コムギ群落における蒸散速度,気孔抵抗に及ぼす土壌乾燥および大気飽差の影響

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Influences of Extractable Soil Water and Vapor Pressure Deficit on Transpiration and Stomatal Resistance in Differentially Irrigated Wheat*

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Abstract : The response of transpiration (Tr) and stomatal resistance (r_s) to extractable soil water and the vapor pressure deficit of the air was investigated over three differentially irrigated wheat plots for an entire growing season. The objective was to develop a physiological basis for remote monitoring of crop and soil water status.

The results indicated that Tr was closely correlated with the extractable soil water (ESW) remaining in the soil when the ESW was less than 40%. When the ESW was greater than 40%, Tr was propotional to the vapor pressure deficit of the air (VPD_a). Stomatal resistance (r_s) was found to increase hyperbolically with decreasing ESW (r=0.82), although r_s was small and independent of ESW at high ESW. No relationship was found between r_s and VPD_a. The correlation between the ratio Tr/VPD_a and ESW was higher (r=0.75) than the correlation between Tr and ESW. Normalizing Tr and ESW values for the water stressed plots to those observed in the well watered plot improved this correlation to r=0.91. Multiple regression analysis showed that r_s^{-1} and VPD_a were highly correlated with ESW (r=0.92-0.97).

Key words : Drought stress, Irrigation, Remote sensing, Stomatal resistance, Transpiration, Vapor pressure deficit, Wheat.

コムギ群落における蒸散速度，気孔抵抗に及ぼす土壌乾燥および大気飽差の影響：井上吉雄**・Ray D. JACKSON・Paul J. PINTER, Jr.・Robert J. REGINATO（農林水産省農業研究センター**, U.S.Water Conservation Lab., USA.)

要　旨：3種類の灌漑条件におけるコムギ群落について，土壌乾燥と大気の蒸発要求度（飽差）に対する蒸散速度および気孔抵抗の反応を全生育期間にわたって調べた．中性子土壌水分計によって測定した体積含水率から利用可能土壌水分（ESW，%）を算出し，これによって土壌の水分状態を経時的に把握した．蒸散速度と ESW との間には，ESW の低い場合に比較的明瞭な正の相関関係があったが，高い場合にはまったく相関がなかった．逆に，蒸散速度と大気飽差の間には，ESW が低い乾燥条件では一定の関係がないのに対して，ESW が高い条件では比較的強い正の相関関係が認められた．したがって，見かけ上，ESW が約40% 以下のときには土壌水分が，それ以上のときには飽差が蒸散速度をそれぞれ律速していた．気孔抵抗は ESW が約40% 以上ではほとんど ESW の影響を受けずかつ非常に小さかったが，それ以下になると ESW の低下にともなって反比例的に増加し，約5% では極度に大きくなった．両者の関係は極めて密接で (r=0.82**)，この関係を土壌水分状態のモニタリングに利用できる可能性が示唆された．また，蒸散速度/飽差の比は ESW と密接に関係していた．土壌乾燥履歴が異なる場合でも，灌水条件での蒸散速度，ESW をそれぞれ基準として算出した相対的な蒸散速度と ESW の間には密接な直線関係が得られた (r=0.91**)．気孔抵抗に対する大気飽差の直接的影響は認められず，少なくとも1日1回日中のモニタリングでは，気孔抵抗に対する大気飽差の影響を考慮する必要はないと考えられた．

キーワード：灌漑，乾燥ストレス，気孔抵抗，コムギ，蒸散速度，大気飽差，リモートセンシング．

Soil water status is a primary determinant of the productivity of crops. In arid and semiarid regions, the measurement of soil water status is important in evaluating irrigation requirements. Even in humid areas, periodic droughts occur, and irrigation is increasingly being used to ameliorate the consequences of drought. When plants are stressed because of insufficient water, stomatal closure lowers photosynthesis, thus restricting growth and reducing productivity.

From the viewpoint of irrigation management, therefore, accurate information on the

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water status of crops and soils on a real-time basis is essential for efficient water use. Recently, remote sensing techniques that use infrared thermometry have been developed to measure crop water status. Jackson et al.[3,7,8] developed a crop water stress index (CWSI) as a practical index for irrigation scheduling. Inoue et al.[4,6] has attempted, furthermore, to estimate transpiration and stomatal resistance with a remote method.

On the other hand, the importance of soil and root water relations in controlling physiological function has recently been reemphasized[13]. Gollan et al.[2] showed that photosynthetic rate and stomatal resistance are more closely correlated to soil water content or soil water potential than with leaf water potential or leaf turgor. Moreover, crop-water relations measured under controlled environmental conditions have been shown to be significantly different from those in the field[9].

Thus, it is necessary to know much more how the stomatal behavior is related to the soil water conditions especially in the field, and also how water stress can be monitored with an accurate and simple means. The purpose of this paper is to quantify the relationship of transpiration and stomatal resistance to the soil water status and the water vapor pressure deficit of the air, and to provide insight into the physiological basis for this relationship in order to improve irrigation management decisions.

Materials and Methods

Experimental

Six cultivars of spring wheat (*Triticum eastivum* L.: 'Ciano 79', 'Genaro 81', 'Pavon 76', 'Seri 82', 'Siete Cerros 66', 'Yecora 70') were planted in mid-December 1982 at Phoenix, AZ, USA. The soil was classified as an Avondale loam (a fine, loamy, mixed calcareous, hyperthermic, Anthropic Torrifluvent). Seeds were planted at a rate of 300/m in N-S rows at 0.18m spacing. Each of the six cultivars was grown in three 12×25m flood irrigation experimental plots. All 18 plots received an irrigation on 4 January, 1983. Thereafter, different irrigation treatments were initiated. Six plots containing the six different cultivars, designated well-watered (W), received six additional irrigations spaced from late-February to early-May. A second group of six plots, denoted D1, received only one additional irrigation (mid-April). The third treatment, designated D2, was irrigated in mid-February and again in mid-April. Each irrigation added from 80 to 100 mm of water to the soil profile. Several rain events occurred early in the season, but only about 25 mm fell after the day of year (DOY) 65. The actual soil moisture in each plot was monitored with a neutron moisture meter throughout the growing season. Data for the two cultivars 'Ciano79' and 'Yecora70' were used for the analysis in this report, because they were most different among the six cultivars in their canopy architecture and yield performance. The approximate dates of heading and maturity were DOY 97 and DOY 140 for 'Ciano79', and DOY 93 and DOY 136 for 'Yecora70', respectively.

Environmental and plant measurements

The dry- and wet- bulb temperatures, and solar radiation were measured automatically every minute at the center of the field, and averaged for every 30-minutes periods. The vapor pressure deficit of atmosphere was calculated from the wet- and dry- bulb temperatures. Soil water contents were measured with a neutron soil-moisture meter in each plot at 0.2-m intervals to a depth of 1.7m, two to three times per week throughout the growing season. A parameter indicating the extractable soil water (ESW, %) remaining in each soil layer was obtained by normalizing the actual volumetric water content to the upper and lower limits. Hence a value of 100% for ESW is essentially field capacity and a value of 0% indicates no available water in the soil. The lower limit was determined as the lowest value observed during the experiment at which the plants died due to drought. Since previous works[11] showed that most of the root system in a wheat crop was distributed within the top 100cm, the mean value of ESW for 0-110 cm depth was used as a representative indicator of available water in the soil.

The transpiration rate and stomatal resistance were measured with a steady state porometer (Li-Cor, LI-1600)[†] once every two days during the period from DOY 69 to 140. The measurements were made for the abaxial surface of several sunlit leaves located near the top of the canopy. Two or three replicate

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[†] Trade names and company names are included for the benefit of the reader. No endorsement is implied.

measurements were made for each plot between 1230 and 1400h. The replicates were averaged for the analysis. Canopy temperatures were measured with a hand-held infrared thermometer (Everest Interscience, model 110)† simultaneously with the porometry measurements. Those data measured just after irrigations were not used in the analysis because of the rapidly changing soil water content. This point is discussed further in the results and discussion section.

Results and Discussion

Seasonal changes in soil and atmospheric moisture conditions, transpiration rate, and stomatal resistance

Fig.1 shows the profiles of ESW in each plot under three typical soil water conditions. On DOY 21 the three plots had almost the same profiles and ESW varied little with soil depth. The mean values of ESW for 0-110 cm depth were close to 90%. By DOY 98 the three plots showed considerable differences not only in their profiles but also in the mean ESW. Toward the end of the season; on DOY 131, the mean ESW remained high in the W plot, but was very low both in D1 and D2 plots. Also, a noticeable decrease in the ESW was evdient at the 70-110 cm depth in the W plot.

In general, changes in the vertical distribution of ESW depend on many factors, such as irrigation or rain, evaporation from the soil surface, drainage into underground, and also absorption by root systems. The absorption is determined by the distribution and activity of the roots which change with growth stage and history of stress. The decreased ESW in the W plot at the depth of 50-90 cm on DOY 98 and at 70-110 cm on DOY 131 suggest that the root system had a high absorbing activity around those layers. Furthermore, the value of the lower limit for calculating ESW needs to be determined for each soil and for each crop. The behavior of water in the soil-plant-atmosphere system is so complicated that it is difficult to estimate separately the relations among the processes. Nevertheless, plants themselves are likely to be the best integrators of their atmospheric and soil environments. Thus, the use of some physiological activity of leaves would seem to be a representative and simple detector of plant and soil water status.

Since the ESW is 100% at the volumetric water content of the field capacity and 0% at the observed driest condition, the ESW directly indicates the residual amount of water available for crop plants. Theoretically, the energy required to drive water from soil to a root should be indicated by the soil water potential (ψ_{soil})[1], which decreases exponentially as ESW decreases. Therefore, ESW may underestimate the intensity of drought stress, particularly, under dry conditions. However, the EWS is an advantageous parameter, especially for practical water management, because it has an explicit relation to the amount of water to be irrigated, and because no continuous and reliable method for measuring ψ_{soil} is available so far.

Fig.2 shows seasonal changes in the mean extractable water remaining in the soil (ESW) during the season. The ESW in the well-watered plot had been kept as high as 50-110% except for the period just before har-

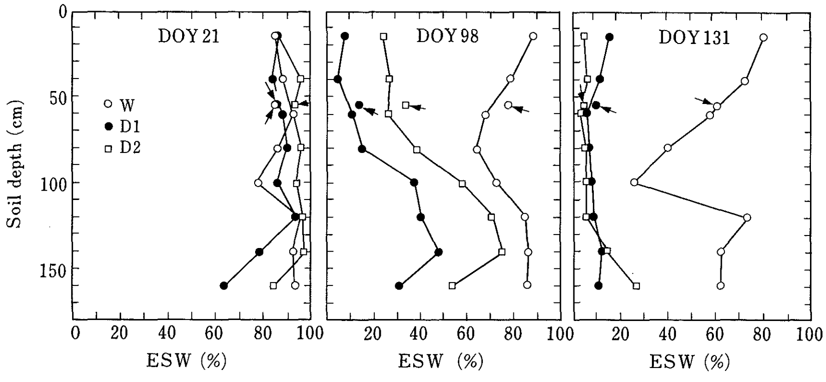

Fig. 1. Typical profiles of extractable water remaining in the soil (ESW, %) measured with a neutron moisture meter in three differentially irrigated plots of the cultivar 'Ciano79'.
Note; Arrows indicate the mean values of ESW for 0-110 cm soil depth. DOY: Day of year.

vesting. The other two plots (D1 plot and D2 plot) had the same ESW as the W plot during the early growing period. Thereafter, however, the two dry plots exhibited water stress. The ESW in D1 plot started decreasing at DOY 50, when the leaf area index (LAI) was still about 1. On the other hand, the D2 plot exhibited water stress after DOY 80 when the LAI approached its maximum value ($\simeq$6.5).

Atmospheric vapor pressure deficit (VPD_a) varied greatly (0.5-3.5kPa) depending on the solar radiation, windspeed, and air temperature. During the periods that the porometry measurements were made, the solar radiation was consistently as high as 800-900 Wm^{-2}, which implies that the solar radiation was not a limiting factor to physiological processes of the wheat plants. Subsequent discussion is based on this assumption.

Transpiration rate (Tr) in each plot varied greatly from 0 to 300 mg m^{-2} s^{-1}, depending on vapor pressure deficit, solar radiation, and stomatal resistance. The stomatal resistance (r_S) under well-watered conditions was consistently small (50-100 sm^{-1}), probably because there was no limiting factor to prevent the stomata from opening. Under drought conditions, as observed in the two dry plots, r_S changed considerably as a result of soil water stress. Nevertheless, no obvious seasonal trend was found both in Tr and r_S.

Influences of extractable soil water and vapor pressure deficit on Tr and r_S

The relationships of the transpiration rate Tr with ESW and VPD_a are shown in Fig.3. A relatively high correlation was found between Tr and ESW at low ESW, while little correlation at high ESW. However, VPD_a was closely correlated with Tr in the W plot, while there was little correlation in the two dry plots. These results imply that Tr is not regulated by ESW but by VPD_a when ESW is greater than 40%.

Fig.4 presents the relationships of the somatal resistance r_S with ESW and VPD_a. A close relation was found between r_S and ESW. The r_S increased hyperbolically with a decrease in ESW and reached extremely high value at around 5% of ESW, although it was little affected by ESW when ESW was greater than about 40%. Point A in Fig. 4a represents a typical data set obtained just after an irrigation. The arrows indicated the direction of change before and after the irrigation. Several days after irrigation were required for r_S to return to the normal line. During this period, r_S behaved as if the plant was still under drought conditions. This fact suggests that r_S does not respond quickly to a drastic change in the soil water conditions, and that a unique relationship cannot be expected for such periods. Duration of the lag varied from two to five days, depending upon the severeness of stress just before the irrigation. From a management point of view, however, it is of little interest to evaluate drought stress immediately after irrigation.

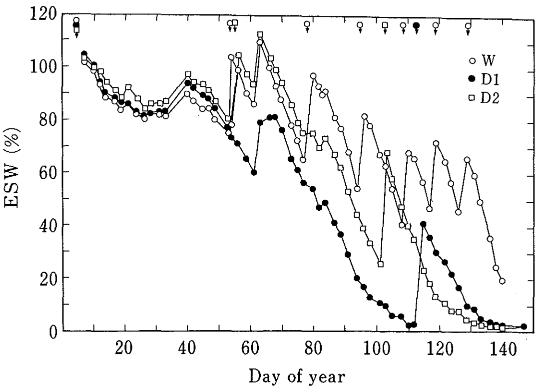

Fig. 2. Seasonal changes in the mean extractable water remaining in the soil (ESW) for the cultivar 'Ciano79'.
Note ; Symbols with an arrow indicate the date of irrigations in each plot.

Since no relation was found between the VPD_a and r_S in Fig. 4b, the processes driven by the VPD_a ; 〔VPD_a increases→Tr increases →plant water potential (ψ_{plant}) dereases→r_S increases〕, and also the direct effect of air humidity on r_S[10,12] do not appear to be detectable from long term and one-time of day measurements. Compared with the ESW, VPD_a changes so rapidly, depending on solar radiation, air temperature or windspeed, that equilibrium cannot be achieved.

The relations shown in Figs. 3 and 4 can be explained by the energy and water balances in the soil-plant-atmosphere system. The relationships among transpiration, stomatal resistance, and vapor pressure deficit can be expressed quantitatively as

$$Tr = Kv \cdot VPD_l / (r_S + r_a) \qquad (1)$$

where r_S and r_a are the stomatal and boundary layer resistances, Tr is the transpiration rate, Kv is the psychrometric constant, and VPD_l is the vapor pressure deficit for leaves. When r_S in Eq. (1) is small and nearly constant (as was found in the W plot), Tr is to be propotional to VPD_l (or roughly to VPD_a). Under stressed conditions (as indicated by low ESW), r_S regulates Tr and the effect of vapor pressure deficit becomes relatively small. On the other hand, the Tr is also related to the impinging energy, as shown in the energy balance equation,

$$2\lambda Tr = R_n - H \qquad (2)$$

where R_n is the net radiation, H is the sensible heat flux from a leaf to the air, and λ is the heat of vaporization of water. When the vapor pressure deficit is high, and the energy supply for evaporation (R_n) is sufficient, the water status of a whole plant is controlled by two

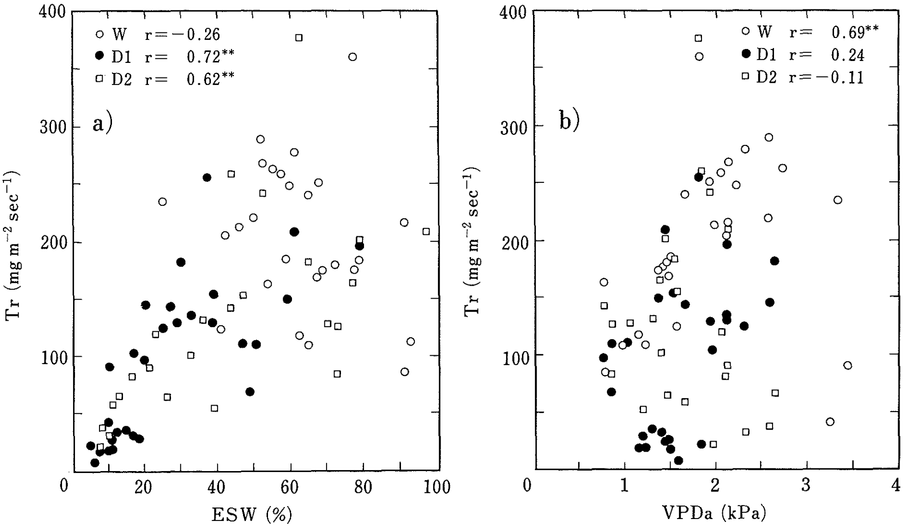

Fig. 3. Relationships of transpiration (Tr) with extractable water remaining in the soil (ESW) and vapor pressure deficit (VPD_a). Note ; **significant at 1% level. Cultivar is 'Ciano79'.

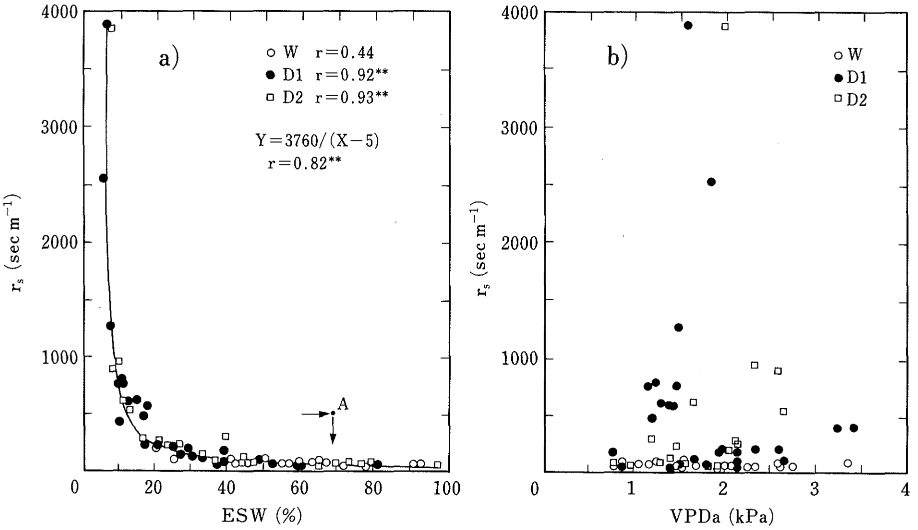

Fig. 4. Relationships of stomatal resistance (r_S) with extractable water remaining in the soil (ESW) and vapor pressure deficit (VPD_a). Note ; The point A represents a typical data obtained just after irrigation, and the arrows indicate the directions of change before and after the day. Cultivar is 'Ciano79'.

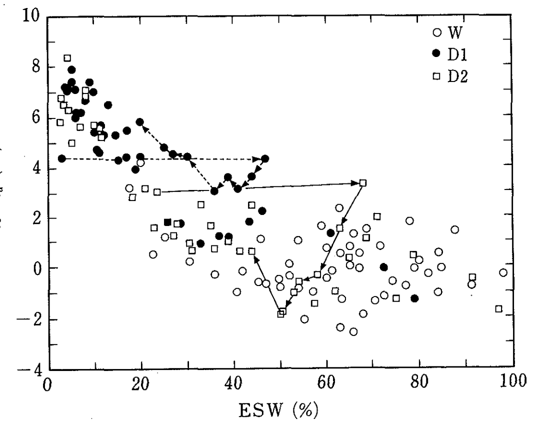

Fig. 5. Relationship between canopy—air temperature difference and extractable soil water ESW. Note ; Arrows trace typical changes just after irrigations. Data just after irrigations are not eliminated in this particular figure. Cultivar is 'Ciano79'.

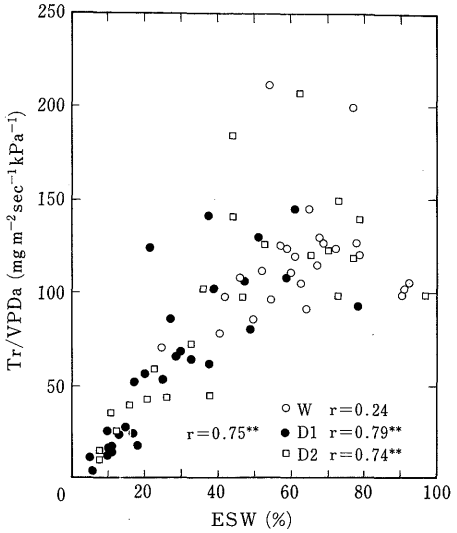

Fig. 6. Relationship between the ratio Tr/VPD$_a$ and extractable soil water ESW. Note ;**significant at 1% level. Cultivar is 'Ciano79'.

factors ; namely, the stomatal resistance r_S and the water supply from the soil. This suggests two hypotheses to explain stomatal behavior as related to drought stress[13]. The first is that stomata do respond directly to the plant water potential, and the second is that water availability to a root system is likely controlling the stomatal behavior. Although stomata could or should be open fully to achieve the high productivity when water supply is sufficient, as water supply decreases the stomata have to close to maintain a favorable internal water status by reducing water loss, i.e. transpiration. Thus, r_S closely responds to the ESW under water-stressed conditions. The relationship between r_S and ESW found here was so close that the soil water status can be inferred from r_S. This suggests that ESW can be estimated remotely, based on energy balance considerations, using infrared canopy temperature and micrometeorological measurements[4,6].

The relationship seems applicable for detecting soil water stress, particularly in cases where the only limiting factor is water, as was the case in the present experiment.

There is considerable evidence that remotely sensed infrared temperatures of vegetation do reflect the plant and soil water status. Fig. 5 shows a significant relationship between the canopy temperature t_c (as measured by infrared thermometry) minus the air temperature t_a and the ESW. The temperature difference increased as the ESW decreased. The arrows in the figure indicate typical changes just after irrigations. The lag in the response is the same sort of time-delay as explained for the response of r_S in Fig. 4. Jackson et al.[3,7,8] used infrared canopy temperatures to evaluate crop water stress for irrigation management. They developed the 'stress-degree-day' and the 'CWSI (crop water stress index)' indices. Recently, Inoue et al.[4,6] developed a model based on biophysical theories, to estimate stomatal resistance r_S with remotely sensed data. The model requires more input data than do the crop water stress indices. Thus, by incorporating the relationship obtained here into that type of model the soil water status can be inferred on the basis of physiological processes.

Three attempts, moreover, were made to relate the Tr, r_S and VPD$_a$ to ESW, with the assumption that all changes detected in Tr and r_S were entirely caused by drought stress.

First, a relation between the ratio Tr/VPD$_a$ and the ESW was examined to see if the effects of VPD$_a$ on Tr were reduced. Equation (1) suggests that a close relationship between the ratio Tr/VPD$_a$ and the stomatal conductance might be expected. The ratio Tr/VPD$_a$ was more closely related to ESW than was Tr (Fig. 6). Since the ratio Tr/VPD$_a$ has shown to be

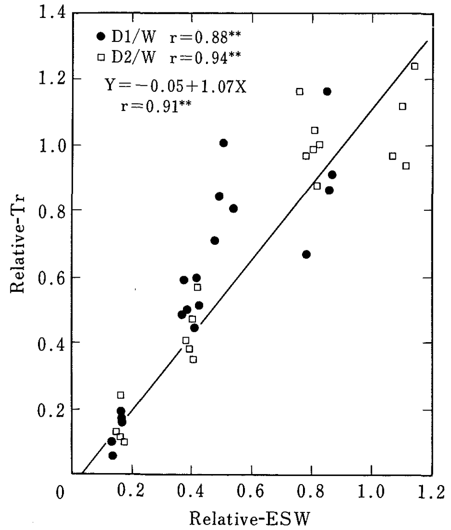

Fig. 7. Relationship between relative Tr and relative ESW normalized using measured values of Tr and ESW in a well-watered plot. Note ;**significant at 1% level. Cultivar is 'Ciano79'. A closer correlation equation was obtained for the data points whose relative-ESW were less than 0.6 ; $Y=-0.16+1.76X$ $(r=0.93^{**})$.

proportional to the photosynthetic rate[5], Fig.6 suggests a rough linear relation between the ESW and the photosynthetic activity. The relation, however, is not sufficiently good to infer the ESW.

Second, values of relative Tr and relative ESW were calculated and compared (Fig.7). The 'relative-Tr' or 'relative-ESW' means the ratio of a measured Tr or ESW in a stressed plot to that in a well-watered plot where wheat plants are postulated to be transpiring at the potential rate. The ratios for each dry plot were closely correlated $(r=0.88^{**}$ and 0.94^{**}, respectively). A high correlation coefficient (0.91^{**}) was obtained for both plots irrespective of differences in their stress histories. Although this type of estimation requires information for well-watered and healthy crops as a basis of comparison, it reduces the influences of all other factors, and its simplicity has a great advantage from a practical standpoint.

The third attempt was a multiple regression analysis to estimate ESW from VPD_a, Tr, Tr/VPD_a, r_S, and/or photosynthetically active radiation (PAR). Consequently, the ESW in each plot was best estimated from the two factors r_S^{-1} and VPD_a, as shown in Eqs. (3)-(6).

Cultivar 'Ciano79'

D1 plot $ESW=13.8+37.3r_S^{-1}-1.4VPD_a$
$r=0.924^{**}$ $(n=29)$ (3)

D2 plot $ESW=38.0+45.8r_S^{-1}-14.6VPD_a$
$r=0.965^{**}$ $(n=24)$ (4)

Cultivar 'Yecora70'

D1 plot $ESW=25.0+36.9r_S^{-1}-7.6VPD_a$
$r=0.958^{**}$ $(n=24)$ (5)

D2 plot $ESW=45.6+44.2r_S^{-1}-16.0VPD_a$
$r=0.921^{**}$ $(n=23)$ (6)

These equations show the negative effect of VPD_a on the ESW, which suggests that even an instantaneous VPD_a could reflect the long term effect of atmospheric demand on ESW. Differences in the coefficients are probably due to the differences in cultivars or stress histories, which would need to be parametarized in order to generalize these equations.

Thus, results from this study show that the critical soil water stress could be assessed quntitatively by detecting changes in the stomatal resistance r_S, transpiration rate Tr and/or the vapor pressure deficit VPD_a. Since, however, the stomatal behavior is dependent on light intensity and time of the day as well, the relations obtained above would be most effective in arid or semiarid areas where the solar radiation is not limiting; that is, the drought stress is liable to be a significant problem. The time of measurement also should be taken into account to minimize the effect of diurnal change.

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