WATER DEFICIT EFFECTS ON POTATO LEAF GROWTH AND TRANSPIRATION: UTILIZING FRACTION EXTRACTABLE SOIL WATER FOR COMPARISON WITH OTHER CROPS

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Abstract

Numerous studies have demonstrated that physiological responses of many crops to the fraction of extractable soil water conforms to a generalizable pattern. This suggests that differences among crops in their drought tolerance are largely due to differences in the total amount of transpirable water the crop can extract. Potato is frequently assumed to be more drought sensitive than other agronomic crops due, at least in part, to a shallow root system. In the research reported here, potato leaf growth and transpiration response to water deficits were determined as a function of fraction transpirable soil water (FTSW). Transpiration was unaffected by water stress until a critical FTSW was achieved when 64% to 80% of the extractable soil water was depleted depending on the cultivar. This was similar to the response reported for 8 other agronomic crops. In terms of transpiration, potato hypersensitivity to drought stress appears to be due to less effective soil water extraction. Leaf growth, however, showed a unique response to soil water deficits. Leaf growth began to decline when 40% of the extractable soil water was depleted. The associated critical FTSW was higher than any previously reported for all other crops. These data indicate that in addition to extracting less soil water, an additional physiological process related to leaf expansion must be contributing to the potato's hypersensitivity to drought.

Compendio

Numerosos estudios han demostrado que las respuestas fisiológicas de muchos cultivos a la fracción extraíble de agua del suelo se comporta de una manera posible de generalizarse. Esto sugiere que las diferencias entre sus tolerancias a la sequía son debidas considerablemente a las diferencias en la cantidad total de agua de transpiración que el cultivo puede extraer. Se considera frecuentemente que la papa es más sensible a la sequía que

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otros cultivos debido, al menos en parte, a un sistema radicular superficial. En la investigación sobre la que aquí se informa, se determinaron las respuestas del crecimiento de las hojas y de la transpiración a los déficits de agua, como una función de la fracción transpirable del agua del suelo (FTSW). La transpiración no fue afectada por el estrés al agua hasta que era alcanzada una FTSW crítica, cuando se consumía del 64% al 80% del agua extraíble del suelo, dependiendo del cultivar. Esto fue similar a la respuesta reportada para otros ocho cultivos. En términos de transpiración, la hipersensibilidad de la papa al estrés a la sequía parece deberse a una extracción menos efectiva del agua del suelo. El crecimiento de las hojas, sin embargo, mostró una respuesta poco común a los déficits de agua en el suelo. El crecimiento de las hojas empezó a declinar cuando se consumió el 40% del agua extraíble del suelo. La FTSW crítica asociada fue mayor que en cualquier otro informe anterior sobre todos los otros cultivos. Esta información indica que además de extraer menos agua del suelo, un proceso fisiológico adicional relacionado a la expansión foliar debe estar contribuyendo a la hipersensibilidad de la papa a la sequía.

Introduction

Potato (*Solanum tuberosum* L.) has long been recognized as being extremely sensitive to drought stress (8) and many researchers have concluded that potato is more susceptible to water deficits than other agronomic crops. Corey and Blake (2) compared soil water extraction by potato, tomato (*Lycopersicon esculentum*) and sweet corn (*Zea mays* L.) and found potatoes extracted less soil water and had shallower root extension than either of the other two crops. Durrant *et al.* (3) found potatoes extracted less soil water at each soil horizon and had only about half the effective rooting depth of sugar beet (*Beta vulgaris*) or barley (*Hordeum vulgare*). These reports suggest shallower and perhaps less efficient rooting systems are responsible for potato's susceptibility to drought. However, in a field study using a root observation chamber, Fulton (6) found that potato, cucumber (*Cucumis sativus*) and corn all had similar rooting depths. In these experiments, potato yields were adversely affected by drought stress at higher soil water potentials (Ψ_s) than were yields of cucumber or corn. Fulton (6) suggested that some other physiological mechanism besides rooting depth was responsible for the different drought responses.

Measurements of physiological parameters associated with water stress in potato have also led to contrasting conclusions. Gandar and Tanner (7) found that leaf growth stopped at leaf water potentials (Ψ_l) between -0.4 and -0.5 MPa in greenhouse grown potato plants. In contrast, Jefferies (9) found the critical range of Ψ_l for leaf growth in field grown potato to be -0.28 to -1.2 MPa, and Epstein and Grant (4) failed to find any relationship between relative leaf water content and stomatal resistance.

Consistent with these findings, Ritchie (15) concluded there was no unique Ψ_l associated with stomatal response, and a parameter with greater generalizability than either Ψ_l or Ψ_s was needed for evaluating crop drought stress responses across species or environmental conditions. He proposed that relative rates of various physiological processes across crop species and soil types should respond similarly to soil moisture deficits when soil water was measured as a fraction of total extractable water. Extractable water was defined as the difference between the highest measured volumetric water content in the field (after drainage) and the lowest measured water content (measured over the entire soil depth through which water extraction occurred) when plant evaporation practically stopped (13). Ritchie (15) proposed that when rates of photosynthesis, transpiration or leaf growth were related to fraction extractable water, plants would respond similarly across a wide range of soil, environmental and meteorological conditions (Figure 1). Specifically, it was proposed that these physiological processes would not be negatively affected by drought stress until a critical fraction extractable soil water content was reached after which, if drying continued, the physiological process would decline linearly with soil water. Most importantly, he proposed that these critical values would be constant across plant species and environmental conditions.

A consistent crop response to fraction extractable water has been widely reported (Figure 1). Sinclair and Ludlow (19) used fraction transpirable soil water (FTSW), (defined as 1 at field capacity and 0 when transpiration of droughted plants reached 10% or less of potential transpiration rates), as a measure of extractable water to access the drought response of 4 grain legumes. While Ψ_l at death varied from -1.8 to -6.3 MPa among cowpea (*Vigna unguiculata*), black gram (*Vigna mungo*), soybean (*Glycine max*) and pigeonpea (*Cajanus cajan*), all four responded similarly to FTSW. Transpiration rates were comparable to those of well watered plants until FTSW reached ~0.2. They concluded that this uniform response to FTSW was not affected by the rate of soil drying and would apply under both greenhouse and field conditions. Similar critical values of FTSW for photosynthesis, transpiration or biomass accumulation have been reported for greenhouse grown cotton (*Gossypium hirsutum* L.), grain sorghum (*Sorghum bicolor* (L.) Moench.), and field grown corn, cotton, grain sorghum, soybean and alfalfa (*Medicago sativa* L.) (13, 14, 16, 21). Critical FTSW values for leaf growth have also been reported for greenhouse grown soybean, cotton and grain sorghum (16, 18) and field grown grain sorghum (16). These values are higher than for transpiration, and leaf growth stops completely before FTSW values of 0 are obtained (Figure 1).

In general, reported plant responses to soil water deficit, when measured as FTSW, are very similar. Most reported critical FTSW values for transpiration and photosynthesis are between 0.2 and 0.3 (see histogram in Figure 1). Leaf growth is more sensitive, with most reported critical FTSW

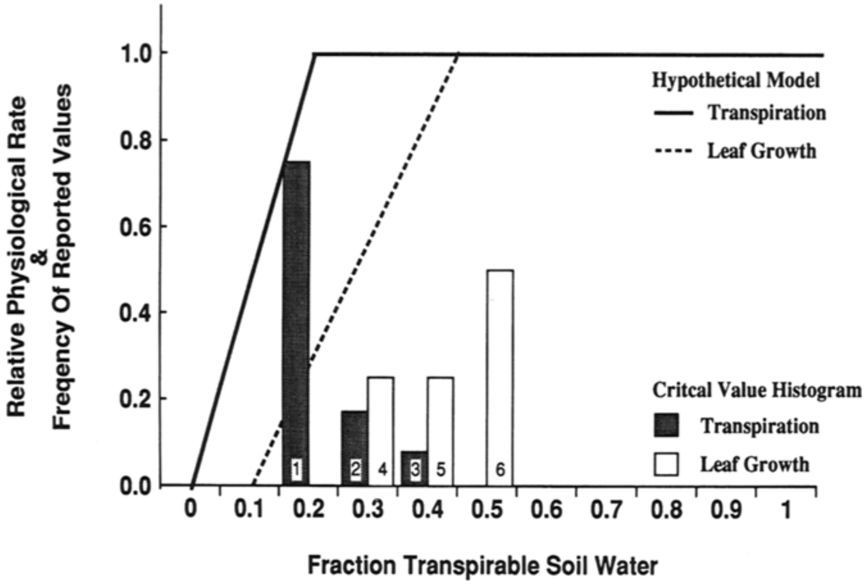

FIG. 1. Generalized model of physiological responses (transpiration; solid line, and leaf growth; dashed line) to soil water deficits measured as fraction transpirable soil water as proposed by Ritchie (15). The model proposes that these physiological rates, relative to non-stressed potential values, should be stable until a critical FTSW is reached. Previously reported values of the critical FTSW at which these physiological rates begin to decline are presented as a histogram showing the degree to which experimental values conform to Ritchie's generalization. For transpiration (histogram bars number 1-3), 1: field grown alfalfa, corn, cotton, grain sorghum and soybean, and greenhouse grown black gram, cowpea, pigeonpea, soybean (13, 14, 21, 20, 19), 2: greenhouse grown grain sorghum and cotton (16) and 3: field grown grain sorghum (16). For leaf growth (histogram bars number 4-6), 4: greenhouse grown soybean (18), 5: greenhouse grown grain sorghum (16) and 6: greenhouse grown cotton and field grown grain sorghum (16).

values between 0.4 and 0.5 (Figure 1). In light of the wide similarity of responses across many crops and conditions, Sinclair and Ludlow (19) suggested that major differences in crop drought response must primarily be due to differences in the magnitude of water a given crop can extract.

The physiological stability of transpiration and leaf growth to changes in FTSW suggest the use of this relationship to explore the apparent sensitivity of potato to drought stress. If potato responded similarly to other crops, (*i.e.* critical FTSW values for transpiration of ~0.2-0.3 and leaf growth of ~0.4-0.5) this would suggest that it's drought sensitivity was due to less effective soil water extraction. This would be consistent with the findings of Corey and Blake (2), Durrant *et al.* (3) and with the conclusions of Sinclair and Ludlow (19). If on the other hand, the response to FTSW was unique, it would indicate that a more fundamental physiological difference existed between the potato and other crops reported to date. The purpose of the experiments reported here was to determine the transpiration and leaf growth response of two potato cultivars to water deficits as measured by FTSW.

Materials and Methods

Greenhouse experiments were initiated in 1989 and 1990 with potato cultivar BelRus (replicates 1 and 2), and in 1991 with cultivar Katahdin (replicates 3 and 4). Each replicate followed the same general experimental plan. Plants of uniform size were assigned to either a well watered control group or a dry down treatment. Plants in the control group were maintained at field capacity throughout the experiment, while plants in the dry down treatment were not watered after the initiation of the experiment which continued until transpiration had stopped. Each day, soil water evaporation, plant transpiration, and plant leaf area associated with each pot were non-destructively estimated. At the end of the experiment, the transpiration rates, leaf growth rates and FTSW values were computed for each pot and normalized to conform to the generalized form presented in Figure 1. Specifics of these procedures follow.

Plant Growth—All plants were grown in sterilized 2.5 liter pots filled with a potting mix consisting of 1 part vermiculite, 2 parts peat, 2 parts sand and 3 parts hagerstown silt loam field soil (Typic hapludalf: fine, mixed, mesic) taken from the soil horizon. Potatoes were started from individual seed pieces approximately 1 cm^3 in size each containing a single eye. The pots were watered to saturation approximately every 3 days. To maintain soil fertility, every other watering (approximately once a week) the pots were saturated with a solution of full strength Peter's Professional Soluble Plant Food (Grace-Sierra Horticultural Products Co.). Supplemental lighting was provided with sodium halide lights to provide a 14 h photoperiod.

When the plants were ~25 cm tall and had ~9 nodes, the pots were randomly divided into a well-watered control, a dry-down treatment, or a group for destructive leaf area sampling. One day before initiating the dry-down, all pots in the control and dry-down treatments were saturated with water and allowed to drain for 24 h. During this time the soil in each pot was covered to a depth of 40 mm with polyvynalchloride beads to minimize soil evaporation during the experiment. Three additional pots with the same volume of soil and covered with polyvynalchloride beads, but without plants were also saturated with water and allowed to drain for 24 h.

Relative Transpiration Rate—The analysis of relative transpiration was similar to that described by Sinclair and Ludlow (19). All pots were assumed to be at field capacity (FTSW = 1) 24 h after saturation and were weighed to determine their initial weight. Each day, the plants in each treatment and the additional three pots without plants were weighed in the early morning on a balance with a resolution of ± 0.1 g. Water of equivalent weight to the daily loss was added back to the pots in the well-watered treatment. Generally, water was not added to the pots in the drought-stressed treatment. However, to assure that the dry-down did not occur too rapidly to be able to collect data across a broad range of FTSW values, daily pot evapotranspiration rates were limited to a maximum of 70 g/day (replicates 1 and 2) or 50 g/day (replicates 3 and 4). On a given day, water was added to any pot in the dry down treatment which exceeded these maximum rates. In these cases, the difference between the maximum allowable rate and the actual pot evapotranspiration was computed and an equivalent amount of water added to the pot.

Transpiration rate was calculated as the difference in pot weights over a 24 h period minus the average evaporative loss from the three pots without plants over the same day. Relative transpiration (RT) rates for each plant in the dry down were first estimated by dividing their daily transpiration rate by the average transpiration rate of the control plants on that same day. To further reduce variation in RT among plants caused by differences in plant size and microenvironmental conditions a second normalization was conducted as defined by Sinclair and Ludlow (19). In this procedure, Sinclair and Ludlow (19) chose a value of FTSW above which RT was constant in all experimental plants. For each plant, the average RT was then computed for all FTSW values above this value, and all initial estimates of RT were then divided by this average. This procedure assures that all plants will have a starting RT value close to 1.0. Furthermore, both this normalization procedure and the exact value of FTSW used in finding an average for each plant does not effect the critical FTSW value which these experiments were designed to determine. For potato, a value of 0.45 FTSW was found to be well above the critical value (see results below), and was used for this normalization.

Relative Leaf Growth Rate—Each day of the dry down, the total leaf area of each plant was non-destructively measured. For BelRus plants, 278 leaves were destructively sampled from potted plants not used in the experiments. For each compound leaf the total leaf length and width (measured at the widest part of the leaf) was measured (mm) using a clear plastic ruler. The leaf area of the same leaf was then determined using a leaf area meter (model # LI-3050A, Li-Cor Inc.). Individual leaf area was then regressed against the product of leaf length times width. During the experiments, the length and width of each leaf on every plant was measured and the derived regression used to non-destructively estimate the plants' leaf area. A similar approach was used for the Katahdin plants in replicates 3 and 4, with minor exceptions. For this cultivar, total compound leaf area for destructively sampled leaves was regressed against the product of length times width of the terminal leaflet. Thus, the length and width of only the terminal leaflets had to be measured during these experiments.

Daily plant leaf growth rates were calculated by fitting a linear regression through the plant leaf areas associated with the previous, same and next day. This three point estimation was used to filter out some of the variability in estimated plant leaf areas associated with the non-destructive technique. Relative leaf growth (RLG) for each plant in the dry down was calculated in a similar fashion as RT described above. The leaf growth rate for each plant was first divided by the average rate observed in the control plants on the same day. A second normalization to reduce variation in RLG among plants caused by differences in plant size and microenvironmental conditions (19) was conducted as described above. A value of 0.6 FTSW instead of 0.45 (used above for RT) was used in this normalization since RLG was stable at FTSW values above this cut off.

Relationship Between RT, RLG And FTSW—The FTSW was calculated as the fraction of the total transpirable water remaining in a pot on a given day. Total transpirable water was the difference between the initial pot weight when the soil was at field capacity and its weight on the day when RT was first 0.1 or less. Values of RT and RLG from each plant were than plotted against FTSW. Critical FTSW values for RT and RLG were computed using a method similar to that of Rosenthal *et al.* (17). The data were modeled as having a constant value of 1 when FTSW was higher than the critical value. After the critical value was reached, RT was assumed to decline linearly until 0 FTSW was reached. The RLG was assumed to decline linearly until a second critical FTSW value was reached when RLG was 0 (*e.g.* Figure 1). These two-step linear models were fit to the data by minimizing the error sum of squares (ESS) (17). After finding the model which minimized the ESS, a non-linear r^2 value was determined such that:

$$r^2 = \frac{TSS - ESS}{TSS} \tag{1}$$

where TSS was the uncorrected total sum of squares.

Replicate Size—Fifty pots were planted to start each replicate. At the start of the experiment, plants not of uniform size or in poor health were discarded. The remaining plants were then randomly assigned to one of three groups: 1) a well-watered control, 2) a dry-down treatment, or 3) a group for destructive sampling to determine the leaf area regression model. Through the course of the dry down, plants that showed disease or insect damage or which were injured in the course of the repeated leaf area measurements were discarded. Consequently, the number of plants remaining at the end of an experiment and included in the data set varied. Replicate one had 6 plants in the control, and 6 plants in the dry-down treatment. Replicate two had 5 plants in the control, and 5 plants in the dry-down treatment. Replicate three had 10 plants in the control, and 17 plants in the dry-down treatment. Replicate four had 8 plants in the control, and 10 plants in the dry-down treatment.

TABLE 1.—*Regression models for the non-destructive estimation of BelRus and Katahdin leaf area. Units of area are cm², units of length are cm.*

Cultivar	Model	r^2	N
BelRus	Leaf Area = 2.97 + 0.38 * (Compound Leaf Length * Width)	0.97	278
Katahdin	Leaf Area = 0.86 * (Terminal Leaflet Length * Width)†	0.98	76

†The intercept was not statistically different from zero, and subsequently dropped from the model.

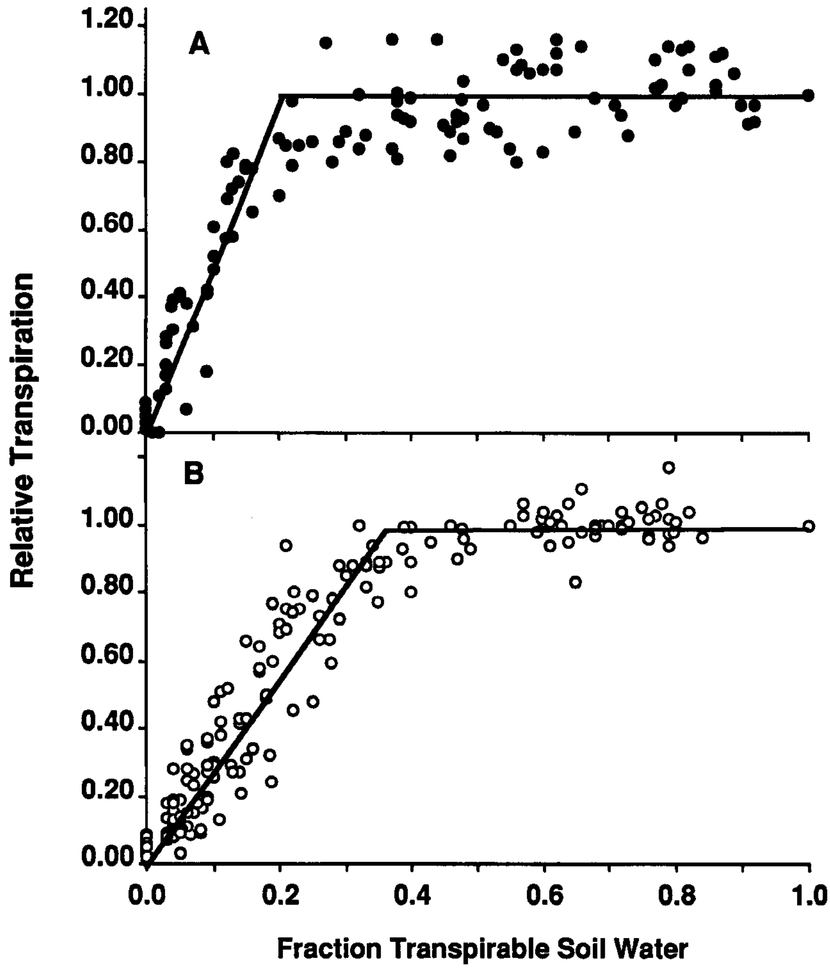

FIG. 2. Relative transpiration rates as related to fraction transpirable soil water for BelRus (A: solid dots) and Katahdin (B: open circles) potato plants.

TABLE 2—*Critical FTSW values and model results for BelRus and Katahdin relative transpiration and leaf growth. CI: confidence interval*

Cultivar	Critical FTSW	FTSW End Point	r^2	N
	Relative Transpiration			
BelRus:	0.20	0.00†	0.99	131
95 % Asymptotic CI	0.18-0.21	-		
Katahdin:	0.36	0.00†	0.97	209
95 % Asymptotic CI	0.35-0.37	-		
	Relative Leaf Growth			
BelRus:	0.56	0.03	0.99	116
95 % Asymptotic CI	0.52-0.59	0.00-0.05		
Katahdin:	0.63	0.09	0.97	147
95 % Asymptotic CI	0.59-0.66	0.06-0.11		
Mean Values:	0.60	0.06		

†FTSW end point for RT is zero by definition (see materials and methods).

Results

Individual leaf areas were well fit using linear regression on the product of leaf length and width for BelRus and of terminal leaflet length and width for Katahdin (Table 1). In both cases, the resultant r^2 values were above 0.9. These regressions were subsequently used to make the non-destructive leaf area determinations during the dry-down experiments.

Relative transpiration rates for BelRus and Katahdin plants were well described using the two step-model. Relative transpiration was largely unaffected by the dry-down until a critical value of FTSW was reached. After that, RT declined proportionally with decreasing FTSW (Figure 2). For BelRus the model fit the data with an r^2 of 0.99 and resulted in a critical value for FTSW of 0.20 (Table 2). The critical FTSW value for Katahdin was 0.36 ($r^2 = 0.99$).

Relative leaf growth also conformed to the two-step model. The RLG for both cultivars was stable until about 40% of the transpirable water was depleted. As FTSW continued to decline, RLG declined linearly until a value of FTSW slightly above zero when RLG stopped (Figure 3). For BelRus and Katahdin RLG, the critical FTSW was 0.55 and 0.63 respectively and the model r^2 values were 0.97 (Table 2) for each cultivar. The 95% asymptotic confidence intervals for the critical FTSW values for these two cultivars overlapped (Table 2) indicating that statistical differences between these two cultivars could not be detected. Thus, the BelRus and Katahdin RLG data were pooled into a single data set (Figure 3). Fitting the two-step model to

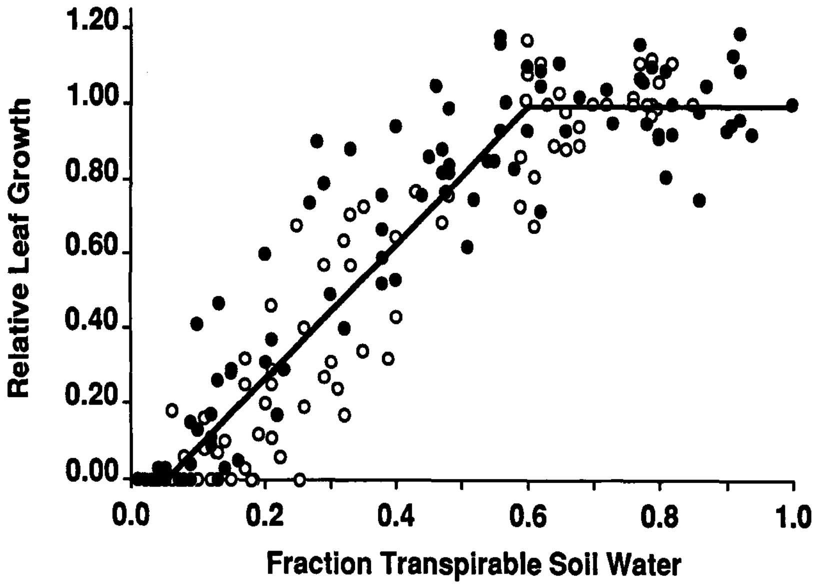

FIG. 3. Relative leaf growth rates as related to fraction transpirable soil water for BelRus (A: solid dots) and Katahdin (B: open circles) potato plants.

the combined data set was complicated since the Katahdin data set was substantially larger than the BelRus data set (see Table 2). Simply fitting the model to the combined data set, would therefore, have resulted in a critical FTSW value biased toward the Katahdin data. For that reason, the average of the individual critical values and end points are presented in Table 2 and were used to construct Figure 3.

Discussion

The data reported here demonstrate that the potato crop responds to soil water deficits in a fashion similar to the generalized model proposed by Ritchie (15) (Figures 1, 2 and 3). Relative rates of leaf growth and transpiration both were unaffected by soil water deficits until a critical value was achieved. With continued dehydration, both processes declined linearly with decreasing FTSW with leaf growth ending slightly before transpiration ceased. Previous research has suggested that such a critical soil water deficit existed for potato. Penman (12), in an analysis of potato yields over a 9 year period, found that yields could be well modeled assuming a critical soil water deficit of 25 mm below field capacity, above which yield was unaffected by water stress, and below which growth stopped. Jefferies (9) reported a critical soil water deficit of 16 mm below field capacity for leaf growth in field grown potatoes. Above this water deficit leaf growth was unaffected by soil water content. Critical absolute water deficit values for potato transpiration have also been previously reported. Burrows (1) reported a critical deficit of ~30 mm for relative transpiration and Jefferies and Mackerron (10) reported a critical soil water deficit of 47 mm for radiation use efficiency. Each of these is consistent with the data reported here, but without converting these absolute units of water deficit to a relative scale like FTSW, comparison among experiments or across species is difficult. To make this conversion requires knowing the water deficit associated with the cessation of transpiration, which these authors did not measure.

To our knowledge, the data reported here represent the first attempt to accurately measure the potato response to FTSW and make comparisons with other reported crops. Potato transpiration was stable until 20% to 36% of the extractable soil water remained depending on the cultivar (Figure 2). This range of critical FTSW values for relative transpiration is within the frequency distribution of values reported for other crops (histogram bars one through three in Figure 1). This indicates that potato transpiration responds to changes in fraction extractable water similarly to other crops studied. In terms of transpiration, the potato's drought sensitivity would appear to be due to an inability to extract as much total transpirable soil water as other crops. This is consistent with numerous studies which have shown potato to have shallow rooting systems (5, 2, 3, 11).

The response of relative leaf growth in potato to FTSW, however, appears to be unique. The critical FTSW value for relative leaf growth was numerically different for the two cultivars studied. However, since these values were not statistically different (Table 2) the RLG data were pooled and the average critical FTSW value (0.60) used (Figure 3, Table 2). Previously reported critical values of FTSW for leaf growth in other crops generally range between 0.4 and 0.5 (histogram bars four, five and six, Figure 1). For potato, the critical value of 0.60 reported here, is higher than previously reported values for any crop, and is outside the leaf growth frequency distribution in Figure 1. It appears that potato leaf growth is compromised by relative water deficits well below those associated with this effect in other crops. This indicates that some other process besides root extension or water extraction is inhibiting potato leaf growth.

These findings support the hypothesis that drought sensitivity in potato is due, in part, to lower total soil water extraction. In terms of transpiration, potato responded similarly to other reported crop species. However, leaf growth appears to respond in a unique fashion and is more sensitive to drought than other crops even at the same levels of extractable water.

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