Chapter 2
Effects of Drought on Maize

Water is vitally needed for every organism in specified amount and any deficiency in that particular amount imposes the stressful conditions. Water requirement is variable across the tissues and across the growth stages of same species of crop plant and maize crop has no exception so, far. Assessment of optimum plant water requirements is prerequisite to determine the water deficiency in plants. Water requirement of maize crop is low at early growth stages then reaches on peak at reproductive growth stages and during terminal growth stages requirement of water again lowers down. During reproductive growth stage, 8–9 mm water is needed per day to single plant. Four weeks are most crucial regarding water requirement which includes two weeks before and two weeks after pollination. Pollination is most critical growth stage for water requirement and all leaves are kept unfolded and grain yield is also decided at this stage. Grain filling and soft dough formation are most sensitive to water deficiency, whereas, pre-tasseling and physiological maturity are relatively insensitive to water deficiency. Drought stress during vegetative growth stages especially during V1–V5, reduces growth rate, prolong vegetative growth stage and conversely duration of reproductive growth stage is reduced (Pannar 2012). Each millimeter of water produces 15.00 kg of kernels and total 450–600 mm is needed across the whole season (Du Plessis 2003). Total 250 l water is consumed by maize plant till maturity (Du Plessis 2003). Relative water contents, stomatal resistance, water potential, leaf temperature and transpiration rate maintain the plant water relation and any imbalance in these or any one of these traits disturb the plant water relation (Anjum et al. 2011b). Relative water contents determine the status of metabolic activities of the cell or tissue. During early leaf development, relative water contents of the leaves were higher and tend to decline towards maturity. Strong correlation is reported between relative water contents, water uptake and transpiration rate. Under drought stress, relative water contents and water potential is reduced, resultantly, leaf temperature is increased due to reduced transpirational cooling (Siddique et al. 2001). It can be easily perceived that plant water status is dependent on stomatal activity (Anjum et al. 2011b).

Transpiration ratio is described as number of water molecules lost in order to fix one molecule of carbon. Soybean, wheat and maize have 704, 613 and 388 transpiration ratio respectively which shows that maize is relatively efficient water user crop (Jensen 1973). Despite of being efficient water user maize is badly affected by

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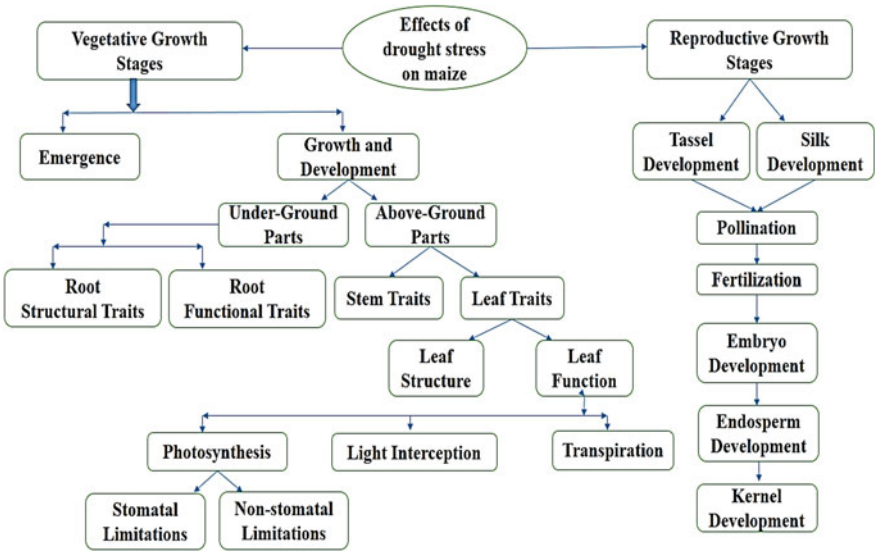

Fig. 2.1 Effects of drought stress on vegetative and reproductive growth stages of maize

drought stress due to hypersensitivity against water deficiency. In maize, developmental stages starting from germination to harvest maturity including seedling establishment, vegetative growth and development and reproductive growth stages are very much prone to drought stress. Effects of drought on maize at different growth stages and organizational levels have been presented in Fig. 2.1 and described in subsequent sessions.

2.1 Effects on Crop Stand Establishment

Crop stand establishment comprised of germination, emergence and seedling establishment. Concepts of germination and emergence prevailed under laboratory conditions and field conditions respectively. Crop establishment accomplished up to development of 7th or 8th leaf. These early growth stages are critical growth stages regarding drought stress. Always there are prominent differences among different levels of water treatments in maize regarding their effects at early growth stages (Fig. 2.2). Proper seed germination is dependent on availability of appropriate moisture contents for metabolic activation to breakdown the dormancy or to convert stored food into consumable form. Crop density or number of emerged seeds, mean time for emergence and synchronization of emergence are characteristic features which determined the efficacy of seedling establishment (Finch-Savage 1995). Crop survival, growth and development are determined by efficacy of seedling establishment (Hadas 2004). Drought stress reduces the germination potential of maize

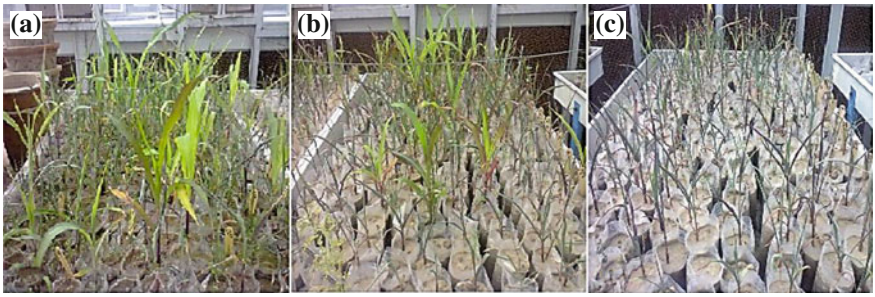

Fig. 2.2 Maize seedlings subjected to different treatments of water deficiency. **a** 75 % of field capacity, **b** 50 % of field capacity, **c** 25 % of field capacity. Visual observations show that same set of maize genotypes is showing different pattern of growth and development due to differences in water availability. Leaf area, seedling height, stem girth and leaf rolling are clearly showing the significant differences among three different treatments. Leaf rolling seems highest in 25 % of field capacity whereas, leaf area, seedling height, stem girth are lower in this treatment relative to others. Under 75 % of field capacity, plant height, leaf area, stem girth seems to be greaterly higher than other two treatments

seeds by reducing their viability. Poor maize seed germination is directly associated with poor post germination performance (Radić et al. 2007). Severity of drought stress is directly linked with poor imbibition, germination and seedling establishment in maize (Achakzai 2009). Germination index (*Box-1*) is reduced by water deficiency (Almansouri et al. 2001). Germination potential, germination rate (*Box-1*) and seedling growth are the studied traits under drought stress because these traits are direct representative of crop establishment and are badly affected by drought stress (Delachiave and Pinho 2003). Germination velocity index (GVI) is corroborated with seed strength and always GVI (*Box-1*) was greater for maize hybrids than landraces due to hybrid vigor (Mabhaudhi 2009).

Maize grain size is greater than other cereals like wheat, rice and barley therefore, water requirement is greater for maintenance of osmotic potential and conversion of stored food into consumable form for proper germination (Gharoobi et al. 2012). Seed vigor (*Box-1*) is considered as important parameter in maize breeding which is badly reduced by drought stress (Khodarahmpour 2011). Water absorption, imbibition and metabolic enzymatic activation are hindered under limited water availability which reduces the maize grain germination. After germination, water deficiency significantly reduced the plumule and radicle growth which resulted in unusual seedling growth (Gharoobi et al. 2012). Hydropriming and osmopriming (*Box-1*) of maize seed result in improved seed germination by regulation of enzymatic activity to break the dormancy which clearly highlights the importance of water availability for exploitation of full germination potential (Janmohammadi et al. 2008). Root and shoot elongations are parameter of seedling growth and these are subjected to reduction by drought stress. At seedling stage in maize, reduction in shoot elongation is more than root elongation under drought stress (Khodarahmpour 2011). Seedling emergence rate of landraces is lower than

hybrids whereas reduction in shoot elongation was less in landraces than hybrids under drought stress (Mabhaudhi 2009). Rate and degree of seedling establishment of maize are critical factors for determination of time of physiological maturity and grain yield (Rauf et al. 2007).

So, it is evident from above discussion that seed vigor, imbibition, germination potential, germination rate, plomule and radicle development and root and shoot growth of maize are adversely affected by drought at early growth stages.

2.2 Effects on Growth and Development

Proper growth and development of crop plants is important for establishment of normal plant structure that carry out all physiological and metabolic processes and give potential yield. Drought stress seriously hindered the growth and development of maize. Growth and development comprised of numerous component parameters which are estimated by different traits like, plant height, leaf area, structural and functional characters of root, plant biomass, plant fresh weight, plant dry weight and stem diameter. Plant height, stem diameter, plant biomass and leaf area are reduced under drought stress (Khan et al. 2001; Zhao et al. 2006).

Growth is described as increase in size of plant which is directly associated with increase in number of cells and cell size. Meristematic tissues are involved in active elongation of plant by active cell division. Cell division and cell size are reduced by reduction in water potential of cells which causes the reduction in plant growth (Nonami 1998).

Leaves in maize are ranged from 8 to 20 and these are present alternatively on nodes. Leaf is comprised of structural and functional components. Leaf growth consists of leaf size and number of leaves which are structural components. Photosynthesis, transpiration and light interception are the functional traits of leaf. Leaf size and number of leaves are reduced in maize by drought stress. Turgor pressure, light interception and flux assimilation are determinant of leaf elongation (Rucker et al. 1995). Wedge shaped motor cells are present on the upper leaf surface and these keep the leaves unfold whereas, under drought stress turgor of leaves is reduced and leaves are curled or folded (Du Plessis 2003). Leaf folding reduces the leaf area and resultantly light interception is reduced which decreases the photosynthetic activity. Leaf area and photosynthesis are directly proportional to each other (Stoskopf 1981). Cell division and cell elongation are reduced under drought stress which reduces the leaf area. Reduction in leaf area under drought stress conditions is taken as adaptive strategy by maize plants. Leaf area index is considered as an important parameter for maize breeding against drought stress (Hajibabaee et al. 2012). Plant water requirement is reduced by reducing the leaf area and probability of plant survival is increased under limited water availability (Belaygue et al. 1996) but chlorophyll contents, chloroplast contents and photosynthetic activity are reduced which reduced the grain yield (Flagella et al. 2002; Goksoy et al. 2004).

Kinases protein family and cyclin-dependent kinases (CDKs) are involved in the active progression of cell cycle. CDK activity is reduced under water deficit conditions which increased the duration of cell division and decrease the number of cell divisions per unit time that ultimately reduces the growth of leaves and plant (Granier et al. 2000). Cell elongation is found to be reduced across all points on leaf. Common regulatory pathway is involved in cell division and cell elongation (Tardieu et al. 2000). Drought stress increases the leaf to stem ratio which is indication of high level of growth retardation in stems than leaves (Hajibabaee et al. 2012). Reduced water potential in roots interrupts the optimal water supply to the elongating cells and resultantly cell elongation is reduced. Water potential less than −10.0 Bars causes the reduction in leaf growth (Tanguilig et al. 1987).

Light interception is reduced after reduction of leaf area. Less interception of solar radiations causes the reduction in biomass production (Delfine et al. 2001). Besides light interception, stomatal activity is also responsible for lower biomass production (Delfine et al. 2001; Medrano et al. 2002). Rise in leaf temperature under drought stress, inhibits the enzymatic activity and reduces photosynthesis (Chaves et al. 2002). Photosynthetic machinery is inactivated by increase in leaf temperature above threshold temperature which is 30 °C (Crafts-Brandner and Salvucci 2002). Stomatal closure, reduced transpiration and its homeostatic effects are the cause of rise in leaf temperature under limited water availability (Jones 1992).

Photosynthetic activity in maize plant is reduced by stomatal and non-stomatal limiting factors. Reduced leaf turgor and root originated signals along with lower plant water status trigger the stomatal closure. Reduction of water potential in the roots transduces the signals for stomatal closure. CO_2 diffusion in the leaves is reduced by stomatal closure and supply of CO_2 to the RUBISCO is hampered (Flexas et al. 2007). Reduced CO_2 diffusion is considered as main reason for decline of photosynthesis. Abscisic acid (ABA) accumulation is increased in the leaves in response to drought induced signals which triggers the stomatal closure (Wilkinson and Davies 2010). Cellular environment becomes alkaline under drought stress. Rise in cellular pH increases ABA accumulation in the leaves (ABA trapping) which induced the stomatal closure (Jia and Davies 2007).

Stomatal closure has protective role in saving the water loss and increasing water use efficiency under mild drought stress but under severe drought stress stomatal closure becomes inevitable evil (Chaves et al. 2009). Stomatal conductance and transpiration rate modulate the CO_2 diffusion in leaves which are directly linked with stomatal opening. CO_2 fixation rate, intercellular CO_2 concentration and net photosynthetic rate are the parameters used for assessment of stomatal conductance and photosynthetic activity under drought stress (Sage and Zhu 2011). Passive and active stomata closures occur under normal conditions and stress prevalence respectively (Fig. 2.3). Different genes are regulated to maintain the production and consumption equilibrium by alteration of redox state in leaves under drought stress. Reactive oxygen species (ROS), electron acceptors and electron carriers have potential role in regulation of stomatal conductance (Chaves et al. 2009).

Leaf structural characters and biochemical parameters are components of non-stomatal inhibition of photosynthesis. According to Von Caemmerer (2000)

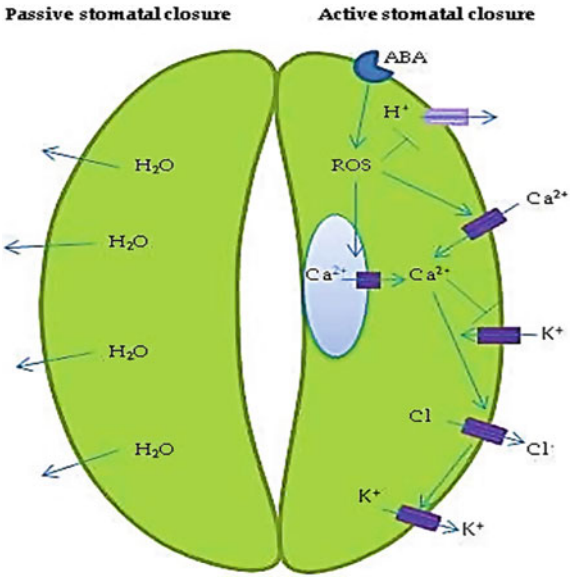

Fig. 2.3 Passive and active stomatal closure. Passive stomatal closure occurs under normal conditions and active stomatal closure occurs under drought stress (Arve et al. 2011). © 2011 Arve LE, Torre S, Olsen JE, Tanino KK. Originally published in [short citation] under CC BY-NC-SA 3.0 license. Available from http://dx.doi.org/10.5772/24661

and Ghannoum (2009) carboxylation is changed by RUBISCO (Ribulose 1,5-bisphosphate carboxylase/oxygenase), PEPC (phosphoenolpyruvate carboxylase) and regeneration of PEP (phosphoenolpyruvate). Activity of the enzymes involved in the photosynthesis are reduced in case of non-stomatal inhibition of photosynthesis. Chlorophyll contents are reduced either by activation of cellular protein degradation or by limited nitrate synthesis (Becker and Fock 1986; Ghannoum 2009).

Maize is C4 plant and it is reported in C4 plants that intercellular spaces and chloroplast positions are misplaced by drought stress resultantly CO_2 diffusion and light penetration are disturbed followed by decreased photosynthetic activity (Flexas et al. 2004). Photorespiration and Mahler's reaction act as alternative electron sinks under drought stress (Ghannoum 2009). Mahler's reaction is involved in generation of reactive oxygen species and develops oxidative stress under drought stress. Oxygen molecule is converted into superoxide as a result of direct reduction reaction in Photosystem-I (Haupt-Herting and Fock 2002). Photosynthetic metabolism is reduced by reduction reaction of carbon substrate. Carboxylation activity of RUBISCO, regeneration of RuBP and ATP are reduced by inhibited CO_2 concentration in the leaves under drought stress (Tezara et al. 1999). CO_2 diffusion through mesophyll is reduced due to change in carbon metabolism and leaf photochemistry under drought stress. Leaf biochemistry, membrane permeability (aquaporin activity), leaf shrinkage, alterations in intercellular spaces, intercellular structure, internal diffusion and internal conductance are altered under drought stress which results in reduction of CO_2 diffusion through mesophyll (Lawlor and Cornic 2002; Chaves et al. 2009).

Roots have the critical importance for plant because these are the primary detectors or sensors of drought stress. Root length, root volume, root density and number of roots are the characteristic structural traits which are disturbed under drought stress and resultantly whole arial plant parts are disturbed. Spatial water uptake and temporal water uptake are functional traits of roots. Root system of maize comprised of axillary and lateral roots. Axillary roots are further comprised of primary, seminal, nodal or crown roots (Cahn et al. 1989). Primary and seminal roots are collectively known as embryonic roots. Seminal roots are permanent and have functional role in growth and development of plant (Navara et al. 1994). Roots of maize plant becomes elongated under mild drought stress to explore the more soil foils for more water uptake whereas, under severe drought stress root length is reduced. Root density, volume and number of roots are reduced under mild and severe drought stress (Nejad et al. 2010).

Requirement of photosynthates and energy is reduced in leaves due to reduced leaf area by leaf rolling or curling under mild drought stress. Photosynthetic assimilates from leaves are directed toward roots for their elongation to increase the water uptake (Taiz and Zeiger 2006). Roots act as primary sensor of water deficiency in soil and transduce signals to the aerial parts to modulate the growth and development. Signal from roots to the aerial parts are transduced through chemical and hydraulic vectors (Davies et al. 1994). Decreased water and nutrient uptake increase the pH of xylem (reduction of negative or positive ions) which transduces ABA-mediated signals to the leaves for preventing water loss by stomatal closure (Bahrun et al. 2002). Reduction in root growth under drought stress is also associated with reduced cell division and cell elongation. Microtubules are critical for cell division and cell elongation because these microtubules are involved in cellular morphogenesis, embryo development, organogenesis, stomatal conductance and organ twisting (Steinborn et al. 2002; Whittington et al. 2001; Marcus et al. 2001; Thitamadee et al. 2002). Reduced root turgor under dehydrated conditions, increases ABA accumulation and plasmolysis. Plasmolysis seriously damages the microtubule skeleton and cellular geometry (Pollock and Pickett-Heaps 2005). Disrupted microtubules in roots induce the ABA accumulation by increasing ABA biosynthesis. Interactions between microtubules, cell wall, plasma membrane and ABA biosynthesis are reported under osmotic stress (Lu et al. 2007).

2.3 Effects on Reproductive Growth Stages

Drought has adverse effects on maize life cycle; particularly reproductive growth phase is most susceptible to drought stress. Translocation of photosynthetic assimilates to the reproductive parts rather than roots for their extensive elongation is most probable reason for more susceptibility of maize plant during reproductive growth stage under drought stress (Setter et al. 2001; Taiz and Zeiger 2006). Sequential effects of drought stress on reproductive growth stages of maize are described in Fig. 2.1. Pollen and silk development, pollination, embryo

development, endosperm development and kernel development are the different component phases of reproductive growth stage which are severely threatened by drought stress.

2.3.1 Pollen Development

Pollens are produced in the tassel which is present on top of the plant. Almost 25 million pollens are produced by single tassel under normal conditions. Modern hybrids produce 2–5 million pollens and landraces produce about 14–50 million pollens on an average (Burris 2001). Breeding efforts are always focused to reduce the tassel size and make tassel smart enough to ensure maximum photosynthetic reserves supply to female inflorescence rather than male inflorescence development because there is no problem of pollen availability in case of maize. Breeding efforts had suppressed the male over-dominance which had reduced the pollen production capability (Duvick and Cassman 1999). Maize pollens are produced in huge bulk and crop yield is not affected even due to 40 % reduction in pollen production (Du Plessis 2003). Timing for pollen shedding is effected negligibly by drought stress so, pollen shedding occurs mostly at normal time even under drought stress but in severe drought cases pollen shedding is adversely affected. Anthesis-silking interval is increased by decrease in silk growth and development rate. Pollen shedding depends on type of variety and environmental conditions; pollen shedding may continue from 2 to 14 days under normal conditions. About 1 h after sunrise is the time for initiation of pollen shedding which remain continue for 4–5 h and maximum pollen shedding occur during 5–8th day of pollen shedding (Burris 2001).

Pollens are affected by drought stress in different ways. Pollen mortality occurred due to dehydration as moisture of pollen is lost due to drying conditions (Aylor 2004). Settling speed, pollen viability, specific gravity, pollen shape and dispersal are seriously affected in dehydrated pollens (Aylor 2002). Increased ABA accumulation and reduced invertase activity are the main reasons for pollen sterility under drought stress (Saini and Westgate 2000). Conversion of sucrose to hexoses is impaired by reduced invertase activity (Sheoran and Saini 1996). Pollens of maize were studied under drought and high temperature stresses which showed that pollen weight, pollen viability, pollen size, pollen tube length and pollen moisture contents were affected by these stresses (Fig. 2.4).

Maize pollens are of large size as compared to other angiosperms and have relatively higher moisture contents. Pollen viability is reduced greatly if pollen moisture contents are reduced below 0.4 g per gram of pollens (Buitink et al. 1996). Pollens absorb moisture from hydrated silk to initiate proper germination so, pollen germination is reduced in case of dehydrated silk under drought stress (Heslop-Harrison 1979). Starch and certain osmolytes are present in the pollens which protect them from losing viability. Drought stress reduced the accumulation of starch in pollens during pollen development which rendered them nonfunctional (Schoper et al. 1987). Upregulation of galactinol and vacuole invertase genes in

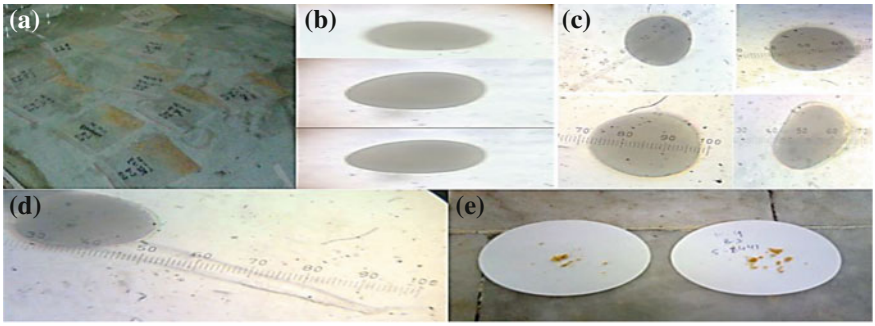

Fig. 2.4 Evaluation of different aspects of maize pollens under drought stress; **a** pollens collected from field and stored in zipper bags, **b** viable pollen grains; **c** measurement of pollen grain size; **d** pollen tube length; **e** pollen moisture contents measurement. These measurements showed that pollen viability, pollen size, pollen tube length and pollen moisture contents were reduced under drought stress

pollen under drought stress showed that these protect the pollens through osmo-protection and prevent the loss of viability (Taji et al. 2002). Gene expression is changed in such a way that cell wall structure and synthesis is impaired which results in loss of pollen viability under drought stress (Zhuang et al. 2007). Severe drought stress at tasseling stage reduce the yield by affecting the number of kernels per row, number of kernel rows, harvest index, number of kernels per cob and grain yield per plant (Anjum et al. 2011b). Increase in ABA accumulation up to 0.5 μM favor the pollen germination and pollen tube elongation but further increase in ABA contents significantly reduces the pollen germination and pollen tube elongation (Zhang et al. 2006).

2.3.2 Silk Development

Silk is female floral part of maize plant and should be receptive for proper pollination and fertilization. Silks remain receptive for 21 days but receptivity tends to reduce 10 days after silking (Du Plessis 2003). Silk elongation starts from the butt of the ear and terminal portion of cob elongated at the end. Large ear size delayed the silk appearance. However, it is reported that silking is delayed by 6–9 days by prevalence of drought stress (Dass et al. 2001). Tassel emerges 2–4 days earlier than silk emergence under normal conditions and this pattern is called protandry. Delay in appearance of silk under drought stress conditions is responsible for increased anthesis-silking interval (ASI) which is very critical index for efficient completion of reproductive growth stage. Lower the value of ASI higher will be the productivity and vice the versa. After silking, silk continue to elongate until it is pollinated and lengthwise it may reach up to 15 cm (Bassetti and Westgat 1993). After fertilization, elongation of silks stops and desiccation starts. Under drought

stress, desiccation of silks starts earlier and pollen tube becomes unable to reach the ovary resultantly no fertilization occurred. Fertilization failure occurs because of earlier silks desiccation due to drought conditions and ear bareness becomes the fate (Dass et al. 2001). So, assimilate partitioning towards the silk and hydration of silks are of prime importance for higher grain yield.

2.3.3 Pollination

Release of pollens in bulk from tassel followed by proper landing on silks is necessary for successful pollination process. Losses due to pollination failure can never be recovered even after rehydration and yield losses may reach up to 100 % (Nielsen 2002). Pollen grain productivity reduces from 3 to 8 % on daily basis under drought stress (Rhoads and Bennett 1990). Pollen shedding is accelerated and silking is delayed by drought prevalence for four consecutive days and this increases the anthesis-silking interval followed by 40–50 % yield losses (Nielsen 2005a, b). Development of silk and ear is dependent on sufficient sugar supply which results in potential seed setting (Zinselmeier et al. 1999). Invertase (carbohydrate transporter) activity is reduced under drought stress which reduces the carbohydrate supply to the developing reproductive plant parts. Glucose contents in the pedicle of ovary are reduced due to IVR2 (soluble invertase) reduction during pre and post pollination under drought stress (Qin et al. 2004). Starch contents of the floral parts are reduced under drought stress due to impaired activity of the enzymes involved in starch metabolism (Zinselmeier et al. 2002). Pollination process is disturbed in following ways by drought stress; (a) silk becomes dried under dehydrated conditions and no more supportive for pollen tube development (Nielsen 2002), (b) pollen shedding occurs before silking which causes increase in anthesis silking interval (Nielsen 2002), (c) silk elongation rate is reduced (Lauer 2012), (d) silk becomes non-receptive for pollen grains under dehydrated conditions along with low humidity (Nielsen 2005a, b). So, the pollination process is badly affected by drought stress in maize causing low productivity at the end.

2.3.4 Embryo Development

Embryonic development is very susceptible to drought stress. During early embryonic development, embryo abortion occurs due to drought or heat stress (Setter et al. 2011). Drought stress prior to fertilization can cause embryo abortion (Andersen et al. 2002). Grain yield in maize is mainly dependent on the tolerance of female reproductive part. Reactive oxygen species are accumulated in the ovary as a result of drought stress and embryo is aborted in oxidative environment (Kakumanu et al. 2012). Embryo sac

development is impaired due to imposition of drought stress during megaspore mother cell formation and resultantly 80–90 % yield losses are reported (Moss and Downe 1971). Insufficient provision of photosynthetic assimilates and sugar substrates to the developing embryo cause their abortion (Feng et al. 2011). Soluble invertases (Ivr2) and cell wall associated invertases are responsible for the provision of hexose to the developing embryos. These invertases are suppressed under drought stress causing check to supply of sugars and assimilate to embryo resulting embryo abortion (Andersen et al. 2002; Feng et al. 2011). Sucrose (substrate for invertase) to hexose ratio is very important for normal embryo development which is impaired during drought stress. Cell wall associated invertases and sugars are involved in signaling pathways and theses signaling pathways are affected by disturbance in expression of invertases and sugars (Kakumanu et al. 2012). Exogenous application of nutrients at reproductive stages rescue the 80 % embryos which proves that assimilate translocation is major reason for embryo abortion relative to lower water potential which causes comparatively less damage (Boyle et al. 1991). Leaves upload sucrose in phloem then it reach to pedicle where invertases hydrolyse sucrose into glucose and sucrose. These hexoses are used for kernel development (Cheng et al. 1996) and starch biosynthesis which participate in ovary development. ABA accumulation triggers the embryo abortion under drought stress (Setter et al. 2001). So, embryo development is very susceptible reproductive growth stage to drought stress which is affected by different ways.

2.3.5 Endosperm Development

Endosperm is storage house of food for embryo in the seed and like other reproductive stages; endosperm development is seriously affected by drought stress. Storage capacity of the endosperm is determined by cell division during early developmental stages of endosperm whereas; final volume of endosperm is determined by cellular elongation and multiplication of cellular organelles (Olsen et al. 1999). Cell division is reduced by imposition of drought stress during endosperm development and resultantly storage capacity is reduced (Ober et al. 1991). Prevalence of drought stress after fertilization, suppresses the cell elongation and multiplication of organelles causing reduction in final endosperm volume.

Process of endoreduplication occurs in the endosperm after mitotic cell division. Endoreduplication is repetition of S phase (synthesis phase) with mitotic cell division. There is no cytokinesis but DNA ploidy becomes double after every repetition of endoreduplication. Cell enlargement, cell differentiation, survival and metabolic activities are the key functions of endoreduplication (Barow and Meister 2003). Comparative evaluation showed that endoreduplication is less affected by drought relative to mitotic cell division (Artlip et al. 1995). Transition from mitotic

cell division to endoreduplication is also affected by drought stress (Mambelli and Setter 1998). Cell division is reduced during early stages (1–10 days after pollination) of endosperm development in the apical kernels whereas; endoreduplication is reduced during terminal stages (9–15 days after pollination) of endosperm development (Setter and Flannigan 2001).

2.3.6 Grain or Kernel Development

Kernel development is very important phase as for as productivity is concerned and comprised of following component stages; blister stage, soft dough stage, milking stage, hard dough stage and dent stage. High moisture contents are needed during blister stage for grain filling and drought stress at this stage results in poor quality kernels. Moisture requirement during soft dough, milking and hard dough stages is higher enough that drought stress at these stages can reduce the kernel quality and yield. Drought stress during hard dough stage causes the premature hanging of the cobs. Water requirement of dent stage is lower relative to pre-dent stages of kernel development but drought stress at this stage still can cause potential loss in yield and quality (Pannar 2012).

Kernel development in maize is comprised of three major stages; (a) lag phase; sink capacity is developed, water contents increase and biomass accumulation reduces (Saini and Westgate 2000), (b) effective grain filling stage or linear phase; maximum biomass accumulation occurs in this stage and kernel size is determined (Westgate et al. 2004), (c) physiological maturity; maximum dry weight is gained and later on grain enters in quiescent phase (Saini and Westgate 2000).

Sink capacity and source strength interact with each other for grain filling. Differences in grain weight are due to difference in source sink ratio. Source strength is determined by photosynthesis and carbohydrate assimilation whereas, sink capacity is determined by sink's activity (Westgate et al. 2004; Yang et al. 2004). Drought stress reduces the photosynthesis and translocation of photosynthetic assimilates followed by reduced grain filling. Source strength and sink capacity are reduced by drought stress in maize. Grain size reduction is caused by reduced remobilization of photosynthetic assimilates (Yadav et al. 2004). Grain filling is also reduced due to decreased activity of sucrose and starch synthesizing enzymes under drought stress (Anjum et al. 2011b). Numbers of kernels are determined during pre-anthesis stages whereas; kernel weight is determined at post-anthesis stages. Drought stress during post-anthesis stages is responsible for kernel weight reduction (Oveysi et al. 2010). Interaction of water and biomass during kernel development are the determinants of final kernel volume. Water contents of the kernel are increased during early developmental stages of kernel and later on water contents decrease followed by increase in biomass accumulation. Biomass accumulation is dependent on source strength and sink's capacity which are seriously reduced by drought stress so final kernel volume is reduced by drought stress (Gambín et al. 2006). Reduced water potential and kernel water uptake

squeeze the duration of kernel filling resultantly kernel size is reduced (Brenda et al. 2007). It is reported that drought stress during, kernel development is responsible for 20–30 % yield losses which are mainly due to under sized kernels (Heinigre 2000). Another report mentioned that drought prevalence during kernel development can cause 2.5–5.8 % yield losses on daily basis (Lauer 2003).

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Drought Stress in Maize (Zea mays L.)
Effects, Resistance Mechanisms, Global Achievements and Biological Strategies for Improvement

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