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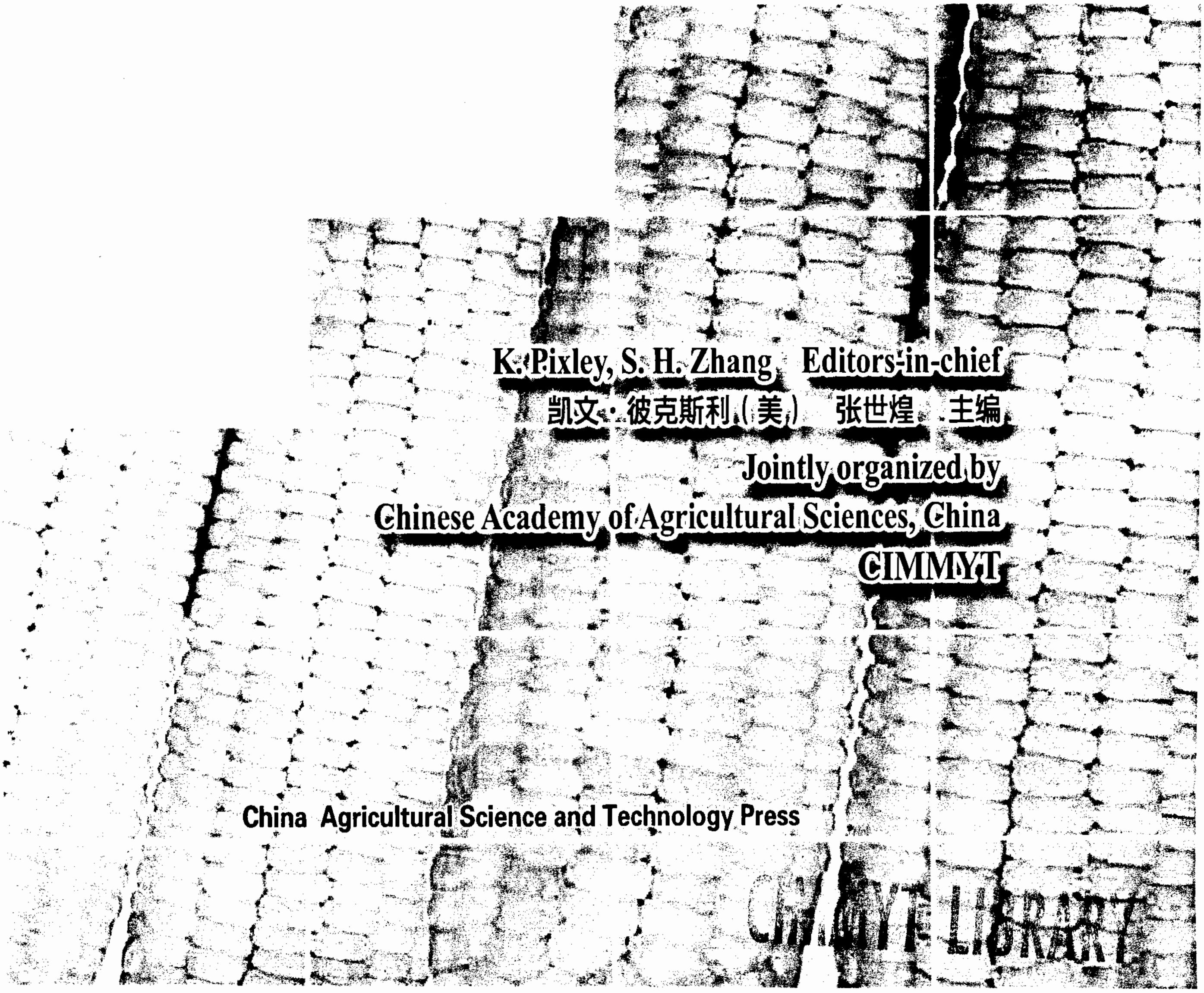

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Physiological Basis of Excessive Soil Moisture Tolerance in Tropical Maize

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Abstract: Response of maize plants to excessive moisture (EM) stress has been studied extensively; however, systematic information on the cascade of events conferring the EM tolerance is yet to be established. This study was undertaken to assess the stress-adaptive physiological changes associated with EM-induced anoxic conditions, and to establish mechanisms of EM tolerance in tropical maize. Tropical/sub-tropical elite maize inbred lines with different genetic backgrounds were used in this study. Germplasm were exposed to EM stress at knee-high stage (V7) by flooding field plots continuously for seven days. EM-induced changes in root geotropism (surface rooting) and increased brace root development were identified as stress-responsive traits, however, only the latter was found to be a stress-adaptive trait resulting in improved tolerance to the stress. Anatomical studies showed drastic changes in the cortical region of root tissues in tolerant genotypes involving the formation of large aerenchymatous spaces. With regard to stress-induced metabolic changes, increased NAD^+-alcohol dehydrogenase (ADH) activity was prevalent in all the genotypes under EM conditions. Although the ADH activity was slightly higher (not statistically significant) in tolerant entries, the product of ADH-activity (ethanol) was relatively much higher in root and leaf tissues of susceptible genotypes. Analysis of ethanol concentration in shoot, root and inundated water showed that the level of ethanol was relatively much higher in the water present in rhizosphere of relatively tolerant genotypes. This finding suggests that EM-tolerant maize genotypes were able to extrude the toxic level of ethanol from root tissues to the rhizosphere. Our findings suggest that mechanisms of EM-tolerance in maize involve morphological and anatomical adaptation through development of brace roots and aerenchyma formation, and metabolic adjustment through regulatory induction of alcohol dehydrogenase (ADH) and extrusion of ethanol out of root tissues.

Key words: Maize, Zea mays, Excessive moisture, Water-logging, Tolerance mechanism

Introduction

In the tropics, maize crops grown during *Kharif* (rainy) season frequently face extreme climatic conditions and various biotic/abiotic pressures that limit yield potential. Among the abiotic stresses, excessive soil moisture caused by contingent/intermittent flooding or water-logging is one of the most important constraints for maize production in the Asian region. In South and SE-Asia alone, over 15% of the total maize growing area is affected by floods and water-logging problems (Rathore *et al.*, 1997). In India, out of a total of 6. 6 million ha of maize, over 2. 5 million ha are prone to excessive moisture conditions, which causes on average 25% ~ 30% loss of the national maize production almost every year.

The extent of damage due to excessive moisture (EM) stress varies significantly with developmental stage; however, considerable genetic variability has been identified in maize (Rathore *et al.*, 1997; Zaidi *et al.*, 2003). The response of maize plants to excessive moisture stress has been studied extensively. At the physiological level, anoxia affects phytohormone homeostasis (Jackson, 1990); affects plant morphology and anatomy (Jackson, 1990); resulted in stunted growth, considerably reduced dry matter accumulation, leaf area development, transpiration, prolonged anthesis-silking interval (ASI) and eventually resulted in poor grain yields (Rathore *et al.*, 1997; Zaidi *et al.*, 2003). However, systematic information on the cascade of events conferring the stress tolerance is not yet established, which is essentially required for genetic enhancement of tropical maize germplasm for improved tolerance to excessive moisture situations. In the present study, we attempted to identify various stress-adaptive changes in the relatively tolerant maize genotypes and their importance in overall performance of the germplasm under excessive moisture stress.

Materials and Methods

The experiment was conducted during *Kharif* (rainy season) 2003 and 2004 at maize research farm, Indian Agricultural Research Institute, New Delhi, India. A total 25 inbred lines were selected from the line evaluation trials conducted on tropical/subtropical lines (S_4-S_n) during the past five years (1998 ~ 2003) to identify the tolerant sources of germplasm for EM-stress. Of the 25 inbred lines selected for this study, 10 were highly susceptible, 7 moderately tolerant and 8 lines (CML-327-4-2-1-3, WL-7-*-*-1, WL14-*-*-1, WL15-*-*-2, WL28-*-*-2, WL29-*-*-2, CML-311-2-1-3-B, CML-425-3) were known for their repeated performance as highly tolerant to EM stress. Entries were grown using cups in which they were exposed to excessive soil moisture from planting until 20 days after sowing (Zaidi *et al.*, 2003). One complete set of the entries was grown under normal moisture conditions. Simultaneously, all the entries were planted in 4-row plots, 3.0 m row length, 0.75 m row-to-row distance, and 0.25 m plant-to-plant distance. The field experiment was planted using a completely randomized block design (RCBD) with three replications. The excessive moisture treatment was applied at knee-high (V7) stage, and consisted of imposing an average ponding depth of 10.0 ± 0.5 cm for 7 days.

Observations on various morphological traits were recorded one week after the completion of the EM stress treatment. Surface rooting was scored using 1 ~ 5 scale (1 = poor to 5 = extensive). Root porosity was measured in underground adventitious roots using the pycnometer method (Noordwijk and Brouwer, 1988). Data on final grain yield were recorded at 15% moisture at harvest. Sampling for ADH-activity and leaf/root ethanol concentrations was done on alternate days, starting from the first day of waterlogging and continuing until 8 days after the stress treatment. Sampling for ethanol concentration was also done on alternate days on the plants exposed to EM stress during "cup screening" and in water samples from the trays holding the cups, starting from the 5th day after planting and continuing until the 21st day.

Analysis of variance was computed using MSTATc with completely randomized block design (2-factors) for the cup experiment and randomized complete block design (2-factors) for the field experiments. For all experiments, data from two years were pooled on the basis of test for homogeneity of error variance of the two-year datasets using Hartley's Fmax test (Ott, 1988). Correlation coefficients and linear regression between secondary traits and grain yield were also computed using MSTATc.

Results

Under excessive moisture conditions a drastic change in root geotropism, i. e. root growth toward the soil surface has been observed in some maize genotypes. Within 2 ~ 3 days of waterlogging in the field a large number of root tips (white tips) were visible around the maize plants. However, the white root tips were relatively more numerous around the plants of susceptible genotypes. The surface rooting might have some temporary role in coping with excessive moisture stress because the visible root tips and shallow roots are under hypoxic rather than anoxic condition, and therefore, may maintain partial aerobic respiration. After the EM stress ended, however, such changes in root geotropism resulted in highly inefficient root systems to support further growth and development of plants (data not shown), and probably have little relationship with yield under EM-stress (Figure 1). In the tolerant genotypes surface rooting was negligible, rather these genotypes responded to EM stress with initiation of aboveground nodal roots. EM-induced nodal roots in maize genotypes have been found to have large air-spaces in their cortical region, which increase root porosity and help increase the supply of oxygen, nutrients and water, and improve anchorage where severe damage of primary roots under excessive moisture has already occurred (Zaidi *et al.*, 2004). In maize, formation of aerenchyma is not a constitutive trait; rather it seems to be a stress-adaptive trait that develops with exposure to excessive moisture stress (Zaidi *et al.*, 2003). Analogous to brace roots, expression of this trait as well was nominal under normal moisture condition, which indicates that it is a stress-induced trait and an adaptive strategy to excessive moisture stress. Root porosity was strongly related to grain yield under excessive moisture stress (Figure 1).

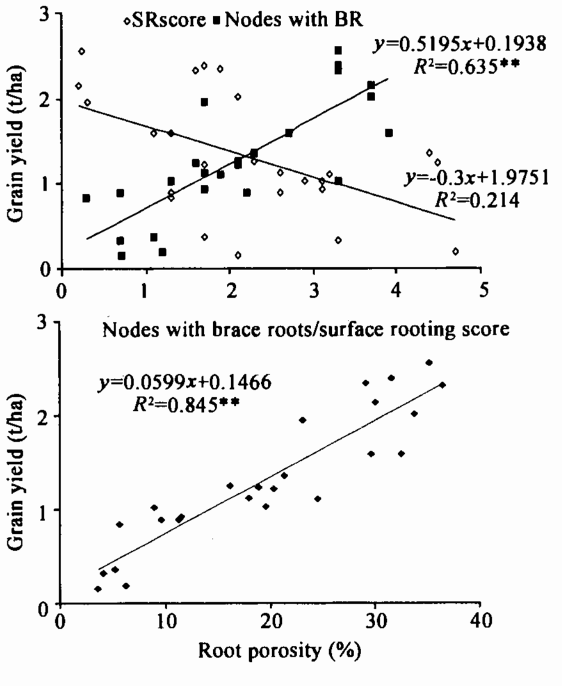

Figure 1 **Grain yield as a function of mean surface rooting score, nodes with brace roots and root porosity in maize inbred lines exposed to excess moisture stress conditions at V7 growth stage**

*** * indicates statistical significance at $P < 0.01$**

Data on ADH activity revealed that the enzyme activity was nominal under normal moisture for both tolerant and susceptible germplasm. However, under excessive moisture conditions there was many-fold increase in ADH activity in both susceptible and tolerant genotypes (Figure 2). ADH activity was slightly higher for tolerant lines as compared to susceptible lines, but this difference was statistically non-significant. Ethanol concentration, both in root and leaf tissues, was comparatively much higher in susceptible genotypes than tolerant ones (Figure 2). Daily monitoring of ethanol in root, shoot and inundated water in cup screening showed that the amount of ethanol in water was comparatively much higher with tolerant entries than susceptible ones. These findings indicate that ethanol was extruded from the roots of tolerant germplasm to the growth medium, which explains the low ethanol concentration in root and particularly in leaf tissues of tolerant entries, in spite of slightly higher ADH activity in these genotypes.

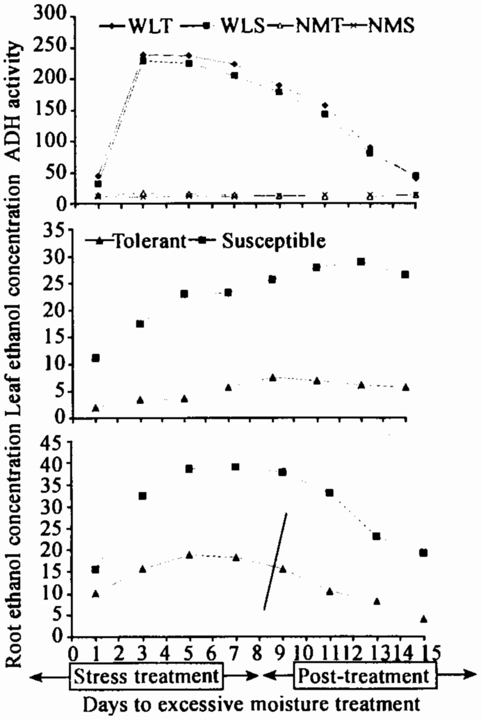

Figure 2 **NAD$^+$-alcohol dehydrogenase activity (unit^{-1} mg protein min^{-1}) and ethanol concentration (μmol/g) in leaf and root tissues of maize inbred lines during excessive moisture stress applied at V7 stage**

Our studies suggest that mechanisms of excessive moisture tolerance in maize involve morphological adaptation through nodal root development, anatomical adaptation through aerenchyma formation in cortex region, and metabolic adjustment through regulatory induction of alcohol dehydrogenase and excretion of toxic level of ethanol from root tissues. However, the contribution of each mechanism, and genotype × environment interactions for the adaptive-responses need to be further investigated.

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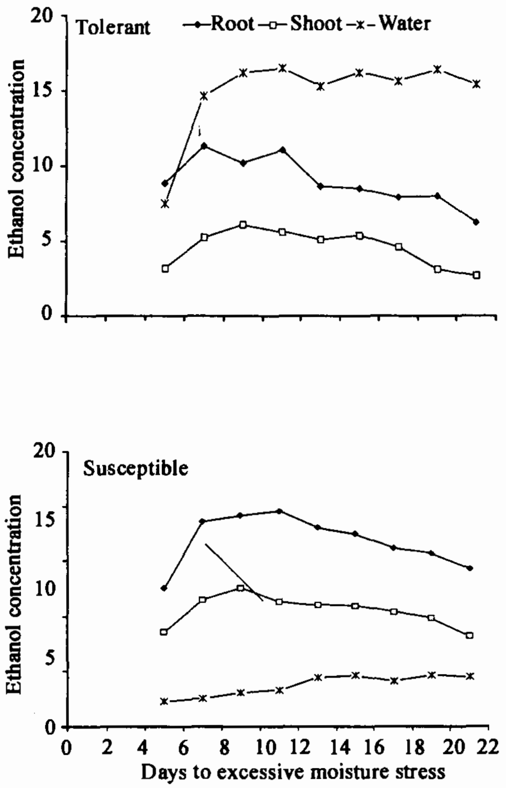

Figure 3 Ethanol concentration(μ mol/g) in shoot, root and water in rhizosphere of maize inbred lines exposed to excessive soil moisture stress at early growth stage using cup method

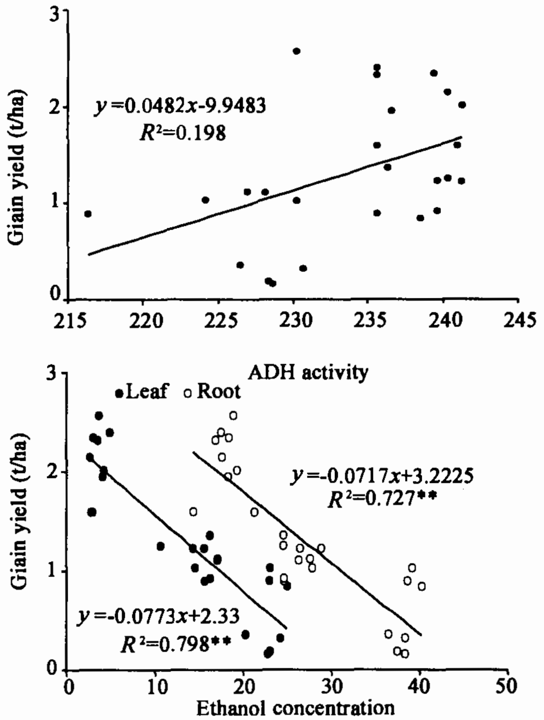

Figure 4 **Grain yield as a function of NAD$^+$-alcohol dehydrogenase activity (unit^{-1}mg protein min^{-1}) and ethanol concentration (μ mol/g) in leaf and root tissues of maize inbred lines exposed to excess moisture stress under field conditions at V7 growth stage**

*** * indicates statistical significance at $P<0.01$**