

Water Relations and Physiological Activity of Potatoes¹

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Abstract. The effects of water stress on internal water potential components and specific physiological processes were investigated in field grown potatoes (*Solanum tuberosum* L. cv. Viking). Leaf water potential (ψ_{leaf}) as estimated by the pressure chamber, was not directly related to soil water potential (ψ_{soil}) until a specific minimum ψ_{soil} was attained. Subsequently ψ_{leaf} did not increase in response to increases in ψ_{soil} . Water stress affected physiological processes such as stomatal resistance, photosynthesis and enzyme activity. A decline in ψ_{leaf} was apparently responsible for increased stomatal resistance and decreases in photosynthetic rates. The activities of ribulose diphosphate carboxylase and phosphoenolpyruvate carboxylase decreased as ψ_{leaf} declined. The relationship between water stress and physiological processes and the inability of ψ_{leaf} to respond to increases in ψ_{soil} after a maximum stress may partially explain the extreme sensitivity of potatoes to even mild water stress.

The limitations imposed by water stress on plant growth are often the result of detrimental effects on physical and physiological processes associated with declining leaf (ψ_{leaf}) and soil (ψ_{soil}) water potentials (10). Growth and yields of potatoes are adversely affected by even mild water stress (6, 14, 18), although the physiological basis for the growth restrictions are virtually unknown.

Epstein and Grant (7) examined the water relations of potatoes under field conditions and observed that leaf diffusive resistances increased with declining availability of soil water. However, a significant relationship between diffusive resistance and relative water content was not evident. Similarly, increases in stomatal and residual resistances concomitant with a decrease in photosynthesis were observed in potatoes as ψ_{leaf} declined (15). Leaf growth of potatoes also appears to be severely inhibited at ψ_{leaf} approaching -4 to -5 bars (8).

Although data are available regarding water stress and physiological activity of plants in controlled environments, limited data are available with respect to field grown plants. The specific objectives of this study were to examine the relationship between plant and soil water relations of potato plants under field grown conditions and determine the response of select physiological parameters to water stress.

Materials and Methods

Seed pieces of 'Viking' potatoes were planted March 24, 1976 on a Friona coarse sandy loam. Each plot consisted of 7 rows, spaced 1 m apart and 6.7 m long oriented in a N to S direction. 'Viking' was utilized because it represents a high yielding fresh market potato commonly grown in the Texas High Plains. Post plant N fertilizer (168 kg/ha) and a Triazine herbicide (Sencor at 1.6 kg/ha) were applied to all plots.

Irrigation treatments were imposed beginning after plant emergence. Soil water content of the 15 to 60 cm profile depth in the plant row was determined by neutron probe analysis. Irrigation was conducted when the available water ($-1/3$ to -15 bars) in the top 45 cm of the soil had been depleted by 40 and 80% for the high and low irrigation treatments, respectively. These correspond to soil water potentials of about -1.5 and -7.0 bars at the 20 cm depth. At each irrigation, water was metered on to insure that 5.0 cm was applied to the high available water treatment and 7.6 cm to the low available water treatment which was sufficient to supply 110% of the water extracted.

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Water flux from the soil to the plant is regulated by water potential gradients. In order to accurately describe the relationship between the plant and soil water status, ψ_{soil} , rather than volumetric water content was used. For comparative purposes, the calibrated relationship between volumetric water content and soil water potential is reported (Fig. 1). In order to establish that the values obtained for soil water potential were representative of the available water in the root zone, root distributions of plants were visually ascertained. The majority of the root system of plants in both treatments was directly below the plant and was limited to the upper 45 cm of the soil profile. Therefore, ψ_{soil} observed in this portion of the profile appeared to be representative of water available to the plants. Two field replications of each irrigation treatment were used.

Fully expanded leaves in the upper and lower portions of the canopy were used for each determination. Leaf water potentials were estimated using the pressure chamber, and osmotic potentials were obtained by freezing leaf tissue in liquid N and thawing at 25°C prior to equilibration in a thermocouple psychrometer. Determinations of ψ_{leaf} of potatoes conducted by Gandar and Tanner (9) indicate that the pressure chamber provides a reliable estimate of ψ_{leaf} provided that sampling is conducted rapidly. Diffusive resistance data were determined with a Lamda LI-60 diffusive resistance meter and a LI-20S sensor calibrated according to the methods of Kanemasu et al. (13). Leaf water potentials and diffusive resistances were obtained at several times during the day and consistently at the same time during the study period. Photosynthetic rates were determined using the ¹⁴CO₂ labeling technique described

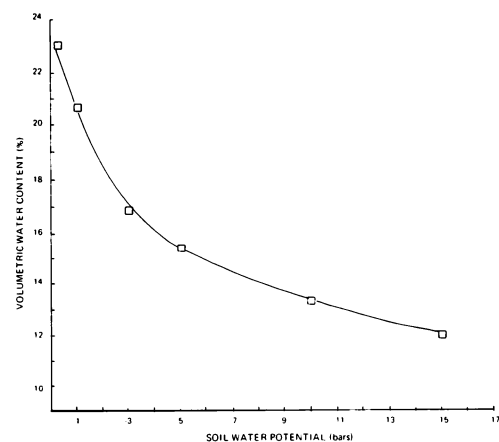


Fig. 1. Relationship between volumetric water content and soil water potential for the surface horizon of Friona coarse sandy loam.

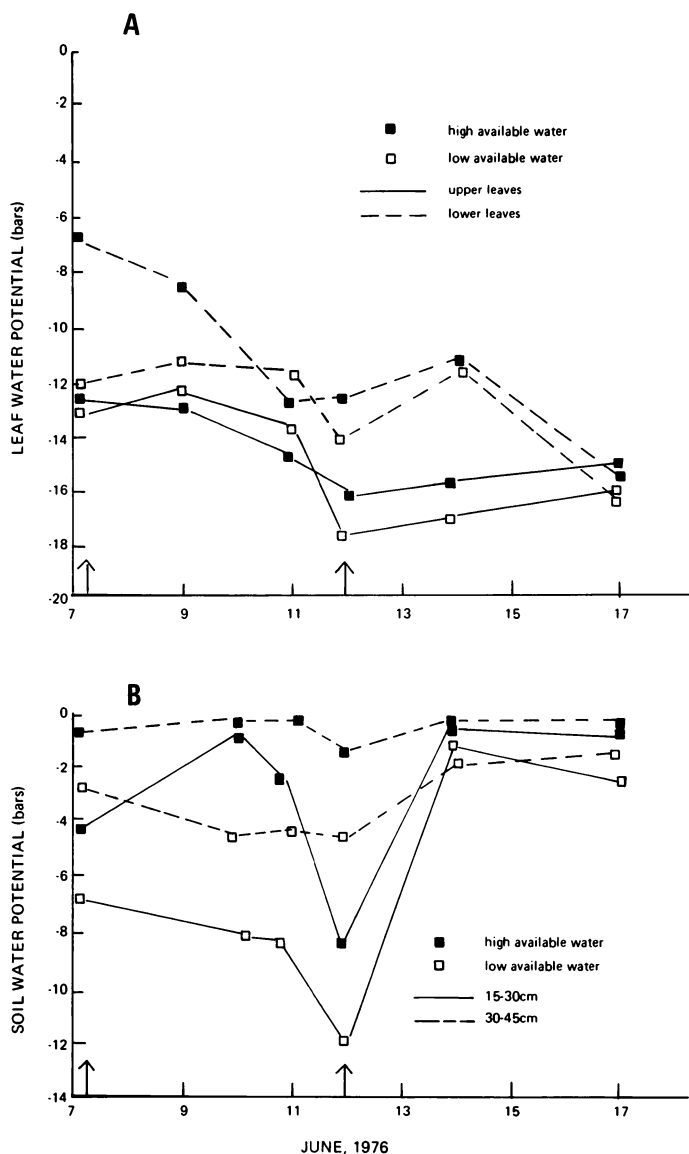


Fig. 2. Midday (~1400-1500 CDT) leaf water potentials (A) of potato leaves and soil water potentials (B) in June 1976. Arrows indicate dates of irrigation of the high available water treatment (June 7) and both treatments (June 12). Values represent the mean of at least 4 observations. The standard deviations for ψ_{leaf} ranged from ± 0.3 to ± 1.0 bars and ± 0.1 to ± 0.2 bars for ψ_{soil} .

by Naylor and Teare (16). The activity of ribulose diphosphate carboxylase (RUDPcase) and phosphoenolpyruvate carboxylase (PEPcase) was determined by methods similar to those previously reported (11).

Results and Discussion

Plant and soil water relations. Midday ψ_{leaf} of upper potato leaves exhibited a pronounced decline during the month of June (Fig. 2A). On June 7, the minimum ψ_{leaf} of plants in both treatments approached -12 to -13 bars even though ψ_{soil} was distinctly different (Fig. 2B). Subsequently, ψ_{leaf} remained essentially unchanged until June 11, when a large decline in ψ_{leaf} was observed. The depression in ψ_{leaf} was apparently the result of a drastic reduction in ψ_{soil} in the 15 to 30 cm profile depth. However, the increased ψ_{soil} after irrigation was not manifest in similar increases in ψ_{leaf} . Rather, ψ_{leaf} increased slowly until June 17 and the increase was relatively small in magnitude. Distinct treatment differences in ψ_{leaf} were evident between June 12 and June 17. The magnitude of the differences appeared to be similar to that observed in the ψ_{soil} during

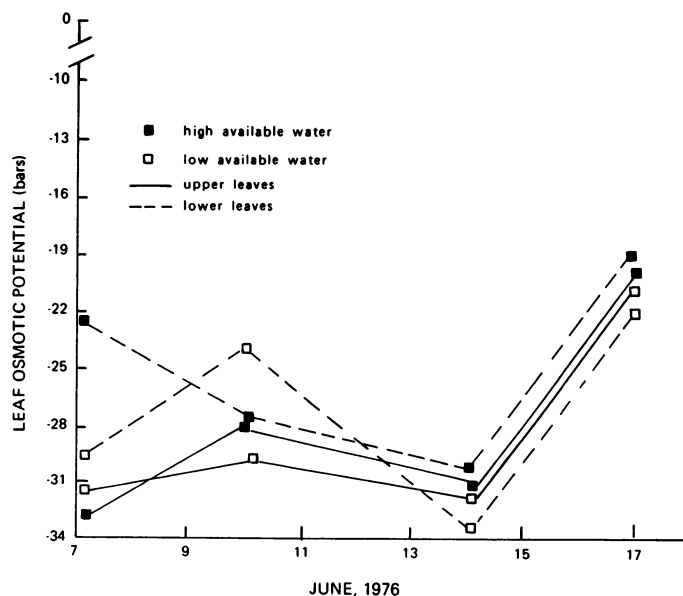


Fig. 3. Leaf osmotic potentials of potato leaves in June, 1976. Values represent the mean of at least 4 observations. The SD for osmotic potentials ranged from ± 0.5 to ± 1.2 bars.

the same period. However, ψ_{leaf} on June 17 were not comparable to those observed on June 7 even though ψ_{soil} was similar or higher. Leaf water potentials observed during the course of this study are in agreement with previous data obtained from field grown potatoes (5).

Leaf water potentials of lower and upper leaves were similar. The general trend was for ψ_{leaf} to decline from June 7 to June 17. Major differences on a treatment basis were observed between June 7 and June 11, when ψ_{leaf} of plants in the high available water treatment were substantially greater than those in the low available water treatment. Thereafter, treatment differences were minimal. Until June 17, ψ_{leaf} of the lower leaves was sufficiently greater than ψ_{leaf} of the upper leaves such that a gradient of water potential was evident. On June 17, the gradient was virtually nonexistent indicating that water flux through the plant would be minimal.

Gandar and Tanner (8) observed no major differences in ψ_{leaf} between stressed and nonstressed potato plants on a daily or diurnal basis, although the rate of recovery of ψ_{leaf} was reduced in stressed plants. The absence of large differences in ψ_{leaf} in this study support their observations, at least with respect to min daily values of ψ_{leaf} . Furthermore, since minimal differences in ψ_{leaf} were observed and large differences in ψ_{soil} were evident, this suggests that ψ_{leaf} may be partially independent of ψ_{soil} . Cary and Wright (5) have observed that ψ_{leaf} in potatoes can be highly dependent on evaporative demand. Campbell et al. (4) have provided a steady state model to account for the relationship between transpiration, ψ_{soil} and ψ_{leaf} . The failure of ψ_{leaf} of potatoes to recover after stress may be due in part to regulation of water flux by the tuber (9) or changes in the internal resistance to water flux (2, 3). The inability of ψ_{leaf} to recover may explain why potatoes are extremely sensitive to mild water stress. A rapid recovery of ψ_{leaf} after irrigation is characteristic of more drought tolerant species such as cotton or sorghum (1).

Between June 7 and June 13, osmotic potentials were of sufficient magnitude to sustain relatively large turgor potentials (Fig. 3). The turgor potentials observed would presumably be of sufficient magnitude to maintain cell extension and growth. Although the data of Gandar and Tanner (8) suggest that leaf growth in potatoes ceases at ψ_{leaf} approaching -5 bars, turgor potential might be the more important criterion in assessing the role of water stress on leaf growth. Minimal levels of turgor po-

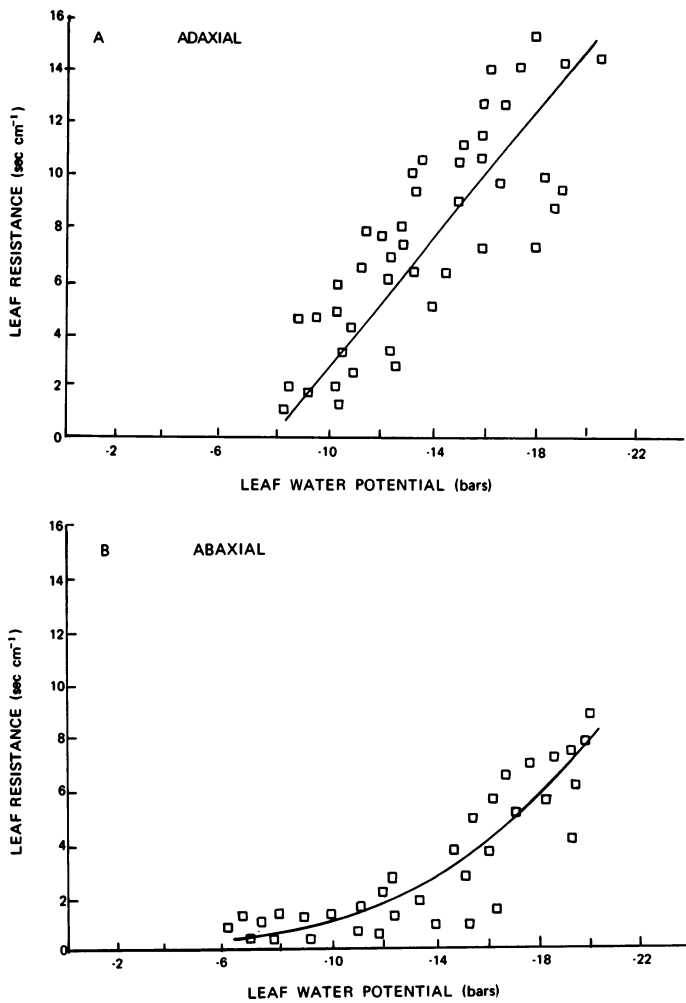


Fig. 4. Relationship between adaxial (A) and abaxial (B) stomatal resistance (R_s) and ψ_{leaf} of potato. Values represent upper and lower leaves at radiation levels sufficient ($\sim 1000 \mu\text{e}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$) to saturate the opening response.

tential were observed June 17, when osmotic potentials increased sharply and ψ_{leaf} were on the order of -16 to -17 bars.

Plant water status and leaf resistance. A significant relationship existed between ψ_{leaf} and leaf diffusive resistance (Fig. 4). The values of diffusive resistance are comparable to those previously reported for potato under similar conditions (7). Rather than assume that adaxial and abaxial stomatal resistances acted in parallel in controlling water flux, the stomatal response of each surface to ψ_{leaf} was examined. A somewhat linear relationship was observed between ψ_{leaf} and adaxial stomatal resistance (Fig. 4A) whereas a more parabolic relationship was observed between abaxial resistance and ψ_{leaf} (Fig. 4B). This response has also been observed in snap beans (12) and clearly indicates a differential abaxial and adaxial stomatal control of water loss. This mechanism may be important in regulating water flux under situations of decreasing water potentials. In addition, this may be important in regulating CO_2 diffusion to the leaf under water stress situations in view of the hypostomatus nature of potato leaves. The significance of this situation becomes apparent when average daily stomatal resistances are considered with respect to time (Fig. 5). Stomatal resistances increased in a characteristic manner between June 7 and June 17, which correlated well with concomitant changes in ψ_{leaf} . Although resistances increased in response to ψ_{leaf} , it is still necessary to maintain water flux through the plant in order to

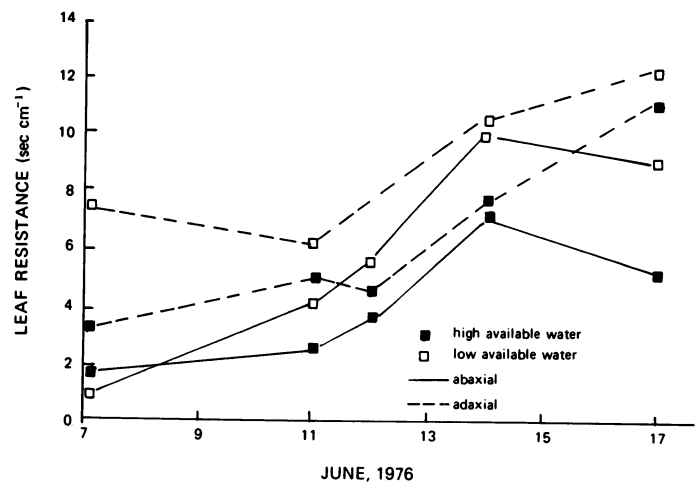


Fig. 5. Average daily stomatal resistance of potato leaves during June, 1976.

sustain growth. Thus, differences in abaxial and adaxial response to ψ_{leaf} on both a daily and seasonal basis could sustain water flux through transpiration. The data also indicate that as water stress progresses, leaves tend to have greater resistances for longer periods of time each day, presumably in response to lower ψ_{leaf} .

Plant water status, photosynthesis and carboxylating enzyme activity. On both a physiological and biochemical basis, water stress and resultant depressions in ψ_{leaf} had pronounced effects on photosynthesis and carboxylating enzyme activity. Maximum rates of photosynthesis were attained on June 12 and a distinct treatment difference was observed which corresponded to differences in ψ_{leaf} (Fig. 6). Thereafter photosynthetic rates declined in plants of both treatments as ψ_{leaf} declined. A notable exception existed with respect to photosynthetic rates of lower leaves of the low available water treatment. However, this may be due to slight increases in ψ_{leaf} of these after irrigation. The data also suggest that upper leaves in both treatments are capable of maintaining higher photosynthetic rates at lower ψ_{leaf} than lower leaves until June 17. Photosynthetic rates on June 17 were similar in both upper and lower leaves. The decrease in photosynthesis may be partially attributed to increased leaf resistance in view of the significant relationship between stomatal resistance and ψ_{leaf} or could be due to stress induced increases in residual resistances as suggested by Moorby et al. (15).

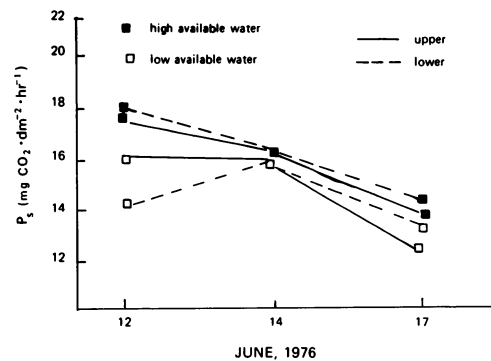


Fig. 6. Photosynthesis of upper and lower leaves of potatoes during June, 1976. Photosynthetic rates of upper and lower leaves are at equivalent radiation levels. Values represent the mean of 4 observations and SD were consistently less than $1.5 \text{ mg CO}_2\cdot\text{dm}^{-2}\cdot\text{hr}^{-1}$. Photosynthetic rates on June 12, 14 and 17 represent days associated with max stress (June 12), 2 days after irrigation (June 14) and 5 days after irrigation (June 17).

Table 1. Activities of ribulose diphosphate carboxylase (RUDPcase) and phosphoenolpyruvate carboxylase (PEPcase) of potato leaves on June 9 and June 21, 1976. Values represent the mean \pm SD of 4 assays.

Treatment	Date	ψ_w (bars)	Activity (μ moles CO_2 -mg Chl $^{-1}$ ·hr $^{-1}$)	
			RUDPcase	PEPcase
High available water				
Upper leaves	June 9	-12.5	253 \pm 21	9.2 \pm 3.0
Lower leaves		-8.0	171 \pm 14	3.7 \pm 0.9
Low available water				
Upper leaves		-12.5	263 \pm 24	8.5 \pm 1.0
Lower leaves		-11.0	136 \pm 16	10.7 \pm 1.0
High available water				
Upper leaves	June 21	-16.5	125 \pm 7.5	3.8 \pm 0.8
Low available water				
Upper leaves		-17.0	126 \pm 1.5	3.7 \pm 0.9

Water stress also appeared to affect the activity of photosynthetic carboxylating enzymes of potato (Table 1). Rates of RUDPcase and PEPcase observed in plants of both treatments on June 9 were comparable to rates characteristic of C₃ species. On June 21, when ψ_{leaf} was -16 to -17 bars the activity of both enzymes was substantially reduced. Thus, the decline in photosynthesis could also be due to reduced enzyme activity associated with low ψ_{leaf} . Recent data have suggested a close relationship between ψ_{leaf} and activity of RUDPcase in snapbean (17). However, Moorby et al. (15) observed that water stress had no effect on RUDPcase in potato.

Our data suggest that both physical and physiological processes of potatoes are strongly dependent on leaf water status. Growth and yield of potatoes growing in conditions where plants are subjected to temporal water deficits might be reduced as a result of stress induced changes of physiological processes and water potential components.

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