Eurasian Journal of Science Engineering and Technology

Review

A REVİEW: MORPHOLOGICAL, PHYSIOLOGICAL AND MOLECULAR RESPONSES OF SWEETPOTATO TO DROUGHT

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ABSTRACT

Sweetpotato is a drought resilient crop that is nutritionally important for the economic uplifting of humans. Sweetpotato has high beta-carotene contents and low glycaemic index that are important sources of vision improvement. It regulates blood sugar level and insulin resistance in diabetic patients, serves a homeostatic property, and maintains healthy blood pressure. The storage roots and the leaves have anti-cancer agents, purifies the liver, and reduce the risk of obesity, diabetes, heart disease, prevents constipation and malnourishment in children, and promotes fertility in women due to its high contents of fibre, irons, and phytochemicals. Sweet potato has high yielding capacity per square meter than other root and tuber crops and played a vital role in famine-relief. The agronomic and nutritional versatility of sweet potato makes it very important food security crop. However, abiotic stress such as drought stress mitigate against the biological and potential yield realization of the crop. This article reviews the effect of drought on the yield and yield traits of sweet potato and the morphological, physiological and the molecular response to the crop to drought effect. Drought impedes photosynthetic activities and disturb the metabolic processes of sweet potato plant causing imbalance in photosynthesis, respiration, translocation, stomatal movement, light absorption, and ion uptake. The economic storage root yield is reduced, increase the number of deformed storage root, reduction in the canopy cover, leaf area index, decrease in the stem length among others. These morphological and physiological effects of drought trigger the generation of reactive oxygen species which generate signal transduction as a mechanism to protect the plant. The detrimental effects of the ROS are buffered, minimised, and scavenged by enzymatic and non-enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), glutathione peroxidase (GPX), glutathione reductase (GR), glutathione S-transferases (GST), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), and dehydro-ascorbate reductase (DHAR) as a defence mechanism to keep the ROS under tight control. In resistant breeding, knowledge of these mechanisms is vital for building resistance and tolerance in sweet potato and other crops to improve yield and yield quality and ensure crop sustainability and food security. The levels of the antioxidants should serve as a guide for agronomists and breeders in selecting and recommending cultivars for drought endemic areas for yield sustainability and food security purposes. In selecting crossing parents for drought tolerance, cultivars with high antioxidants should be used to increase the chance of drought tolerance and eliminate the episode of crop failure due to drought stress.

Keywords: Sweet potato, Drought stress, Yield and yield traits, Antioxidants, ROS

1. INTRODUCTION

Sweet potato (Ipomoea batatas) is a nutritionally important crop belonging to the Convolvulaceae family. Sweet potato occurs cytologically as a diploid 2n=30, tetraploid 2n=60 and hexaploid 2n=90 (cultivated forms) with more than 100 known species. Its origin is in Mexico and Venezuela in the Central or South Americans continent. Sweet potato has become the 3rd largest cultivated root crop after potato and cassava globally based on its nutritional and agronomic resilience and food security properties [1, 2]. The crop was introduced into Europe around 1604, Asia during the Spanish colonial era (1521-1598) and Africa in the early 1600s by the Portuguese traders [3]. Today, sweet potato is cultivated in over 120 countries worldwide [2] with over 133 million tons of annual production. Continentally, Africa and Asia are the leading producers of sweet potato with 95% of production coming from developing countries, bringing sweet potato to the 5th and 6th important food crop respectively in developing countries and in the world.

Sweet potato is nutritionally an important source of beta-carotene, a precursor of vitamin A (vision protection), vitaminsB6, and C [4]. The storage roots are rich starch reservoirs with carbohydrates, dietary fibre, minerals, and vitamins for human consumption and animal feeding [5]. Sweet potato helps in the economic uplifting of humans and serving as a food security crop. It maintains healthy blood pressure, prevents constipation due to its high fibre content, has anti-cancer agents, reduces the risk

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Recieved: 15.10.2021 Accepted: 29.11.2021

of obesity, diabetes, heart disease, and overall mortality in humans [6] and serve as a liver purification crop. The high fibre, phytochemicals, and iron content in sweet potato promote fertility in women [7, 8]. Sweet potato contains a low glycaemic index scale, regulates blood sugar level and insulin resistance in diabetic patients, and thus serves a homeostatic property in human health. The glycaemic index of sweet potato reduces the risks of stroke by 24% [9]. Only small percentage of the global human population meet the daily dietary potassium requirements, thus the high amounts of potassium in sweet potato help reduce this by 2 %. Potassium also helps mob up excess reactive oxygen species (ROS) in the human system and thus improve their general well-being [10]. Sweet potato is used in the production of alcoholic beverages, flour for biscuits, and noodles [11].

Agronomically, sweet potato has high yield per square meter than any other tuber crop and its yield can be increased by 25% with a slight improvement in agronomic practices [12]. It has high promising dry matter and requires less capital with a short duration of cultivation and is the foremost root vegetable with the highest calories. In its storage roots, carbohydrate and ethanol quantities are triple that of corn though cultivar dependent [2]. Sweet potato is especially earmarked for its higher yield than other root and tuber crops and played a vital role in famine-relief over the years and has been re-evaluated as a health-promoting food [13, 14]. The agronomic and nutritional versatility of sweet potato captured global attention as a resilient food crop to fight food and nutrition insecurities which is expectant of bridging food shortages because it is a high-yielding energy crop per unit area [12].

However, abiotic stress such as drought stress over the years has been a major setback affecting sweet potato production. Drought in agricultural sense is the inadequacy of soil moisture for crop plants utilization for maximum yield output. In the meteorological sense, drought is the shortage of precipitation. In agricultural production, drought, or water deficiency is a major limiting factor that prevents crops from achieving their genetically determined potential maximum yield. Drought adversely affects crop growth and yield, and it has been identified as the primary constraint on rainfed crop production especially in rice, potato, soybean, wheat, maize, groundnut, and sweet potato [15, 16].

Globally, drought is a major abiotic stress factor prevalent in sweet potato production areas. About two-thirds of the world including Southern Africa, West- and North-Africa, central America, west and mid-west of North America, southern and eastern parts of South America, the Near East, and Central Asia; and three-quarters of Western Europe, India, Western Australia, and Northern China are prone to drought and desertification due to drought affecting 52 million humans annually [17, 18]. Drought negatively affects plant growth through various biochemical, morphological, and physiological processes. It inhibits photosynthetic activities and disturb the metabolic processes of the crops, resulting in imbalance in photosynthesis, respiration, translocation, stomatal movement, light absorption, and ion uptake [19, 20, 21]. It also causes reduction in mineral nutrient uptake and disorder in many various metabolic processes.

Although sweet potato is generally said to be a drought tolerant crop, selection of appropriate genotypes for drought conditions is still essential. Almost all plants have drought tolerance however the degree of the tolerance varies from one species to another and even within the same species due to i) different severity of drought, ii) duration of drought, iii) the organizational level of the plant, and iv) the developmental stage of the plant species [22, 23, 24]. Hence, understanding the morphological and physiological responses of sweet potato to drought can help to determine the traits to be used as selection criteria in breeding programs for yield improvement under drought conditions [25].

In the context of climate change, the frequency and the severity of drought is expected to rise most especially in Africa in the coming decades [18, 26]. Different drought response mechanisms in sweet potatoes such as drought escape (earliness), drought avoidance (root depth), and drought tolerance (maintaining assimilation under drought conditions) need to be identified and new sweet potato varieties should be improved using this information to combat the negative effect of drought to the sweet potato cultivation [18]. Therefore, this review assessed the effect of drought on the morphological, physiological, and molecular traits in sweet potato.

2. EFFECT OF DROUGHT ON STORAGE ROOT OF SWEET POTATO

Plants respond to soil moisture deficit conditions through the root zone by sensing the soil drought at the cellular level and through the whole root system architecture [27, 28]. The sensed changes in the soil moisture caused morphological and physiological changes aimed to absorb water and nutrients in the soil [29, 30]. The growth and architecture of roots are plastically a complex system. It is associated with several gene interaction and expression with an array of factors such as biological, and physical, features in the soil.

In crop production, root system serves as a good selection criterion for drought tolerant crop varieties under drought and is stated to positively correlate with yield under drought stress. In sweet potato, the drought tolerance ability is affected by root quantity, morphology, distribution, and physiology. Deep and dense rooting system increases the drought tolerance and root yield of sweet potato due to maximum uptake of mineral nutrients and water. In sweet potato, drought causes extensive structural changes in the root by increasing the root branching and density. In sweet potato as in other crops, drought stress causes small root system configuration and reduction in size of root system which is dependent on the magnitude of water shortage. The rate and availability of nitrogen (N) affect sweet potato root architecture development [28] especially at storage root formation stage

[31]. The adventitious roots of sweet potato differentiate into storage roots from the stems during the early growth period. This is affected by environmental factors such as soil moisture and N content [31].

[27, 28] revealed that the application of N fertilizer caused early development and differentiation of sweet potato roots. They further indicated that drought stress reduced root biomass ranging from 47.23% to 75.19%. Sweet potato root growth and differentiation is delayed in the presence of excess soil nitrogen [28]. This apparently causes great reduction in the storage root yield of sweet potato. The negative effect of drought on the root development of sweet potato can be alleviated by appropriate nitrogen (e.g., N75) treatment and thus enhance their tolerance levels while excess soil nitrogen (N150) significantly reduces root biomass and morphological parameters such as root volume, total root length, and root surface area that affect the number of differentiated marketable (diameter greater than 3.0mm) storage roots [32]. In fact, drought stress has greater negative impact on sweet potato root architecture. The difference in root architectural response of different sweet potato varieties to drought or water deficit present the bases for drought tolerance of the varieties.

For improvement of drought resistance of sweet potato varieties, deep root system is the identified target. Sweet potato varieties with deep and thick roots increase the drought stress tolerance of the plants due to positive correlation with xylem vessel area. The xylem vessel area helps the plants to meet the evaporative demand by conducting soil water to all parts of the of the plant [32, 33]. Drought stress in sweet potato crop is characterised by small root development. For optimum growth and development of crops, [34] reviewed that, large and vigorous root system and the continued production of new root hairs are required for maximum response to nutrients supply and increase dry matter accumulation within the shoot in drought conditions.

Drought stress has two main effects on sweet potato root development. It declines the rate of root meristematic activity and decreases the root elongation. This causes negative effect on mineral nutrient and water uptake and suberization of the root system as whole. Drought stress also adversely reduces the fresh and dry biomass production of sweet potato due to the inhibited uptake of nutrients and water by the small root architecture [35]. This situation disrupts the dry matter portioning and temporal biomass distribution, resulting in a decrease in crop yield. Thus, for drought resistance breeding, high dry weight under water stress conditions is a desirable characteristic for survivability of the plant under water stress conditions.

3. EFFECT OF DROUGHT ON THE STORAGE ROOT YIELD OF SWEET POTATO

Sweet potato breeders aim to obtain varieties with high yielding and nutritious storage root in their breeding program, especially under drought conditions. Under favourable condition, the yield potential of a variety is important to determine the variety's yielding ability under water stress. Drought stress critically affect sweet potato yield at three critical stages, seedling, vegetative development, and anthesis. These stages are highly affected by water stress, resulting in reduction in the yield. Sweet potato is susceptible to water stress at plant establishment stage. At this stage water limitation causes lignification of developing roots which impair the potential lateral thickening, a sign of proper photosynthate sink [36]. Different sweet potato cultivars have varied drought response and sensitivity.

In a field study to assess the response of sweet potato to prolonged drought, [37] stated that drought stress caused cracking on storage roots. This increased the accessibility of insects to the storage roots and caused a greater degree of root damage depending on the cultivar. Drought stress caused three different underground effect on the sweet potato, decreased storage root yield, unmodified storage root yield, and increased storage root yield. Indicating that, the effect of drought stress on the yield and yield components such as the number of storage root and single storage root weight of sweet potato is cultivar dependent. Based on this, sweet potato genotypes have been classified as susceptible, neutral, and resistant sweet potato genotypes based on their drought stress response strategy. [37] demonstrated that under water stress conditions, the marketable yield of sweet potato cultivar "Toka Toka Gold" decreased by 77% under drought conditions. They concluded that drought stress had a severe negative significant impact on storage root yield of all sweet potato cultivars. It has been noticed that severe water deficit caused drastic reduction in storage root yield and biomass of sweet potato. Thus, in paramount to say that sweet potato experiences huge yield losses under severe water stress conditions. This effect can be attributed to the decrease in assimilates translocation towards storage roots.

To select suitable cultivar under water deficient environment, drought tolerance index has been used as an important criterion to screen for drought tolerant varieties [38, 39]. Drought tolerance index is calculated based on the loss of yield under drought condition in correlation to water sufficient condition [40]. Drought stress aside causing drastic storage root yield reduction, it results in a decrease in stem length and leaf size of genotypes.

It is further stated that drought stress has severe effect on the yield of sweet potato, though sweet potato is said to be a drought tolerant crop. This was confirmed by [41] assessing the effect of drought on sweet potato using seven cultivars and six elite lines under three water treatments (100% water availability as control treatment; 60% water availability as mild stress; and 30% water as severe stress). Very great effect and significant genotypic differences were found for the storage root yield, leaf area index (LAI), stem length and stomatal conductance (gs). In terms of stem length, Purple Sunset and Blesbok sweet potato cultivars were found to strive much better under drought stress conditions. For total biomass and root yield, Bophelo, Resisto, and 199062 produced the highest yield at the mild stress with positive significant correlation with LAI, stem length, and stomatal conductance. With this, [41] suggested that the underground traits of sweet potato are directly influenced by the above-ground growth with LAI and stomatal conductance playing a very important role in achieving storage root yield. This can be useful indicators for screening drought tolerant sweet potatoes.

During the storage root development and establishment stage of sweet potato, drought stress is the most limiting factor. It causes reduction in the cells swelling pressure and inhibit cell growth, which reduce the plant root growth and differentiation [28, 34], sweet potato root biomass, total root length, root surface area, and root volume [27, 28]. The intensity and duration of the drought determine the extent of decrease in storage root yield which also depend on the number of lateral roots formed. It also reduces the plant establishment, inhibits the growth, causes damage to the photosynthetic apparatus which leads to decrease in net photosynthesis, and reduction in the mineral nutrient uptake [18]. Many scientific reports stated that sweet potato is particularly susceptible to drought at the root initiation and bulking stages which cause great effect to loss of yield, hence require adequate available soil moisture from planting till harvest [17, 18].

4. EFFECT OF DROUGHT STRESS ON THE LEAF CANOPY AND DENSITY

Drought stress is a very important factor for plant growth and affects both elongation and expansion growth. It is a major abiotic stress affecting agricultural production and productivity around the world, resulting in yield loss. Drought reduces soil water availability and increased evaporation. The cell size, intercellular volume and leaf area of the plants are reduced in drought stress conditions [42], especially in sweet potato. This amongst others is mostly due to the reduction in the soil moisture content which lead to lowering the leaves water content. The water loss in the leaves leads to a decrease in turgor pressure of guard cells, resulting in reduction in the stomatal pore sizes and the stomatal closure.

Drought stress causes reductions in the height and branching of cereals, legumes, root, and tuber crops including sweet potato. It also reduces LAI and biological yield of the plants. In soybean crops, water stress has been noticed to cause reduction of seed weight, total biomass, pods per plant, seeds per plant, seeds per pod, 100-grain weight, and ultimately caused a decline in soybean yield due to reduction in the LAI [39]. The reduced LAI reduced the absorption of photosynthetically active radiation by the plant which results in the yield reduction and the other parameters being affected. In sweet potato, drought stress at the early stages causes early profuse flowering and delayed canopy growth and development. Research by [37] on the effect of drought on sweet potato revealed that, the canopy growth and expansion of some varieties of sweet potato such as Beauregard, S1819, S1818, S1816 and S1787 were highly affected (reduced) throughout the growth period.

5. MORPHOLOGICAL, PHYSIOLOGICAL, AND MOLECULAR EFFECTS OF DROUGHT ON SWEET POTATO

Plants encounters water stress or drought due to no rainfall, high salt concentrations that cause reverse osmosis, low temperature, and transient loss of turgor at midday. At the molecular levels, plants during long-term water stress produce stress proteins, chaperones, up-regulate antioxidants, and accumulates compatible solutes [43, 44]. These mechanisms aim to increase root growth, and reduce leaf and stem growth, as they are the effects of drought stress on the growth of plants. Physiologically, plants during water stress produce and accumulate abscisic acid (ABA) and solutes in the leaves and roots that are transported to the guard cells. Also, reactive oxygen species (ROS) () are produced which inhibits the membrane protein pumps and increase influx of Ca^{2+}, causing efflux of anions and K^+ of the cells [42, 45, 46]. These actions cause conversion of malate to starch leading to reduction in the osmotic potential and turgor pressure, and reduction in the cell volume. The resultant effect of this physiological effect is closure of the stomata. In sweet potato, drought causes stomatal closure that affect the photochemical efficiency in the photosystem I and II and quantum generation this cause metabolic breakdown and reduction of photosynthesis [47, 48]. Drought also disrupts the cyclic and non-cyclic types of electron transport in the light phase. It is stated that, photosynthetic reduction in plants is due to qualitative and quantitative reduction or total stoppage of the photosynthetic pigment chlorophyll and carotenoids pigmentation production, photo-oxidation, and degradation of the pigments [49].

[49] found a significant reduction in the stomatal conductance of the sweet potato under drought conditions. Other researchers also reported that, stomatal conductance of plants is an indication of their drought tolerance ability. In breeding and agronomical evaluations for drought tolerant cultivars, stomatal conductance, relative water content, and photochemical efficiency of photosystem II are the important physiological traits to be considered.

It was stated that drought stress caused a reduction in photosynthesis rate ranging from 71.2% to 98.7%, in stomatal conductance between 34.4% and 47.1% and in chlorophyll content of *Triticum aestivum* [50, 51, 52]. In sweet potato and potato, the closure of the stomata prevents the capture of CO_2 by the carboxylation centre and increases the internal leaf temperature. This causes the degradation of the chlorophyl apparatus and lead to photosynthetic rate depletion and the inhibition of the plant growth. [53] revealed that drought is the main inhibitory factor for growth of plants. This effect among others is caused by the low absorption of CO_2 by the carboxylation centre due to stomata closure. The low or prevention of CO_2 capturing by the plant leaves results in reduced photosynthetic rate leading to the low growth and yield of the crops.

In a study to assess the effect of drought stress on chlorophyll content, proline content, stomatal conductance, photosynthesis and transpiration, and yield characteristics in chickpea cultivars (drought tolerant Bivaniej and ILC482 and drought sensitive Pirouz), [54] concluded that all physiological and biochemical parameters of the varieties were significantly affected. The concentration of chlorophyll, transpiration, stomatal conductance was drastically decreased while the proline content was substantially increased. Among other researchers, [54] stated that plants were especially affected at physiologlal level by drought occurred at vegetative or anthesis stages. Plants physiologically respond to drought by accumulation of proline. The rise in proline indicates impairment of photosynthesis due to stomatal (stomatal closure) and nonstomatal (impairments of metabolic processes) factors [55, 56, 57]. The photosynthetic sensitivity of a plant to drought is determined by its mesophyll resistance under drought conditions.

Morphologically, [58] stated that the above ground biomass and morphology of potato cultivars were greatly affected by drought stress treatments and the impact escalated when combined drought and heat stress. This resulted in less abundant leaves, foliage and shorter stems of the stress treatment as compared to their controls varieties. [58] noticed a drastic reduction in the photosynthetic rates and leaf relative water content of all cultivars (Agria, Desiree, Russet Burbank, and Unica) being either drought resistant or sensitive under drought conditions. Furthermore, a significant increase in proline and MDA was observed in the drought treated cultivars in potato [58, 59]. The results of various research on the effect of drought on crops shows that drought affects at morphological, physiological, and biochemical level.

Plants have evolved several survival mechanisms at morphological, physiological, and molecular levels to withstand the various environmental impediments they encounter due to their sessile nature (Figure 1). Some plants adapt to the effect of drought by developing deep and defused root systems to absorb soil moisture as much as possible, small leaves to prevent much water loss through transpiration. Crops including sweet potato are photosynthetically sensitive to drought and thus exhibit diffusive stomatal resistance, leaf water retention, osmotic adjustment, rolling of the leaves, regulation of the closing and opening of stomata and its position, and leaf senescence. The limited water in the soil serves as a prime signal perception to detect the available water and act as a signal for ABA (abscisic acid) biosynthesis that regulates stomata closure to prevent the water loss [60, 61]. The consequential impact of this response is reduction in the CO_2 absorption and assimilation in the dark reaction of the photosynthesis. It also affects the photons' energy levels in the light reaction in the photosystem II. This restricts the H_2O oxidation in the chloroplastic organelle and lowers the quantum yield (Fv/Fm).

At the molecular or cellular levels, plants such as sweet potato adjust their osmotic pressure by synthesizing and accumulating carbohydrates, proline, sugar alcohols, polyamine and glycine betaine that serve as osmoprotectants [63, 64, 65]. For instance, proline, a nontoxic and non-enzymatic small neutral aromatic amino acid molecule accumulated during the episode of drought stress, is synthesized by sweet potato in the cells through the glutamate and/or ornithine pathway to play a key role in osmotic adjustment. More so, [10, 66, 67, 68, 69] among other researchers stated that proline among other non-enzymatic compounds such as ascorbic acid, carotenoids, glutathione, and tocopherol are synthesized to reduce the negative effect of reactive oxygen species (ROS) and keep them in balance during drought stress. The activities of enzymatic antioxidants including ascorbate peroxidase, glutathione transferase, catalase, and superoxide dismutase are also increased to scavenage the accumulated ROS under drought [70, 71]. This detoxification of the ROS by the enzymatic and nonenzymatic antioxidant defence systems decreases the harmful effect of ROS. The ROS are mainly generated by the chloroplasts and mitochondria. Plants have developed a versatile and cooperative antioxidant system and defence mechanism that modulates intracellular ROS content and sets the redox status of the cell in balance and under tight control [72, 73, 74, 75]. A slight increase in ROS production under drought conditions initiates a signal transduction to trigger plant defence mechanism which is linked to abscisic acid (ABA) and Ca^{2+} fluxes in the cell resulting in acclimatization to the environment [60, 66, 72, 74]. The higher accumulation of ROS under drought conditions damages the cells, even causes cell death due to protein denaturation, lipid peroxidation, and DNA degradation. Sweet potato and other plants also produce aquaporins (AQP), drought-responsive genes (DRG), late embryogenesis abundant proteins (LEAP), transcription factors (TF), heat shock proteins (HSP), dehydrins, proline (pro), glycine betaine (GB), and cyclic adenosine 50-diphosphate ribose (cADPR), inositol-1, 4, 5-triphosphate (IP3), NO and soluble sugar (SS) [39, 59] in response to drought stress aiming for the crop to survive. These results in morphological and physiological changes through signal transduction directly or indirectly [76] by the action of calcium-dependent protein kinases (CDPKs), mitogen-activated protein kinases (MAPKs), HD-zip/bZIP, AP2/ERF, NAC, MYB, and WRKY [20] known as regulatory gene products that enables the successful survival of the plants in the environment.

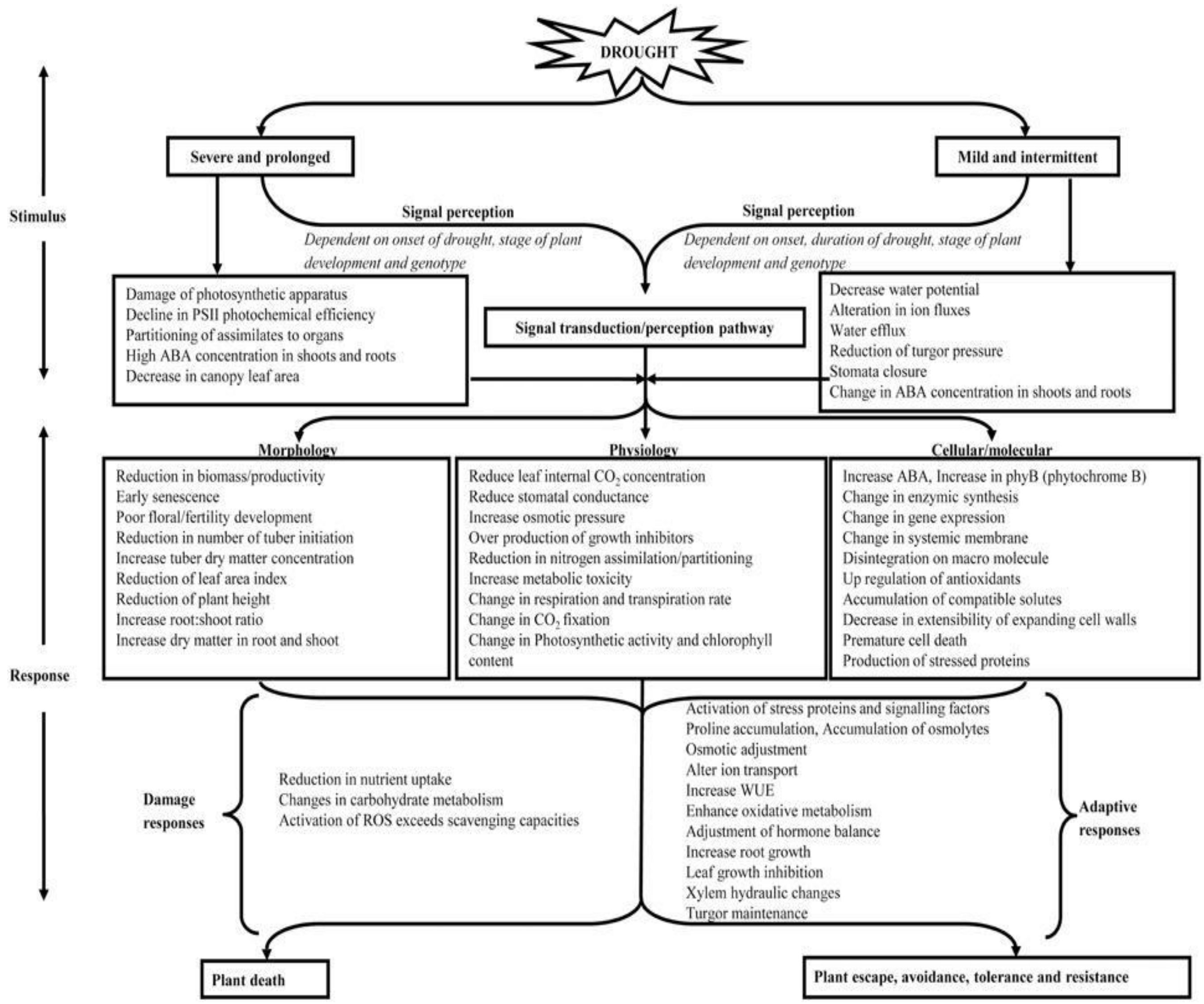

Figure 1: Morphological, physiological, and molecular response of plants to drought stress conditions; obtained from [62]

The enzymatic antioxidants defence system includes superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6), guaiacol peroxidase (POX, EC 1.11.1.7), glutathione peroxidase (GPX, EC 1.11.1.9), glutathione reductase (GR, EC 1.8.1.7), glutathione S-transferases (GST, EC 2.5.1.18), ascorbate peroxidase (APX, EC 1.11.1.11), monodehydroascorbate reductase (MDHAR, EC 1.6.5.4), and dehydroascorbate reductase (DHAR, EC 1.8.5.1) (Rajput et al., 2021). During stress episodes, the antioxidant enzymes effectively buffer, minimize and scavenge the ROS. The superoxide (O_2^-) radical is catalysed by SOD to form molecular oxygen (O_2) and hydrogen peroxide (H_2O_2), a less reactive ROS (Figure 2). The each of CAT, APX, POX, and GPX detoxifies the H_2O_2 to water [70, 77, 78]. The levels of these antioxidants in sweet potato are highly enhanced under drought conditions that makes the sweet potato moderate or highly resistant to drought.

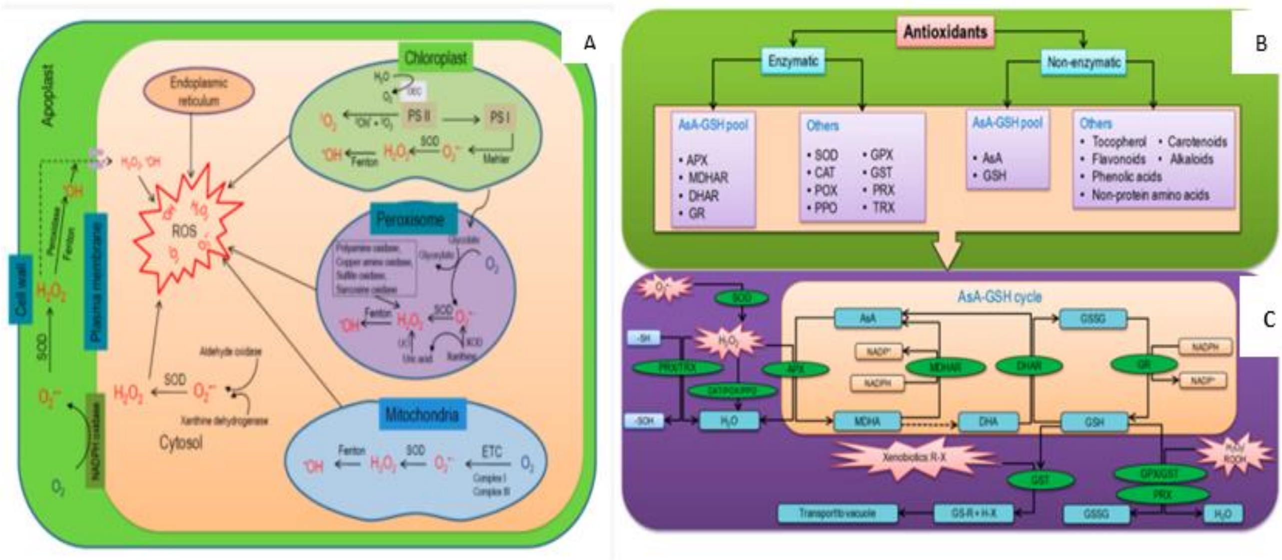

Figure 2: Localization and processes for the generation (A), Enzymatic (B) and non-enzymatic (C) antioxidants and their scavenging activity of ROS; (modified from [70]). Ascorbate peroxidase (APX), Ascorbate (AsA), Catalase (CAT), Dehydro-ascorbate (DHA), , Dehydro-ascorbate reductase (DHAR), Glutathione peroxidase (GPX), glutathione reductase (GR), reduced glutathione (GSH), oxidized glutathione (GSSG), glutathione S-transferase (GST), hydrogen peroxide (H_2O_2) monodehydroascorbate (MDHA), monodehydroascorbate reductase (MDHAR), nicotinamide adenine dinucleotide phosphate (NADPH), superoxide anion ($O_2•^-$), peroxidases (POX), peroxiredoxins (PRX), R, aliphatic, aromatic, or heterocyclic group; ROOH, hydroperoxides;, thiolate (–SH), superoxide dismutase (SOD), sulfenic acid (–SOH), thioredoxin (TRX), sulfate (X), nitrite, or halide group. hydroxyl radical (•OH), urate oxidase (UO), xanthine oxidase (XOD), electron transport chain (ETC), PS photosystem I (PSI), photosystem II (PSII), nicotinamide adenine dinucleotide phosphate (NADPH)

Sweet potato also responds to drought by alterations in gene expressions. These genes are classified into functional and regulatory genes [76]. Functional genes directly resist environmental stress, whiles the regulatory genes indirectly respond to stress through the actions of protein kinase genes, protein phosphatase genes, phospholipid metabolism-related genes, and stress-related transcription factor genes assisting in signal transduction and regulation of gene expression [27, 28, 79]. The functional genes include aquaporin genes, osmoregulatory factors synthase genes, and protective proteins genes. These proteins act by participating in plant stress signal transduction pathways or by regulating the expression and activity of other effector molecules.

6. CONCLUSION AND FUTURE PERSPECTİVES

The sessile nature of plants causes them to be highly exposed to environmental effects such as drought stress. Drought stress is the major abiotic stress affecting about two-third of global cultivation land area. In sweet potato cultivation, drought negatively affects the agronomic and economic output due to several morphological, physiological, and biochemical changes. It causes reduction in root yield, branching, canopy cover, leaf area index, stem height and length, stomatal closure, leaf sizes, and photosynthesis in sweet potato. Drought triggers oxidative stress that generate reactive oxygen species (ROS) being harmful to the plants. To survive the effect of these ROS and other negative pressures of drought, sweet potatoes synthesize and accumulate some molecules such as carbohydrates, proline, sugar alcohols, polyamine, and glycine betaine to adjust their osmotic pressure and serve as osmoprotectants. The activities and synthesis other enzymatic and non-enzymatic antioxidant compounds such as ascorbate peroxidase, glutathione transferase, catalase, superoxide dismutase, ascorbic acid, carotenoids, glutathione, and tocopherolare increased during drought stress to scavenge and keep the ROS under tight control. The drought resistant and tolerant nature of sweet potato is mainly due to the high antioxidant levels which effectively keep the generation and effects of the ROS under check. In sweet potato breeding, the levels of the antioxidants in a genotype may serve as a marker for breeders to select drought resistant/tolerant individuals for drought prone areas for yield sustainability and food security purposes. For plant breeders, to increase the drought tolerant levels of cultivar, the genotypes with high antioxidants levels might be used as crossing parents. Such genotypes may have the possibility to increase drought resistance and tolerance levels of sweet potatoes to eliminate the high yield reductions under severe drought conditions.

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