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Early Responses of Drought-Resistant and -Susceptible Tomato Plants Subjected to Water Stress

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Abstract. Three-week-old seedlings of one drought-susceptible tomato cultivar (*Lycopersicon esculentum cv. "New Yorker"*) and two drought-resistant species of tomato (*Solanum pennellii* and *Lycopersicon chilense*) were subjected to various degrees of PEG 8000-induced water stress from −0.017 to −1.0 MPa for a duration of 24 h so that their early responses to water stress could be compared. Such a comparison would determine if there was a relationship to root cytokinin levels following sudden induction of water stress in the drought-resistant species. Transpiration rates of leaves were monitored throughout the 24-h period, shoots were evaluated for leaf water potential (LWP), and roots were extracted for levels of *t*-zeatin riboside (*t*-ZR) and dihydrozeatin riboside (DHZR) using a monoclonal antibody enzyme immunoassay. Transpiration rates were evaluated gravimetrically by difference every 6 h up to 24 h. Transpiration rate decreased with increasing PEG levels and passage of time in all three species, measured at 6 and 12 h, logarithmically in the case of the two *Lycopersicon* species and linearly in the case of *Solanum*. From 12–18 h (while plants were in darkness), transpiration rate was a function of the level of PEG only and not time in all three species. When light resumed from 18–24 h, only *S. pennellii* showed no further decrease in transpiration rate over time with increasing PEG. Drought-susceptible *L. esculentum* had a stronger linear decrease in LWP with increasing PEG 8000 concentration than the other two species. *L. esculentum* also had a higher initial transpiration rate than did either of the drought-resistant species. The two drought-resistant species showed less change in LWP with *S. pennellii* having a small decrease and *L. chilense* having little change. Only *S. pennellii* exhibited a decrease in root *t*-ZR levels, which may imply a role for root cytokinin within the first 24-h exposure to water stress in this species. *L. esculentum* exhibited no change in root *t*-ZR. The levels of *t*-ZR in *L. chilense* were less than that of *L. esculentum* but showed only a slight decrease with increasing PEG. *S. pennellii* and *L. chilense*, although both drought-resistant tomato species, showed different patterns of response with respect to pattern of decline in transpiration rate, LWP, and root *t*-ZR levels.

Different mechanisms have evolved in plants that minimize tissue dehydration and allow metabolism to continue (Aspinall 1980). Tomato has been used extensively in water stress research and has wild relatives that exhibit different mechanisms in response to drought conditions (Dehan and Tal 1978, Rick 1986). Although it has been proposed that cytokinins—which retard aging and senescence (Richmond and Lang 1957)—play a role in the water stress response, this role has not been fully investigated beyond the fact that water-stressed plants exhibit a decrease in endogenous levels of cytokinins. This may be a result of less synthesis or reduced transport from the root (Itai and Vaadia 1965, Itai et al. 1968). High concentrations of cytokinins can promote stomatal opening even in the presence of abscisic acid (ABA) (Blackman and Davies 1983). If roots can detect water stress and convey that condition to the shoot before there are measurable changes in the water status of the shoot, the plant may be able to compensate its pattern of water usage. It has been proposed that reduced transport of cytokinin from the root is a more sensitive indicator of water stress than increased synthesis of a stomatal-opening inhibitor, such as ABA. This is supported by the partial closure of stomata in leaves of *Zea mays* which had half of

their root system exposed to water stress but no change in leaf water potential (LWP) or ABA in leaf tissues (Blackman and Davies 1985).

Little work has been done to investigate the physiological responses during the onset of water stress, the first 24 h after exposure to severe drought or osmotic stress, and to correlate these changes with endogenous root cytokinin levels. This study examined the effects of increasing levels of drought stress on transpiration rates during the first 24 h of exposure in three species of tomato, one drought susceptible and two resistant. LWP and the concomitant changes in endogenous cytokinin in the root was also compared among the species using a commercially available monoclonal antibody immunoassay.

Materials and Methods

Seeds of the drought-susceptible *Lycopersicon esculentum* Mill. cv. "New Yorker," a commercially available cultivated tomato plant, and the drought-resistant species, *Solanum pennellii* Corr. and *Lycopersicon chilense* Dunn., were sown in vermiculite in 5-cm diameter plastic pots. The plants were watered daily with full-strength Hoagland's nutrient solution (Gamborg and Wetter 1975) and kept in a Rheem MP1 constant environment chamber (Puffer-Hubbard Environmental, Weaverville, NC, USA) at 25°C, 50% relative humidity, and a 14-h photoperiod with a light intensity of 260 $\mu mol \cdot m^{-2} s^{-1}$ (Plaut and Federman 1985). Plants were exposed to a light period from 6:00 a.m. to 8:00 p.m., and a dark period from 8:00 p.m. to 6:00 a.m.

Stress Conditions

Three-week-old seedlings were stressed by adding sufficient quantities of polyethylene glycol (PEG 8000; Sigma Chemical Co., St. Louis, MO, USA) to the Hoagland's solution to obtain water potentials of −0.1, −0.3, −0.5, −0.7, and −1.0 MPa (Plaut and Federman 1985). The control, containing only Hoagland's solution, had a water potential of −0.017 MPa. Water potentials of the solutions were measured using a thermocouple psychrometer (Decagon Devices, Pullman, WA, USA).

Measurement of Transpiration Rates

Each pot containing one 3-week-old seedling was placed in an airtight Glad bag with only the shoot exposed. Nonporous foam rubber was placed carefully around the stem to prevent injury, and the bags were held shut with paper clips adjacent to either side of the stem. The experiment was initiated at 10:00 a.m. (t = 0 h), and the normally scheduled dark period was allowed to occur at t = 10–18 h. Each plant/pot unit was weighed at 6-h intervals on a Mettler PB300 top-loading balance, and the difference in weight taken as water lost through transpiration. At the end of the experiment, the total leaf area of each plant was measured with a ΔT area meter (Delta T Devices, Decagon Devices). Transpiration rates for each 6-h period were then calculated as water lost per unit leaf area ($\mu g \cdot cm^{-2} s^{-1}$) (Neill and Horgan, 1985).

Measurement of LWP

LWP was measured at the end of the 24-h treatment period using an SC-10 thermocouple psychrometer with the NT-3 nanovoltmeter–thermometer (Decagon Devices). Three leaf strips (12 × 45 mm) from the largest fully expanded leaves for each treatment–species combination were used to measure LWP. Due to the length of time it took for leaf samples to equilibrate to a stable temperature (10–15 min), and because the experiment was time-dependent, microvolt readings were uniformly taken after 3 min and then converted to megapascals (SC-10 Operator's Manual 1983).

Determination of Root Cytokinin Levels

After 24 h, the roots of each plant were excised, blotted, weighed, and immediately frozen in liquid nitrogen. Root weights per plant ranged from 0.25–0.35 g. The entire root was extracted in 80% methanol in quantities of 20 ml solvent/g fresh weight (Wood 1986). Butylated hydroxytoluene (BHT) and EDTA (Stewart and Barthe 1986) were added to the solvent at 10 $mg \cdot L^{-1}$, and polyvinylpyrrolidone (PVP) at 10 $g \cdot L^{-1}$ (Sigma Chemical Co.). The extraction solvent was kept at a temperature of −20°C. BHT, an antioxidant that helps prevent oxidation of the plant growth substance, and EDTA, a chelating agent, have improved percentage recovery of cytokinins (Stewart and Barthe 1986). Challice (1984) successfully used PVP for the separation of cytokinin as a class from co-occurring phenolics. Its purpose in the extraction solvent is to reduce the number of cleanup steps (Wood 1986).

The plant roots were homogenized using a rotor stator generator probe on a Janke & Kunkel Tissumizer (Tekmar Inc., Cincinnati, OH, USA) at a setting of 6 for 15 s (Wood 1986). The probe was then rinsed with an equal volume of extraction solvent. Samples were extracted for 24 h at −20°C and then centrifuged for 5 min at 3000 *g* in a Beckman TJ-6 refrigerated centrifuge. The supernatant was saved and the pellet discarded.

Primary Purification

A sample aliquot of 2 ml from each treatment was passed through a Sep-Pak disposable chromatography cartridge, and the cartridge was then washed with 1 ml ice-cold extraction solvent. The cartridges had been premoistened by passing 2 ml ice-cold extraction solvent through them prior to sample entry. The eluents obtained were evaporated to dryness at room temperature using a nitrogen gas stream and then reconstituted in 1 ml of 20 mM Tris-buffered saline (20 mM Tris-HCl, 100 mM NaCl, 1 mM $MgCl_2$, 0.1% sodium azide) at pH 7.5 containing 10 $mg \cdot L^{-1}$ BHT and EDTA.

Enzyme Immunoassay of Cytokinins

Aliquots of 100 μl each were removed and measured for *t*-zeatin riboside (*t*-ZR) and dihydrozeatin riboside (DHZR), using a monoclonal antibody enzyme immunoassay (MAb ELISA) called Phytodetek (Idetek, Inc., San Bruno, CA, USA) specific for each compound. The antibody-coated plates, tracer, substrate, wash solution, and stopping reagent were those supplied in the MAb ELISA kit.

All the reagents and standard solutions were prepared accord-

ing to kit instructions (Idetek 1985). The microwell plates coated with antibodies to *t*-ZR were removed from −20°C storage, and 100 µl of standard solution or supernatant sample solution was placed into each well. Then, 100 µl of tracer was added to each well. The wells were mixed, covered with a plate sealer, and incubated for 3 h at 4°C. After incubation, the plates were removed and the solutions decanted. The wells were washed three times by adding 200 µl of the wash solution to each well and then decanting. Two hundred microliters of the substrate solution was added to each well, the plates were covered, and incubated for 1 h at 37°C. The plates were then removed from the incubator and the enzyme reaction stopped by adding one drop of stopping reagent to each well. Absorbance was read at 405 nm on a Titertek Miniskan vertical-path, single-channel photometer (Flow Laboratories Inc., McLean, VA, USA). Optical density was converted to concentration in pmol · $(0.1\ ml)^{-1}$ using the standard curve and its resultant regression equation and then further converted to concentration per gram fresh weight. A series of known concentrations was included each time an assay was run to plot a standard curve unique to each run.

The Phytodetek immunoassays measured both *t*-ZR and DHZR. The standard curve equations were as follow: *t*-ZR: $y = -0.928x - 1.009$ ($r^2 = 0.999$) and DHZR: $y = -1.018x - 0.966$ ($r^2 = 1.000$).

Statistical Design

The experimental design was a split plot with species and stress levels factorially arranged as the main plots and repeated observations over time treated as the split. Three replications were used with pots randomly arranged within replications in the growth chamber. The initial ANOVA on all three species indicated significant differences among species; thus, the data were separated by species and subsequently analyzed separately. Only those factors with a significant F value in the ANOVA were used for determination of the regression equations. Pearson correlation coefficients were determined for leaf water potential, root *t*-ZR concentration and transpiration rates over the three species (SAS Institute 1982).

Multiple regression analyses were separately conducted on transpiration rates versus two independent variables—time (transpiration measured at three time periods: t = 6–12 h, t = 12–18 h, and t = 18–24 h) and stress levels (as measured by polyethylene glycol concentration). Each time period or pair of transpiration measurements was used independently to generate a polynomial model as a function of stress level and time to eliminate any confounding effect due to the scheduled dark period from t = 10–18 h. Regression models were compared evaluating the stress level as a linear, natural logarithm, or exponential function and the best model selected for use. A simple regression analysis of LWP versus stress level and cytokinin concentration versus stress level was also conducted.

Results

Transpiration Rates

There was a sharp decrease of transpiration rate measured at t = 6 h versus t = 12 h in all three species (Figs. 1–3) with the greatest decrease occurring in *L. chilense* (Fig. 3). The drought-susceptible

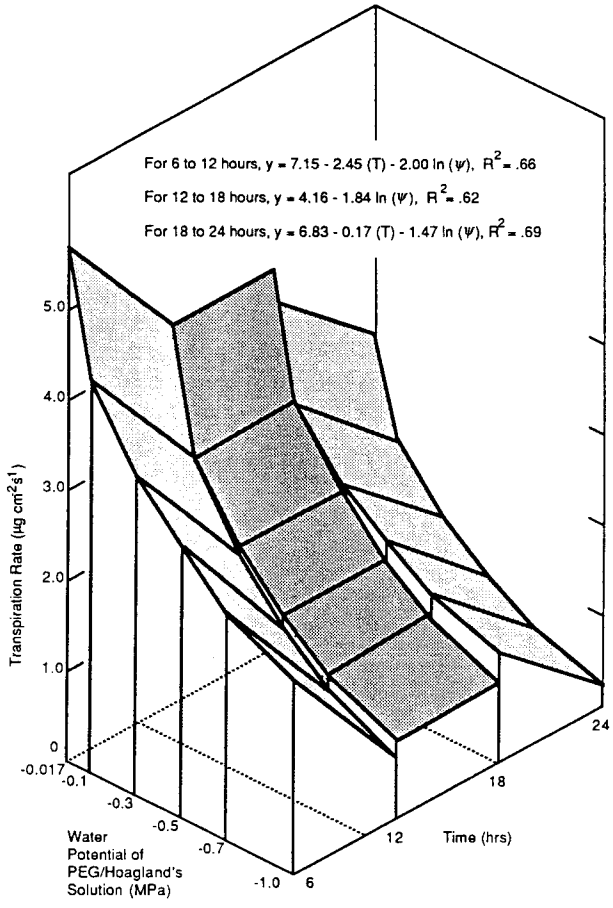

Fig. 1. Transpiration rates of *Lycopersicon esculentum* as a function of increasing levels of osmotic stress and duration of exposure to osmotic stress. The levels shown are the predicted values using the regression equation given for each time period. The gray area on the time axis indicates when the scheduled dark period occurred between t = 10–18 h.

L. esculentum had the greatest initial transpiration rate (Fig. 1) and *S. pennellii* had the least of the three species (Fig. 2). Transpiration rates stabilized during the period from t = 12 h and t = 18 h (the dark period) in all three species and could be expressed as a function of water potential only and not time. In both drought-resistant species, the transpiration rate was less in the dark period than in the drought-susceptible *L. esculentum*. There was no recovery of the transpiration rates to the predark levels with the resumption of the light period at t = 18 h in either of the *Lycopersicon* species (Figs. 1 and 3). At the highest level (−1.0 MPa), there was an almost total cessation of transpiration after only 18 h of exposure to stress in both *L. esculentum* and *L. chilense*. The drought-resistant *S. pennellii* was able to sustain a stable rate of transpiration in the 6 h of light which followed the dark period, in spite of

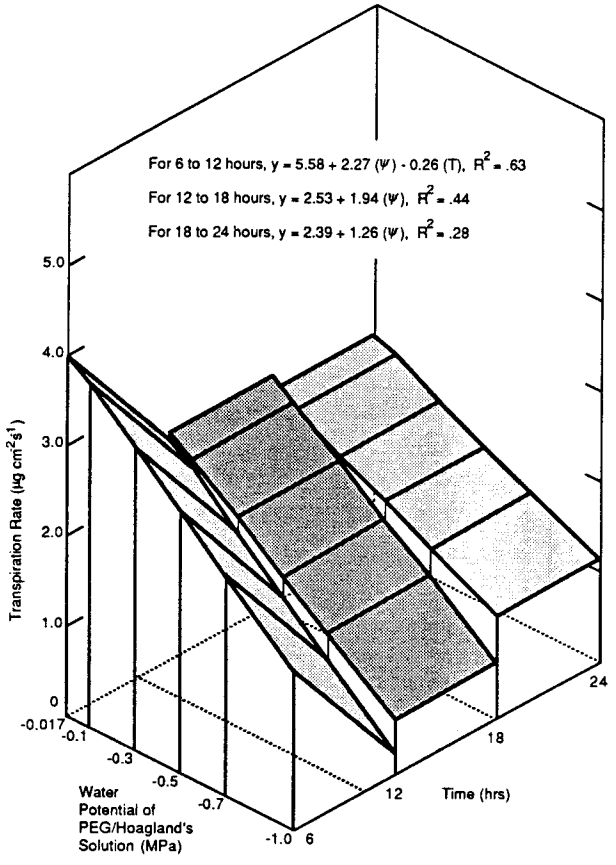

Fig. 2. Transpiration rates of *Solanum pennellii* as a function of increasing levels of osmotic stress and duration of exposure to osmotic stress. The levels shown are the predicted values using the regression equation given for each time period. The gray area on the time axis indicates when the scheduled dark period occurred between t = 10–18 h.

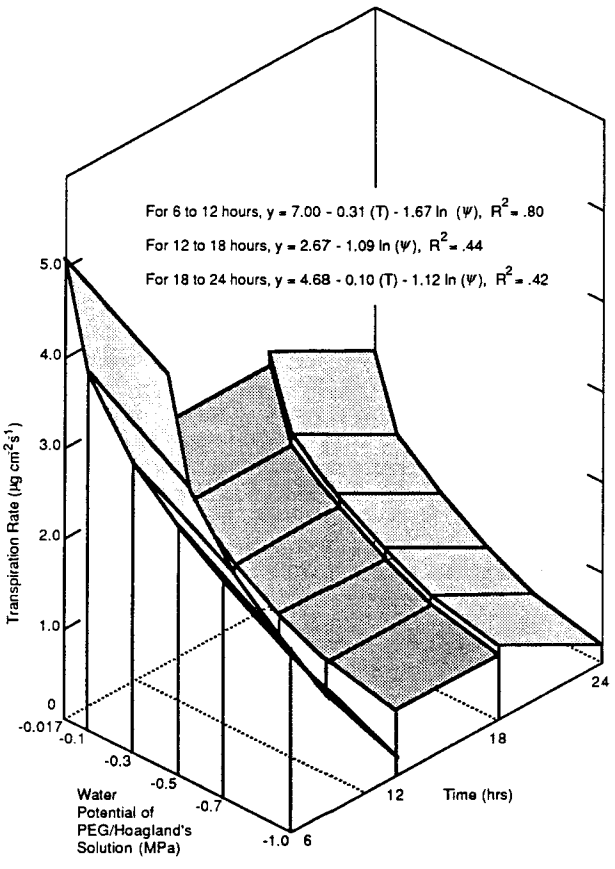

Fig. 3. Transpiration rates of *Lycopersicon chilense* as a function of increasing levels of osmotic stress and duration of exposure to osmotic stress. The levels shown are the predicted values using the regression equation given for each time period. The gray area on the time axis indicates when the scheduled dark period occurred between t = 10–18 h.

the prolonged period of exposure to water stress. The decrease of transpiration and increase in the stress level were functions of the natural logarithm of the ψ of the PEG solution in the two *Lycopersicon* species, the most severe decrease occurring in the first 6 h, and a linear function in the case of the *Solanum* species.

LWP

The three species showed different trends with respect to changes of LWP measured at the end of 24 h, with increasing water stress level (Fig. 4) and had different slopes of the linear regression equations describing those trends. The drought-susceptible *L. esculentum* exhibited a strong linear decrease (slope = 2.51) in LWP with increasing stress. *S. pennellii* exhibited a slower decrease intermediate

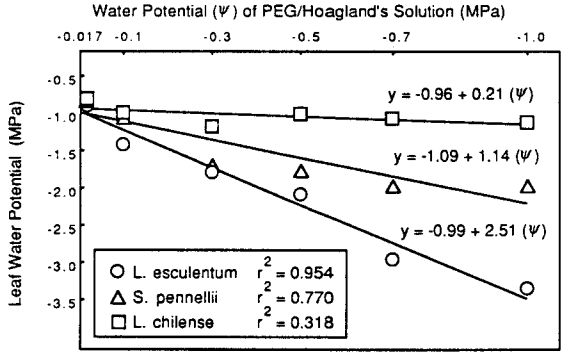

Fig. 4. Endpoint LWP of three tomato species subjected to varying levels of drought stress for a 24-h period.

in slope (1.14) between *L. esculentum* and *L. chilense*. The other drought-resistant species, *L. chilense*, exhibited little change of LWP (slope = 0.21) in response to increasing levels of water stress.

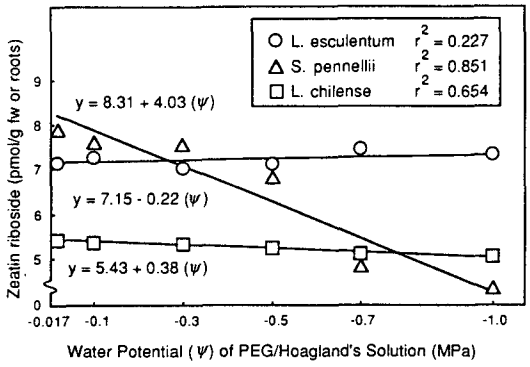

Fig. 5. Endpoint zeatin riboside concentration of three tomato species subjected to varying levels of drought stress for a 24-h period.

Endogenous Root Cytokinin Levels

Both drought-resistant species, *L. chilense* and *S. pennellii,* exhibited a linear decrease with increasing stress, in endogenous levels of root *t*-ZR. However, there was a significant difference in the magnitude of these trends (Fig. 5). The level of *t*-ZR in *S. pennellii* decreased rapidly from a control level of 8.3 to 4.4 pmol · g^{-1} in the most severe stress treatment (−1.0 MPa). The concentration of *t*-ZR in controls of *L. chilense* was much lower (5.4 pmol · g^{-1}) than that of *S. pennellii.* The decrease in *t*-ZR concentration observed in *L. chilense* over increasing water stress levels was also much smaller (a regression slope of 0.38) as opposed to a slope of 4.03 in the case of *S. pennellii.* The concentration of *t*-ZR in the drought-susceptible *L. esculentum* was affected only very slightly by increasing stress, with a small increase in levels as the water potential became more negative. Although a DHZR standard curve could be obtained, no levels of DHZR in the roots could be detected when measured with the ELISA. This was true for all three species at all levels of stress.

There was a highly significant 0.71 correlation between LWP and *t*-ZR concentration, a significant 0.50 correlation between *t*-ZR concentration and transpiration rate, and a nonsignificant 0.15 correlation between LWP and transpiration rate over all three species, times, and PEG concentrations.

Discussion

The hormonal aspect of a plant's response to drought stress has most often centered on ABA. The premise that cytokinins are involved in the response to water deficits arises from the observation that cytokinins are transported from the roots to the shoots in many plants (Henson and Wareing 1976) and that the concentration in the sap exuded from detopped plants is reduced by previously applied stress (Itai et al. 1968). The investigation of cytokinin in this study was an attempt to further elucidate this hormone's role particularly early in the onset of the drought-induced response.

The dramatic decline in levels of root *t*-ZR in *S. pennellii* after 24 h of increasing stress suggests that this cytokinin is either transported to the shoot or is rapidly metabolized into other inactive or storage forms (Letham and Palni 1983), or that synthesis is reduced. The report that cytokinin concentrations decrease in xylem sap of water stressed plants (Itai et al. 1968) argues for metabolism or reduced synthesis in the drought-resistant *S. pennellii* during 24 h of stress, but the fact that transpiration rates stabilized even after 18 h of stress exposure argues for increased transport to the shoot. The *t*-ZR concentration in the roots of *L. chilense* after 24 h decreased slightly as stress increased, indicating a reduction in cytokinin production or, conceivably, an increase in degraded or stored form. Assuming that cytokinin helps to maintain open stomata in some species (Livne and Vaadia 1965, Luke and Freeman 1968), it is possible that in this species there is reduced transport of cytokinin from root to shoot, thereby accounting for the reduced transpiration observed. Another possible explanation for the fate of root cytokinins is that the other physiologically active form *t*-zeatin could be present. When using the Phytodetek kit for *t*-ZR, there is a 47.3% cross reactivity for *t*-zeatin. Therefore, *t*-zeatin could be active in cell division in the root apices, increasing root mass—another adaptive mechanism against drought (Levitt 1980).

The measurement of the ribosides is prudent, considering that they are important translocation forms (Letham and Palni 1983); however, the fate of their metabolites has to be considered. The functions of these metabolites are unclear, the most common concept being that they are storage forms and physiologically inactive (Letham and Palni 1983; McGaw and Horgan 1985). Another aspect to consider is compartmentation of the cytokinins and their metabolizing enzymes (Burch and Stuchbury 1987). Why levels of root DHZR were undetectable, even in the unstressed plants, is unclear. One possibility is that DHZR is rapidly translocated out of the root, or is metabolized to *t*-ZR. However, the absence of the Δ^2 double bonds makes the dihydroform of cytokinin resistant to cytokinin oxidase attack and apparently incapable of being oxidized to *t*-ZR (McGaw and Horgan 1985). Conjugation provides another mechanism by which this compound can be metabolized. The resultant glucoside conju-

gates are most probably storage forms (McGaw and Horgan 1985); therefore, this may be the fate of DHZR. A simpler possibility is that DHZR is normally produced in very small amounts in the roots below the detection range of the assay.

There is a definite stomatal response by *S. pennellii* to darkness and the resumption of light. Although under stress, the guard cells of the leaf were able to function in response to diurnal periodicity. Transpiration rates are decreased linearly as stress is increased. This indicates a less sensitive response to less severe levels of water stress than in the drought-susceptible *L. esculentum* and the drought-resistant *L. chilense,* which both responded to increase stress levels in a logarithmic manner. In this study, inability of *L. esculentum* to reopen its stomata after the light period had resumed was probably due to the severity of the water stress effect. Water stress has an overriding influence on the behavior of the stomata, and this behavior is dictated by factors specific to the species and cultivar. In the case of "Alisa Craig," a different susceptible cultivar of *L. esculentum,* there was a decrease in transpiration rate in the dark and a subsequent increase following the reintroduction of light (Neill and Horgan 1985). The tapering off of the transpiration rate decrease after stress level −0.5 MPa suggests that *L. esculentum* had become unresponsive to further stress at that point and increasing stress did not bring about any major stomatal response.

Lycopersicon chilense, also a drought-resistant tomato species, responded by complete cessation of transpiration after only 18 h of water stress at the most severe level of −1.0 MPa. This, coupled with the fact that LWP remained high, indicated that *L. chilense* is a drought avoider, as defined by Levitt (1980). As transpiration rates decrease, it is expected that LWP of the stressed drought-resistant plant will remain at a relatively high level. This is observed in *S. pennellii.* This tomato species is drought-tolerant and has a high capacity to absorb and retain atmospheric water (Taylor et al. 1982a). The levels of LWP measured in the present study show that there is some loss of water from the leaves, indicative of a plant which tolerates drought at a low water potential but has a high turgor potential (Levitt 1980).

Ludlow (1980) described a threshold water potential for stomatal closure, which varies among species and cultivars, and appears to be associated with the environment to which that plant has adapted. A drought-susceptible plant will have a limited capacity for this sort of stomatal adaptation. The dramatic decrease in LWP of *L. esculentum* is probably due to the plant's inability for total stomatal closure under stress. Studies on different cultivars of this species show a similar response of LWP to increasing water deficit (Taylor et al. 1982b).

The results of the present study show that *L. chilense,* by exhibiting very high LWP and cessation of transpiration, possesses the characteristics of a drought avoider, and more specifically, a water saver (Levitt 1980). The high LWP and cessation of transpiration in this species and not in *L. esculentum* probably contributed to the nonsignificant correlation between these two parameters. However, *L. chilense* also possesses an extensive root system, a distinct characteristic of a water spender, when found in its natural habitat (Rick 1986). Thus, the species appears to utilize both resistance mechanisms, a common characteristic among drought-resistant species (Jones et al. 1981). The other drought-resistant species, *S. pennellii,* exhibits characteristics of a drought-tolerant plant (lowered LWP, possible osmoregulation). However, its ability to retain atmospheric water in its foliage (Taylor et al. 1982a), and subsequently high turgor, is indicative of a drought avoider.

Cytokinin levels in roots responded differently (as did LWP and transpiration rates) in the three different tomato species to the induction of water deficit. A species and varietal difference in the o-xylosyl derivitization of *t*-Z and DHZ has been shown for *Phaseolus* (Mok and Mok 1987). Cytokinin derivitization, transport, and metabolic systems could differ among the tomato species as well. The evidence indicated that the three tomato species each possess different mechanisms for the early responses to water deficit. The twofold reduction in the amount of *t*-ZR detected in the roots of *S. pennellii* may be capable of eliciting change in the shoot. Incubation of half of the roots of individual maize plants resulted in restricted stomatal aperture even though there was no change in LWP or turgor when at most only a twofold reduction in materials transported from the root could be expected. This reduction in aperture was reversed by less than a 10-fold increase in kinetin (Blackman and Davies 1985). Changes in endogenous levels of *t*-ZR can occur as early as 24 h after induction of PEG-induced drought stress which suggests that cytokinins as well as ABA could play a role in rapid response to drought stress or that cytokinins in the roots are affected very quickly when the plant is exposed to water stress.

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