Responses of Different Physiological Indices for Maize (*Zea mays*) to Soil Water Availability*1

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ABSTRACT

Knowledge of plant responses to soil water availability is essential for the development of efficient irrigation strategies. However, notably different results have been obtained in the past on the responses of various physiological indices for different plants to soil water availability. In this study, the responses of various plant processes to soil water availability were compared with data from pot and field plot experiments conducted on maize (*Zea mays* L.). Consistent results were obtained between pot and field plot experiments for the responses of various relative plant indices to changes in the fraction of available soil water (FASW). A threshold value, where the relative plant indices began to decrease with soil drying, and a lower water limit, where the decline of relative plant indices changed to a very slow rate, were found. Evaporative demand not only influenced the transpiration rate over a daily scale but also determined the difference in transpirational response to soil water availability among the transient, daily and seasonal time scales. At the seasonal scale, cumulative transpiration decreased linearly with soil drying, but the decrease of transpiration from FASW = 1 in response to water deficits did not affect dry weight until FASW = 0.75. On the other hand, the decrease in dry weight was comparable with plant height and leaf area. Therefore, the plant responses to soil water availability were notably different among various plant indices of maize and were influenced by the weather conditions.

Key Words: dry weight, evaporative demand, fraction of available soil water, plant growth, transpiration


INTRODUCTION

On the semi-arid Loess Plateau of China, maize (*Zea mays* L.) is a major irrigated crop. Since irrigation water comes from diversions or dams on the Yellow River, which has had recurrent and increasingly low flow volumes in recent years, irrigation water needs to be used efficiently to avoid serious water shortages in this area. Knowledge of plant responses to soil water availability is essential for the development of sustainable agriculture on the Loess Plateau.

Soil water deficits are often the greatest constraint on plant growth and, consequently, research on soil water availability to plants has attracted considerable interest. Available soil water is generally considered to be the amount of water held by a soil between its field capacity (FC) and permanent wilting point (PWP). A number of studies have examined changes in soil water availability in the range of FC to PWP. Veihmeyer and Hendrickson (1950) stated that the soil water availability to plants was the same over the entire range of FC to PWP based on their yields. However, Richards and

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Response to soil water availability of different physiological indices is variable due to their dissimilar water stress sensitivities. Sadras and Milroy (1996) reviewed published threshold values for various physiological indices and found that threshold values for tissue expansion were higher than those for gas exchange, including transpiration and photosynthetic rates. Nable et al. (1999), Soltani et al. (2000), and Casadebaig et al. (2008) observed the same phenomenon when studying threshold values of sugarcane (Saccharum spp. cv. Q115) and sorghum (Sorghum bicolor L.), chickpea (Cicer arietinum (L.) Moench s. lat.), and sunflower (Helianthus annuus L.), respectively. However, Lecoeur and Sinclair (1996) reported that transpiration and leaf area expansion had the same threshold values for peas. Furthermore, Lecoeur and Guillon (1998) obtained smaller threshold values for leaf production than those for transpiration and leaf area expansion. Due to plant responses to soil water availability being different for different species or cultivars and experimental conditions such as soil texture (Erickson et al., 1991; Robertson and Fukai, 1994) and evaporation demand (Denmead and Shaw, 1962; Novák et al., 2005), these results are difficult to compare directly and to use as guides for water management of other plants. Therefore, studies are needed to be done to assess the responses of a wide range of physiological indices to soil water availability for the same soil and plant type, and to explain the differences among various indices.

The objectives of this study were to compare different physiological processes occurring in maize in response to induced soil water deficits, and to define irrigation strategies for a more efficient use of water. The plant physiological indices selected for this study were plant growth indices, including increments in plant height, leaf area and dry weight, and transpiration indices including daily plant transpiration rate, leaf transient transpiration rate and cumulative transpiration.

MATERIALS AND METHODS

Site description

The study was conducted at the Irrigation Experiment Station, Northwest A & F University, Shaanxi Province, China (34° 20' N, 108° 24' E). The test maize cultivar was Zhengdan 958. The soil was a silt loam soil belonging to the loess series (Zhu, 1989) with the sand, silt and clay contents of 55.9, 665.5 and 278.6 g kg⁻¹, respectively; soil bulk density and particle density of 1.35 and 2.65 g cm⁻³; organic content of 10.46 g kg⁻¹; and the FC and PWP values of 0.28 and 0.12 cm³ cm⁻³. The FC value was estimated for a corresponding pressure head of −0.06 × 10⁶ Pa from soil water characteristic curves determined in this study, and the PWP values was defined for a pressure head of −1.5 × 10⁶ Pa.

Pot experiment

A pot experiment was conducted in an open-sided greenhouse with a glass roof in 2008. Maize seeds were sown on July 15 in 18 pots uniformly packed with 10 L of silt loam soil at a bulk density of 1.35 g cm⁻³. Nitrogen (0.7 g N L⁻¹ soil) was mixed with the soil before packing, and the soil surface was covered with a layer of 80 g of perlite gravel to reduce soil evaporation. In order to avoid soil crusting, irrigation water was provided through a supply tube (2 mm inner diameter) inserted from the soil surface down to a depth of 5 cm above the bottom of the pot. After three leaves had expanded, two viable plants were established in each pot. The water regimes were soil water contents established as a fraction of the field capacity: 90% to 100% (WC1), 80% to 90% (WC2), 75% to 80% (WC3), 65% to 70% (WC4), 60% to 65% (WC5), and 50% to 60% (WC6). Initially, all the pots were kept well-watered. From August 23 in the jointing stage, soil water treatment levels were created by either drying or adding water to reach the intended soil water content for each
pot. Once the soil water content of the most stressed water treatment (WC6) was reached on September 6, all pots were weighed and water was added to maintain the desired water contents at intervals of two to five days. Before and after irrigation, soil water contents in each pot were also determined using the weighing data.

Field plot experiment

Due to lower available soil volume, the rooting environment in pots may differ from that in the field in a number of ways including soil temperature, water availability and nutrient efficiency (Townend and Dickinson, 1995; Hurley et al., 1998), which could have significant effects on plant physiology. So a field experiment was also conducted with six elementary plots. The plots were arranged in two rows with three elementary plots in each row. A rainout shelter, open-sided with a glass roof, covered the entire plot area in order to prevent the addition of rainwater to the soil. Each plot measured 1.0 m × 0.8 m × 1.5 m (length × width × depth) and was bordered by a cement wall to prevent water exchange between adjacent plots. The base of each plot was sealed with an impermeable cement layer to prevent water flow into the subsoil and covered by a 10 cm layer of coarse sand, where a pipe facilitated water drainage from the plot. Soil water content was measured by a time domain reflectometry system (TDR100, Campbell Scientific Inc., Logan, Utah) with 20 cm probes (3-rod). Ten TDR probes were placed horizontally in the center of each plot at different depths while filling the plots with a silt loam soil packed to a bulk density of 1.35 g cm⁻³. The TDR probes were placed at every 0.1 m for depths between 0.1 and 0.6 m and at every 0.2 m between 0.6 and 1.5 m depth. The probes remained in position throughout the experiment. The TDR probes were calibrated in the field by comparing the volumetric soil water contents, determined from soil samples collected with a soil corer, with the TDR readings during the experimental period in each plot. Nitrogen (0.29 g N L⁻³ soil) was applied to the top 20 cm of each plot before planting. Maize seeds were sown on June 24, and eight plants were established in each plot after three leaves had expanded. Water treatments began to be established from July 19. Soil water contents were recorded manually every 5–10 d using the TDR system prior to irrigation. The initial soil water contents were approximately 0.27 cm³ cm⁻³. Three irrigation water treatments (WP1, WP2, and WP3) with two replications were then applied to randomly selected plots: WP1, WP2, and WP3 received a total of 112.5, 50 and 0 mm of irrigation, respectively, during the period July 19 to October 10. In WP1, 50, 37.5, and 25 mm were added during the boot, flowering and maturing stages, respectively; and in WP2, 25, 12.5 and 12.5 mm were added at the three stages, respectively.

Measurements of physiological indices

Plant height (PH) and the length and maximum width of every leaf blade were measured from the beginning of the water treatment at intervals of about 10 d until the leaves turned yellow. Plant height was measured from the stem at the soil surface to the pulvinus of the upper unrolled leaf (Wielgolaski, 1999; Rodiyati et al., 2005). The product of leaf length and the maximum width was multiplied by 0.75 to estimate the area of individual maize leaf blades (LA) (Montgomery, 1911).

Transient transpiration rate (mmol H₂O m⁻² s⁻¹) was measured at 10:00–11:00 in the morning on sunny days using portable photosynthetic systems (Li-6400, Li-Cor Inc., Lincoln, Nebraska). Two measurements, with three replicates for each water treatment level, were made in the pot experiment, while one measurement, with three replicates in each plot, was made for the plants grown in the field experiment. The soil water content was determined at the same time by weighing the pots or from the TDR100 measurements.

A water balance equation incorporating the difference in weight of the soil pots (or the difference in water storage of the plots) and the mass of water added to them was used to calculate water consumption over time for both pot and plot experiments. Evaporation from the soil could be ignored as it was very low due to the layer of perlite gravel in the pot experiment and the dense canopy during the experimental period in the plot experiment. Thus, the daily transpiration rate was the daily average water consumption determined for each 2–5 day period for the pot experiment and each 5–10 day period for the plot experiment.

One plant in each pot or plot was cut at the beginning of the water treatments. The above-ground parts were put into an oven for 30 min at 105 °C and then dried at 70 °C until a constant weight was attended, and then weighed to determine the dry weight (DW). The dry weight was also determined after harvesting on October 21 for the pot experiment and on October 4 for the plot experiment.
Data analysis

The soil water availability in each pot or plot was expressed as a function of soil water content. In the pot experiment, the fraction of available soil water content (FASW) were calculated as FASW = (SWC−PWP)/(FC−PWP), where SWC is the actual average soil water content of each pot in each measurement period. In the plot experiment, the FASW of the soil profile was calculated from the actual water storage in the whole profile, determined from the SWC at each soil depth using the TDR system and the water storage at FC and PWP, which was assumed to be the same in all the profile since the soil was packed uniformly.

A linear-plateau equation (Sadras et al., 1993; Casadebaig et al., 2008) and a logistic function (Muchow and Sinclair, 1991; Lucape et al., 1998) were used to describe the responses of various relative physiological indices to changes in soil water availability in the pot experiment. The data from the plot experiment were compared with those from the pot experiment. The linear-plateau equation is given by:

\[
\begin{align*}
RP &= 1 & \text{FASW} \geq \text{FASW}_0 \\
RP &= 1 + k \times (\text{FASW} - \text{FASW}_0) & \text{FASW} < \text{FASW}_0
\end{align*}
\]

where \( RP \) is the relative values of plant physiological indices, \( \text{FASW}_0 \) is the threshold value of the FASW and \( k \) is the slope of the linear part of the equation.

The logistic equation is given by:

\[
RP = \frac{A - 1}{1 + \exp([\text{FASW} - B]/C)} + 1
\]

where \( A, B \) and \( C \) are regression coefficients.

As proposed by Ray and Sinclair (1997), transpiration rates were normalized to account for time variations in weather conditions and differences in initial plant sizes among different water treatments. For each water treatment, the relative daily transpiration rate (RDT) of the three replicates was estimated by dividing the average daily transpiration rate (ADT) of that treatment by the average daily transpiration rate from the well-watered treatment (ADT_w). The daily normalized transpiration rate (NTR) was obtained by dividing RDT by the average relative transpiration rate (ART) corresponding to the period when all treatments were well watered.

\[
\text{NTR} = \frac{\text{RDT}}{\text{ART}}
\]

As for the plant growth indices, the relative plant height (RPH), relative leaf area (RLA) and relative above-ground dry weight (RDW) were estimated by dividing the increments of these indices in every pot by the average increment in the well-watered pots. The increment of plant height or leaf area in each pot was the difference between the initial value, measured at the beginning of the water treatment, and the maximum value. The increment of dry weight was the difference between the initial value and the value determined after harvesting. The relative transient transpiration rate (RTT) was estimated by dividing the average leaf transient transpiration rate of each water treatment by the average value in the well-watered treatment.

In the plot experiment, the relative transpiration rate was calculated for each water treatment by dividing the average daily value of the index by the daily potential evapotranspiration rate. The daily potential evapotranspiration rate was calculated using the FAO method (Allen et al., 1998) by multiplying the crop coefficient determined with the LAI, as in Kang et al. (2003), and the potential evapotranspiration estimated by the Penman-Monteith equation using weather data collected from the standard weather station near the field plots at the Irrigation Experiment Station. Other relative indices were calculated by dividing the average value of the individual index for each water treatment by its average value determined for the most watered treatment (WP1). This ratio was then multiplied by the predicted value for the index from Eq.1 for an FASW value equal to the average water content of WP1; note that Eq. 1 was derived from data from the pot experiment.

Curves were fitted using the SAS NLIN procedure (SAS Institute, 1998) with a significance level set at \( P < 0.05 \). The coefficient of determination (\( R^2 \)) and the root of mean square error (RMSE) of the pot experiment were used to evaluate the precision of the simulations. In order to compare the difference between the pot and plot experiments, RMSE2 between the experimental plot data and the fitted linear-plateau or logistic equations was also calculated. The RMSE is given by:

\[
\text{RMSE} = \left[ \frac{1}{n} \sum_{i=1}^{n} (S_i - M_i)^2 \right]^{1/2}
\]

where \( S_i \) and \( M_i \) are the simulated and measured va-
values for the $i$th observed value and $n$ is the total number of observations.

Analysis of variance (ANOVA) among water treatments was performed for FASW, plant height, and leaf area for both pot and plot experiments using the ANOVA procedure of SAS at $P < 0.05$.

RESULTS

Available soil water content and plant growth

Fig. 1 showed that the average FASW during each weighing interval for both the pot and the field plot treatments varied with time for different water treatments. In the pot experiment, the FASW in each water treatment was successfully maintained around the desired value during the experimental period (Fig. 1). The average FASW values observed for treatments WC1–WC6 were 0.99, 0.82, 0.67, 0.52, 0.36 and 0.23, respectively. The coefficient of variance (CV) of the daily FASW was generally less than 10% except for that of WC6, which was higher (about 32%) because it included the longer period required to dry the soil to the intended FASW (Fig. 1). The soil water contents of the various water treatments were all found to be significantly different ($P < 0.05$). In the plot experiment, the FASW decreased with time as drying occurred under the three different irrigation treatments (Fig. 1). The fractions of water contents during the experimental period ranged between 0.45 and 1.00, 0.20 and 0.81, and 0.05 and 0.78 for WP1, WP2, and WP3, respectively, with average values of 0.72, 0.50 and 0.40 that were significantly different ($P < 0.05$). The average available soil water storage of the WP1 treatment was 163 mm during the experimental period, which together with the irrigation of about 112.5 mm, was 1.07 times more than the potential evapotranspiration (258 mm) during the entire water control period. Therefore, the water in WP1 met the water requirements for maize yield production (Kang et al., 2003; Keller and Seckler, 2004). The total available soil water (average available soil water storage plus irrigation) in WP2 and WP3 was about 62% and 34% of the potential evapotranspiration, which would limit the growth of above-ground biomass (Keller and Seckler, 2004).

Both pot and plot experiments resulted in changes of plant height and leaf area that followed similar patterns with time for all the water treatments (Fig. 2). From the beginning of the water treatments, plant height increased to a maximum height within approximately 25 days for the pot experiment and 40 days for the plot experiment, and then remained constant after that time (Fig. 2). The maximum plant height and the height growth rate both increased with decreasing levels of water stress (Fig. 2). The leaf area for all water treatments also demonstrated similar relationships that were positively related to the soil water content (Fig. 2). However, from the beginning of the water treatments the maximum value was reached within 20 to 25 days for the pot experiment and 30 to 40 days for the plot experiment, after which the leaf area slowly declined with time (Fig. 2) because of leaf senescence as grain developed. Using ANOVA, significant differences ($P < 0.05$) were found among the water treatments for the measurements of plant height and leaf area during the water control periods in both pot and plot experiments. The absolute plant heights and leaf areas were significantly higher ($P < 0.05$) for maize plants grown in all three water treatments in the plot than those in best watered treatment in the pot.
Fig. 2 Plant height and leaf area of maize grown in the pot experiment containing different soil water contents representing increasing levels of water stress (WC1–WC6) and in the plot experiment receiving a total of 112.5, 50 and 0 mm irrigation (WP1–WP3) as a function of time from the beginning of the water treatment.

**Effect of soil water availability on different plant indices**

The responses of plant physiological indices (plant height, leaf area, dry weight, daily transpiration and leaf transient transpiration) to changes in FASW for both the pot and plot experiments are shown in Figs. 3 and 4. In the pot experiment, NTR calculated for a 2 to 5-day period might result in great variability. However, we did not observe a large variability. Regression analyses indicated that the relationships between these plant indices and the FASW were essentially the same.

Fig. 3 Relative plant height (RPH), leaf area (RLA) and dry weight (RDW) as a function of the average fraction of available soil water (FASW) in the pot and plot experiments. Regression lines of the linear-plateau equation and logistic function were fitted to the data from the pot experiment.
Fig. 4 Normalized daily transpiration rate (NTR) and relative leaf transient transpiration rate (RTT) plotted as a function of the fraction of available soil water (FASW) in the pot and plot experiments. Signals with three potential evapotranspiration (PET) levels (low PET: < 2.0 mm d$^{-1}$; medium PET: 2.0–3.0 mm d$^{-1}$; high PET: $\geq$ 3.0 mm d$^{-1}$) are the data from pot experiment. Regression lines of the linear-plateau equation and logistic function were fitted to the data from the pot experiment.

and were statistically significant ($P < 0.0001$). The linear-plateau and logistic equations both provided good descriptions of these relationships as indicated by high $R^2$ values and low RMSE values (Table I). Figs. 3 and 4 also indicated that the plant responses to soil drying were consistent in both pot and plot experiments. This was also indicated by the RMSE$_2$ values between the experimental plot data and the fitted linear-plateau or logistic lines for the various indices, which were in the range of 0.023–0.135 with an average of 0.080 (Table I) and that were generally in the range of the RMSE$_1$ (0.074–0.147) values determined between the experimental pot data and the fitted lines.

The responses of RPH, RLA and RDW to changes in FASW (Fig. 3) were comparable and had similar threshold values and slope values for their fitted linear-plateau equations (Table I). The plant growth indices were essentially unchanged until the soil dried to a FASW of 0.72–0.76. Fig. 4 shows the responses of NTR and RTT to changes in soil water availability. The threshold value of FASW, at which plant NTR began to decline with the reduction of FASW, was 0.84, which was higher than the FASW$_0$ value for RTT (Table I). After the threshold value, NTR and RTT decreased at a similar rate. Although the response of NTR to FASW appeared to be similar to those of RPH, RLA and RDW, NTR began to decrease at a higher FASW and then declined at a lower rate than other plant growth indices. Notably, a linear relationship between relative cumulative transpiration (RCT) and FASW is shown in Fig. 5. It indicated that the threshold value of RCT was close to the field capacity.

The potential evapotranspiration rates (PETs) during the water treatment period in the pot experiment calculated using the Penman-Monteith equation were in the range of 1.0–4.1 mm d$^{-1}$. To evaluate the influence of meteorological conditions on the relationship between NTR and FASW, we divided the data of daily transpiration rate into three groups according to the levels of evaporative demand: PET < 2.0 mm d$^{-1}$, 2.0 $\leq$ PET < 3.0 mm d$^{-1}$, and PET $\geq$ 3.0 mm d$^{-1}$. Fig. 6a and b show the linear-plateau and logistic relationships, respectively, between NTR and FASW under the three levels of PET. The threshold values increased as the PET increased and a significantly higher threshold value existed at the high PET level (PET $\geq$ 3.0 mm d$^{-1}$) relative to the low PET level (PET < 2.0 mm d$^{-1}$) (Fig. 6, Table II).
TABLE I
Parameters$^a$ (FASW$_0$, k, A, B and C) and statistical properties$^b$ of the fitted linear-plateau equation and logistic function for various plant indices related to the fraction of available soil water (FASW)

<table>
<thead>
<tr>
<th>Index</th>
<th>Linear-plateau equation</th>
<th>Logistic function</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FASW$_0$ k $R^2$ RMSE$_1$ RMSE$_2$</td>
<td>A B C $R^2$ RMSE$_1$ RMSE$_2$</td>
</tr>
<tr>
<td>Growth index</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Relative plant height</td>
<td>0.76 1.68 0.91 0.111 0.033 0.20 0.53 0.069 0.91 0.108 0.129</td>
<td></td>
</tr>
<tr>
<td>Relative leaf area</td>
<td>0.72 1.94 0.87 0.141 0.085 0.21 0.52 0.051 0.87 0.140 0.117</td>
<td></td>
</tr>
<tr>
<td>Relative dry weight</td>
<td>0.75 1.77 0.86 0.146 0.072 0.18 0.53 0.069 0.85 0.147 0.074</td>
<td></td>
</tr>
<tr>
<td>Normalized daily transpiration rate</td>
<td>0.85 1.24 0.92 0.083 0.135 0.26 0.57 0.093 0.94 0.074 0.090</td>
<td></td>
</tr>
<tr>
<td>Relative transient transpiration rate</td>
<td>0.75 1.10 0.89 0.083 0.023 0.46 0.51 0.080 0.88 0.081 0.044</td>
<td></td>
</tr>
<tr>
<td>Transpiration index</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$FASW$_0$ is the threshold value of FASW where the relative indices begin to decline; k is the slope of the linear part of the linear-plateau function; A, B and C are regression coefficients of the logistic function.

$^b$RMSE$_1$ is the root of mean square error between the fitted function and the experimental pot data; RMSE$_2$ is the root of mean square error between the fitted function and the experimental plot data.

Fig. 6 Normalized daily transpiration (NTR) plotted with the fitting of the linear-plateau equation (a) and the logistic function (b) as a function of the fraction of available soil water (FASW) at different potential evapotranspiration (PET) levels: low PET (< 2.0 mm d$^{-1}$), medium PET (2.0–3.0 mm d$^{-1}$) and high PET (≥ 3.0 mm d$^{-1}$).

TABLE II
Parameters and statistical properties for the fit to normalized daily transpiration data in response to the fraction of available soil water (FASW) for different potential evapotranspiration (PET) conditions

<table>
<thead>
<tr>
<th>Function</th>
<th>PET level mm d$^{-1}$</th>
<th>Parameter$^a$</th>
<th>$R^2$$^b$</th>
<th>RMSE$_1$$^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FASW$_0$ k A B C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Linear-plateau</td>
<td>1.0–2.0</td>
<td>0.80 1.25 - -</td>
<td>0.96 0.060</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.0–3.0</td>
<td>0.85 1.26 - -</td>
<td>0.96 0.063</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3.0–4.0</td>
<td>0.90 1.36 -</td>
<td>0.95 0.066</td>
<td></td>
</tr>
<tr>
<td>Logistic</td>
<td>1.0–2.0</td>
<td>- - 0.26 0.52 0.093</td>
<td>0.97 0.056</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.0–3.0</td>
<td>- 0.27 0.58 0.090</td>
<td>0.98 0.048</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3.0–4.0</td>
<td>- 0.27 0.64 0.088</td>
<td>0.96 0.064</td>
<td></td>
</tr>
</tbody>
</table>

$^a$FASW$_0$ is the threshold value of FASW where the relative indices begin to decline; k is the slope of the linear part of the linear-plateau function; A, B and C are regression coefficients of the logistic function.

$^b$Determination coefficient.

$^c$Root of mean square error between the fitted function and the experimental pot data.
Furthermore, in Figs. 3 and 4, using the logistic function simulation, the plant indices decreased quickly at first below the threshold values (0.70–0.85), and then decreased slowly below about 0.3 of FASW in response to soil drying. While in Fig. 6b, the lower limit, where soil water availability began to decrease slowly, ranged between 0.4 and 0.3 of FASW as the potential transpiration rate decreased. This lower limit of soil water availability was about 60%–65% of field capacity.

**DISCUSSION**

In this study, there were significant differences ($P < 0.05$) in the absolute plant height and leaf area between plants grown in the pot and plot experiments with different soil volumes. Due to lower available soil volume, the rooting environment in the pots may differ from that in the field in a number of ways including soil temperature, water availability and nutrient efficiency (Townend and Dickinson, 1995; Hurley et al., 1998), which have been shown to be the factors that cause soil volume to affect plant growth (Whiley et al., 1999; Wang et al., 2001). Therefore, the available soil volume was the main factor leading to the greater plant height and leaf area in this experiment. Studies have shown that pot size greatly influenced plant growth and transpiration, but had little influence on the response of the NTR to soil water availability (Ray and Sinclair, 1998). In this study, the responses of relative plant indices, such as the increment of plant height, leaf area and dry weight, and daily and transient transpiration rate to soil water availability, in the pot experiment were identical with those in the plot experiment (Figs. 3–5). In the plot experiment, soil water content decreased progressively (Fig. 1), NTR was calculated for a 5- to 10-day period and FASW was calculated for a 1.5 m soil profile. In the pot experiment, the soil water content of each water treatment remained constant. The different water treatment regimes in the pot and plot experiments did not induce different responses of the relative plant indices to soil water availability. Lecoeur and Guilioni (1998) reported that the change with time of the relative leaf production did not depend on the rate and duration of soil drying, but solely on the actual soil water content. Therefore, we can conclude that the responses of relative plant indices to soil water availability obtained in the pot experiment are applicable to the field.

The threshold values for all the plant indices selected in response to soil drying were in the range between 0.72 and 0.85. These values were very near the field capacity (85%–90% field capacity) and were much larger than the widely recognized threshold values where two-thirds of the available soil water content was removed from the soil. We also found a lower water limit in the range between 60%–65% of field capacity below which plant indices decreased more slowly than above it. This dynamic characteristic is comparable with Shao et al. (1987), who reported that cumulative root uptake of winter wheat grown in the same soil in response to soil water availability declined quickly near the field capacity, but declined slowly after 80% of field capacity. Therefore, deficit irrigation with the soil water content below 65% of field capacity for maize on the Loess Plateau is feasible.

By dividing transpiration rate into three groups according to the evaporative demand and analyzing the responses of transpiration rates to soil water availability, we found that meteorological conditions did affect the threshold value, as reported in Denmead and Shaw (1962) and Novák et al. (2005). The threshold values increased as the potential transpiration rate increased from 1.0 to 4.0 mm d$^{-1}$, and significant differences were observed between the potential transpiration rates below 2.0 and above 3.0 mm d$^{-1}$.

In the mathematical study of Novák and Havrila (2006), the threshold soil water content of maize only significantly increased after about 3.0 mm d$^{-1}$. Our experimental results were consistent with their numerical results. Therefore, it is suggested that water management would be different under different weather conditions especially when the potential transpiration rate is higher than 3.0 mm d$^{-1}$.

It should be noted that the plant physiological indices selected were relevant to three different time scales: a transient time scale (RTT), a daily scale (NTR) and a seasonal scale (RPH, RLA and RDW, RCT). For the indices related to the seasonal scale, RPH and RLA determined before the leaves started to turn yellow represent the effect of water stress before the filling stage. In contrast, RDW and RCT indicated the effect of water stress over the entire experimental period. The threshold value of soil water availability has been investigated at both the transient and daily scales (Sadras and Milroy, 1996). However, the differences in the threshold values for different scales were not compared in their study. In our study, for different time scales and taking RTT, NTR and RCT as examples, plant transpiration over the seasonal time scale (RCT) declined at the beginning of soil drying at the field capacity and RTT began to decrease later than
NTR. This illustrates that scale may also be an important factor influencing the dynamics of soil water availability. The transient transpiration rates were taken at a time when the evaporative demand was not very high, and the cumulative transpiration aggregated the evaporative demand effects on the daily transpiration response to water stress during the whole experimental period. Therefore, evaporative demand may be one of the determinants for the different reaction of plant transpiration to soil drying at different time scales. Over the seasonal scale, RDW, RPH and RLA had similar threshold and slope values. The reason may be attributed to the influence of leaf area on dry matter production as reported by Jones (1992). Leaf area plays an important role in light interception and hence influences dry matter production and plant growth. The smaller threshold value for RDW as compared to RCT indicates that dry weight is less sensitive in response to soil water deficits than plant transpiration. Fig. 7 showed that dry weight production per hectare with a density of 75,000 plants was related to total transpiration and that the decrease in transpiration cumulated from the late jointing stage to the end of the experiment did not contribute to the decrease in dry weight production at a relatively higher transpiration level. This is similar to the results of Calviño et al. (2003), who investigated maize yield in response to the water use from 20 days before to 20 days after flowering. Results of Novák and Havrila (2006) showed that biomass production is linearly related to transpiration during the vegetation period. Therefore, irrigation in the vegetation period would be fully used by crops during biomass production; however, a large amount of irrigation provided in the reproductive period would be wasteful.

CONCLUSIONS

Characteristic responses of the various plant indices to changes in the FASW obtained in the pot experiment were applicable to the field, although large differences were found between the plants grown in the pots and plots when considering their absolute plant height or leaf area. The response of various physiological indices (i.e., relative plant height, relative leaf area, relative transient transpiration rate, and normalized transpiration rate) to decreases in the FASW decreased slowly near the field capacity, and more rapidly decreased below threshold values of FASW in the range between 0.72 and 0.85, but then decreased slowly below a lower limit ranging between 0.3 and 0.4 of FASW. However, RCT was linearly related to the change of FASW. By comparing the threshold values for various plant indices at different time scales and the normalized transpiration rate under different weather conditions, we found that evaporative demand affected the plant responses to soil water availability and that the growth indices responded to soil drying later than the transpiration indices did. Therefore, deficit irrigation was considered to be feasible and practical. It was suggested that water management would be different under different weather conditions and at different growing stages.

REFERENCES


