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Drought Responses on Physiological Attributes of *Zea mays* in Relation to Nitrogen and Source-Sink Relationships

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Abstract

Maize is the staple food crop and essential for world food security. Maize plants' water requirement is high for proper growth and development at vegetative stage and grain formation at reproductive stage. Drought is the major abiotic stress that affects almost all the growth stages of maize crop and it has a strong impact on all the physiological process of maize plants. Similarly, N metabolism is of central importance during drought stress. Nitrogen (N) is one of the macronutrients; it is a major requirement for crop growth and grain yield of maize. Therefore, nitrogen and water separately or in combination are the two most critical factors in maize production. Drought modifies source-sink relations and weakens the source and sink strength, which disturbs plant's growth, plant's adaptation to stress, and consequently affects crop productivity.

Keywords: maize, drought, nitrogen, source-sink relationship

1. Introduction

Plants are nonmotile, and they protect themselves from various biotic and abiotic stresses through structural and metabolic changes like altering leaf orientation, transpirational cooling, or adjustment of membrane lipid compositions [1]. Maize is a staple food crop that grows under optimal environmental conditions and throughout their life span is often exposed to various abiotic stresses [2] like either combined stresses like drought and heat, drought and salinity, drought and low-N stresses, or singly drought. In combined stress, plants show a wide range of responses that brings changes in growth and morphology, and the plants' ability to withstand these stresses greatly varies from species to species [3]. However, drought along with high frequencies, longer durations, and large ranges occur almost yearly across the globe, even in wet and humid regions [4, 5]. Water deficit is the most detrimental environmental stress that adversely affects the maize productivity. The effect of drought is manifested at cellular, physiological biochemical, metabolic, proteins, and gene levels. Water is an essential component for plants; it maintains cell turgidity and keeps the structure intact (by keeping the pressure inside cells high) so that they are fully expanded (i.e., turgid). In wilted plants, when turgor pressure approaches to zero, the cell membranes collapses, damage and becomes

leaky, the key enzymes proteins denatured and their structure altered. To ensure high survival rates and production under drought conditions, maize plants rely on several strategies, including drought avoidance, escape, and tolerance [6–8]. Nitrogen plays a major role in plant nutrition and also combats with several abiotic stresses like salinity, drought, heat stress, etc. [9–13], but this mineral element is most often deficient in arable soils. Though the requirement of nitrogen is greatest among all mineral elements, its deficiency limits the plant's growth and development [14–16]. There is a tight regulation of carbon and nitrogen metabolism in photosynthesis and N uptake [14, 17–19]. In a review, Aziz Khan et al. [20] outline the nitrogen (N) responses in crop production and to ameliorate abiotic stresses for better crop production. Further they emphasize that nitrate and ammonium nitrogen are essential nutrients for successful crop production [21]. Moreover, shortage and N excess affect assimilate partitioning between vegetative and reproductive organs [22]. Mineral nutrition influences the physiological response of plants to water stress [23]. While Waraich et al. [24] discussed the role of macro- and micronutrients to decrease the adverse effect of drought in crop plants. Therefore, water and nitrogen affects the crop growth, development, and production either separately or in combination. Humbert et al. [25] observed the physio-molecular changes in response to water and nitrogen and finally concluded that the responses of plants to the combination of these two stresses may cause additional effect that was different from the individual effects, and hence, cannot be inferred from the end results obtained from different stresses applied individually. Drought affects maize grain yield to some degree at almost all growth stages, but the crop is the most susceptible during flowering [26, 27]. At the reproductive phase, N availability affects assimilate partitioning between vegetative and reproductive organs and N metabolism in young ear shoots [28]. Therefore, the timing and intensity of stress determine the extent to limits yield either due to source or sink limitations.

2. Maize response under drought stress

2.1 Effect of drought on morpho-physiological parameters

The water deficit conditions Boyer [29] showed the decrease in leaf area attributed to decrease rate leaf initiation and expansion or increase leaf senescence or shedding. Though the number of leaves per plant did not reduce in early vegetative maize growth in severe nonlethal water deficit conditions, Abrecht and Carberry [30] also demonstrated the gradual reduction in plant height in maize with increasing water deficit. Further supported by Moss and Downey [31] showed the significant reduction in plant height with increase in water stress. While, dry matter yield accumulation depends on the leaf area and leaf dry weight because leaf area is the major assimilatory surface for most crop any factor that affects the leaf area also affects dry matter [32]. In similar way, the short term responses of corn to a pre-anthesis water deficit, delayed leaf tip emergence and reduction in leaf area. While long-term consequences of water deficits have reduced final sizes of the leaves and internodes [33]. Drought stress significantly repressed relative leaf water content, leaf size, and photosynthesis-related parameters in maize seedling [34]. Drought affects various morpho-physiological processes including plant biomass, root length, shoot length, photosynthesis, water use efficiency (WUE) and leaf water content [35, 36]. At early growth stage 50 maize genotypes for drought tolerance was assessed. Principal component analysis revealed important morpho-physiological traits (FSL, FRL, DSW, DRW, RWC, and TDM) plays key role in drought tolerance. Later, Ali et al. [37] identified various

morpho-physiological traits that have higher heritability, genetic advancement, and correlation and which contribute for improved maize grain yield. A set of 24 genotypes bred at different centers in India as well as in CIMMYT showing variability for drought tolerance were selected for molecular and morpho-physiological characterization. Phenotyping of inbred by morpho-physiological traits revealed that there was a positive relationship among root length, chlorophyll content, relative water content while anthesis-silking interval (ASI) have negative relationship with all these traits [38]. Water stress occurring during vegetative and tasseling stages reduced plant height, as well as leaf area development [39].

2.2 Photosynthesis under drought stress

In a study Anjum et al. [40] showed that drought stress in maize led to considerable decline in net photosynthesis (33.22%), transpiration rate (37.84%), stomatal conductance (25.54%), water use efficiency (50.87%), intrinsic water use efficiency (11.58%) and intercellular CO₂ (5.86%) as compared to well water (WW) control. The main cause of reduced photosynthesis under drought stress is due to decreases in both assimilation (A) and internal CO₂ concentration, that finally inhibits total photosynthetic metabolism [41]. Besides there are other several non-stomatal effects during drought which are responsible for stomatal closure. These include photophosphorylation, ribulose-1,5-bisphosphate (RuBP) regeneration [42, 43], rubisco activity, and ATP synthesis [44, 45]. The response of growth and some physiological characteristics were compared in two maize (*Zea mays* L.) cultivars, one drought-resistant (PNR473) and the other drought-sensitive (SR52). Drought-resistant (PNR473) had a higher growth rate and deeper rooting than the drought-sensitive cultivar under water stress treatment. But the drought-resistant cultivar had a higher transpiration rate and lower diffusive resistance during the onset of water stress, and higher relative water content and levels of abscisic acid and proline throughout the period of water stress [46]. While, Jama and Ottaman [47] reported delay in the irrigation during early growth stages of a corn plant (including anthesis) decreased plant dry weight. The responses of maize (*Zea mays* L.) from the third leaf stage to maturity for different soil water levels (well watered, moderately stressed, and severely stressed) indicated that drought stress relied on drought intensity and duration, with more severe drought stress creating more serious effects on maize. It is well known that leaf water status always interacts with stomatal conductance through plant hormone abscisic acid, increased production of ABA would help the plants to survive under drought stress [48]. According to Bray [49], dry soil induced and increased ABA concentrations in the roots to maintain root growth, increase root hydraulic conductivity, through these process shoot water uptake increases thus drought induced root-to-leaf signaling. Also direct correlation between the xylem ABA content and stomatal conductance has been demonstrated [50]. The role of other phytohormones like Brassinosteroid is for plant growth, as they are involved in main plant antioxidant processes encompassing the regulation and enhancement of plant tolerance against different environmental stresses [51].

2.3 Metabolic changes under drought stress

To maintain cell turgor and to lower the osmotic potential plants accumulate different types of organic and inorganic solutes in the cytosol [52]. Primary metabolites, such as sugars and amino acids, have also been reported to accumulate during water stress [53]. Two maize (*Zea mays* L.) cultivars, 704 and 301, accumulate soluble sugars, starch, and proline content in shoots and roots in response to drought stress. This suggests role of sugars in osmotic adjustment whereas, proline

minimized the damage caused by dehydration [54]. The high salt concentration of soil causes a water deficit in crops [55], exogenous application of SA mitigated the adverse effects of salinity on maize plants by osmoregulation which is possibly mediated by increased production of sugar as well as proline [9]. Besides, the ROS (including oxygen ions, free radicals, and peroxidases) forms major by-product of normal metabolism and in abiotic stress conditions. However, during environmental stress such as drought, ROS levels increase dramatically resulting in oxidative damage to proteins, DNA, and lipids [56]. Among six maize genotypes (A638, B73, Grace-E5, Lo964, Lo1016, and Va35) studied, the drought-sensitive maize genotypes accumulated significantly more reactive oxygen species (ROS) and reactive nitrogen species (RNS). In addition, they showed rapid increases in enzyme activities involved in ROS and RNS metabolism compared to tolerant genotypes. However, antioxidant enzyme activities were higher of tolerant genotypes than in the sensitive genotypes [57]. In a study, the protective role of biochar (date and wheat) in combination with Me and P against water stress in two maize varieties were examined. The maize variety Mallika performed better and was more drought-tolerant with its increased osmolyte production and an efficient antioxidant defense system that eliminated ROS. Hence, ROS elimination further alleviated the damage to the photosynthesis system induced by water stress. On other hand, Azam variety was more sensitivity to drought [58]. Plants tolerate the water deficit conditions by adjusting their physiological and biochemical approaches. Maize leaves subjected to water deficit rigorously down-regulated NR activity and photosynthesis, also a correlation between maximal extractable foliar nitrate reductase (NR) activity and the rate of CO₂ assimilation was observed [59]. The assimilatory sulfate reduction in roots and leaves of the staple crop maize demonstrated the organ specific impact of drought upon sulfate metabolism. Under drought stress, the allocation of sulfate was significantly shifted to the roots allowed for significant increase of thiols derived from sulfate assimilation in roots. This enabled roots to produce biomass, while leaf growth was stopped. Therefore, sulfur metabolism related alterations at the transcriptional, metabolic and enzyme activity level are consistent with a promotion of root growth to search for water at the expense of leaf growth. The results provide evidence for the importance of antagonistic regulation of sulfur metabolism in leaves and roots to enable successful drought stress response at the whole plant level [60]. During the silking and blister stages moderate stress significantly change the relative water content (RWC) and also change the relative conductivity (RC) ($P < 0.05$) of the leaves; however, severe stress significantly decrease ($P < 0.01$) the leaf RWC and increase ($P < 0.01$) membrane permeability (leaf relative conductivity). Furthermore, under severe drought stress antioxidant enzyme activities declined ($P < 0.01$) in later stages, namely for superoxide dismutase (SOD) the tasseling and blister stages, for peroxidase (POD) the milk stage, and for catalase (CAT) during the tasseling, blister, and milk stages. Meanwhile, membrane lipid peroxidation (measured as malondialdehyde content) significantly increased ($P < 0.01$) in all stages [61].

2.4 Drought-tolerance mechanism

Phytohormones like, ABA, IAA, CKs, GA, SA, BRs, JA, ethylene, and triazole are directly or indirectly involved in plant responses to a wide range of stresses. They play critical roles in regulating plant growth and development, and stress tolerance to promote survival and acclimatize to varying environments [10]. Abscisic acid accumulates in response to drought stress and displays its well characterized effect on stomatal closure and promotes root growth in maize

seedlings at low water potential [62]. Another possible role of endogenous ABA is to modulate glycinebetaine (GB) metabolism in maize particularly at the seedling stage in drought stress. The leaves of two maize cultivars, Zhengdan 958 (ZD958; drought-tolerant), and Jundan 20 (JD20; drought-sensitive) after exposure to integrated root-zone drought stress (IR-DS) shows increased betaine aldehyde dehydrogenase (BADH) activity and choline content the key enzyme and initial substrate, in GB biosynthesis. The peak of ABA content reached earlier than that of GB in the leaves of drought-stressed maize plants. Therefore, endogenous ABA seemed to be involved in modulating GB accumulation by enhancing BADH activity, thereby improving leaf RWC and enhancing shoot DM in drought-stressed maize plants, especially in the drought-sensitive cultivar (JD20) [63]. Similarly, Si application (400 mg L^{-1}) had positive effect on photosynthesis, water use efficiency, stomatal conductance, chlorophyll contents, Rubisco activity, and Rubisco activation state at 20 days of drought. Possibly Si may have direct or indirect role in maintenance of more active Rubisco enzyme and Rubisco activase and more stable proteins for carbon assimilation under stress conditions [64]. Maize was subjected to drought at the start of tasseling (6 days) followed by foliar spray of BR (0.1 mg l). Exogenous application of BR remarkably improved the gas exchange attributes, plant height, leaf area, cobs per plant, seedling dry weight both under drought and well-watered conditions [40]. The formation of cortical aerenchyma (RCA) in maize roots is associated with drought tolerance. RCA reduces root respiration by converting living cortical tissue to air volume. It has been hypothesized that RCA or large cortical cell size (CCS) increases drought tolerance by reducing root metabolic costs, permitting greater root growth and water acquisition from drying soil [65, 66]. Maize growth and yield responses were related to ROS production, osmolyte accumulation, and activation of anti-oxidative defense system under drought conditions. The regulation of these physio-biochemical responses of plants can be used as markers for drought stress tolerance [67]. Drought-tolerance mechanism is difficult in maize this may be due to complex genetic makeup. Metabolic traits provides better substitute to unravel the genetic mechanism of drought tolerance. The physiological status of plants can be monitored by metabolites that interconnect the visible phenotype with core genome, so that gene or gene loci could be identified and selected which are less affected by environmental factors [68–71]. However, the negative effects of abiotic stresses can be minimized by adopting the genetic approaches or by inducing resistance through transgenic approaches [3]. The importance of QTLs-based approach is associated to improve the maize crop performance under various abiotic stresses and in achieving increase in maize yield. Besides, QTLs with large effect and linked with stress-tolerance traits provides several modes to investigate the various components affecting source sink relationships of maize plants under abiotic stress [72]. Chen et al. [73] compares the role of drought resistance and drought recovery in drought adaptation in maize seedlings. After recovery most of the physiological parameters (like leaf water content, water potential, osmotic potential, gas exchange parameters, chlorophyll content, Fv/Fm and nitrogen content, and increased H_2O_2 accumulation and lipid peroxidation) rapidly return to normal level. Correlation analysis shows that physiological bases of drought adaptability closely related to drought recovery ($r = 0.332$) and not to drought resistance and ($r = 0.714^{**}$) both are definitely different. Under drought stress higher chlorophyll content ($r = 0.874^{***}$) and Fv/Fm ($r = 0.626^*$) contributes to drought recovery. In addition, leaf water potential, chlorophyll content, and Fv/Fm could be used as efficient reference indicators in the selection of drought-adaptive genotypes.

3. Nutrient status in drought

The role of N metabolism regulation in maize drought tolerance was comprehensively studied [74]. Drought have strong impact on all the physiological process of plants and N metabolism is of central importance during drought stress because to survive drought and to maintain growth plants adaptive strategies includes such as improved nutrient uptake and transport, photosynthesis regulation, and to produced solutes and proteins that contains N compounds such as amino acids, amides and betaines. While Kant et al. [75] reported that relationship between drought and N nutrition consists of a complex network of regulatory interactions that affects almost all physiological processes in plants. Nitrogen (N) is one of the macronutrients, its major requirement for crop growth and grain yield of maize, whereas maize water requirement is highest in the reproductive stage [76]. Therefore, nitrogen and water separately or in combination are two are most critical factors in maize production. According to Saud et al. [77] the use of nutritional soil with a proper nitrogen rate remained effective in ameliorating the adverse influence of drought stress. However, a contrast study showed low field capacity irrigation and low nitrogen fertilizer rates application improves water use efficiency and nitrogen recovery efficiency (NRE) simultaneously [78]. Water and nutrient availability influence root system architecture and development [79, 80]. During vegetative stages of corn, under moderate drought stress rooting depth typically increases, allowing more efficient uptake of water and nutrients from deeper within the soil profile [81]. The increase in plant height related with increasing N fertilizer application under drought stress [82, 83]. Andrade [84] reported that N deprivation reduced leaf area index, leaf area duration, radiation interception, and radiation use efficiency. Improved tolerance to various abiotic stresses alternative breeding strategies are adopted, one of them is to select and inbreed maize plants under high population density to improved tolerance for low-N and drought [85]. Although under dense plant population maize prone to lodging due to increase in plant height and reduced culm diameters makes the stem weaker [86]. The mechanism underlying tolerance to high population density and low-N diverse tropical germplasm were grown under optimal, high plant population density and low-N. The association between ASI and grain yield, delayed senescence (expressed as chlorophyll concentration or number of green leaves above the ear) and ear/tassel weight ratio was observed in low-N. Also, grain yield negatively correlated with abortion rate. While under optimal and high population density, a positive association was reported between ovule number and abortion rate, suggesting a source limitation for C products [87]. In the same way selection of hybrid progenies for mid-season drought tolerance was due to improvements in morpho-physiological secondary traits such as reduced anthesis-silking interval, increased ears per plant, delayed senescence and relatively high leaf chlorophyll during late grain filling [88]. Drought at one of the sensitive growth stages, caused up to 40% grain yield losses. However, prolonged water stress during tasseling and ear formation stages leads to yield loss of 66–93% greater magnitude [39].

3.1 Effect of nitrogen at vegetative stage under drought stress

Variation in N supply affects both growth and development of maize plants [89]. Uhart and Andrade [90] reported that N deprivation reduced leaf area index, leaf area duration, radiation interception, and radiation use efficiency. However, nitrogen fertilizer changes canopy size which has an effect on the radiation use efficiency (RUE) of the crop thus affect plant growth and productivity [91]. According to Bänziger et al. [92], about 50% of all N in the leaf is directly involved

in photosynthesis as either enzymes or chlorophyll. Thus, if the N supply is insufficient, photosynthesis is decreased by reducing the leaf area and photosynthesis rate as well as accelerating leaf senescence. Longer duration of green leaf area is one of the most important ways to improve maize yields. Bertin and Gallais [93] found that leaf senescence was highly correlated with a nitrogen nutrition index, mainly at low levels of nitrogen input. Using a comparative proteomic analysis of *Zea mays*, Prinsi et al. [94] found that the nitrogen status of plants may affect the post-translational modification of phosphoenolpyruvate carboxylase (PEPCase) that plays a role in phosphorylation in leaves. Several studies have reported that drought stress decreases N uptake and assimilation in plants [24, 95, 96]. Maize growth and many physiological processes associated with it are enhanced by N supply [97]. Nitrogen efficiency is a complex trait, to identify for N-efficiency 16 tropical maize cultivars, studied for leaf senescence under N deficiency (short-term nutrient solution experiment). Leaf chlorophyll contents and photosynthesis rates were used as measures for leaf senescence. The results show that the photosynthetic capacity of senescing leaves correlated with the N efficiency of the cultivars, rather than leaf chlorophyll content [98]. The effect of nitrogen on maize leaves at three level of drought stress (normal, mild, and severe stress) was examined, The NO content and nitrate reductase (NR) activity of maize leaves were significantly reduced under drought stress, while moderate nitrogen supply promoted the accumulation of NO and an increase in the Nitrate Reductase activity. Also, abscisic acid content increased and was positively correlated with the nitrogen concentration under drought stress. Together, these results indicate that moderate nitrogen supply increases plant resistance to drought stress, while high or low nitrogen concentrations increase the sensitivity of maize to drought stress [99]. Maize (*Zea mays* L.) crop was subjected to different periods of deficit irrigation and N rates in the field. The results indicated that optimum use of both water supply and N application will maximize the maize production. Deficit irrigation during early vegetative growth modestly reduced LAI, plant height, CGR, N uptake and total biomass production as compared to reproductive stage [100] also N uptake decreased with greater water and N deficits. Two maize hybrids differencing resistance to drought were fertilized with two different forms of nitrogen fertilizers, $\text{Ca}(\text{NO}_3)_2$ and $(\text{NH}_4)_2 \text{SO}_4$, and after fourth leaf stage they were exposed to drought stress. The results shows that two maize hybrids different in adaptability to two nitrogen treatment. NH_4 treated plants maintain the high turgor by improved osmotic adjustment under drought stress. Whereas, chlorophyll a, b values significantly higher in NH_4 treated plants compared to NH_3 treated plants in which chlorophyll content decreased throughout the drought stress [23]. Similar work Zhang et al. [101] indicated increased NO_3 nutrition played a favored anti-oxidative metabolic role, as compared with NH_4 nutrition, in the plants thereby increasing tolerance to drought stress. Further, two maize genotypes were accessed for effect of nitrogen rates and water stress. Under water stress, Shaadan 9 accumulates higher dry matter, grain yield, anti-oxidative enzyme activity, and lower MDA content than Shaadan 911. However, the addition of nitrogen increased dry matter and grain yield as well as activities of SOD, POD, and CAT to different levels and significantly decreased MDA content under water stress, higher for Shaandan 911 than for Shaandan 9. Thus, drought-sensitive variety showed its full potential after adding nitrogen in water stress condition [102]. The dry matter accumulation and nitrogen uptake were compared in sorghum and maize. Drought reduced nitrogen availability in soil for both the crops, although sensitivity of maize crop to nitrogen is more. Directly, maize crop shows less accumulation of dry matter in water deficit condition and indirectly because of nitrogen nutrition [103]. Twenty maize inbred lines were phenotype in response to two levels of water and nitrogen supply (control and stress) and combined nitrogen and water

deficit. Image analyses study provide the opportunity for new traits, identified several color-related traits and kinetic chlorophyll fluorescence (PSII). For biomass production ability in maize, kinetic chlorophyll fluorescence (PSII) is relevant traits particularly under severe stress conditions. While architectural traits, like greater leaf area which provide good discrimination of resistant cultivars to abiotic stresses under climate change scenarios [104].

3.2 Effect of nitrogen at reproductive stage under water deficit condition

Maize crop tolerant to N-deficit conditions at early vegetative stage than later reproductive phase [105]. There is a synergistic relationship between water availability and N use efficiency in maize [106]. When N supply is limited, grain yield is more associated with N deficiency than drought stress, but with adequate N supply, drought stress is the main yield-limiting factor [97]. Similarly Halvorson et al. [107] described maize yield as a function of available water and nitrogen. Maize plants selected for tolerance to mid-season drought also provide tolerance toward nitrogen stress. This may be due to an increase in both the number of kernels per plant and kernel weight. Hence consistently increases grain yield across N-level [108]. The pre-anthesis drought significantly reduced the number of kernel rows, the number of kernels per row, as well as the 1000-kernel weight. The 80 kg N ha⁻¹ was sufficient to achieve maximum grain yield under pre-anthesis drought. It is hypothesized that the adverse effects of pre-anthesis drought on grain yield can be mitigated if varieties are selected for roots which rapidly penetrate the soil and exploit the water resources in deep soil layers [109]. The effects of water stress imposed at low-sensitive growth stages (vegetative, reproductive, and both vegetative and reproductive) and level of nitrogen (N) supply (100 and 200 kg ha⁻¹) on the physiological and agronomic characteristics of the two hybrids of maize (*Zea mays* L.) were studied. The results showed that proline content increased and the relative water content, leaf greenness, 100-kernel weight, and grain yield decreased under conditions of water deficits. The limited irrigation imposed on maize during reproductive stage resulted in more yield reduction than that during vegetative stage. The 100-kernel weight was the most sensitive yield component to determine the yield variation in maize plant when the WD treatments were imposed in low-sensitive growth stages. The increase of N supply improved yield and IWUE when maize plant endured once irrigation shortage at vegetative stage. But, the performance of high N fertilizer reduced and eliminated when water deficit imposed once at reproductive stage and twice at vegetative and reproductive stages, respectively [110]. Further, the hybrids B73 × LH38, FS854, B73 × Mol7, and US13 were subjected to drought stress from the seventh leaf stage to evaluate differences in carbon and nitrogen accumulation and partitioning under drought. The results indicate that the greater drought tolerance of B73 × LH38 and FS854 to stress imposed during vegetative and early reproductive development resulted from their more active N uptake and assimilation and sugar production during the later portion of grain fill and from their more efficient partitioning of assimilate to the developing kernels [111]. Drought severity decreased grain yield sharply, but grain yield increased with nitrogen fertilizer. The time taken for pollination, grain weight, and total number of grains/ear were also affected. Increased proline content significantly under drought stress conditions shows activation of osmotic adjustment mechanism [112]. In a field study (carried out from 1995 to 1997) the effect of irrigation and water stress imposed at different development stages on vegetative growth, grain yield and other yield components of corn (*Zea mays* L.) was determined. The results of this 3-year study show that water stress occurring during vegetative and tasseling stages reduced plant height, and also leaf area development. Short-duration water

deficits during the rapid vegetative growth period caused 28–32% loss of final dry matter weight. Whereas, single irrigation omission during one of the sensitive growth stages, caused up to 40% grain yield losses. Although prolonged water stress during tasseling and ear formation stages the predictable loss could be much greater (66–93%) [39]. Though, stay-green and kernel numbers are affected by nitrogen uptake and use efficiency, and by nitrogen remobilization [113]. Whereas, insufficient N supply combined with water deficit reduces per-plant kernel number and mass, total aboveground dry matter (DM) yield, and harvest index (HI) [114, 115].

4. Source-sink relationship under drought

Higher plants are heterotrophic, leaves are the major organs that are photosynthetically active sources with tissues that synthesize sugars and translocate mainly sucrose to other parts of the plants, which are photosynthetically less active or inactive sinks such as roots, fruits kernel, and tubers. This physiological dynamics is not static and changes with each different phenological stages. The plant life cycle begins from embryo (sink) that mobilize nutrient from storage organ seed (source). During vegetative stage the source organ are photosynthesizing leaves ($\text{fixed CO}_2 + \text{H}_2\text{O} = \text{sugars}$) that export carbohydrates to various developing sink organs, like, emerging leaves, roots for their utilization in growth and development. During reproductive stage, sugars and other nutrients are mobilized from mature leaves to developing seeds, kernel, fruits, and tubers. This sink transition and various competing sinks changes with respect to sink strength and all compete for carbohydrates allocation. This carbohydrate production (source) and carbohydrate partitioning (sink utilization of carbon) is also influenced with various other factors such as nutrients, hormones, environmental factors. This coordinate regulation of source activity and sink strength determine the carbon allocation throughout the plant and has been crucial for defining yield of the crop [116]. The balance between source-sink is disturbed due to insufficient sink strength or slow carbohydrates export leading to accumulation of carbohydrates in source organ causes feedback inhibition which in turn, down regulate the photosynthesis in leaves [117]. Drought, modify source-sink relations that disturb plant growth, also adaptation to stress and consequently affect crop productivity. Source-sink altered under water deficit condition because the growth primacies of plant changes. Since the source organ unable to supply assimilates to various competitive vegetative organ growth, to maintain reproductive structures and adaptation to stress. This decrease in photo assimilates reduces sink number and size [118]. They also emphasize the role of several metabolic and hormonal factors influencing not only the source strength, but especially the sink activity and their interrelations and their potential to improve yield stability under drought and salinity stresses. Further, Fahad et al. [10] highlighted the regulatory circuits of different phytohormones and cross talks among ABA, indole ABA, CKs, GA, SA, BRs, JA, ETHY, and TR at physiological and molecular levels on exposure to salinity. The decline in source and sink strengths during water deficit leads to important reductions in crop yield [3]. In the present climate change model [119], drought periods are becoming more frequent and severe [120, 121], and future crop varieties have to be more resilient to this stress. Maize is the third most important crop after wheat and rice, mainly grown for food, feed, and fodder. Plant breeding and agronomic practices have major role in genetic contribution to improved grain yield. Two main important physiological processes involved are sustained leaf photosynthesis during grain filling, which contributes to increases in dry matter accumulation, and second, an increase in kernel number due to higher partitioning to the kernels during the sensitive period of kernel number

determination. Water use in corn is greatest during the late vegetative through early grain filling stages [76]. There are several factors that contribute to high plant performance under drought stress, like better portioning of biomass to the developing ear that results in faster spikelet growth which may results reduction in the number spikelet formed on the ear thus, facilitate overall seed set by reducing water and carbon stress per spikelet [122].

4.1 Source limitation and strength under drought stress

4.1.1 Source limitation

Growth conditions are favorable during pre-flowering and flowering, and a certain maize crop therefore establishes a large leaf area and many kernels and ears. Drought occurs after flowering causing the leaves to senesce early. The supply of assimilates will limit grain yield in this crop, and the plant will have many small kernels, thus limiting the source.

4.1.2 Regulation of source activity

Leaves are the main source organs; in maize, leaves ranged from 8 to 20 and these are present alternatively on nodes, and drought stress reduced the leaf size and number of leaves. Alternatively, reduced leaf areas under drought stress consider as an adaptive strategy. This may reduce the plant water requirement by reducing the leaf area and probability of plant survival is increased under limited water availability [123] but decrease in chlorophyll contents, chloroplast contents and photosynthetic activity reduced the grain yield [124, 125]. The important characteristics of superior germplasm include, more biomass allocation to leaf relative to stem weight, more leaf area, longer active leaf area duration [126] under different growing conditions. However features like morpho-physiological attributes such as leaf area, chlorophyll content, the rate and duration of photosynthesis, time of flowering, dry matter partitioning during silking, and leaf stay green plays key role in dry matter accumulation, harvest index and grain yield of corn [127]. Selection for stress tolerance has improved the grain yield in maize and it depends on higher leaf area per plant and higher harvest index (HI). Moreover, “stay green trait” or leaf greenness or reduction in the rate of leaf senescence during grain filling was one of the distinctions between older and newer hybrids [128]. Lafitte and Edmeades [129] selected maize cultivars in low and high N and secondary traits (Such as increased plant height, leaf area, chlorophyll concentrations, and delayed senescence) to improved grain yields. However, selection based in low-N to increase grain yield disturbs the balance of source and sink. Various secondary traits like water depletion pattern, leaf rolling, canopy temperature, reveals root potential and water extraction capacity. Whereas chlorophyll concentration quantifies the stay green trait of leaf. Flowering traits are associated with specific developmental stage, while, photosynthetic rate indicates the plant growth rate throughout the plant life cycle. Thus, these secondary traits are a related to specific mechanism and they contribute to enhance grain yield under drought stress [130]. Monneveux et al. [131] indicate that the traits of source organs contribute marginally to drought tolerance; variation of leaf or root traits seems to be less important than variation in tassel parameters for increasing drought tolerance. Further progress in drought tolerance in maize, the solution might reside in the manipulation of sink organs. It is therefore suggested that selection for even greater number of ears, bigger grains and smaller tassels may help to increase grain yield under water limited environments in the near future. Selection based on crop ideotype by Bolaños and Edmeades [132]

was successful in producing drought-tolerant cultivars that were able to partition the assimilates to ear at flowering. However, Gambin et al. [133] indicated maize reproductive efficiency in kernel set is not constant across different plant growth rates (PGR) around flowering, therefore PGR per kernel used during this period as an indicator of source availability per kernel. The curvilinear response relating kernel number per plant and PGR around flowering, increased PGRs resulted in higher PGR per kernel around this period ($r^2 = 0.86$; $p < 0.001$). Grain filling duration was partially explained ($r^2 = 0.27$; $p < 0.01$) by the ratio between PGR per kernel during the effective grain filling period and kernel growth rate. Together, these results support the importance of source availability per kernel during early grain filling on the determination of maize potential sink capacity and final KW.

4.2 Sink limitation and strength under drought stress

4.2.1 Sink limitation

Growth conditions are favorable during pre-flowering and a certain maize crop therefore establishes a large leaf area. There is stress during flowering time and therefore the crop can establish only few ears and kernels. After flowering, the growing conditions may be favorable again, but the demand for assimilates by the kernels and their capacity to absorb the available assimilate will limit grain yield, thus limiting the sink.

4.2.2 Regulation of sink activity

Flowering is the most crucial stage for silk growth, pollination, and kernel setting in maize [134] and is the utmost susceptible stage to drought stress. An asynchrony between silk emergence and pollen shedding under drought stress before and during flowering increases the anthesis-silking interval (ASI) and primarily causes yield loss [135–138]. High-temperature stress also hampered the pollen characteristics. However, exogenous application of various PGRs significantly reduced the damaging effects of high temperature, compared with control. Further, pollen characteristics can be exploited as screening tools for varietal development but selection must focus for those germplasm sources which can tolerate temperature above 38°C [1, 11, 12]. Under drought stress, a positive correlation was observed between flowering and kernel number per plant ($r > 0.8$), barrenness ($r > 0.7$), and ASI ($r = -0.4$ to -0.7) in tropical maize [136]. In maize, increased abiotic stress tolerance increased yield and yield stability in some tropical and temperate maize germplasm [139, 140]. Canadian maize hybrids show increased tolerance toward various stress factors like high population density, weed interference, low night temperature, low soil moisture, and low-N stress due to the features such as increased leaf longevity, increased nutrient and water uptake, and greater assimilates supply during grain filling [140]. Similarly, tropical maize shows decreased kernel and ear abortion, selected for mid-season drought [141, 142]. Therefore, constitutive stress-tolerance mechanism may be operative in maize germplasm, which may be related to the creation of sink size [92]. The ovule, ear and kernels are the reproductive sinks, for their proper development assimilates supply above threshold level are necessary. In unstressed condition, ear abortion may occur due to insufficient assimilates supply that led to barren plants. Thus, ovule fails to extrude silk due to slow growth, whereas kernel aborted following pollination [141, 143, 144]. The corn was subjected to low water potential (C_w) for 5 days at the time of pollination [145]. Zinselmeier et al. [145] observed that embryos formed but abortion occurred and kernel number decreased markedly. Besides, during this

abortion, all of the intermediates in starch synthesis were depleted and the starch contained in the ovary almost disappeared. The period for ovule, kernel, and ear abortion falls 1 week before until 2 weeks after silking; during this period, stress factors like drought, shade, high density, and low-N stress accelerate these processes [27, 90, 146, 147]. Physiological reasons for abortion of reproductive structures under various stresses have shown that concurrent photosynthesis is required to maintain the flux of carbohydrates to the young ear around flowering but under drought it not possible to remobilize carbohydrate reserve for the support of ear development [148–150]. Drought also reduces invertase activity in ovaries and this will reduce the flux of hexose sugars; starch reserves of ovaries are depleted and it leads to the ovaries abortion [151]. In tropics, maize yield could be increased by improving the balance between the source supply and sink demand [152]. The main focus of maize breeding program is to increase the grain yield under high N; this practice resulted in an increase in both the source and sink in size and efficiency [153]. However, in N-limited conditions, not only the importance of C but also for N associates with source and sink [154] the N required during the exponential phase of grain growth to sustain the kernel number per plant and grain yield. The role of glutamine synthetase (GS) and asparagine synthetase (AS) (their main function in plant nitrogen remobilization) was determined in two maize varieties (ZD958 and NH101) in relation to post-silking drought stress (PD) nitrogen partitioning. The results indicate the PD stress increased nitrogen remobilization, and in ear leaves, the expression of *ZmGln1-3* was enhanced for both varieties. While under PD treatment, three AS genes (*ZmAS1*, *ZmAS2*, and 10 *ZmAS3*) were differentially regulated, of which the expression of *ZmAS3* was stimulated at the late stage of leaf senescence. In developing kernels, there were no significant differences in expression patterns of GS and AS genes between the well water (WW) and PD plants. Therefore, at the whole plant level, PD stress showed more influence on leaf nitrogen status, and the upregulation of GS and AS genes may contribute to the higher leaf nitrogen remobilization when exposed to PD treatments [155]. Genotypes selected for high grain yield under normal growing conditions also had a high level of dry-matter accumulation and partitioned more assimilates to the grain under water deficit conditions. The improved genotypes produced more numbers of ears/plant and kernels/ear [156]. Leaf growth and ASI are the main determinants of source and sink strengths of maize.


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