

## A MODEL DESCRIBING SOIL-PLANT-WATER RELATIONS FOR POTATOES<sup>1</sup>

M. D. Campbell, G. S. Campbell, R. Kunkel, and R. I. Papendick<sup>2</sup>

### Abstract

A simple steady state model is derived which describes the diurnal water potential fluctuations in leaves and tubers of potatoes. The magnitude of these fluctuations is shown to depend on transpiration rate, hydraulic properties of the soil, rooting depth and density, resistance to flow of water within the plant, and the leaf water potential at which stomatal closure occurs. Model predictions agree quite well with measurements made in the field and in the growth chamber. The model is used to predict the lower limit of readily available moisture for potatoes and shows the important environmental and plant factors.

### Resumen

Se ha derivado un modelo simple de equilibrio dinámico para describir las fluctuaciones diurnas del potencial de agua en hojas y tubérculos de papa.

La magnitud de estas fluctuaciones muestra dependencia en la tasa de transpiración, propiedades hidráulicas del suelo, profundidad y densidad de enraizamiento, resistencia al flujo del agua dentro de la planta, y el potencial de agua de la hoja al cual ocurre el cierre de los estomas.

Las predicciones del modelo concuerdan bastante bien con medidas hechas en el campo y en las cámaras de crecimiento. El modelo se usa para predecir el límite más bajo de humedad fácilmente disponible para papa y muestra la importancia de los factores ambientales y de la misma planta.

The relationship between soil water potential and plant transpiration rate and growth is subject to considerable influence by soil, plant, and atmospheric factors. With most irrigation systems, it is desirable to maintain the soil water potential sufficiently high to maximize growth. Much research has been conducted to determine the lower limit of available water to plants and the relative availability of water at various soil water potentials. These determinations are often confounded by the influences of transpiration, leaf osmotic potential, root density and distribution, and

<sup>1</sup>Scientific Paper No. 4335 College of Agriculture Research Center, Washington State University, Pullman. Work supported in part by the Washington Potato Commission. Received for publication December 17, 1974.

<sup>2</sup>Former N.D.E.A. Fellow, now Soil Scientist, Bureau of Reclamation, USDI, Yuma Project Office, Yuma, Arizona, Associate Professor of Biophysics and Associate Soil Scientist, Horticulturist, and USDA-ARS Soil Scientist, Washington State University, Pullman, Washington.

hydraulic conductivity of the soil. The purpose of this paper is to describe a soil-plant-water flow model which takes these factors into account and apply it to determine the optimum soil water potential for maximizing potato growth.

### Theory

A steady state model is developed similar to that of Gardner (1960) and Cowan (1965) to relate transpiration rate to soil and plant characteristics. Consider a root of radius  $r_1$  removing water from soil out to radius  $r_2$  with water potentials  $\psi_r$  at  $r_1$  and  $\psi_s$  at  $r_2$ . Water flux from  $r_2$  to  $r_1$  may be described by

$$\frac{q}{2\pi r l} = k \frac{d\psi}{dr} \quad (1)$$

with  $q$  the volume flux,  $k$  the unsaturated hydraulic conductivity which is a function of soil water content or potential,  $2\pi r l$  the area of a hypothetical cylinder coaxial with the root, and  $d\psi/dr$  the potential gradient at the cylinder perimeter. An empirical relation for  $k$  that is adequate for water potential in the plant growth range (Hillel and Gardner, 1969) is

$$k = k_s (\psi_e/\psi)^n \quad (2)$$

where  $k_s$  is the saturated hydraulic conductivity,  $\psi_e$  is the air entry water potential (potential at which the largest pores just drain) and  $n$  is an empirical constant. To simplify calculations,  $\psi$  is expressed as cm of water tension so that  $\psi$  and  $\psi_e$  are both positive numbers; then the result is divided by  $-1017 \text{ cm bar}^{-1}$  to convert to water potential.

At steady state the fluxes toward and away from the plant are equal but of opposite sign so

$$\frac{q}{l} = \frac{-E}{DL} \quad (3)$$

where  $E$  is the transpiration rate ( $\text{cm day}^{-1}$ ),  $D$  is rooting depth, (cm) and  $L$  is rooting density in units of root length per unit of soil volume ( $\text{cm cm}^{-3}$ ). Substitution of equations (2) and (3) into equation (1) followed by separation of variables and integration between  $r_2$  and  $r_1$  and  $\psi_s$  and  $\psi_r$  leads to:

$$\frac{E(1-n)}{4\pi DL k_s \psi_e^n} \ln(\pi r_1^2 L) = \psi_s^{1-n} - \psi_r^{1-n} \quad (4)$$

Where  $\psi_s$  is the soil water potential at a distance  $r_2$  from the root axis and  $\psi_r$  is the water potential in the zone of root absorption, a distance  $r_1$  from the root axis. Radius  $r_2$  has been represented by (Gardner, 1960)

$$r_2 = (\psi L)^{1/2} \quad (5)$$

Except  $E$ , all values on the left side of equation (4) are constant for a given soil-plant system at a particular time and are set equal to  $B$ . The equation may be rearranged to evaluate water potential at the absorbing surface:

$$\psi_s = [\psi_s^{1-n} - EB]^{1/n} \quad (6)$$

Steady state water flux through the plant and, therefore, loss from the plant may be described by the equation (Cowan, 1965)

$$E = \frac{\psi_1 - \psi_r}{R} \quad (7)$$

where  $R$  is plant resistance to flow of liquid water and  $\psi_1$  is leaf or plant water potential. Substitution of equation (6) into equation (7) yields

$$E = \frac{\psi_1 - [\psi_s^{1-n} - EB]^{1/n}}{R} \quad (8)$$

Equation (8) gives the rate of transpiration for a given leaf water potential and a given set of conditions described by the parameters  $B$  and  $R$ . Since there is a leaf water potential at which stomatal closure begins (resulting in reduction in  $E$  and in photosynthesis), equation (8) can also be used to compute maximum transpiration rate for a given soil plant system. Conversely, if the maximum transpiration rate during the day is known as well as the required soil and plant properties, one could predict the soil water potential at which wilting occurs. If  $\psi_{cl}$  is the leaf water potential at stomatal closure and  $E_m$  is the maximum transpiration rate, then the soil water potential,  $\psi_{sl}$  at which transpiration is first reduced is

$$\psi_{sl} = [(\psi_{cl} - RE_m)^{1-n} + E_mB]^{1/n} \quad (9)$$

Note that  $\psi_{sl}$  is not constant, but depends on soil hydraulic properties, transpiration rate, and plant properties of  $\psi_{cl}$ ,  $R$ , rooting depth and root density.

### Materials and Methods

Potatoes (*Solanum tuberosum*, L. var. Russet Burbank) were grown in a growth chamber at Pullman, and in furrow-irrigated plots in the Columbia Basin near Othello, Washington. For the growth chamber, a seed piece was planted in each of several containers  $30 \times 30 \times 32$  cm deep filled with Novara silt loam from Othello. The plants were maintained well watered with nutrient solution until full establishment (2 months), and after that with tap water. Fluorescent lights supplied 11,000 to 15,000 lumens  $m^{-2}$  at the soil surface during a 14-hour day. Air temperatures were maintained at 30 and 22 C during the day and night, respectively, throughout the experiment.

The field planting was made in mid-April by conventional methods. Nitrogen, phosphorous, and potassium fertilizer at rates of 300 kg/ha was applied as sidedress at planting. Irrigation was initiated at mid-June and consisted of applying water for 24 hours to alternate furrows every 2.5 days.

The required soil parameters were evaluated from soil water-retention relationships and a single hydraulic conductivity measurement at saturation. Tensiometer readings or pressure plate extractions using undisturbed soil cores were made followed by a determination of water content. The retention function was taken as  $\psi = \psi_e(\theta/\theta_s)^{-b}$  (Campbell, 1974) where  $\psi$  is the soil water potential (cm) at water content  $\theta(\text{cm}^3 \text{cm}^{-3})$  and  $\psi_e$  is the air entry water potential. The constant,  $b$  is evaluated from the slope of the line on a log-log plot of  $\theta$  vs  $\psi$ . From these,  $n$  in equation (2) is given by  $2 + \frac{3}{b}$  (Campbell, 1974). Saturated hydraulic conductivity of the soil,  $k_s$  was measured on undisturbed cores using standard techniques (Klute, 1965). Values obtained were  $\psi_e = 12.4$  cm,  $k_s = 17.5$  cm/day,  $b = 3.18$ ,  $n = 2.94$ , and  $\theta_s = 0.44$ .

The root diameter, density, and rooting depth were determined by direct measurement. Root radius was measured with a graduated ocular on a microscope. Rootlets with protruding root hairs were excavated from the soil and the distances from the axial center of the rootlet to the ends of the root hairs were measured. It was assumed that absorption takes place in the root hair zone. Root density was measured using undisturbed volumes of soil by counting the roots that intersected a plane of known area and dividing the number obtained by the area. Variations in distribution were averaged to arrive at a number for the density,  $L$ . The rooting depth for both the growth chamber and field were estimated during excavation of soil from several plants.

Soil water potential in the growth chamber was measured with tensiometers placed 10 cm below the soil surface and 5 cm from the plant stems. In the field tensiometric measurements were made in the row at depths of 15, 30, and 40 cm.

Leaf water potentials were determined *in situ* using specially constructed psychrometers (Campbell and Campbell, 1974). Psychrometer and leaf temperatures were measured with thermocouples. Leaf osmotic potentials were measured with a commercial sample chamber psychrometer (Wescor, Inc., Logan, Utah) using sap extracted from leaves which had been frozen on dry ice. Tuber water potentials were determined for some tubers in the field. Midway along an intact tuber, a hole was made with a cork borer and drill, and a soil psychrometer (Wescor, Inc., Logan, Utah) was sealed in place with a wax-lanolin mixture after flushing the hole with distilled water to diminish wound healing.

Transpiration rates were measured by monitoring weight changes of the containers in the growth chamber and were taken as equal to class A pan evaporation for the field.

Plant resistance,  $R$  is known to vary with soil temperature, aeration, and transpiration rate (Slatyer, 1967). For the purposes here it is treated as constant during the time the model is applied. The uncertainty in  $R$  due to environmental factors was minimized by determining it under conditions similar to those obtained during the validation run. The increase in resistance at night is not accounted for in this model (though a simple extension of the model would account for it (because our primary concern was to simulate daytime water potentials. Resistance can be found by measuring  $\psi_1$ ,  $\psi_s$ , and  $E$  when the soil is wet so that  $\psi_s$  approaches  $\psi_r$ .

## Results and Discussion

### *Growth Chamber Test*

Figure 1 compares transpiration rate, and soil and leaf water potentials calculated from equation (8) with measured values. Plant resistance was taken as the difference between soil and leaf water potential on day 2 divided by the transpiration rate. The leaf water potential at which transpiration began to be controlled by the system was taken as  $-3.4$  bars which was the lowest water potential reached (day 4) when transpiration was first noted to decrease. Predicted and measured soil water potentials agree very well. The predicted transpiration rate drops somewhat faster than the measured. By changing  $B$  in equation (8) from  $3.5 \times 10^{-6}$  to  $2 \times 10^{-6}$ , the calculated transpiration matched the experimental values. This is probably well within the error limits of  $B$ , since there is considerable variation in several of the parameters used to determine  $B$ .

The daytime leaf water potentials are described reasonably well by the model (figure 1). The low water potentials measured on day 1 may have been caused by a previous mild stress cycle from which the plant was recovering. The model fails to describe the water potential of the leaf after wilting on day 5 because of the simplifying assumption that the leaf water potential cannot go below some preset limit. In nature this limitation does not exist, although plant mechanisms begin to control water loss at this potential, thus tending to limit further reduction to leaf water potential.

Two factors are probably involved in the poor agreement between measured and calculated nighttime leaf water potentials (Figure 1). First, the weighing device did not have adequate sensitivity to give reliable estimates of nighttime transpiration rates. Higher rates than those used would have given lower predicted leaf water potentials. Also, constant plant hydraulic resistance was used throughout for the model. In reality, the nighttime resistance is probably 10 times the daytime resistance because of increased resistance to water flow at low transpiration rate.

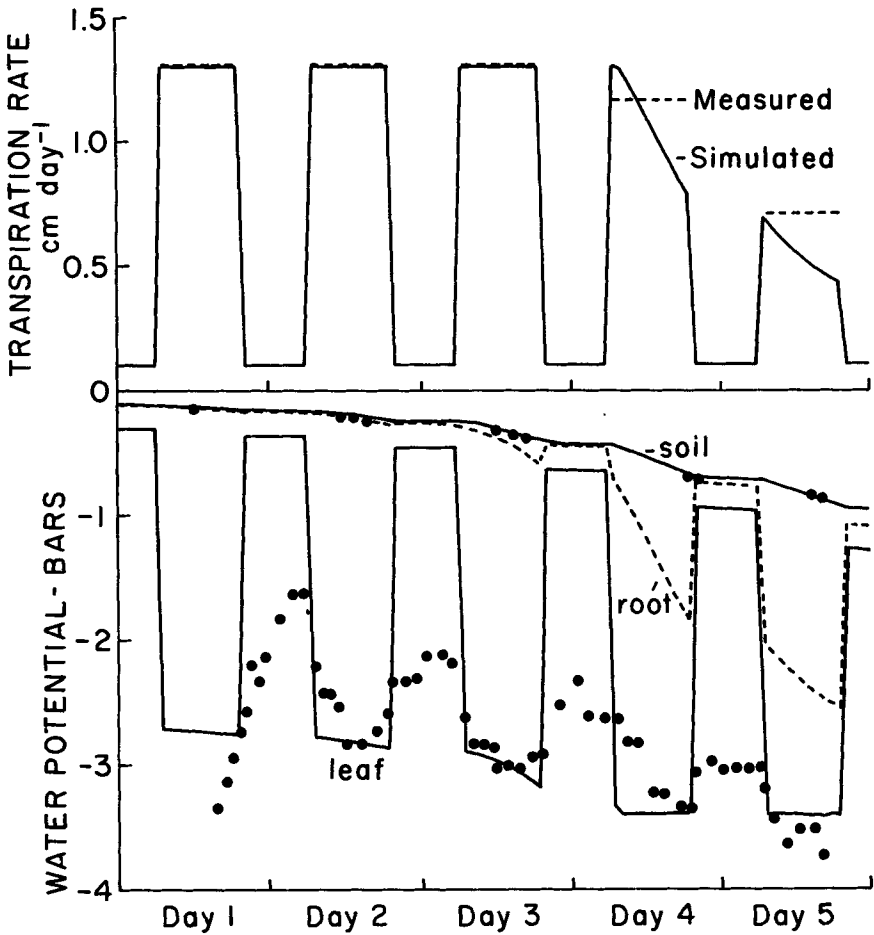


FIG. 1. Simulations and measurements for the growth chamber experiment. The upper curves show the simulated (—) and measured (-----) transpiration rate. The lower curves show simulated soil, root and leaf water potentials (lines) and measured values (\*).

Incorporation of this information into the model would provide better predictions of nighttime leaf water potentials. However, since the lower limits of leaf and soil water potential were the main interest, this modification was not warranted for the present study.

Osmotic potentials of light exposed leaves were approximately  $-8$  bars. However, transpiration began to be reduced at leaf water potentials between  $-3$  and  $-4$  bars. A possible explanation as to why transpiration would be reduced at leaf water potentials well above the osmotic potential is that leaves on the plant varied in osmotic potential, ranging from about

-5 to -8 bars, depending on whether the leaves were shaded or exposed. Stomata of shaded leaves would close at higher water potentials than those of exposed leaves because of low turgor pressures in these leaves.

Departure of root surface water potential from bulk soil water potential on day 3 (Figure 1) indicates resistance to water flow in the soil is beginning to limit water flow in the soil-plant system. Note that stomatal closure, as indicated by reduced transpiration, is nearly concurrent with the decrease in root surface water potential. Under this condition stomatal closure would have occurred no matter what the leaf water potential had been because the soil resistance to water flow increases rapidly with drying after the soil water potential decreases to a certain level. Thus, the transpiration curves would likely not have changed much from those shown in Figure 1 even if the limiting leaf water potential had been set at -8 bars.

*Field Tests*

Field data and model predictions for one day in August and 3 consecutive days in September are summarized in Figure 2. Pan evaporation on August 4 was 0.9 cm day<sup>-1</sup> in contrast to an average loss for September 2, 3,

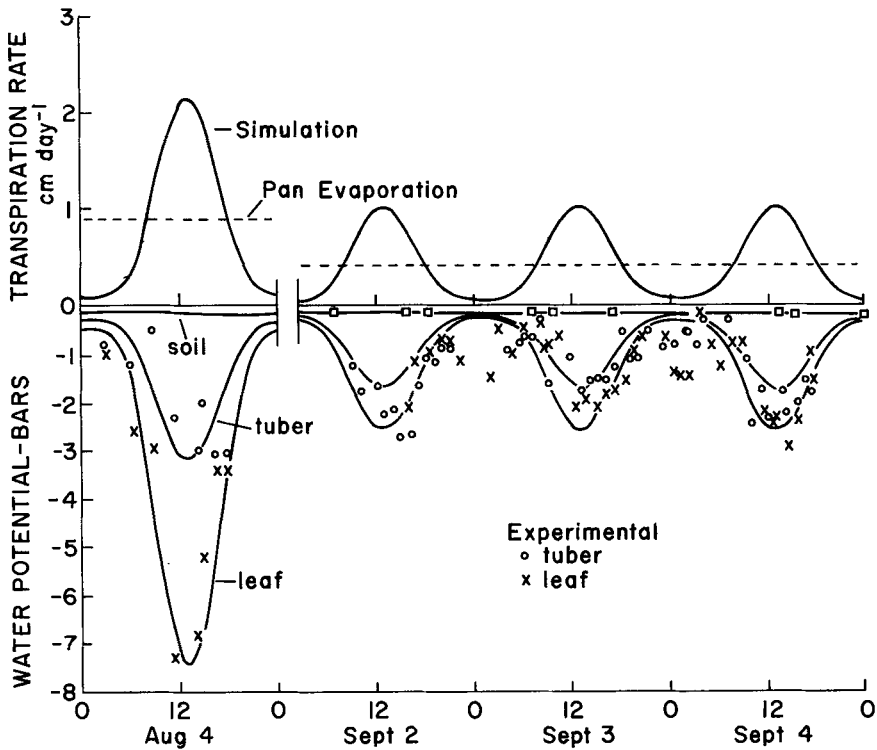


FIG. 2. Simulated (solid lines) and measured (points) transpiration rate, soil water potential ( $\square$ ), and tuber ( $\circ$ ) and leaf ( $\times$ ) water potentials for field-grown potatoes.

and 4 of  $0.43 \text{ cm day}^{-1}$ . The September days were overcast and followed humid weather. Since only mean daily transpiration rates were known (and these only approximately), it was necessary to approximate the diurnal transpiration rate by some expression which would give instantaneous rate from the mean. An expression which was found to fit unpublished data of the authors obtained in another study is

$$E = 2.3\bar{E} [0.05 + \sin^4(7.5t - 9.75)]$$

where  $E$  is the instantaneous transpiration rate (cm/day),  $\bar{E}$  the mean daily rate and  $t$  is time in hours. The peak to mean ratio for this expression is about 2.4 with a nighttime rate of about 5% of the peak daytime rate. The ratio depends on day length, and for summer months the value we have used should be representative. For example, summertime data for alfalfa near Phoenix, Arizona, given by van Bavel (1966) show peak to mean ratios of about 2.8. Summer days are longer in the Columbia Basin of Washington than in Phoenix, Arizona, so that the lower value of the ratio is reasonable.

Plant resistance was calculated separately for the August and September data, and was found to be 3400 days for the day in August, and 2400 days for the days in September. Resistance to water flow from the absorbing surfaces to the tuber was found to be 1400 days for the day in August and 1500 days for the days in September.

For the field, the leaf water potential for stomatal closure was taken as  $\psi_{cl} = -10$  bars which was the mean osmotic potential of leaves exposed to the sun.

Agreement between the model predictions and measured values is reasonable, and is especially good between measured and calculated values of leaf water potential. Differences between measured and calculated values in most cases are probably due primarily to departures in actual transpiration rate from that simulated by the model. Stomates of well-watered potatoes do not necessarily remain closed at night (Loftfield, 1921), so appreciable water loss at night could be caused by advected heat. This could cause the observed reduction in nighttime water potentials.

Fluctuations in tuber water potential, as observed in this study, are likely the result of fluctuations in tuber water content, since one would expect the tuber osmotic potential to remain relatively constant (measurements made in this study indicate that the tuber osmotic potentials averaged about  $-8$  bars). Kunkel and Gardner (1965) showed cases where tuber mass increased with transpiration rate and cases where the reverse occurred. In a related study, measurements generally showed an increase in tuber mass with increased transpiration rate during a diurnal cycle (Campbell, 1972). It is possible that the apparent mass increase can be attributed to changes in stolon turgor (Meinel, 1965). Very rough calculations from data given for tomato leaves by Slatyer (1967) show that mass should change by about 2% of fully turgid weight per bar water potential. Diurnal



fluctuations of 3 bars, as were observed in August, would result in mass fluctuations of about 6%. This appears to be about the size fluctuation reported by Kunkel and Gardner (1965) for the tuber which lost weight during the day.

#### *Prediction of the Lower Limit of Readily Available Moisture*

The simple model described here appears to adequately describe plant water potential during the day and take into account the effect of the important variables in the system such as soil hydraulic properties, plant rooting depth and density, and transpiration rate. Thus, the model can be used to predict the soil water potential at which potato plants should be irrigated to minimize reduction in growth. Equation (9) can be used to predict the soil water potential at which stomatal closure occurs ( $\psi_{cl}$ ). Figure 3 (curve a) shows the maximum instantaneous transpiration rate ( $E_m$ ) as a function of the soil water potential at which flow becomes limiting

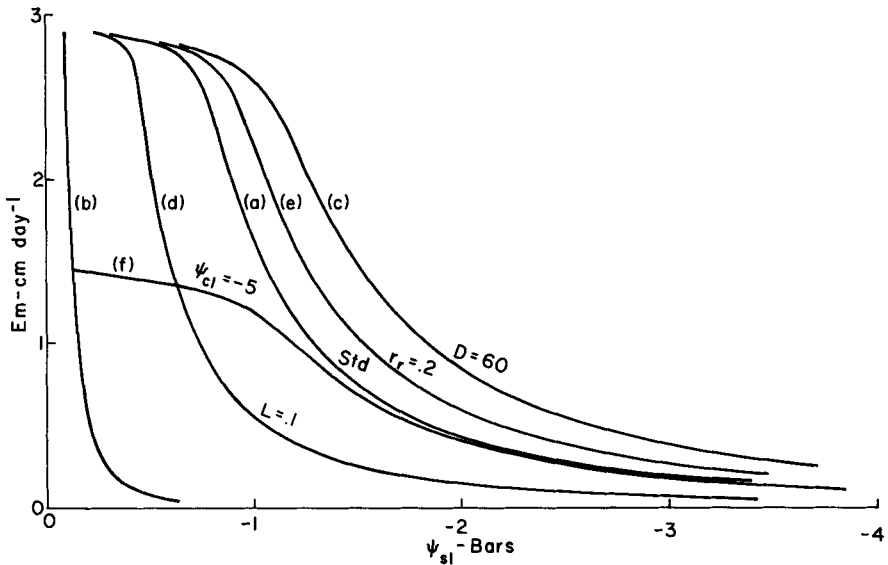


FIG. 3. Maximum transpiration rate which can be sustained in a soil-plant system as a function of soil water potential. Curve A is standard with  $R = 3600$  Day,  $\psi_{cl} = -10$  bars,  $L = 0.25$  cm<sup>2</sup>,  $r_r = 0.1$  cm,  $D = 30$  cm,  $\psi_e = 12.4$  cm,  $k_s = 17.5$  cm day<sup>-1</sup>,  $n = 2.94$ . For other curves only the following were changed: B:  $\psi_e = 3.0$  cm,  $n = 2.75$ ,  $k_s = 35$  cm day<sup>-1</sup>, C:  $D = 60$  cm, D:  $L = 0.1$  cm<sup>2</sup>, E:  $r_r = 0.2$  cm, F:  $\psi_{cl} = -5$  bars.

( $\psi_{sl}$ ) for the conditions existing on August 4 at Othello. This figure would be used to determine the limiting soil water potential by first determining  $E_m$ . If the mean daily transpiration rate to be expected were 1 cm day<sup>-1</sup> and the peak to mean ratio were 2.4, as was assumed here,  $E_m$  would be 2.4 cm day<sup>-1</sup>. The limiting water potential would therefore be  $-0.8$  bar. It should

be pointed out that this is not the lower limit for plant growth, rather it is the water potential below which growth will be reduced by stomatal closure.

Lines b, c, d, e, and f (Fig. 3) show the effects of changing soil hydraulic properties, rooting depth, root density, root diameter, and  $\psi_{cl}$  respectively. If other factors are held constant a heavy soil with high saturated conductivity will supply water to lower potentials than will a sandier soil. Increased root depth and density decrease the lower limit of available water and increase the water available to the plant at any given transpiration rate. Root diameter and  $\psi_{cl}$  are shown to have a relatively minor effect on the lower limit of available water (Figure 3).

It should be pointed out again that a number of simplifying assumptions were made in the model which will need further examination as the model is made more general. These are: a) water is withdrawn from a volume of soil with uniformly dense rooting into which no water flows, b) a single value of  $\psi_{cl}$  applies for the entire plant, c) the plant water potential cannot drop below some predetermined value, d) the plant resistance remains constant, e) no root growth occurs, and f) steady state obtains. We are presently refining the model to take into account variable root density and water flow in the soil. Other modifications of the model must await a more thorough understanding of water relations of the potato plant. Of particular interest is the possibility that growth is limited by turgor loss rather than stomatal closure (Hsiao, 1974). Turgor induced growth reduction would occur at even higher soil water potentials than those shown in Figure 3.

#### Literature Cited

1. Campbell, G. S. 1974. A simple method for determining unsaturated conductivity from moisture retention data. *Soil Sci* 117:311-314.
2. Campbell, G. S., and M. D. Campbell. 1974. Evaluation of a thermocouple hygrometer for measuring leaf water potential in situ. *Agron J* 66:24-27.
3. Campbell, M. D. 1972. The lower limit of soil water potential for potato growth. Ph.D. Thesis, Washington State University, Pullman (Univ. Microfilm order # 73-35).
4. Cowan, I. R. 1965. Transport of water in the soil-plant-atmosphere system. *J Appl Ecol* 2:221-239.
5. Gardner, W. R. 1960. Dynamic aspects of water availability to plants. *Soil Sci* 89:63-73.
6. Hillel, D., and W. R. Gardner. 1969. Steady infiltration into crust-topped profiles. *Soil Sci* 108:137-142.
7. Hsiao, T. C. 1973. Plant Responses to Water Stress. *Annu Rev Plant Physiol* 24:519-570.
8. Klute, A. 1965. Laboratory measurement of hydraulic conductivity of unsaturated soil, p. 253-261. In C. A. Black (ed.) *Methods of Soil Analysis. Part 1.* Am Soc of Agron, Madison, Wisconsin.
9. Kunkel, R., and W. H. Gardner. 1965. Potato tuber hydration and its effect on blackspot of Russet Burbank potatoes in the Columbia Basin of Washington. *Am Potato J* 42:109-124.
10. Lottfield, J. V. G. 1921. The behavior of Stomata. Carnegie Institution of Washington (D.C.) #314.

11. Meinel, G. 1965. The growth and water supply of individual organs of the potato. *In* B. Slavik (ed.), *Water Stress in Plants*. W. Junk Publishers, The Hague. p. 223-226.
12. Slatyer, R. O. 1967. *Plant-Water Relationships*. Academic Press, New York. 366 p.
13. Van Bavel, C. H. M. 1966. Potential evaporation: the combination concept and its experimental verification. *Water Resour Res* 2:455-467.