al., 2016). Currently, about 45% of the world's total agricultural land has been affected by drought (Dos Reis et al., 2012). The effect of drought has become more severe with the climate change. Intergovernmental Panel on Climate Change (IPCC) reports that the air and ocean temperatures have risen, and the concentrations of greenhouse gases have increased over time (Edenhofer, 2015). Both these factors affect the plant growth and crop productivity (Stocker et al., 2013) as they result in elevated temperatures and infrequent and erratic precipitations and thereby contributing to the development of drought-prone areas (Zhao et al., 2017). Therefore, with the increment of global warming and rising of population, it is crucial to take measures for the development of drought tolerance in crops, in order to meet the demand. In this review, the efforts that have been made so far to improve crop productivity under water-limiting conditions, and to develop drought tolerant crops have been discussed with special reference to tropical palm trees.

Drought tolerance in plants

Drought tolerance is defined as the ability of a plant to survive, grow, and reproduce satisfactorily with limited water supply (Turner, 1979). Crop plants should have both the ability to survive under drought and the ability to produce a harvestable yield under adverse conditions. In order to cope with environmental stresses, plants possess different strategies and among them, drought escape, dehydration avoidance and dehydration tolerance are important in facing and responding to drought (Levitt, 1980). Simply, drought escape strategies include the completion of the full life cycle of the plant prior to approaching a drought event. Dehydration avoidance strategies include the morpho-physiological features that enable the plant to maintain hydration whereas dehydration tolerance strategies include the features that allow the plant to maintain proper functionality in severe dehydrated state. However, these three broad strategies include a cascade of physiological, biochemical and molecular events and they will be discussed in detail.

Drought escape

As mentioned earlier drought escape can be described as the ability of a plant species to complete its life cycle before the commencement of drought. Plants which possess this strategy are usually ephemerals and they can regulate the vegetative and reproductive growth depending on the availability of water, thereby avoiding the experiencing of the drought stress. Two main mechanisms are identified in association to this strategy namely the rapid phenological development and development plasticity (Basu et al., 2016). Rapid phenological development includes the rapid plant growth with early flowering and production of minimal number of seeds before the depletion of the soil water (Abobatta, 2019). However, such plants do not possess with any special morphological, physiological, or biochemical adaptations for drought (Basu et al., 2016). Plants with mechanisms of developmental plasticity show retarded growth during the dry season, with very few flowers and seeds, but in wet seasons they grow indeterminately, producing a large number of seeds.

Dehydration avoidance

When considering the morphological adjustments of plants to cope with heat stress or drought, the root system lies in front. The root of the plant can be considered as the key organ providing mechanical support and it facilitates the absorption and transportation of water, oxygen, nutrients, and hormones to the aboveground tissues. As it has an important role in the abiotic stress tolerance, crop performance and yield production in response to environmental variations, the root modifies its architecture to a level in which it increases the water uptake efficiency. In response to drought stress, many plants prefer to increase the primary root elongation while suppressing the lateral root branching (Oosten et al., 2016). Studies have identified several genetic components contributing to root architecture that has the potential to limit crop loss due to adverse environmental conditions. Moreover, plants re-model the root system during stresses by activating programmed cell death in the root apical meristem and thereby removing the apical root dominance (Oosten et al., 2016). Drought tolerance is a complex composite resulting from the interaction of root and shoot traits (Lu et al., 2007). The size and activity of the root system determines the rate at which the shoot system can produce photosynthates. Therefore, despite of the less well studied nature of roots due to lack of ready visibility and issues in replicating the conditions in which they grow, there is a higher potential in exploitation and manipulation these root traits to optimize crop growth and adaptation to water stress. (Den Herder *et al.*, 2010).

Physiological adjustments that maintain turgor pressure are important under changing environmental conditions. Water transportation in roots is affected by various components such as root anatomy, water availability and salts in the soil (Boursiac *et al*., 2005). All these factors are influenced by the activity of aquaporins, which are integral membrane proteins that function as channels to transfer selected small solutes and water (Vandeleur *et al.*, 2014).

Stomata is another key player in dehydration avoidance as they control and regulate the evapo-transpiration of water to the external environment (Pirasteh-Anosheh et al., 2016). Stomata usually occur mostly on the lower surface of the leaf and new stomata are generated continually during leaf growth. Stomatal closure is a well-known first responsive reaction of plants to drought stress in many crops (Nemeskeri et al., 2015). Stomatal closures are more closely related to soil moisture content compared to leaf water status. Stomatal responses to drought stress are mainly controlled by chemical signals such as ABA that are produced in dehydrating roots. According to Taiz and Zeiger (2002), stomatal closure can be observed under severe drought conditions along with other physiological processes such as inhibition of cell division, inhibition of wall and protein synthesis, accumulation of solutes and inhibition of photosynthesis. However, stomata closure does not always depend on the or drought stress signals arising from leaves. In fact, stomata closure is directly sensitive to soil dehydration, even before any significant reduction in leaf mesophyll turgor pressure occurs (Mahajan and Tuteja, 2005).

Many studies have indicated that drought stress results in increasing stomatal density in sorghum, wheat and in some other plants (Yang and Wang, 2001; Xu and Zhou, 2008). Stomatal morphological traits such as size, density, and distribution may affect gas exchange quite remarkably and their relationships with key environmental factors such as water status (Xu and Zhou, 2008). Moreover, some studies have shown that drought stress decreased stomatal size, which indicated these changes in stomatal morphology could increase the plant adaptation to drought stress conditions (Martinez et al., 2007). Yadollahi et al. (2011) revealed that leaf stomatal cells of an Almond had strong mechanisms to keep the leaves turgid and active, even during drought periods. The lack of relationship between stomatal density and drought stress in some plants showed that they possibly use another mechanism for drought resistance such as stomatal conductance.

Dehydration tolerance

Exposure to drought leads to cellular dehydration where water removes from the cytoplasm resulting in decreasing of cytosolic and vacuolar volumes (Forni et al., 2017). In response to this, plants increase the production of specific sets of primary and secondary metabolites that act as osmo-protectants, osmolytes, antioxidants, and stress signals which are specifically involved in stress tolerance (Fang and Xiong, 2015).

Osmo-protectants involve in preserving the cells and cellular components from the detrimental changes caused by dehydration, without interfering with the normal metabolic processes at the cellular level and thereby restoring homeostasis. These solutes include amines (polyamines and glycine betaine), amino acids (proline), soluble sugars (glucose, sucrose, trehalose), and polyols (mannitol, sorbitol and inositol) (Szabados and Savouré, 2010). The accumulation of these compounds aid in protection of protein structures and stabilization of cellular membranes as cells dehydrate, maintenance of cell turgor and thereby providing abiotic stress tolerance (Zlatev and Lidon, 2012).

However, some crops have low levels of these compounds, and hence such plants manipulate the genes involved in osmo-protectant biosynthesis pathways and it is considered as one of the strategies to improve stress tolerance in plants (Reguera et al., 2012).

Polyamines (PAs) are small aliphatic nitrogen compounds that are ubiquitous in all organisms. In plants, PAs act as regulatory molecules involved in vital cellular processes such as embryogenesis, floral development, and pollen tube growth (Tiburcio et al., 2014). A significant accumulation of the three most common PAs, namely; Putrescine (Put), Spermidine (Spd), and Spermine (Spm) could be identified during the biotic and abiotic stress conditions (Wen and Moriguchi, 2015).

Glycine Betaine (GB) is a quaternary ammonium derivative of glycine and is one of the major osmolytes involved in protection of the cell membrane. They are involved in encouraging water influx into cells and maintain the intracellular osmotic equilibrium while regulating the signal transduction cascades (Ranganayakulu et al., 2013). In many plant species these GBs are accumulated in chloroplasts and other plastids in response to various abiotic stresses such as drought.

Proline, a versatile amino acid that is essential both as a component of the protein and as a free amino acid contributing to osmotic adjustment in response to different abiotic stresses (Zandalinas *et al*., 2017). Proline facilitates water uptake and reduces the accumulation of Na^+ and Cl^- (Ashraf and Foolad, 2007) and avoid dehydration. Therefore, accumulation of proline under stress conditions in many plant species has been correlated with stress tolerance.

Other than the above-mentioned compounds, plant hormones also play major roles in abiotic stress tolerance. Abscisic acid (ABA) is one of the most important hormones involved in abiotic stress tolerance such as drought, cold, heat and wounding (Zhang et al., 2006). ABA also is considered as a major chemical involved in root-to-shoot stress signal transduction (Schachtman and Goodger, 2008), inducing inhibition of leaf expansion and stomatal closure. Osmotic stress also results in the synthesis or catabolism of several other growth regulators, including Auxin, Cytokinins, Ethylene, Gibberellins, Brassinosteroids and Jasmonic acid which are involved in the regulation of physiological processes through their action as signal molecules in signaling networks (Nakashima and Yamaguchi-Shinozaki, 2013).

In addition to the above strategies, plants also enhance intracellular Ca^{2+} levels with the support of several signal molecules such as Inositol Trisphosphate, Inositol Hexaphosphate and Diacylglycerol (Hirayama and Shinozaki, 2010) during stress. Calcium binding proteins, functioning as Ca^{2+} sensors, perceive these elevated Ca^{2+} levels (Kudla *et al*., 2010) and it will lead to the activation of calcium dependent protein kinases. The activated kinases or phosphatases can phosphorylate or dephosphorylate specific transcription factors (TFs), thus regulating the expression levels of stress-responsive genes (Reddy *et al*., 2011). TFs play important roles in stress tolerance. Many abiotic stress-related genes and TFs have been isolated from different plant species mainly in wheat and maize and overexpressed in transgenic plants to improve stress tolerance. The stress-inducible TFs include members of the DREB, ERF, WRKY, MYB, bHLH, bZIP, DOF, and NAC families (Mittal *et al*., 2017).

Another important cellular mechanism conferring drought tolerance is the regulation of Reactive Oxygen Species (ROS) (Hirayama and Shinozaki, 2010). ROS are chemically reactive molecules containing oxygen and they are formed in the metabolism of oxygen and have important roles in cell signaling and homeostasis. Increased levels of ROS have been reported during biotic and/or abiotic stresses, such as pathogen attack, wounding, UV irradiation, high light, drought, salinity, and chilling (Sharma *et al*., 2012). Accumulation of ROS causes oxidative stress, which in turn results in oxidative damage to proteins, DNA and lipids (Gill and Tuteja, 2010). Acclimation of plants to drought and salinity is often associated with increased levels of ROS, such as superoxide anion (O^{2-}), hydrogen peroxide (H_2O_2), hydroxyl radical (HO), and singlet oxygen (O_2), which are toxic to the cells (Grover *et al*., 2011). During non-stress conditions, ROS are efficiently eliminated by non-enzymatic and enzymatic antioxidants. However, during drought and salt stress, the production of ROS exceeds the capacity of the anti-oxidative systems to remove them, causing oxidative stress (Vanderauwera et al., 2012). In these conditions, the elimination of ROS is a key response to tolerate drought stress. This is mainly achieved by antioxidant compounds such as ascorbic acid, glutathione, thioredoxin, and by oxyreductant enzymes such as glutathione peroxidase, superoxide dismutase, and catalase. It has been established that 1–2 % of oxygen absorbed by plants is used to produce ROS in plants (Bhattacharjee, 2005). Over accumulation of ROS from abiotic stress contributes to major losses of crop productivity and is an important economic problem for cultivated plants worldwide (Gill and Tuteja, 2010).

The above discussed different strategies used by plants as drought tolerance mechanisms are summarized in Figure 1.

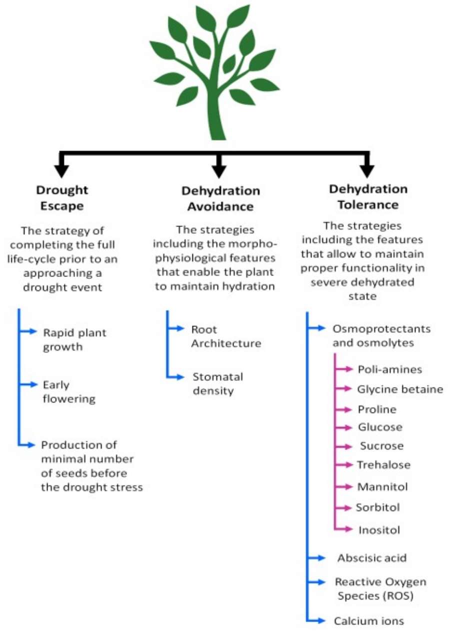

Figure 1: Different mechanisms used by plants to cope with drought stress (Only the major strategies are illustrated.)

Improving drought tolerance in crops

With the scarcity of water and frequent droughts due to climate change, the worldwide agricultural ecosystems are facing the challenge of combatting drought. Therefore, breeding for water saving and drought tolerant crops is a priority in the current world for ensuring world food security. A significant progress has been achieved in this aspect during the last decade (Luo et al., 2019) with the advancement of technology and novel findings.

Breeding strategies include several methodologies such as breeding and selection in the field, Quantitative Trait Loci (QTL) mapping or Genome Wide Association Studies (GWAS), comparative transcriptome analysis, precise high-throughput phenotyping, and characterization of drought-resistance genes, to induce drought-resistance in different crops.

Understanding the genetic basis of drought tolerance in plants is vital in developing superior genotypes resistant to drought. Generally, drought tolerance is a quantitative trait (Fleury *et al.*, – 2010) controlled by multiple genes. Therefore, the underpinning mechanisms of drought tolerance are more complex than the traits of biotic stresses that are generally characterized by monogenic resistance. However, studies have shown that single genes also are important in drought tolerance in plants (Morgan, 2000) and these genes include the genes controlling flowering time, plant height, and osmotic adjustment which might have important roles in adaptation to drought-prone environments (Forster *et al.,* 2004).

At present, majority of the data available on drought tolerance are based on segregation mapping and QTL analysis . Identification of drought-resistance QTLs is essential to provide valuable targets in crop breeding. Drought related QTL information for majority of the plant species is available in open source databases like GRAMENE (http://www.gramene. org) and Phytozome (https:// phytozome. jgi.doe .gov /pz/portal.html) which can be utilized freely for further research. When considering the drought related QTLs for several crops they coincide with the other specific traits such as yield and root traits (Verma et al., 2004) which can be used in improving drought tolerance in crops using marker assisted selection. For instance, Lanceras et al. (2004), showed that favorable alleles for yield components were located in a region of rice chromosome 1 where QTLs for many drought-related traits like root dry weight, relative water content, leaf rolling and leaf drying which have been previously identified. However, due to the polygenic nature of drought tolerance and the interaction with the environment, a genetic linkage between a specific DNA marker and a target locus allele established by QTL studies can be broken. As a result, Marker Assisted Selection for drought tolerant QTLs has been extremely difficult (Francia et al., 2005). Cloning of DNA sequences underlying QTLs is considered to be a key step towards the application of molecular techniques in breeding for drought. Even though most plant QTLs have been cloned so far, no QTL for drought tolerance has been cloned in crop species (Cattivelli et al., 2008). However, ERECTA gene, a sequence beyond a QTL for transpiration efficiency has been cloned in Arabidopsis (Masle et al., 2005).

Generation of molecular/function maps or molecular linkage maps based on candidate genes is one of the means in determining the functional markers in plants with larger genomes (Causse et al., 2004). As this candidate gene strategy can be utilized to bridge the gap between quantitative genetic and molecular genetic approaches to study complex traits, it has been applied to identify the putative genes involved in drought tolerance in barley and rice (Zheng et al., 2003; Tondelli et al., 2006). With the benefit of the conserved biochemical pathways which involves in stress tolerance in plants, the genetic information in model plants can be utilized to exploit the genome synteny in crops. Several studies have identified the regulatory components of the drought response in soybean, wheat and barley using this approach (Li et al., 2005; Shen et al., 2003; Mare` et al., 2004).

At present, the novel approaches such as GWAS have broaden up the horizons in stress tolerance breeding. For example, Li et al. (2018) have identified four genomic regions containing Single Nucleotide Polymorphisms (SNPs) significantly associated with several different traits in chickpea under drought stress. This result has indicated the pleiotropic effects of drought-resistance associated QTLs. Moreover, Gudys et al. (2018) have identified 11 candidate QTLs of physiological and biochemical traits associated with drought-tolerance in Barley on a high-density function map. Furthermore, they have prioritized 143 candidate genes by their potential involvements in certain biological processes based on Gene Ontology annotation. Cui et al. (2018) has provided a new method to identify QTLs for drought-tolerance in rice by comparing the allele frequency between drought-resistant introgression lines and random populations and identified 13 major QTLs of drought-tolerance in rice using the joint segregation distortion method. The most exciting result of this study was the detection of the large-effect QTLs locate upstream of the genetic networks as putative regulators, which could contribute significantly to drought-tolerance in rice. In addition, they also suggested the designed QTL pyramiding strategy that is feasible for improving drought-tolerance in rice. Even though there are hundreds of QTLs for the diverse traits related to drought resistance have been mapped, only a small portion of them can be repeatedly detected in different environments and populations and a few have been verified and cloned so far (Hu and Xiong, 2014).

Selection and breeding in the field have been used as the fundamental strategy in different crop species to build up drought tolerance in the upcoming progenies (Sallam et al., 2019). A crucial aspect in all field studies dedicated to drought tolerance is the assessment of the degree of drought tolerance of different genotypes (Avramova et al., 2016). However, in many studies the identification of tolerant and susceptible cultivars is based on a few physiological measures related to drought response. With the difficulty in identifying a physiological parameter as a reliable indicator of yield in dry conditions, it has been suggested that the yield performance over a range of environments could be used as the main indicator for drought tolerance (Voltas et al., 2005). Furthermore, a number of regression techniques of yield against environmental indices as independent variables were developed to evaluate genotype adaptability. Several indices were proposed to describe yield performance of a given genotype under stress and non-stress conditions or in comparison with the average yield or the yield of a superior genotype (Finlay and Wilkinson, 1963).

Improving drought tolerance in tropical palms

When considering the attempts made so far to improve drought tolerance in perennial tree crops, it is interesting to look at the improvement of the palm species such as oil palm (*Elaeis guineensis* Jacq.), date palm (*Phoenix dactylifera* L.) and coconut (*Cocos nucifera* L.). Oil palm and coconut are the two most important plantation crops grown in the wet tropics. Even though oil palm is considered as a drought tolerant crop , negative impact of drought on the yield can be identified. Several attempts have been made to identify drought tolerant genotypes of oil palm via selection and progeny testing in the field as well as in controlled environments (Ubara et al., 2017). Physiological parameters such as the root biomass, potential root extraction ratio, rate of stomatal conductance and photosynthesis were used in these studies (Murugesan et al., 2017). Also, studies have indicated that the tolerant oil palm genotypes consisted of higher total root length, total root surface area and potential root water extraction ratio than the susceptible genotypes based on half-distances between roots and the distance of water migration from soil to root (Nodichao et al., 2011).

Furthermore, interspecific hybrids like (*E. guineensis* × *E. oleifera*) have been produced and they have shown positive responses for drought tolerance (Barcelos et al., 2005).

Application of Silicon (Si) increases oil palm resistance to drought (Sacala, 2009), by aiding the oil palm plants to maintain water contents in the tissue, and increase photosynthetic activity

(Bharwana et al., 2013), to support the establishment of leaves, to maintain the structure of xylem vessels under conditions of rapid transpiration rate, to improve the balance of nutrients, to reduce mineral toxicity and to increase the mechanical strength of plant tissues (Sacala, 2009). Other benefits of application of Si are greater water use efficiency by reducing the rate of water loss, elimination of cuticular transpiration and increase in the CO_2 assimilation rate and stomatal conductance (Sacala, 2009).

From recent studies conducted using genomic and transcriptomic approaches, genes, pathways and networks responding to drought have been identified in oil palm (Wang et al., 2020). This study on root transcriptomic response of oil palm seedlings to drought stress has revealed over thousand differentially expressed genes. These genes were involved in different molecular processes implying the complex nature of the response to drought. The differently expressed genes have been identified under different functional groups including cell wall biogenesis and functions, phenylpropanoid biosynthesis and metabolisms, ion transport and homeostasis and cellular ketone metabolic process, as well as small molecule biosynthetic processes.

Date palm (*Phoenix dactylifera* L.) is another important tree crop contributing to the food security in arid regions of the world particularly in the Middle East and North Africa (Hazzouri et al., 2020). Irrespective of the drought tolerant quality gifted by nature, studies have been conducted in several research areas to explore and improve the drought tolerance in date palm. According to Xiao et al. (2019), date palm develops a tuber-like anatomical structure known as the cotyledonary petiole and it helps to protect the developing embryo in the soil. Furthermore, this study reported that date palms maintains suberized and lignified xylem, phloem and bundle cells in roots and also produce pneumatophores accounting for the drought and salinity tolerance.

Yaish (2015) studied the possibility of using proline as a biochemical marker in selecting for drought tolerance and found that date palm seedlings accumulate proline not only in response to drought but also as a response to salinity, extreme temperatures and abscisic acid treatments. As a result, it was concluded that the proline would be an unsuitable marker to use in traditional breeding programmes. Even though proline production is a common response for a variety of stresses, there is a potential for utilizing proline production as a possible marker in date palm breeding programs aiming to improve abiotic stress tolerance.

With the improvement of cutting-edge technologies, several omics studies also have been conducted on the drought tolerance of date palm. For example, genes involved in salt and drought tolerance in *P. dactylifera* have been identified by a proteomics study (Rabey et al., 2016). The group have identified 47 genes in total of which 17 are responsive for drought stress. Furthermore, Safronov et al. (2017) have conducted a transcriptomic and metabolomic profiling to characterize the response to heat and drought stress in date palm. The results have shown similar effects on both the stresses including the up regulation of soluble carbohydrates and increased antioxidant activity in the cytosol, chloroplasts, and peroxisomes. Moreover, differentially expressed genes involved in circadian and diurnal

Moreover, differentially expressed genes involved in circadian and diurnal rhythm in response to combined heat and drought were reported in the study implying a novel stress-avoidance strategy in date palm.

When considering coconut, it is mainly a rain-fed crop and faces summer drought spells each year in addition to the frequent drought years. Due to its perennial nature, coconuts have a long duration of about 37 months from the initiation of inflorescence primordia to nut maturity which contains a longer pre-fertilization period (About 26-27 months) and a shorter post fertilization period (11 months) (Perera et al., 2010; Ranasinghe, 2013). Therefore, any drought spell experienced at any of these critical stages affect the nut yield and the performance of the palm for about three consecutive years (Naresh Kumar, 2002). As it takes about 4 years for a coconut palm to recover in the worst affected conditions under a stress, improving the drought tolerance has been the need of the hour.

For the improvement of coconut for drought tolerance, the fundamental and promising approach which have been used is selection and progeny testing. Different coconut germplasm has been screened so far based on the essential anatomical and physiological traits such as the cell size and number, the size of the sub stomatal cavity, stomatal frequency, thickness of the epicuticular wax on leaflets, photosynthetic rate and water use efficiency (Naresh Kumar et al., 2000). Therefore, such desirable traits which reflects overall palm–water relationships could be used in identifying coconut cultivars with different levels of drought tolerance (Rajagopal et al., 2000). Based on drought tolerance indexes the germplasm also have been screened. For example, in Sri Lanka, the two cultivars San Raman tall and Ambakelle special have been identified as drought tolerant (Wikramartne, 1987). Ambakelle special is a cultivar that is resulted from a selection of the tall coconut palms providing stable yield even under adverse climatic conditions over 16 years from the tall coconut population in the Isolated seed garden at Ambakelle, Sri Lanka. Currently, three generations of Ambakelle special cultivar have been produced by paired crossing between the selected palms and they are in further evaluation at multi-locational sites for drought tolerance (Samarasinghe et al., 2018a; Samarasinghe et al., 2021).

In Cote d'Ivoire, PB-121 was identified as drought tolerant while West African Tall was identified as moderately tolerant to drought. According to the studies conducted at the Central Plantation Crops Research Institute (CPCRI), India have indicated that the Tall palms and the hybrids with the mother parent being Talls had shown a higher degree of drought tolerance than the dwarf palms and the hybrids with the mother parent being dwarf (Rajagopal and Kumar, 2005). With this background, in Sri Lanka, several attempts were taken to develop drought tolerant coconut cultivars through inter and intra varietal hybridization. For example, the CRISL98 (TSR) produced in 1998 by crossing of Sri Lankan Tall x San Raman Tall (Philippine cultivar) was initially recommended as a cultivar suitable to grow in the dry zone with drought tolerant traits. However, these inter and intra varietal hybrids developed with unselected Sri Lankan tall germplasm failed to develop cultivars withstanding drought and temperature stresses (Samarasinghe et al., 2018b; Waidyarathne and Perera, 2020; Samarasinghe et al., 2021) and the recommendation of CRISL98 has been revised as to grow them in wet and intermediate zones only due to the poor performance in the dry zone. Therefore, attempts have been currently made to use the putative drought tolerant second generation Ambakelle special palms as the maternal parent in developing new coconut cultivar CRISL2020.

Use of molecular techniques and novel omics approaches for improving the drought tolerance in coconut has been attempted at CPCRI (Rajagopal and Kumar, 2005) and some of the putative stress responsive genes to water deficit have been uncovered (Ramesh et al., 2020). Furthermore, they revealed differential molecular response of genotypes to water stress.

Even though the omics outcomes of drought and other abiotic stresses are nonspecific (Yaish, 2015) and there are only a few records of potential molecular markers for improving the drought tolerance, several attempts are in progress to uncover the putative genes/metabolic pathways accounting for drought tolerance in coconut and other palm species using integrated approaches and to utilize them accordingly in improving the drought tolerance in coconut.

2. CONCLUSION

Drought tolerance is a quite complex phenomenon which is controlled by a combination of anatomical, physiological and biochemical parameters. At different developmental stages, plants adopt different mechanisms to confer drought resistance. Even though it is difficult to evaluate drought resistance of a given plant species, several attempts have been made and are in progress to uncover the secrets behind drought stress tolerance in plants. However, in this genomic era it is important to have an integrated approach of omics tools to unwrap the linkage of traits, metabolic networks and protein interactions associated with drought stress tolerance in plants and to utilize them accordingly in improving the drought stress tolerance in plants.

3. REFERENCES

Abobatta W. F. (2019). Drought adaptive mechanisms of plants – a review. *Advances in Agriculture and Environmental Science*. 2(1): 42−45.DOI: 10.30881/aaeoa.00021

Al-Amin, A. Q., Leal, W., de la Trinxeria, J. M., Jaafar, A. H. and Ghani, Z. A. (2011). Assessing the impacts of climate change in the Malaysian agriculture sector and its influences in investment decision. *Middle-East Journal of Scientific Research*, *7*(2), 225-234.

Ashraf, M. F. M. R. and Foolad, M. R. (2007). Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and experimental botany*, *59*(2), 206-216.

Avramova, V., Nagel, K. A., AbdElgawad, H., Bustos, D., DuPlessis, M., Fiorani, F. and Beemster, G. T. (2016). Screening for drought tolerance of maize hybrids by multi-scale analysis of root and shoot traits at the seedling stage. *Journal of Experimental Botany*, 67(8), 2453-2466.

Barcelos, E., Cunha, N.R.W., & Nouy, B. (2005). Genetic resources of oil palm (*Elaeis guineensis* Jacq. and *Elaeis oleifera* (Kunth) Cortes) available at EMBRAPA and its use. In: BORÉM, A and VIANA, GV Plant Breeding, Viçosa, UFV. 525 p

Basu, S., Ramegowda, V., Kumar, A. and Pereira, A. (2016). Plant adaptation to drought stress. F1000Research, 5, F1000 Faculty Rev-1554. https://doi.org/10.12688/f1000research.7678.1

Bharwana, S. A., Ali, S., Farooq, M. A., Iqbal, N., Abbas, F. and Ahmad, M. S. A. (2013). Alleviation of lead toxicity by silicon is related to elevated photosynthesis, antioxidant enzymes suppressed lead uptake and oxidative stress in cotton. *Journal of Bioremediation and Biodegradation* 4(4), 187.

Bhattacharjee, S. (2005). Reactive oxygen species and oxidative burst: roles in stress, senescence and signal transduction in plants. *Current Science*, 89,1113–1121.

Boursiac, Y., Chen, S., Luu, D. T., Sorieul, M., van den Dries, N. and Maurel, C. (2005). Early effects of salinity on water transport in Arabidopsis roots. Molecular and cellular features of aquaporin expression. *Plant physiology*, *139*(2), 790-805.

Cattivelli, L., Rizza, F., Badeck, F. W., Mazzucotelli, E., Mastrangelo, A. M., Francia, E. and Stanca, A. M. (2008). Drought tolerance improvement in crop plants: an integrated view from breeding to genomics. *Field crops research*, *105*(1-2), 1-14.

Causse, M., Duffe, P., Gomez, M. C., Buret, M., Damidaux, R. *et al.* (2004). A genetic map of candidate genes and QTLs involved in tomato fruit size and composition. *Journal of Experimental Botany*, *55*(403), 1671-1685.

Cui, Y., Zhang, W., Lin, X., Xu, S., Xu, J. and Li, Z. (2018). Simultaneous improvement and genetic dissection of drought tolerance using selected breeding populations of rice. *Frontiers in plant science*, *9*, 320.

Daryanto, S., Wang, L., and Jacinthe, P. A. (2016). Global synthesis of drought effects on maize and wheat production. PloS one, 11(5), e0156362.

Den Herder, G.D., Isterdael, G.V., Beeckman, T. and Smet I.D. (2010) The roots of a new green revolution. Trends Plant Sci 15:600–607. doi:10.1016/j.tplants.2010.08.009

Dos Reis, S. P., Lima, A. M. and de Souza, C. R. (2012). Recent molecular advances on downstream plant responses to abiotic stress. *International journal of molecular sciences*, 13(7), 8628–8647. https://doi.org/10.3390/ijms13078628

Eberhart, S. T., & Russell, W. A. (1966). Stability parameters for comparing varieties 1. *Crop science*, 6(1), 36-40.

Edenhofer, O. (2015). *Climate change 2014: mitigation of climate change-IPCC* (Vol. 3). Cambridge University Press.

Fang, Y. and Xiong, L. (2015). General mechanisms of drought response and their application in drought resistance improvement in plants. *Cellular and molecular life sciences*, 72(4), 673-689.

Finlay, K. W. and Wilkinson, G. N. (1963). The analysis of adaptation in a plant-breeding programme. *Australian journal of agricultural research*, *14*(6), 742-754.

Fleury, D., Jefferies, S., Kuchel, H. and Langridge, P. (2010). Genetic and genomic tools to improve drought tolerance in wheat. *Journal of experimental botany*, 61(12), 3211-3222.

Forni, C., Duca, D. and Glick, B. (2017). Mechanisms of plant response to salt and drought stress and their alteration by rhizobacteria. *Plant and Soil*, 410(1/2), 335-356

Forster, B. P., Ellis, R. P., Moir, J., Talame, V., Sanguineti, M. C. *et al.* (2004). Genotype and phenotype associations with drought tolerance in barley tested in North Africa. *Annals of applied Biology*, *144*(2), 157-168.

Francia, E., Tacconi, G., Crosatti, C., Barabaschi, D., Bulgarelli, D., Dall'Aglio, E. and Valè, G. (2005). Marker assisted selection in crop plants. *Plant Cell, Tissue and Organ Culture*, *82*(3), 317-342.

Gill, S. S. and Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant physiology and biochemistry*, *48*(12), 909-930.

Grover, A., Singh, A. and Blumwald, E. (2011). Transgenic strategies toward the development of salt-tolerant plants. Agricultural salinity assessment and management, 2nd edn, pp. 235–274.

Gudys, K., Guzy-Wrobelska, J., Janiak, A., Dziurka, M. A., Ostrowska, A., Hura, K. and Szarejko, I. (2018). Prioritization of candidate genes in QTL regions for physiological and biochemical traits underlying drought response in barley (*Hordeum vulgare* L.). *Frontiers in plant science*, *9*, 769.

Hazzouri, K.M., Flowers, J.M., Nelson, D., Lemansour, A., Masmoudi, K. and Amiri, K.M.A. (2020). Prospects for the Study and Improvement of Abiotic Stress Tolerance in Date Palms in the Post-genomics Era. *Frontiers in plant science*. 11:293. doi: 10.3389/fpls.2020.00293

Hirayama, T. and Shinozaki, K. (2010). Research on plant abiotic stress responses in the post-genome era: past, present and future. *Plant Journal*, 61, 1041–1052. doi: 10.1111/j.1365-313X.2010. 04124.x

Hu, H. and Xiong, L. (2014). Genetic engineering and breeding of drought-resistant crops. *Annual review of plant biology*, 65, 715-741.

Jung, J. K. H. M. and McCouch, S. R. M. (2013). Getting to the roots of it: genetic and hormonal control of root architecture. *Frontiers in plant science*, 4, 186.

Kudla, J., Batistic, O. and Hashimoto, K. (2010). Calcium signals: the lead currency of plant information processing. *Plant Cell*,22, 541–563. doi: 10.1105/tpc. 109.072686

Lanceras, J. C., Pantuwan, G., Jongdee, B. and Toojinda, T. (2004). Quantitative trait loci associated with drought tolerance at reproductive stage in rice. *Plant Physiology*, 135(1), 384-399.

Morgan, J. M. (2000). Increases in grain yield of wheat by breeding for an osmoregulation gene: relationship to water supply and evaporative demand. *Australian Journal of Agricultural Research,* 51(8), 971-978.

Murugesan, P., Aswathy, G. M., Sunil Kumar, K., Masilamani, P., Kumar, V. and Ravi, V. (2017). Oil palm (*Elaeis guineensis*) genetic resources for abiotic stress tolerance: A review. *Indian Journal of Agricultural Sciences, 171*, 12-17.

Nakashima, K. and Yamaguchi-Shinozaki, K. (2013). ABA signaling in stress-response and seed development. *Plant Cell Reports*, 32, 959–970. doi: 10.1007/s00299-013-1418-1.

Naresh Kumar, S. (2002). Agro-meteorology and drought management in coconut. In: Training manual on drought stress and its management in plantation crops. Central Plantation Crop Research Institute, Kasaragod, India.

Naresh Kumar, S., Rajagopal, V. and Karun, A. (2000). Leaflet anatomical adaptations in coconut cultivars for drought tolerance. pp 225-229. In: N Muralidharan and R Raj Kumar (eds). *Recent advances in plantation crop research*. Allied Pub. Ltd, New Delhi, India.

Nemeskéri, E., Molnár, K., Vígh, R., Nagy, J. and Dobos, A. (2015). Relationships between stomatal behaviour, spectral traits and water use and productivity of green peas (*Pisum sativum* L.) in dry seasons. *Acta physiologiae plantarum*, *37*(2), 34.

Nodichao, L., Chopart, J. L., Roupsard, O., Vauclin, M., Aké, S. and Jourdan, C. (2011). Genotypic variability of oil palm root system distribution in the field. Consequences for water uptake. *Plant and soil*, *341*(1), 505-520.

Oosten, M.J.V., Costa, A., Punzo, P., Landi, S., Ruggiero, A., Batelli, G. and Grillo, S. (2016). Genetics of Drought Stress Tolerance in Crop Plants. In. Hossain et al. (eds.), *Drought Stress Tolerance in Plants*, Vol 2, Springer International Publishing Switzerland. Pp: 39-70 DOI 10.1007/978-3-319-32423-4_2

Perera P.I.P., Hocher L.K., Weerakoon D.M.D., Yakandawala S.C. and Fernando J.L.V. (2010). Early inflorescence and floral development in *Cocos nucifera* L. (Arecaceae: Arecoideae). *South African Journal of Botany* 76: 482-492

Pirasteh-Anosheh, H., Saed-Moucheshi, A., Pakniyat, H. and Pessarakli, M. (2016). Stomatal responses to drought stress. *Water stress and crop plants*, 24-40.

Rabey, H. E., Al-Malki, A., and Abulnaja, K. (2016). Proteome analysis of date palm (*Phoenix dactylifera* L.) under severe drought and salt stress. *International Journal of Genomics*. 2016:7840759.

Mittal S., Arora K., Rao A. R., Mallikarjuna M. G., Gupta H. S. and Nepolean T. (2017). Genomic selection for drought tolerance using genome-wide SNPs in maize. *Frontiers in plant science*. 8:550 10.3389/fpls.2017.00550

Lata, C. and Prasad, M. (2011). Role of DREBs in regulation of abiotic stress responses in plants. *Journal of Experimental Botany*, 62, 4731–4748. doi: 10.1093/jxb/err210

Levitt, J. (1980). *Responses of plants to environmental stresses*. 2nd edn. (Academic Press: New York).

Li, X. P., Tian, A. G., Luo, G. Z., Gong, Z. Z., Zhang, J. S. and Chen, S. Y. (2005). Soybean DRE-binding transcription factors that are responsive to abiotic stresses. *Theoretical and Applied Genetics*, *110*(8), 1355-1362.

Li, Y., Ruperao, P., Batley, J., Edwards, D., Khan, T., Colmer, T. D. and Sutton, T. (2018). Investigating drought tolerance in chickpea using genome-wide association mapping and genomic selection based on whole-genome resequencing data. *Frontiers in plant science*, *9*, 190.

Lipiec, J., Doussan, C., Nosalewicz, A. and Kondracka, K. (2013). Effect of drought and heat stresses on plant growth and yield: a review. *International Agrophysics*, 27(4), 463-477.

Lou, Q., Chen, L., Mei, H., Xu, K., Wei, H. *et al*. (2017). Root transcriptomic analysis revealing the importance of energy metabolism to the development of deep roots in rice (*Oryza sativa* L.). *Frontiers in plant science*, *8*, 1314.

Lu, P. L., Chen, N. Z., An, R., Su, Z., Qi, B. S., Ren, F. *et al.* (2007). A novel drought-inducible gene, ATAF1, encodes a NAC family protein that negatively regulates the expression of stress-responsive genes in Arabidopsis. *Plant molecular biology*, 63(2), 289-305.

Luo, L., Xia, H. and Lu, B. R. (2019). Crop breeding for drought resistance. *Frontiers in plant science*, *10*, 314.

Mahajan, S. and Tuteja, N. (2005). Cold, salinity and drought stresses: an overview. *Archives of biochemistry and biophysics*, *444*(2), 139-158.

Mare, C., Mazzucotelli, E., Crosatti, C., Francia, E. and Cattivelli, L. (2004). Hv-WRKY38: a new transcription factor involved in cold-and drought-response in barley. *Plant molecular biology*, *55*(3), 399-416.

Martinez, J.P., Silva, H., Ledent, J.F. and Pinto, M. (2007), Effect of drought stress on the osmotic adjustment, cell wall elasticity and cell volume of six cultivars of common beans (*Phaseolus vulgaris* L.), *European Journal of Agronomy*, 26, 30-38.

Masle, J., Gilmore, S.R. and Farquhar, G.D. (2005). The ERECTA gene regulates plant transpiration efficiency in Arabidopsis. *Nature* 436, 866–870.

Rajagopal, V., Bai, K. K. and Kumar, N. (2005). Breeding for drought tolerance in coconut: Status and potentials. *Coconut Genetic Resources*, 282.

Rajagopal, V.., kasthuri Bai, K.V. and Naresh Kumar, S. (2000). Drought management in plantation crops. Pp 30-35. In: P.Rethinam, Khan H.H, Reddy V.M, Mandal P.K and Sudash K (eds). Plantation crops research and development in the new millennium. *Abstracts of PLACROSYM XV*, 10-13 December 2002, Mysore, India.

Ramesh, S. V., Hebbar, K. B., Rajesh, M. K., Sukumar, P. A., Raj, K. G. and Bobby, A. (2020). Transcriptome Analysis of *Cocos nucifera* L. Seedlings Having Contrasting Water-Use Efficiency (WUE) under Water-Deficit Stress: Molecular Insights and Genetic Markers for Drought Tolerance. *1st International Electronic Conference on Plant Science* Vol. (1), p. 15.

Ranganayakulu, G. S., Veeranagamallaiah, G. and Sudhakar, C. (2013). Effect of salt stress on osmolyte accumulation in two groundnut cultivars (*Arachis hypogaea* L.) with contrasting salt tolerance. *African Journal of plant science*, *7*(12), 586-592.

Reddy, A. S., Ali, G. S., Celesnik, H. and Day, I. S. (2011). Coping with stresses: roles of calcium and calcium/calmodulin-regulated gene expression. *Plant Cell*, 23, 2010–2032. doi: 10.1105/tpc.111.084988

Reguera, M., Peleg, Z. and Blumwald, E. (2012). Targeting metabolic pathways for genetic engineering abiotic stress-tolerance in crops. *Biochimica et Biophysica Acta (BBA)-Gene Regulatory Mechanisms*, *1819*(2), 186-194.

Sacala, E. (2009). Role of silicon in plant resistance to water stress. *Journal of Elementology*, 14(3), 619-630.

Safronov, O., Kreuzwieser, J., Haberer, G., Alyousif, M., Schulze, W. et al. (2017). Detecting early signs of heat and drought stress in *Phoenix dactylifera* (date palm). PLoS One 12: e0177883. doi: 10.1371/journal.pone.0177883

Sallam, A., Alqudah, A. M., Dawood, M. F., Baenziger, P. S. and Börner, A. (2019). Drought stress tolerance in wheat and barley: advances in physiology, breeding and genetics research. *International journal of molecular sciences*, 20(13), 3137.

Samarasinghe, C. R. K., Meegahakumbura, M. K., Dissanayaka, H. D. M. A. C. and Perera, L. (2018a). Performance of the second generation of Ambakelle special variety under varying rainfall and climatic conditions. *Proceedings of the 7th Annual Research symposium of the Young Scientist Forum of the National Science and Technology Commission* (NASTEC), Sri Lanka; pp: 122-125

Samarasinghe, C. R. K., Meegahakumbura, M. K., Dissanayaka, H. D. M. A. C., Kumarathunge, D. and Perera, L. (2018b). Variation in yield and yield components of different coconut cultivars in response to within year rainfall and temperature variation. *Scientia Horticulturae*, 238, 51-57.

Rajagopal, V., Bai, K. K. and Kumar, N. (2005). Breeding for drought tolerance in coconut: Status and potentials. *Coconut Genetic Resources*, 282.

Samarasinghe, C. R. K., Meegahakumbura, M. K., Kumarathunge, D. P., Dissanayaka, H. D. M. A. C., Weerasinghe, P. R. and Perera, L. (2021). Genotypic selection approach made successful advancement in developing drought tolerance in perennial tree crop coconut. *Scientia Horticulturae*, 287, 110220.

Ranasinghe C.S. (2013). Impact of climate change on coconut and identification of adaptation measures with special emphasis on reproductive development. In: Gunasena H.P.M., Gunathilake H.A.J., Everard J.M.D.T., Ranasinghe C.S. and Nainanayake N.P.A.D. (Eds), *Proceedings of the International Conference on Climate Change Impacts and Adaptations for Food and Environment Security* 'Sustaining Agriculture under Changing Climate', pp 101-114. Coconut Research Institute, Lunuwila, Sri Lanka; Ministry of Environment and Renewable Energy, Sri Lanka, World Agroforestry Centre, Regional Office, New Delhi, India.

Schachtman, D. P. and Goodger, J. Q. (2008). Chemical root to shoot signaling under drought. *Trends Plant Science*, 13, 281–287. doi: 10.1016/j.tplants.2008.04.003

Sharma, P., Jha, A. B., Dubey, R. S. and Pessarakli, M. (2012). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *Journal of botany*, Vol. 2012, Article ID 217037, doi:10.1155/2012/217037

Shen, Y. G., Zhang, W. K., He, S. J., Zhang, J. S., Liu, Q. and Chen, S (2003). An EREBP/AP2-type protein in *Triticum aestivum* was a DRE-binding transcription factor induced by cold, dehydration and ABA stress. *Theoretical and Applied Genetics*, *106*(5), 923-930.

Stocker, T. F., Qin, D., Plattner, G. K., Alexander, L. V., Allen, S. K. *et al.* (2013). Technical summary. In *Climate change* 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 33-115). Cambridge University Press.

Suresh, K., Nagamani, C., Ramachandrudu, K. and Mathur R.K. (2010). Gas-exchange characteristics, leaf water potential and chlorophyll *a* fluorescence in oil palm (*Elaeis guineensis* Jacq.) seedlings under water stress and recovery. *Photosynthetica*, 48:430-436

Szabados, L. and Savouré, A. (2010). Proline: a multifunctional amino acid. *Trends in Plant Science*, 15, 89–97. doi: 10.1016/j.tplants.2009.11.009

Taiz, L. and Zeiger, E. (2002). *Plant physiology*. 3rd edn. (Sinauer Associates: Sunderland, MA, USA).

Tiburcio, A. F., Altabella, T., Bitrián, M. and Alcázar, R. (2014). The roles of polyamines during the lifespan of plants: from development to stress. *Planta*, 240(1), 1-18.

Tondelli, A., Francia, E., Barabaschi, D., Aprile, A., Skinner, J. S. *et al.* (2006). Mapping regulatory genes as candidates for cold and drought stress tolerance in barley. *Theoretical and Applied Genetics*, 112(3), 445-454.

Turner, N. C. (1979). Drought resistance and adaptation to water deficits in crop plants. *Stress physiology in crop plants*, 343-372.

Ubara, U. E., Agho, C. A., Aye, A. I., Yakubu, M., Eke, C. R. and Asemota, O. (2017). Identification of drought tolerant progenies in oil palm (*Elaeis guineensis* Jacq.). *International Journal of Advanced Research in Biological Sciences*, *4*, 120-127.

Van Oosten, M. J., Costa, A., Punzo, P., Landi, S., Ruggiero, A., Batelli, G. and Grillo, S. (2016). Genetics of drought stress tolerance in crop plants. *Drought Stress Tolerance in Plants*, 2, 39-70.

Vandeleur, R. K., Sullivan, W., Athman, A., Jordans, C., Gilliham, M., Kaiser, B. N. and Tyerman, S. D. (2014). Rapid shoot-to-root signalling regulates root hydraulic conductance via aquaporins. *Plant, Cell & Environment*, 37(2), 520-538.

Vanderauwera, S., Vandenbroucke, K., Inzé, A., Van De Cotte, B., Mühlenbock, P., De Rycke, R. and Van Breusegem, F. (2012). AtWRKY15 perturbation abolishes the mitochondrial stress response that steers osmotic stress tolerance in Arabidopsis. *Proceedings of the National Academy of Sciences*, 109(49), 20113-20118.

Verma, V., Foulkes, M.J., Worland, A.J., Sylvester-Bradley, R., Caligari, P.D.S. and Snape, J.W. (2004). Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. *Euphytica*, 135, 255–263.

Voltas, J., Lopez-Corcoles, H. and Borras, G. (2005). Use of bi-plot analysis and factorial regression for the investigation of superior genotypes in multi-environment trials. *European Journal of Agronomy*, *22*(3), 309-324.

Wang, L., Lee, M., Ye, B. and Yue, G. H. (2020). Genes, pathways and networks responding to drought stress in oil palm roots. *Scientific reports*, 10(1), 1-13.

Waidyarathne K.P. and Perera S.A.C.N. (2020). 'Extreme weather events and crop yields: a case study with coconut', In: *Adapting to Climate Change: A Sri Lankan perspective*. Caldera, H.I.U. and Perera, S.A.C.N. (Eds.), Institute of Biology Sri Lanka, Colombo. pp.153-166

Wen, X. and Moriguchi, T. (2015). Role of polyamines in stress response in horticultural crops. In: *Abiotic stress biology in horticultural plants*. Kanayama, Y. and Kochetov, A. (eds) Springer, Japan, pp: 35–45.

Wickramaratne, M. R. T. (1987). Breeding coconuts for adaptation to drought. *Coconut Bulletin* (Sri Lanka).

Xu, Z. and Zhou, G. (2008). Responses of leaf stomatal density to water status and its relationship with photosynthesis in a grass. *Journal of experimental botany*, 59(12), 3317-3325.

Yaish, M.W. (2015). Proline accumulation is a general response to abiotic stress in the date palm tree (*Phoenix dactylifera* L.). *Genetics and Molecular Research* 14: 9943–9950

Yadollahi, A., Arzani, K., Ebadi, A., Wirthensohn, M. and Karimi, S. (2011). The response of different almond genotypes to moderate and severe water stress in order to screen for drought tolerance. *Scientia Horticulturae*, 129(3), 403-413.

Yang, H. M. and Wang, G. X. (2001). Leaf stomatal densities and distribution in Triticum aestivum under drought and CO_2 enrichment. *Chinese Journal of Plant Ecology*, 25(3), 312.

Zandalinas, S. I., Sales, C., Beltrán, J., Gómez-Cadenas, A. and Arbona, V. (2017). Activation of secondary metabolism in citrus plants is associated to sensitivity to combined drought and high temperatures. *Frontiers in Plant Science*. 7,1954. doi: 10.3389/fpls.2016.01954

Zhao, C., Liu, B., Piao, S., Wang, X., Lobell, D. B. *et al*. (2017). Temperature increase reduces global yields of major crops in four independent estimates. *Proceedings of the National Academy of* Sciences. U.S.A. 114, 9326–9331. doi: 10.1073/pnas.1701762114

Zheng, B. S., Yang, L., Zhang, W. P., Mao, C. Z., Wu, Y. R. *et al*. (2003). Mapping QTLs and candidate genes for rice root traits under different water-supply conditions and comparative analysis across three populations. *Theoretical and Applied Genetics*, *107*(8), 1505-1515.

Zhang., Y.P., Wang, Z.M., Wu, Y.C., and Zhang, X. (2006). Stomatal characteristics of different green organs in wheat under different irrigation regimes, *Acta Agronomica Sinica*, 32, 70-75.

Zlatev, Z. and Lidon, F. C. (2012). An overview on drought induced changes in plant growth, water relations and photosynthesis. *Emirates Journal of Food and Agriculture*, 24, 57–72. doi: 10.9755/ejfa.v24i1.10599