LITERATURE REVIEW

Adaptive Response of Plant to Water Stress

Morphological Responses

One of the most important responses of crops to water deficits is marked reduction in leaf area. A reduction in leaf area could result in a reduction of the transpiring surface (Begg,1980). Reduction increased leaf senescence which results in less water use (Turk and Hall, 1980). 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).

Water stress reduces leaf area by accelerating the rate of senescence of the physiologically older leaves (Begg, 1980). Hall *et al.* (1979) reported that leaf senescence in cereals could confer an adaptive advantage if it was accompanied by a substantial reduction in transpiration because the old shaded leaves which senesce first supplied relatively little carbohydrate to the developing grain. Hsiao *et al.* (1984) also attributed that water stress accelerated the senescence of lower leaves in maize, and cultivars with increased capacity for osmotic adjustment have shown to have delayed leaf senescence under drought. Wolfe *et al.* (1988) found that senescence was influenced by the balance between water and N supply, and the demands for water (as affected by canopy size) and N (as affected by reproductive sink size).

Plants 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. Bolaños *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 one tropical maize population.

Physiological Responses

Stomatal closure occurs when leaf water potential decreases, especially during water deficit. However, for the stomata to close, the leaf water potential must drop to a critical threshold value. Critical threshold values of leaf water potential which can induce stomatal closure in maize are about -0.9 to -1.0 MPa (O'Toole and Cruz, 1980) and -0.81 to -0.96 MPa (Neumann *et al.*, 1974), while field data show values of -1.6 MPa (Turner, 1974) and -1.9 MPa (Bolaños *et al.*, 1993). Boyer (1970) found that at leaf water potential below -0.4 MPa, enlargement was completely suppressed in sunflower, but continued at low rates in soybean and maize. Moreover, stomata on the upper surface of leaves are more sensitive to water stress than those on the lower surface and leaf resistances are also higher for the upper than the lower surface. (Soinit and Kramer, 1976).

Plant temperature may be a valuable index with which to differentiate plant water regimes. Increases in canopy temperature have been correlated with declines in leaf relative turgidity (Wiegand and Namken, 1966), soil water content (Bartholic *et al.*, 1972) and leaf water potential (Blum *et al.*, 1982 ; Ehrler *et al.*, 1978 ; Pandey *et al.*,1984a). Furthermore, a linear negative relationship has been established between canopy temperature elevations and grain yield of maize under stress (Clawson and Blad, 1982). Pandey *et al.* (1984b) suggest that genotypes which maintain a cooler canopy in a dry environment will be able to maintain their physiological function to thereby produce higher seed and dry matter yield. Leaf temperature differences, measured by portable hand-held infrared thermometer, have been used to provide an indirect field measure of dehydration avoidance and plant water status in several crop breeding programs (Jackson, 1982 ; Blum, 1988 ; Bolaños *et al.*, 1993). The principle of the technique is that when stomates close because of reduced leaf water status, leaf temperature rises above ambient air temperature (Ludlow and Muchow, 1990).

Growth Analysis as Related to Water Stress

Assimilate produced from photosynthesis was normally used for growth of plant organs, and some of it is stored in vegetative parts and then translocated into seed (Yoshida, 1972). Growth analysis is a set of procedures the following in the dynamics of growth and yield in terms of dry weight and leaf area measured by sequential sampling at different growth stages (Gardner *et al.*,1985). Growth analysis parameters in terms of crop growth rate (CGR), leaf area index (LAI), specific leaf weight (SLW) ; leaf area duration (LAD) , have been used to describe the responses of several crop plants to drought stress (Pandey *et al.*, 1984b).

The effects of water stress on crop growth rate have been reported in several crops, including grain legumes (Pandey *et al.*, 1984b), soybean (Senthong *et al.*, 1986), mungbean (Pandey *et al.*, 1988) and maize (Bennett and Hammond, 1983). Senthong *et al.* (1986) indicated that cultivars which had a high CGR, tended to produce a high yield in the dry environment and had high partitioning efficiency of photosynthate into seed.

Several reports have suggested that reductions in leaf area may be responsible for a drought-induced reduction in seed yield (Boyer, 1970 ; Legg *et al.*, 1979 ; Rawson and Turner, 1982). Increasing moisture stress resulted in progressively less LAI (Wien *et al.*, 1979 ; Pandey *et al.* 1984b ; Wolfe *et al.*, 1988). The relationship of LAI to seed yield under water stress has been shown in cowpea (Turk and Hall, 1980), soybean (Senthong *et al.*, 1986) ; grain legumes (Pandey *et al.*, 1984b) and maize (Bennett and Hammond, 1983 ; Wolfe *et al.*, 1988).

Field studies with maize demonstrated a correlation between LAD during grain filling and yield (Wolfe *et al.*, 1988). Fischer and Kohn (1966) showed that the yield of wheat under dryland conditions was inversely related to the LAD after anthesis which, in turn, was related to the plant water deficit. Pandey *et al.* (1984b) found that the larger LAD in peanut was due to less leaf senescence, while early leaf senescence was prominent in soybean. The differences in LAD were primarily due to leaf senescence, leaf area, and crop duration (Pandey *et al.*, 1984b).

SLW increased with increasing levels of water stress (Turk and Hall, 1980 ; Pandey *et al.*, 1984b). Change in SLW due to drought has proviously been reported in cowpea (Turk and Hall, 1980), grain legumes (Pandey *et al.*, 1984b) and desert shrubs (Fischer and Turner, 1978). SLW changes were used to indicate that leaf thickness appeared to be an adaptive mechanism to drought (Pandey *et al.*, 1984b).

Effect of water stress on yield and yield component of maize

The level of yield reduction by a water deficit will depend on the degree, duration, and timing of the deficit and on the proportion of the total yield that comprises the economic yield of the crop (Begg and Turner, 1976). Studies on the timing of drought stress have indicated that drought imposed at flowering can result in a 50% or greater yield reduction in maize (Boyer and McPherson, 1976 ; Eck, 1986 ; Grant *et al.*, 1989) and that the flowering stage is very susceptible to stress. It has been shown that the vegetative growth and grain filling are also sensitive to drought, but to a much less degree. Eck (1986) found that drought imposed during vegetative and grain filling stage resulted in reduction of 46 and 33 % ,respectively, in seed yield. However, it is difficult to compare these figures because stress itself is difficult to quantify.

Water deficits during flowering stage could result in reduced kernel number due to the effect of carbohydrate deprivation on sterility of the female gametophyte (Westgate and Boyer, 1986 ; Grant *et al.*, 1989). Schussler and Westgate (1991) found that a large proportion of the kernel loss may be explained by lack of current assimilate production. Kernel development could depends on remobilization of reserves, at low leaf water potential but the ear is a weak sink and cannot attract stored assimilates. Although increasing the level of carbohydrate reserve under field conditions has not proven beneficial, selecting for rapid ear or ovary growth during pollination may be an affecting method for increasing grain yield of maize in areas of recurrent drought stress (Schussler and Westgate, 1995).

Nitrogen Partitioning in Maize

The morphological and physiological responses of maize to continuous stress caused by low N include reductions in plant size, leaf area, radiation-use efficiency, accelerated senescence, delayed silking, reduced ear biomass, increased mobilization of vegetative N to developing kernels, and reduced plant N concentration (Lemcoff and Loomis, 1986 ; Muchow, 1988a ; Muchow, 1988b ; Muchow and Davis, 1988 ; Lafitte and Edmeades, 1994 ; Uhart *et al.*, 1995).

In the case of maize, such reduction in N application rate may lead to reduced yield as the result of N deficit during ear development. During reproductive growth of maize, there are two sources of N for kernel development : concurrently absorbed N from soil and remobilized N from vegetative tissues. Under conditions of low N fertility, however, available soil N is in short supply during grain filling (Ta and Weiland, 1992), remobilization of N from vegetative tissues becomes particularly important for kernel growth.

In maize, translocation of nitrogen from one plant part to another occurred to a significant extent only after grain formation began. About one-half of the nitrogen in the grain at maturity appeared to have been translocated from other above ground plant parts (e.g., the cob, husk, stalk and leaves) (Hanway, 1962). Thus, the stalk is an important reserve of nitrogen for grain development (Beauchamp *et al.*, 1976, and Ta and Weiland, 1992).

CERES-Maize model

Crop growth model is developed as a tool for studying in responses to the environment and to management. They are useful to decision makers and those who analyse to risk of crop cultivation in a given area. The CERES-Maize model , developed by Jones and Kiniry (1986) , is one of the CERES family of cereal crops models which include rice, wheat, perl millet, sorghum and barley. The CERES-Maize model like other cereal models requires input data, namely daily weather data, soil data, crop management data and genetic coefficient parameters (Jones *et al.*, 1994). The CERES-Maize model allows the quantitative determination of growth phenology and yield of crops. Its features involve predicting the phase of development, biomass production and partitioning, root system dynamics, yield, soil water balance, carbon balance and nitrogen balance (Jones *et al.*, 1994 ; Jongkaewwattana, 1995). It has been used successfully in several countries (Piper and Weiss, 1990 ; Agrotechnology Transfer, 1992).