CHAPTER 2

LITERATURE REVIEW

Drought stress is one of the major global problems, causing an extensive loss to agricultural production worldwide (Boyer 1982). Drought limits plant growth, and crop yield. Recently, the Food and Agricultural Organization of the United Nations (FAO) pointed out that one way to insure future food needs of the increasing world population should involve a better use of water by the development of crop varieties less demanding of water and more tolerant to drought (Andersen *et at.*, 1999). Yield loss may be moderated or even prevented by plants' response to water deficit and adapt to drought conditions through various physiological and biochemical changes including phenological modifications (Monneveux and Belhassen, 1996). In maize, drought stress is one of the most important factors limiting production in most areas of the world (Edeades *et al.* 1989).

2.1 Effects of water stress on maize growth and yield

Effects of water deficits on crop growth and yield depend upon degree of stress and developmental stages at which stress occurs (Hsio and Acevedo, 1974; Sullivan and Eastin, 1974). Early drought can limit leaf area and root growth. Low water potentials during anthesis and early grain filling can be especially critical (Westgate and Boyer, 1985).

The most important responses of crop to water deficits are marked reduction in leaf area. A reduction in leaf area could result in a reduction of the transpiring surface

(Begg, 1980), but drought also hastens leaf senescence which results in loss of photosynthetic capacity (Turk and Hall, 1980). The leaf area has been identified as one of the most sensitive components of plant growth to water stress based on numerous reports (Begg and Turner, 1976; Turk and Hall; 1980; Pandey *et al.*, 1984b; Senthong and Pandey, 1989).

Kummerow (1980) found that, water deficits not only reduce the dry matter production of plants and stands of plant but also change the partitioning of carbohydrates among organs. In general, shoot growth is reduced more then root growth because more severe water deficits develop in the transpiring shoot and probably persist longer, although there seem to be few data on the latter point. Thus, root-shoot ratios are generally increased by water stress, although the absolute weight of roots usually decreases. Also, the root-shoot ratio is generally supposed to be larger for plants arid regions than for plant of humid regions, but there some uncertainty about this.

Water deficits can reduce photosynthesis by reduction in leaf area, closure of stomata, and decrease in the efficiency of the carbon fixation process. Reduction in leaf area by water stress is an important cause of reduced crop yields because the reduced photosynthesis surface persists after the stress is removed. Reduction in rate of photosynthesis in water stressed plants has usually been attributed chiefly to stomata closure, but this is now being questioned. It is true that rate of water loss and CO2 uptake often decease at the same rate in plants subjected to increasing water stress (Barrs, 1968; Brix, 1962).

6

Moreover, stomata on upper surface of leaves are more sensitive to water stress than those on the lower surface and leaf resistance are also higher for the upper than lower surface (Soinit and Kramer, 1976). Crop requires plenty of water throughout its growing period, especially during rapid growth, pollination and grain development. The transpiration ratio was found to very from 261-445 in different seasons (Kiesselbach, 1916).

Begg and Turner (1976) found that the level of yield reduction by water deficit will depend on a degree, duration, and timing of the deficit and on the proportion of the total yield that comprises the economic yield of crop, or harvest index.

2.1.1 Nutrient uptake under water stress

Drought is undoubtedly deleterious for plant growth (Garg et al., 2004; Samarah et al., 2004). It is known that low water availability under drought stress generally results in reduced total nutrient uptake and frequently reduces the levels of mineral nutrients in crop plants (Marschner, 1995; Baligar et al., 2001). In plants growing in drying soil, the development of the root system is usually less affected than shoot growth (Sharp and Davies, 1989).

Nutrient uptake by plants is decreased under drought stress conditions due to reduced transpiration, impaired active transport and membrane permeability resulting in reduced root absorbing power (Tanguilig et al., 1987). Nutrient supply to the root surface l is also likely to be adversely affected in dry soil as mass flow of water through the soil to the root is slowed down.

Water stress-induced increase of deposition of hydrophobic substances in the walls of epidermal root cells has even been found when soil moisture was only locally decreased in basal root zones, and thus did not affect the root growth rate (Watt *et al.*, 1996). Deposition of hydrophobic substances in the walls of root cells may reduce the hydraulic conductance of the roots (Cruz *et al.*, 1992), and also affect apoplastic nutrient transport and apoplastic accessibility of the membranes for nutrients (Ferguson and Clarkson, 1976; Peterson, 1987).

Plant species and genotypes within a species vary in their response to mineral uptake under drought stress (Garg, 2003). The drastic effect of drought stress observed is on the transport of nutrients to the root and on the root growth and extension (Alam, 1999). Inorganic nutrients such as N, P, K+, Ca2+ and Mg2+ ion play multiple essential roles in plant metabolism. Potassium plays an important role in osmoregulation, activates enzymes of respiration and photosynthesis and has a role in stomatal regulation. Calcium is the component of cell membrane and thus plays a significant role in plant growth (Lahaye & Epstein, 1971). Nitrogen is a constituent of many cell components and P plays a role in cellular energy transfer, respiration and photosynthesis (Alam, 1999). The supply of each of these nutrients, which must be maintained at an optimum concentration range for proper growth, may be affected by drought.

2.1.2 Vegetative growth under water stress

Maize is very susceptible to drought damage due to the plant's requirement for water for cell elongation and it's inability to delay vegetative growth. Therefore, there is always the danger of yield loss regardless of the timing of dry weather. The good way of maize production is that highest yields will be obtained only where environmental conditions are favorable at all stages of growth. The amount of yield loss that occurs during dry weather depends on what growth stage the maize is in and how severe the dry conditions become (Heinigre, 2000).

Water stress during vegetative development of maize had decreased dry matter yield at harvest by reducing leaf area development, stalk dry matter accumulation, and potential grain-filling capacity of plant (Wilson and Allison, 1978; Eck, 1984; Lorens et al., 1987). Drought stress during the vegetative stage has a large effect on a number of morphological traits of plant, such as leaf rolling, leaf expansion, leaf death and plant height (O'Toole and Cruz, 1980).

Visible syndromes of plant exposure to drought in the vegetative phase are leaf wilting, decrease of plant height, number and area of leaves, and delay in occurrence of buds and flowers (Boyer 1982, Passioura et al. 1993).

Shaw (1977) and Cakir (2004) reported that maize is relatively insensitive to water stress imposed during early vegetative growth stages because water demand is relatively low at this point, and the plants are able to adapt to water stress to reduce the effect of subsequent periods of water stress.

Plant growth from emergence to V8 (eighth leaf full emerged or about 4 weeks after planting) determines the size that the plant achieves and the size of the individual leaves. Dry weather during this period will reduce plant and leaf size. Impact on yield will be based on the reduction in leaf area available for photosynthesis. Minor reductions in leaf size will have little impact on yield while major reductions (all leaves removed from the plant) could reduce potential yields. Extended dry weather that results in leaf burning and loss will have the greatest impact on yield (Heinigre, 2000).

Water deficit is one of the most important constraints in maize production. Water stress given at the vegetative stage delays leaf emergence and reduces the leaf area and biomass production, and that given at reproductive stage delays tassel and silk emergence and reduces grain yield (Dwyer and Stewart, 1985; Nesmith and Ritchie, 1992).

2.1.3 Reproduction and yield under water stress

Grain yield of maize is governed by (a) ear size, which determined by the number of florets; (b) successful fertilization of the florets or grain set; and (c) ability of the plants to fill the grain with photosynthate. All of these are affected by drought, but to different degrees. Water stress around flowering and pollination delays silking, reduces silk length, and inhibits embryo development after pollination. Moisture stress during this time reduces maize grain yield 3 to 8 percent for each day of stress. Silking or the onset of the reproductive stage is the most sensitive stage for drought stress. Drought during silking coupled with high temperatures can result in 100 percent yield loss. High daytime temperatures can kill pollen before it can reach the silks. High humidity often results in heavy dew which can help pollen reach the maize silk. However, severe yield

10

reductions can occur due to incomplete pollination and the loss of kernel number (Lauer, 2003).

Drought after silking stage up to maturity affects kernel weight. Severe drought can reduce maize yields during this period by 20 to 30 percent. Again, the key factor is how long the drought occurs and how late in this period it occurs. Drought immediately following silking has the largest impact, and can reduce yield substantially. Drought latter in this period is less damaging, but can hasten maturity. While each stage is important, drought during some stages can be especially devastating. The key stage is silking followed by the V8 to V16 period and then the grain fill period from silking to maturity. Dry weather that starts early and covers several growth periods will have a compounding effect with severe reductions in maize yields (Heinigre, 2000).

The water deficits at flowering may also decrease maize grain yield even if pollination occurs (Schussler and Westgate, 1994). And Westgate (1994) reported that large yield reductions for maize resulted when drought occurred at flowering and early seed development. These yield reductions were primarily due to decreases in seed numbers per plant. At flowering stage is very susceptible to stress and it has been shown that the vegetative growth and grain filling are also sensitive to drought, but to much less degree (Boyer and MgPherson, 1976; Eck, 1986; Grant et al. (1989).

Heinigre (2000) reported that plant growth from V8 to V16 (all leaves emerged, start of tasseling; from 4 weeks to 66 days after plant emergence) determines ear size and the number of kernels set. From V8 to V14, ear size is set. Drought during this period will reduce ear size and potential yield. Potential yield losses could range from 10 percent

to 30 percent. From V14 to tasseling, the number of kernels that can be fertilized are determined. Drought during this period can reduce maize yields 10 to 50 percent. Throughout the V8 to V16 period the key question is how long the drought stress is present.

Water stress during grain-filling increases leaf dying, shortens the grain-filling period, increases lodging and lowers kernel weight. Water stress during grain-filling reduces yield 2.5 to 5.8 percent with each day of stress. Kernels are most susceptible to abortion during the first two weeks following pollination. Kernels near the tip of the ear generally are last to be fertilized and are less vigorous than the rest, so they are most susceptible to abortion. Once kernels have reached the dough stage of development, further yield losses will occur mainly from reductions in kernel dry weight accumulation (Lauer, 2003).

The physiological and biochemical effects discussed thus far operate in the protoplast. Thus, there has been a lively interest, especially among European physiologists, in the effects of dehydration on the physical condition of the protoplasm itself, especially permeability and viscosity. Their ideas are set forth in reviews by Iljin (1957), Stocker (1960), and Henckel (1964). Stocker stated that dehydration occurs in two stages: first the reaction phase and than the restitution and hardening phase. The reaction phase is characterized by increased permeability to water, urea, and glycerol, increased proteolysis, and increased respiration. If water stress continues, there is a restitution phase involving increased viscosity, decreased permeability to water and urea,

and decreased respiration. This course of events is said to occur during gradual dehydration, and if it does not go too far the processes are reversible.

Water is a major limiting factor affecting plant growth, development and yield mainly in arid and semiarid regions where plants are often exposed to periods of water deficit stress also known as drought stress. Drought is one of the major causes for crop loss worldwide, reducing average yields with 50% and over (Wang et al., 2003).

In maize, the reduction in grain yield caused by drought ranges from 10 to 76%, depending on the severity of the drought and the growth stage at which it occurs (Bolaoos et al., 1993). Although total root length influences water and nutrient uptake, maintenance of roots that are viable and active in water and nutrient uptake during drought may be more important for plant tolerance to drought (Huang et al., 1997).

2.2 Drought tolerance in maize

Tolerance to drought in crops depend on an ability of plants to (i) avoid the condition of water stress by adaptive mechanisms such as closure of stomata to prevent water loss or deep rooting to find water deeper in the soil, (ii) escape water stress by early maturity, and (iii) able tolerate lower water potential in the cell, and (iv) recover from transient water stress (Levitt, 1980; Fukia and Cooper, 1995). Under drought condition the plant tries to avoid drought, but low tissue water potential still occur especially during the reproductive phase. Therefore it is necessary to distinguish the drought tolerance mechanism that enable the protoplasm to survive and allow the plant to recover from stress after rain and those that enable the plant to adapt to low tissue (by osmotic adjustment). Drought can also cause significant changes in the diurnal courses of

transpiration and CO_2 assimilation. During the course of a year, one peaked curves of CO_2 uptake and water loss change with increasing atmospheric and soil drought into two-peaked patterns (Stocker, 1960; Schulze *et al.*, 1975a). Roots are the most important for plant adaptation to soil water deficits, which was supposed to take up water and necessary solutes from the soil (Turner 1979).

2.2.1 Mechanisms of drought tolerance

Plants can adapt to water stress by increasing root depth and root density, which enhance the ability of the root system to extract soil water. Blum (1982) reported that high root mass production in rice was associated with drought resistance. Begg (1980) and Tanguilig *et al.* (1987) also indicated that an increase in available assimilates resulting from the reduction in shoot growth permits osmotic adjustment and additional root growth.

Bolanos *et al.* (1993) found that increases in grain yield under drought were associated with reduced root biomass in the upper 50 cm of the root profile in tropical maize population.

The traits of plants can resistance more than one mechanism at the time drought occurs (Mitra, 2001).

Drought escape is defined as the ability of a plant to complete its life cycle before serious dry soil and plant water deficit develop (Mackill *et al.*, 1996). This mechanism for drought escape involves rapid phonological development (early flowering and early maturity), developmental plasticity (variation in duration of growth period developing on the extent of water-deficit), and remobilization of pre-anthesis assimilates to grain. The

differences in the timing and severity of drought in association to the timing of plant growth and development are used as the basic for category in to different types of drought (Pantuwan *et al.*, 2002).

Drought avoidance is performed by increasing rooting depth, efficient root system and increase hydraulic conductance uptake maximum water and by reduction of water loss through reduced epidermal (stomatal and lenticular) conductance, reduced absorption of radiation by leaf rolling or folding, and reduced evaporation surface (leaf area) (Lebreton *et al.*, 1995; Courtois *et al.*, 2000). The varieties with a high deep root weight to shoot weight ratio exhibit enhance drought avoidance.

Begg (1980) and Tanguilig *et al.* (1987) also found that an increase available assimilates resulting from the reduction shoot growth permits osmotic adjustment and additional root growth.

2.2.2 Genotypic variation in drought tolerance (in maize, in other crops)

The yield performances of genotypes grown under water stresses are reflective of both plant responses to stress and of potential yield levels. Four main aspects of behavior relative to drought that can be linked with yield are modification of leaf area, root growth, efficiency by which leaves exchange water for CO2, and processes involved in setting and filling of seeds (Passioura, 1994).

Ribaut *et al.* (1997) reported that maize is susceptible to drought at flowering stage than any other crop. Baenziger *et al.* (2000) reported that drought leads to reduced leaf, silk, stem, root and grain development. Maize is very sensitive to drought. It is exposed to more hazards and it is a higher risk crop in general (Misovic, 1985). Drought

is an important climatic phenomenon, which after soil infertility, ranks as the second most severe limitation to maize production (Sallah *et al.*, 2002). Roots are usually the site of highest resistance in pathways for liquid-phase movement of water through the soil-plant --atmosphere continuum (Kramer and Boyer, 1995). Efficiency of soil water uptake by roots is the key for determining rates of water transpiration and plant tolerance to drought. Water uptake by roots is complex and depends on structure, anatomy and pattern by which different root parts contribute to overall water transport (Cruz *et al.*, 1992). Salih *et al.* (1999) reported that drought tolerance was associated with higher water extraction efficiencies, fewer nodal roots per plant, fewer late metaxylem vessels per nodal roots, smaller leaf areas, and more well-developed sclerenchyma cell.

For early maturing cultivars often have higher grain yields than late maturing cultivars when drought occur, because late maturing cultivars suffer drought stress during productive or grain filling growth periods, while early maturing cultivars are able to escape drought during these critical growth periods. Drought resistance mechanisms in crop plants are often related to physiological traits or processes. Some of these are (a) moderated water use through reduced leaf area and shorter growth duration, (b) ability of root to exploit deep soil moisture to provide for evapotranspirational demands, (c) capacity for somatic adjustment in leaf cells so they can retain turgor and protect meristems from extreme desiccation, and (d) control of nonstomatal water lostses from leaves (Nguyen *et al.*, 1997).

In addition, genetic variation exists in and among plant species for dehydration avoidance (maintenance of relatively high leaf water potentials under conditions of soil

moisture stress), osmotic adjustment, tolerance in plant or organ growth rate, plant recovery upon rehydration, tolerance of photosynthetic systems or their components, tolerance of enzyme activities, tolerance of translocation systems, stability of cellular membranes, proline accumulation, root growth attributes, plant development or moephological attributes, leaf area per plant, leaf orientation, tiller survival, and organ pubescence (Blum, 1983).

Cultivating tolerant genotypes is the most attractive approach to attenuate the negative effects of drought on crop production. Drought escape, dehydration avoidance and drought tolerance are the plant strategies to crop with physiological events associated with drought (Blum, 1988).

The mechanisms can involve different cell pathways resulting in the expression of stress-response genes. Drought tolerance of a crop is seen as the minimum difference in yield between stress and non-stress environments (Fischer and Maurer 1978; Langer et al. 1979). It is also defined as the relative yield of a genotype compared with other genotypes subjected to same drought stress (Hall *et al.*, 1993).

Significant difference of drought tolerance among maize germplasms implicates the hope of improving production of maize varieties under drought stress. However, breeding for drought tolerance is particularly challenging because of the genetic complexity of this trait, the variability in the timing and severity of drought, and the strong genotype by environment interactions that affect trait phenotype (Edmeades *et al.* 1993; Fu *et al.* 2008).

Senthong and Pandey (1989) found that in medium and late maturity genotypes showed the less value of drought susceptibility index tended to have a higher grain yield and tolerated greater water stress than the short maturity ones. Manupeerapan *et al.* (1997) also demonstrated that drought tolerance maize genotypes produced the largest value of drought index and had a relatively short anthesis-silking interval.

Drought tolerance is believed to be the result of cooperative interactions among multiple morphological, physiological and biochemical characters. Moreover, different genotypes may have different responses to drought stress (Bohnert *et al.* 1995; Bray 1997; Jia *et al.* 2006; Ludlow and Muchow 1990; Shinozaki and Yamaguchi-Shinozaki 1997).

Muir et al., (1992; Cooper and Delacy (1994) and Cooper et al., 1996b) reported that, the genotype by environment (GxE) interaction variance component can be partitioned in to important components: (i) heterogeneity of genetic variance among environments and (ii) lack of genetic correlation among environments.
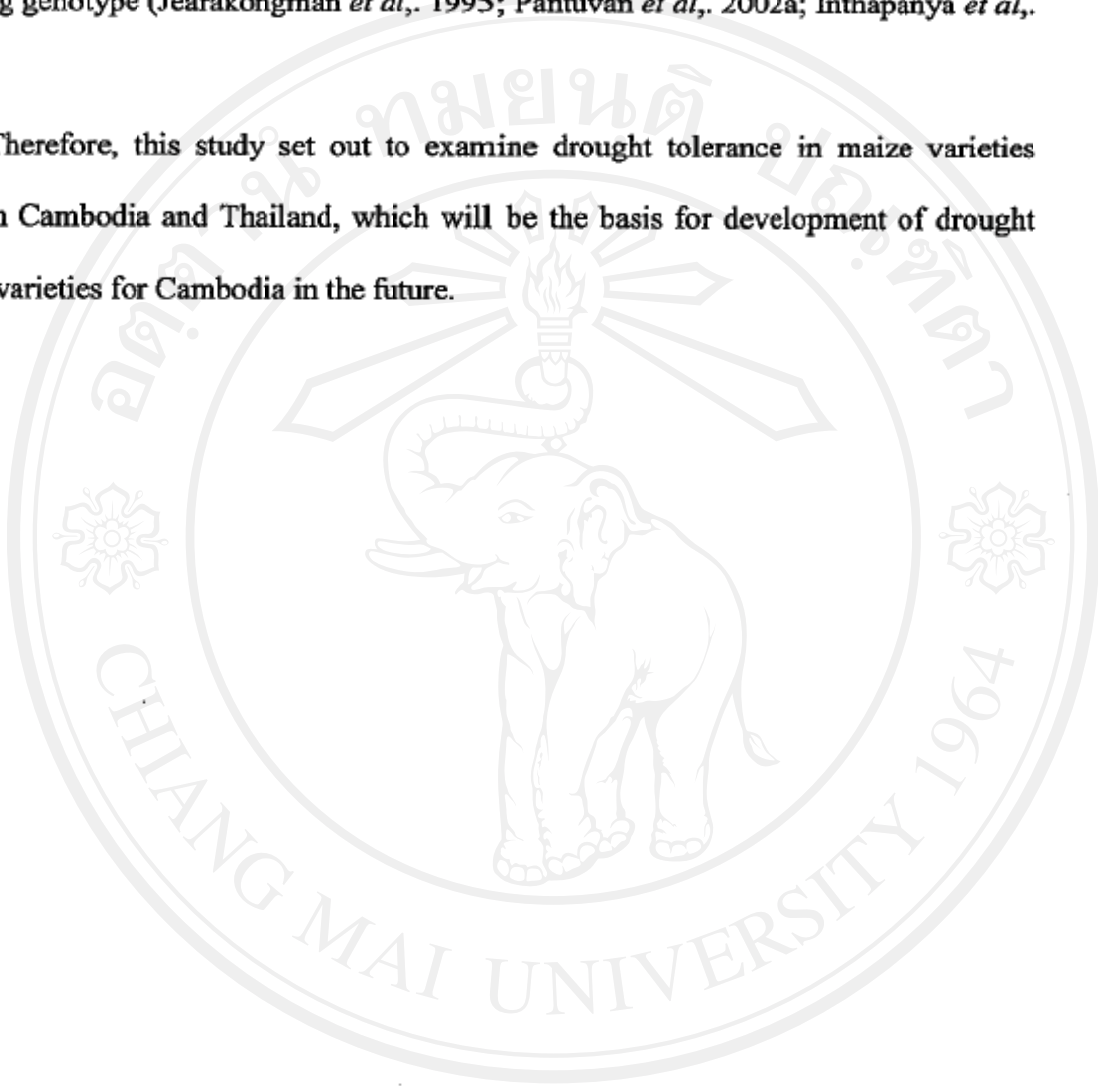
Fukai and Cooper (1995) suggested that the timing and intensity of drought determines the effect of drought on crop yield observed in muti-environment trials.

Cooper and Somrith (1997) evaluated 62 rice genotypes under rainfed lowland and under condition at 13 sampling sites in Thailand and Laos. Thy found a large effect of GxE interaction, which were mainly explained by genotypic variation for flowering time and environmental variation in the timing and severity of drought.

In rainfed lowland rice, flowering time plays an important role in determining grain production, particularly when late season drought develops. Under such drought

conditions, grain yield of late flowering genotypes are more affected than the early flowering genotype (Jearakongman *et al,.* 1995; Pantuvan *et al,.* 2002a; Inthapanya *et al,.* 1997).

Therefore, this study set out to examine drought tolerance in maize varieties grown in Cambodia and Thailand, which will be the basis for development of drought tolerant varieties for Cambodia in the future.