1977

Modeling Soil Water Movement into Plant Roots

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ABSTRACT

mathematical model was developed which describes uptake of water by plant roots as a function of leaf and soil water potentials. The model was used to estimate transpiration from corn grown in a controlled environment under soil drying conditions. The model predicted daily transpiration quite well for the period modeled.

INTRODUCTION

Current methods of estimating evapotranspiration use an estimate of potential evapotranspiration that is reduced as soil water decreases. Methods are needed for estimating evapotranspiration which are based on the physics and physiology of evapotranspiration. This study was undertaken to develop and evaluate a model to quantify transpiration which incorporates the interaction of plant growth and soil water depletion on transpiration.

Transpiration may be defined as the process by which water is absorbed by plants and evaporated into the atmosphere. Thus in vegetated areas, transpiration is generally regarded as the principal component of evapotranspiration. Estimates of the amount of water lost from the soil by transpiration vary considerably depending on whether or not the transpiration is considered to remain constant or decreases as soil water diminishes. The differing views concerning transpiration rate are based mostly on experimental evidence from particular soils and plants. Recent theoretical investigations indicate that the availability of soil water for transpiration depends on soil water content and other variables (Gardner, 1960; Cowan, 1965; Molz, et al., 1968).

Recently researchers have developed methods of estimating evapotranspiration as a function of potential evapotranspiration (Haan, 1972; Ritchie, et al., 1972). In these methods, once estimates of potential evapotranspiration have been obtained, estimates of actual evapotranspiration are computed on the basis of available soil water. The difficulty with such methods lies in finding a meaningful description of available soil water.

The generally accepted theory is that water movement through the soil-plant-atmosphere-continuum (SPAC) is a result of a gradient of decreasing water potential from the soil, through the plant, and to the atmosphere. The total water potential ($\varnothing$) as applied to the SPAC is generally written

$$\phi = \psi + Z \qquad \qquad \qquad \qquad \qquad \qquad [1]$$

where ψ is the water potential (cm) derived from the chemical potential of water and Z is the gravitation potential (cm).

The concept of water potential is applicable to all three components of the SPAC (Hillel, 1971). The major water storage components in the SPAC are the soil and the atmosphere. The plant also functions as a storage component, but more importantly the plant is the biotic or living part of the system and in this role has the ability to control the transpiration stream.

Attempts to mathematically model water movement through the SPAC have involved segment models to describe flow behavior in different parts of the system (Van de Honert, 1948; Slayter and Gardner, 1965; Philip, 1966: Cowan and Milthorpe, 1968). The segments through which water movement may be considered to occur are: movement within the soil, movement from the soil to the root, movement through the plant, and movement from the plant to the atmosphere. The model discussed in this paper combines three of the segment models to describe water movement within the soil, movement to the root and movement through the plant. Movement from the plant to the atmosphere is not considered in this paper.

Soil Models

Two of the three segment models utilized in the combined model involve movement of water in the soil. Most processes involving soil water flow in the root zone of most plants occur while the soil is in an unsaturated condition. The general equation of flow for unsaturated soil may be expressed as

$$C \frac{\partial \psi}{\partial t} = \nabla \cdot [K(\psi) \nabla \phi] \qquad \qquad \qquad [2]$$

where $K(\psi)$ is the unsaturated hydraulic conductivity of the soil in cm/hr, t is time, C is the water capacity

$$\left(\frac{d\Theta}{d\psi} \right)$$

and Θ is the volumetric soil-water content $\Theta = \Theta(\psi)$.

Equation [2] fails to take into account the hysteresis of soil water characteristics. In this study hysteresis was avoided by considering only a continuously drying soil.

If in addition to Darcian flow, water is removed from a point at a rate S in such a way that it is not included in the flow velocity, equation [2] must then be modified to

$$C\frac{\partial \psi}{\partial t} = (\nabla \cdot [K(\psi)\nabla\phi]) + S \quad \dots \dots \dots \dots \dots \dots [3]$$

The quantity S is an extraction term having negative values and may be a function of space, time, water content, or a combination of these variables. It expresses water withdrawal per unit volume of soil $cm^3/hr\text{-}cm^3$. Models utilizing equation [3] are referred to as extraction term models or macroscopic models and have been employed by a number of investigators to study water withdrawal by plant root systems (Whisler, et al., 1968; Molz, 1970, 1971; Molz and Remson, 1970, 1971; Kilic, 1973; Nimah and Hanks, 1973; Feddes, et al., 1974; Feddes and Rijtema, 1972). In this paper equation [3] is referred to as the macromodel.

If the flow of water to individual roots is considered as radial flow, the general equation of flow for such a system may be developed from equation [2] after making appropriate assumptions. These assumptions are as follows: the root is an infinitely long cylinder of uniform radius and water-absorbing properties, water moves in the radial direction only, and the effects of gravity are negligible and may be ignored. Equation [2] in cylindrical coordinates, assuming radial symmetry, is

$$C\frac{\partial \psi}{\partial t} = \frac{1}{\rho}\frac{\partial}{\partial \rho}[\rho \, K(\psi)\frac{\partial \psi}{\partial \rho}]. \quad \dots \dots \dots \dots \dots \dots [4]$$

where ρ is the radial coordinate.

A useful variation of equation [4] is a model which considers flow in a hollow cylinder (Lang and Gardner, 1970; Whisler et al., 1970; Cowan, 1965). The radius of the root is ρ_1 and it is surrounded by a shell of soil with an outer radius ρ_2. Thus ρ_2 may be considered to be one-half the distance between roots spaced uniformly in the rooting medium and is referred to as the radius of influence. In this paper equation [4] is referred to as single-root or micromodel.

The Plant Model

Flow of water through a plant may be quantified in terms of gradients in water potential by the relationship

$$F = \frac{\psi_r - \psi_L}{R} \quad \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots [5]$$

where F is the rate of water flow between the root surface and the leaf surface, ψ_r and ψ_L are the water potentials at these surfaces, respectively, and R is resistance to flow within the plant. This relatively simple relationship was formulated by Van den Honert (1948).

The three models discussed above represent segment models describing the flow of water in the three segments considered in this paper. Viewed separately, each has significant limitations. However, a combination model which describes flow through these three segments may be developed which utilizes the strong points of each while minimizing these limitations.

THE COMBINED MODEL

The combined model may be developed by first considering the rooting system of a growing plant to extend downward and outward about a vertical axis of symmetry. Thus, at any time t, the root density may vary with depth and radial distance as shown schematically in Fig. 1. The cross-hatched area does not represent a dimension vertically but serves to show the relative root density at each depth and radial increment. The total rooting depth might extend to L

and the radial extent of the root zone X may be viewed as representing 1/2 of the row or plant spacing. The rooting domain of the plant is thus represented by a cylinder of soil of radius X and depth L. The model which can best describe water movement within this zone is the macromodel represented by equation [3] for which a known source term flow is described throughout the root zone.

If the source term is considered as a function of time and space only, it may be written as S (r, z, t). Equation [3] may now be rewritten in terms of radial coordinates and, if radial symmetry is assumed, becomes effectively a two-dimensional equation.

$$C\frac{\partial \psi}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}[rK(\psi)\frac{\partial \psi}{\partial r}] + \frac{\partial}{\partial z}[K(\psi)\frac{\partial \psi}{\partial z}] + \frac{K(\psi)}{\partial z}$$

$$+ S (r, z, t) \quad \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots [6]$$

where r is the distance radially outward from the main plant axis and z is the vertical coordinate.

Equation [6] is a second order, non-linear, partial differential equation of the parabolic type which expresses water potential distribution as a function of time and space. Since this equation has no known analytical solution, a finite difference approach is taken.

The initial condition applied to this model is

$$\psi(r, z) = \psi_0(r, z) \text{ at } t = 0 \quad \dots \dots \dots \dots \dots \dots \dots \dots [7]$$

$$0 \leqslant z \leqslant L \text{ and } 0 \leqslant r \leqslant X$$

where L is the depth of the soil system and X is the radius of the soil system.

If evaporation from the soil surface is prevented, the upper boundary condition is a no flow condition. Likewise the lower and lateral boundary conditions are no flow conditions. With the assumption of radial symmetry, one additional effective boundary condition is a no flow condition at r = 0.
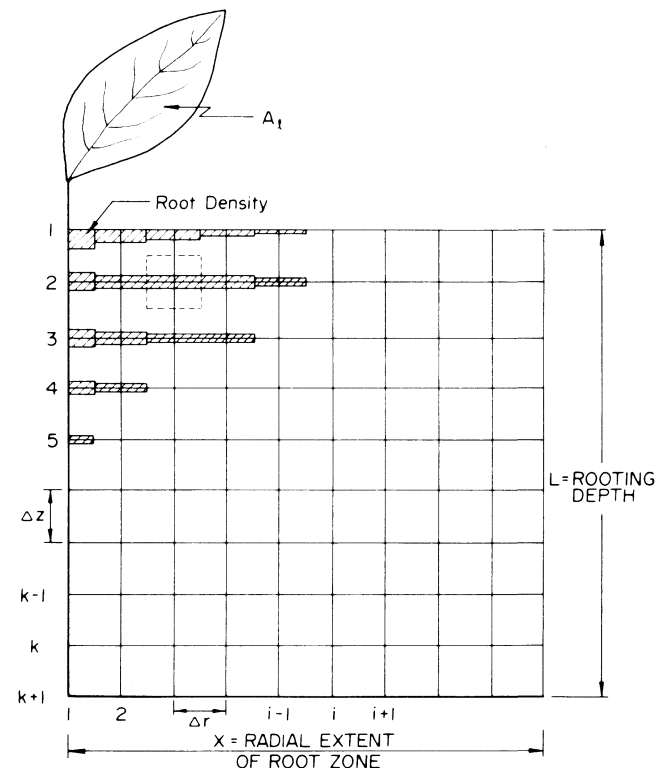

FIG. 1 Schematic of combined model showing macromodel solution grid.

Within the cylinder of soil in which the plant is growing, water is removed only by the negative source term of equation [6]. The space grid system for numerical solution of equation [6] is shown in Fig. 1. A source term is needed only at those grid points which represent soil volumes containing roots.

To obtain a solution of equation [6] it is necessary to evaluate the source term. This is accomplished by application of the single-root model of equation [4] to those nodes representing soil volumes containing roots. It is assumed that all the roots within the annular ring of soil enclosed by the dashed line of Fig. 1 may be represented by a single root with a length equal to the total length of all roots within that volume and a radius, ρ_1, equal to the mean radius of those roots. This root is surrounded by a shell of soil of radius ρ_2 computed so that the total volume of soil surrounding the root is equal to the soil volume within the annular ring corresponding to node i,k. Thus flow to the root may be treated as flow within a hollow cylinder.

THE SINGLE-ROOT MODEL

The general equation for flow to a single root is equation [4]. The initial and boundary conditions which apply to the single-root system are:

1. $t = 0; \psi = \psi_0; \rho_1 \leqslant \rho \leqslant \rho_2$ . . . . [8a]

2. $t > 0; \psi = \psi_{root} = \psi(t); \rho = \rho_1$ . . . . [8b]

3. $t > 0; \dfrac{\partial \psi}{\partial \rho} = 0; \rho = \rho_2$ . . . . [8c]

where ψ_0 is the initial water potential assumed to be constant throughout the soil volume considered and $\psi(t)$ is the water potential at the root surface which may be a function of time.

The water flow rate across the root-soil interface is given by

$$q(t) = 2\pi\rho_1 K(\psi) \frac{\partial \psi}{\partial \rho} \bigg|_{\rho = \rho_1} \quad \text{. . . . . [9]}$$

where q(t) is the flow rate per unit length of root in cm³/(hr-cm). The amount of water removed by roots from the soil volume represented by node i,k is then

$$Q_{i,k}(t) = q_{i,k}(t) \, RL_{i,k}(t) \quad \text{. . . . . [10]}$$

where RL(t) is the total length of root within the annular ring. Equation [10] may be applied to each node in the root zone and the results summed to obtain the total water uptake by the plant which, with the assumption of no water storage in the plant, is equivalent to the transpiration rate or

$$T(t) = \sum_{i=1}^{NR+1} \sum_{k=1}^{ND+1} Q_{i,k}(t) \quad \text{. . . . . [11]}$$

where T(t) is the transpiration rate for the entire plant cm³/(hr) and NR and ND are the number of space increments in the radial and vertical directions, respectively, so that the number of nodes in the two directions is NR+1 and ND+1, respectively.

A difficulty encountered in attempting to apply boundary conditions of equation [8] to equation [4] is that Ψ_{root} is not readily determined experimentally.

Thus it would be difficult to define this condition and experimentally verify the results. This difficulty is overcome by including flow through the plant in the model and using leaf water potential as the upper boundary since several reliable methods are available for in-situ determination of leaf water potential (Newman and Thurtell, 1972; Hoffman and Rawlins, 1972; Campbell and Campbell, 1974; Hoffman and Hall, 1976).

The total flow through the plant or total transpiration is expressed as

$$T(t) = A_L(t) \frac{(\psi_r - \psi_L)}{R(t)} \quad \text{. [12]}$$

where $A_L(t)$ is the leaf area. To illustrate the method of including flow through the plant in the model, it is necessary to develop the numerical relationships leading to solution of the model. Equation [12] applies to the entire plant while equations [4] and [9] represent a single root at node i,k. To obtain a solution of equation [4] with boundary conditions [8] and include the effect of flow through the plant, it is necessary to determine the fraction of total transpiration T(t) supplied by the single root. The relationship expressing this fraction is developed in detail elsewhere (Slack, 1975). The expression is:

$$F_{i,k}(t) = \frac{RL_{i,k}(t) \ K(\psi_{i,k}) \ (\psi_{s,i,k} - \psi_L)}{\displaystyle\sum_{i=1}^{NR+1} \sum_{k=1}^{ND+1} RL_{i,k}(t) \ K(\psi_{i,k}) \ (\psi_{s,i,k} - \psi_L)}$$

. . . . [13]

where $F_{i,k}(t)$ is referred to as the transpiration fraction and ψ_s is the water potential in the soil.

The amount of transpiration attributed to any single root can be equated to the flux of water to that root (equation [9]) yielding

$$F_{i,k}(t) \, A_L(t) \frac{(\psi_{r,i,k} - \psi_L)}{R(t)} = 2\pi\rho_1 K(\psi_{i,k}) \frac{\partial \psi}{\partial \rho} \bigg|_{\rho = \rho_{1_{i,k}}}$$

. . . . [14]

Noting that

$$D(\psi) = K(\psi) \frac{d\psi}{d\Theta} \quad \text{or} \quad D(\psi) = \frac{1}{C} K(\psi) \quad \text{. . . . . [15]}$$

where $D(\psi)$ is diffusivity (Childs and Collis-George, 1950), equation [4] may be expanded to yield

$$\frac{\partial \psi}{\partial t} = \frac{1}{C} \frac{\partial \psi}{\partial \rho} \frac{\partial K}{\partial \rho} + D \frac{\partial^2 \psi}{\partial \rho^2} + \frac{D}{\rho} \frac{\partial \psi}{\partial \rho} \quad \text{. . . . . [16]}$$

Equation [16] is nonlinear, second order, partial differential equation of the parabolic type and has no known analytical solution. However, its solution may be approximated by finite difference techniques (Amerman, 1969; Carnahan et al., 1969). The numerical procedure used is described in detail by Slack (1975) and includes the root-to-leaf segment as defined by equation [14] in the solution matrix. The time-space solution grid used is shown in Fig. 2. Note that the distance from space node j=1 to j=2 which represents the plant is not directly defined but is included in the resistance term. Thus from node 1 to 2, equation [14] is used and from node 2 through MP2, equation [16] is used in setting up the solution matrix.

The initial and boundary conditions required for solution are those given in equations [8] with the exception that with the inclusion of flow through the plant, the boundary at the root surface is now replaced by a boundary condition at the leaf surface.

$$t > 0; j = 1; \psi = \psi_{leaf} = \psi(t) \quad \dots \dots \dots \dots \dots \quad [17]$$

The water potential at the root-soil interface (node 2) is computed by the model. An implicit method of solution is used and thus no restriction is placed on the relative magnitudes of Δt and $\Delta \varrho$ for stability. The numerical formulation used is a modified form of the O'Brien, et al. method discussed by Ames (1969). The modification is necessary due to the nonlinearity of the equation.

SOURCE TERM EVALUATION

The source term of equation [6] represents a moisture extraction rate per unit volume of soil. In the process of solving equations [14] and [16] a solution is also obtained for equations [9] and [10]. The source term for node i,k is then obtained by dividing the solution of equation [10] by the corresponding volume of soil surrounding the root at node i,k. The source term for each node of the combined model is thus obtained by solving the single root model at each node. Total plant transpiration for each time step Δt may be obtained by summing the solutions of equation [10] over the entire root zone as indicated in equation [11].

SOLUTION OF THE MACROMODEL

With the source term evaluated it is now possible to solve equation [6]. Although several finite difference methods are available for solution of parabolic equations in several variables (Ames, 1969), an implicit method of solution is desirable primarily because of the associated unconditional stability. The alternating direction implicit (ADI) method is such a method and has the practical effect of considering only one dimen-

Space Node I = Leaf water potential
Node 2 = Water potential at soil-root interface
Node MP2= Water potential at outer radius of zone of influence

FIG. 2 Time-space solution grid for solving the single root model.

sion at a time so that the tridiagonal matrix and its rapid solution may be utilized. The ADI Method, as modified by Amerman (1969) for nonlinear equations, is the method employed in solving equation [6]. A detailed description of the method and algorithms for a system in radial coordinates with radial symmetry is given by Slack (1975).

SOLUTION OF THE COMBINED MODEL

The complete model of water flow through the soil and plant segments of the SPAC requires interconnection of the three segment models discussed in this paper. Some of the interconnection has been explained by the inclusion of the plant in the solution of the single-root model and by the evaluation of the macromodel source term from results of the single-root model. Operation of the complete model through several time steps will now be discussed.

The combined model consists of solving the single-root model at each macronode i,k to obtain water uptake for some time period $n\Delta t$ for each incremental soil volume within the root zone. These solutions provide the negative source terms required for the solution of the macromodel for some time step $\Delta \tau = n\Delta t$ where Δt is the time step for solution of the single-root model. Since the single-root model does not consider gravitational flow components or flow due to potential gradients within the bulk soil, the potential within each incremental volume as determined by the single-root model must be adjusted using results of the macromodel prior to initiation of each $n\Delta t$ series of calculations. The method of adjustment is discussed in detail by Slack (1975).

The single-root model is solved for each incremental soil volume containing roots following the procedure previously outlined. At the end of each Δt and $\Delta V_{i,k}$ solution, where $\Delta V_{i,k}$ indicates the incremental volume associated with macronode i,k, transpiration for the volume $\Delta V_{i,k}$ is calculated.

The source term for each macronode is determined for each $\Delta \tau$, starting with the same initial water potential throughout the soil as existed prior to initiation of the single-root model. The macromodel includes the entire root zone whether or not the roots are present, while the single-root model operates only where roots are present.

At the end of 12 hr of operation, the single-root model ceases to operate since the leaf stomates are assumed to close with darkness. However, the macromodel continues to operate. In some cases it may be possible to cover the entire 12-hr period of darkness with one time step since the source term is zero for this period.

At the end of the 12-hr period of darkness, root growth and leaf growth information may be incorporated into the model. The single-root model is then operated again starting with the initial water potential distribution in each radius of influence as a constant value which corresponds to the water potential existing at the corresponding macronode as a result of macromodel operation. This process is repeated for each 24-hr period modeled.

In order to operate and check the combined model, a FORTRAN computer program was written for operation with a digital computer. Using a CDC CYBER 74 computer, between 2 and 3 min of computer time
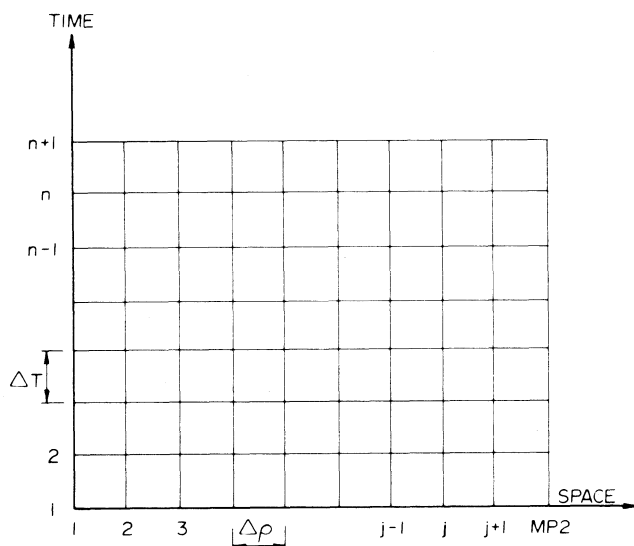
were required to simulate 23 days of real time in the model. The program consists of a main program called MULTROOT which calculates soil volumes, root densities, etc., and solves the single-root model for each incremental soil volume within the root zone. Subroutine MACRO is called for solution of the macromodel after the single-root model has operated through a time period equal to $\Delta\tau$ and the corresponding source terms have been calculated. In addition to these main procedures, the program also contains two function subprograms TABEX and TABEC. The former is a table-interpolating procedure for the water characteristic relationship and the latter is the same program for the water capacity relationship. Fig. 3 is a skeletal flow diagram for the program.

EXPERIMENTAL PROCEDURE

To evaluate the model and obtain boundary conditions, corn was grown in nalgene pots with an inside diameter of 27.5 cm and a depth of 65 cm. The pots were filled with thoroughly mixed Maury silt loam soil from the Ap horizon. To further insure uniformity and minimize particle segregation, only the soil which passed through a 5.0 mm sieve and was retained on a 1.0 mm sieve was used. The soil water characteristic for this soil was determined with a pressure plate apparatus.

Corn plants were grown in a greenhouse in four pots. In two of the pots ten thermocouple psychrometers were installed in the soil to monitor soil water potential. In addition tensiometers were installed at levels of 5, 15, 30, 45 and 60 cm from the soil surface at a radial distance of 5 cm from the center of the pot.

In each container a performated pipe of 1.27 cm diameter was installed on the bottom of the container and covered with 5 cm of coarse sand. When the remainder of the container was filled with soil, this pipe was used to supply and drain water from the pot. The soil psychrometers and tensiometers were installed as the soil was placed in the pots.

The two instrumented pots were used to determine soil hydraulic conductivity by the instantaneous profile method (Wells, 1974). After hydraulic conductivities had been determined, these pots were used to grow the corn for which daily transpiration was modeled. In addition, corn was grown in two other pots for the purpose of collecting root density samples without disturbing the plants used to evaluate the model. The root density pots were uninstrumented.

After hydraulic conductivity determinations were completed, all pots were resaturated, then drained until drainage ceased. At the cessation of drainage the top 5 cm of soil was removed from each pot and replaced with perlite to minimize evaporative loss and temperature variability at the surface while providing adequate opportunity for gaseous exchange. The drainage pipes were then closed, and one healthy pre-germinated corn seedling one week old was planted in the center of each of the four pots. No further water was added for the remainder of the experiment.

Soil water potential was determined in the pots with tensiometers for high water potentials and thermocouple psychrometers for water potentials of -1/2 bar or lower. The thermocouple psychrometers used were of the peltier type developed by Spanner (1951). They were single-junction psychrometers enclosed in ceramic cups and provided with a temperature measuring junction. The soil psychrometers were commercially manufactured and were obtained from WESCOR, Logan, UT.

Leaf water potential was monitored by means of a silver foil leaf thermocouple psychrometer of the type developed by Hoffman and Rawlins (1972). These psychrometers were fabricated at the University of Kentucky using components from various sources. Both soil and leaf psychrometer output was read with a 24-point thermocouple psychrometer recorder which was fabricated at the University of Kentucky following the design of Meeuwig (1972).

The silver foil leaf psychrometers were attached to the leaf by coating the lip of the psychrometer with a silver impregnated, water based conductive coating, and pressing it against the abaxial side of the leaf. The psychrometer was supported and several washers with a diameter equal to that of the psychrometer were placed on top of the leaf until the silver coating dried to prevent curling and to ensure a complete seal.

During preliminary investigations it was found that the silver coating damaged the leaves of young plants less than 10 days old. In addition, a satisfactory seal could not be obtained between the leaf and psychrometer when the psychrometer extended across the midrib of the leaf. For these reasons the psychrometers were not installed on the plants used for model evaluation until the plants were 10 days old. Satisfactory seals were not obtained until the plants were 13 days old. The adaxial side of the leaf immediately opposite the psychrometer was shaded as suggested by Hoffman and Hall (1976).

To obtain an estimate of plant resistance, corn plants were grown in plexiglass containers 7 cm in diameter and of variable depth depending on the desired water potential in the root zone. Root growth was restricted to the top portion of the container filled with soil by placing a #400 screen immediately below
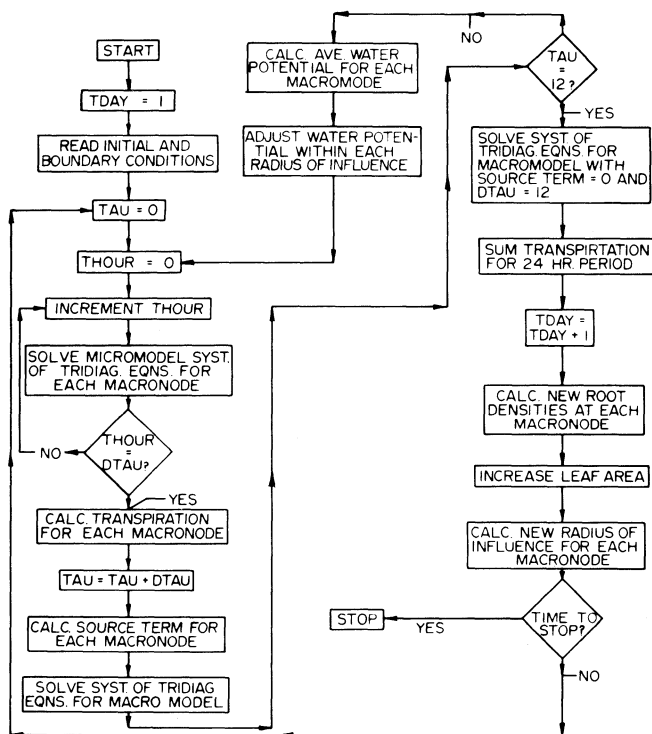

FIG. 3 Skeletal flow diagram of program MULTROOT.

the soil. The screen was underlain by coarse sand for the remaining depth of the container. Water potential in the root zone was controlled by maintaining the water level in the coarse sand at a fixed level during periods of constant transpiration. This method has been described in greater detail by Haan and Barfield (1971) and Hsieh et al. (1972).

Water potential in the root zone was measured with a tensiometer and leaf water potential was measured with the leaf psychrometer described previously. Water or nutrient solution was supplied to the sand column from a burette. Transpiration was then calculated on a per unit leaf area basis by dividing the amount of water used during a given time period by the total leaf area of the plant and the time elapsed since the last measurement. The plants were supplied with a full Hoagland nutrient solution to ensure that plant growth was not limited by nutrient availability. The water potential of the Hoagland solution was determined to be about -1.0 bar using the WESCOR soil psychrometer. Plant resistance was calculated by solving equation [12] for the resistance term.

The root density was measured as a function of depth, radius, and time by taking core samples every 10 days from the two uninstrumented pots in which corn was grown. Samples were taken from each pot at 5 and 10 cm from the main plant axis. The cores extended to the bottom of the soil and samples were extracted in increments of 5 cm. Each 5 cm increment of soil from each core was dried at 60 °C and then stored until analysis could be performed.

The root length for each sample was determined using the random line intersection theory developed by Newman (1966). Root density was obtained by dividing the total length of root in the 5 cm sample by the original sample volume giving cm root/cm³ soil. These data were then analyzed to determine root density as a function of depth, radius and time.

Leaf area for all plants was determined daily from emergence until termination of the experiment. Leaf area was estimated using the method of Montgomery (1911).

EXPERIMENTAL RESULTS AND DISCUSSION

The soil water characteristic was used in tabular form. The hydraulic conductivity data for pot No. 1 was described by the regression equation

$$K(\psi) = 0.8768 \, (\psi)^{-1.1348} \qquad \ldots \ldots \ldots \ldots \ldots \ldots \ldots [18]$$

where $K(\psi)$ is expressed in cm/hr. The coefficient of determination (R^2) for equation [18] is 0.68. A similar relationship was obtained for pot No. 2.

The tensiometer data from the experiment was used to provide initial conditions for the computer model, and estimates of daily transpiration were made from the corresponding water content profiles. The water potential profiles for pot No. 1 are shown in Fig. 4. The water potential changed very slowly until the plant was 21 days old. From that time on the daily decrease was quite large throughout the profile.

Leaf water potential was determined hourly between 14 and 37 days after emergence.

For the computer model the actual leaf water potential data was modified to yield an "equivalent" 12-hr leaf water potential which was assumed constant for a 12-hr period and then increased to zero for the re-

maining 12 hr of each day. The 12-hr equivalent leaf water potential was determined by first integrating the water potential-time curves over a 1-day period beginning at midnight to obtain the area under these curves and then solving for a 12-hr value of leaf water potential which would give an equivalent area.

The resulting equivalent leaf water potentials for plant No. 1 at various times after emergence are shown in Fig. 5. The cyclic variation is quite large and is greater than one might expect under relatively constant conditions of temperature and humidity. However, since the plants were exposed to sunlight in the greenhouse, leaf temperature varied considerably from day to day depending on cloud conditions. The greenhouse was cooled by ventilating fans so that during periods of percipitation the relative humidity within the greenhouse often reached a maximum of 80 percent and then decreased rapidly to between 35 and 40 percent.

Given this large variation in ambient conditions and realizing that leaf water potential is dependent upon evaporative demand, the rather large variations in leaf water potential are not as unreasonable as they may appear at first.
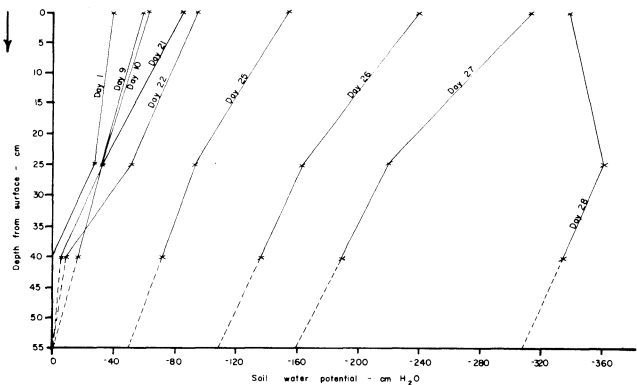

FIG. 4 Water potential profiles for pot No. 1 for selected days.
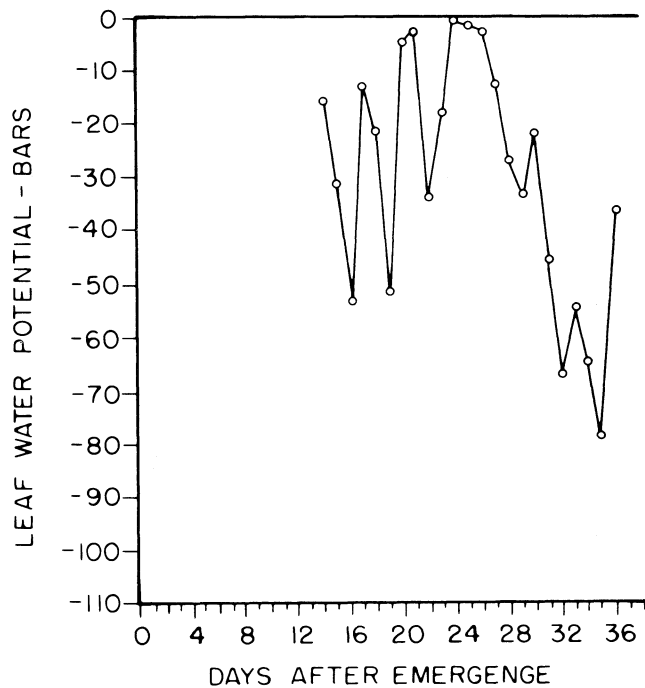

FIG. 5 Equivalent 12 hr average leaf water potential versus days after emergence for plant No. 1.

Since the plant was initially growing in a well watered condition, as exhibited by leaf exudation through the 28th day, one would expect leaf water potential to respond primarily to ambient conditions. This is illustrated somewhat by the summary of leaf temperature, leaf water potential and relative humidity data shown in Table 1. Maximum and minimum values of leaf water potentials did not always coincide exactly with corresponding minimum and maximum temperatures and/or maximum and minimum relative humidity. However, periods (within one or two days) of large fluctuations of leaf water potential corresponded to periods of large fluctuations in ambient conditions.

Plant resistance was determined as discussed earlier. Resistance determinations were made over a wide range of plant ages, leaf areas, and potential gradients. The literature indicates that plant resistance appears to be a function of stage of growth (Hailey et al. 1973) and plant water potential (Macklon and Weatherly, 1964; Stoker and Weatherly, 1971; Millar et al. 1971). Inspection of the experimental data indicated that resistance appears to be highly dependent upon leaf water potential and to a lesser extent leaf area. In view of this the data were analyzed using stepwise regression techniques and the following relationship obtained:

$$RP = 69.4 \left| \psi_L \right|^{1.09} \quad \dots \dots \dots \dots \dots \dots \quad [19]$$

Where RP is the plant resistance in hours and $|\psi_L|$ is the absolute value of plant leaf water potential in centimeters of water. The coefficient of determination (R^2) for equation [19] is 0.69. Much of the variation not explained by equation [19] appears to be due to individual plant characteristics which were not readily measurable (i.e. characteristics other than leaf area, age, leaf water potential, leaf temperature, etc.). Resistance values obtained from equation [19] and the "equivalent" leaf water potential data range from 5.8×10^4 to 1.5×10^7 hr. These values appear to encompass the range of values reported for corn

by Neumann et al. (1974) which ranged from 3.6×10^5 to 8.2×10^5 hr. However, in this experiment the values show considerably more variation than was noted by Neumann.

Root density data from the two pots of corn grown for this purpose were analyzed together using stepwise regression techniques. The resulting relationship expressing root density as a function of radius, depth, and leaf area is

$$DRoot = 4.5301 - 0.099682r - 0.031273z + 8.8528 \times 10^{-4} AL$$

$$\dots \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots \dots [20]$$

where
DRoot = root density (cm root/cm^3),
r = radial distance from pot center (cm),
z = depth from soil surface (cm), and
AL = leaf area (cm^2).

The coefficient of determination (R^2) for equation [20] is 0.43.

Leaf area of plant numbers 1 and 2 for time t, days after emergence, is shown in Fig. 6.

MODEL PERFORMANCE WITH EXPERIMENTAL DATA

The model was operated using input data from plant No. 1 for day 14 through day 36 after emergence. This interval was chosen because leaf water potential data was not available prior to the 14th day for the reasons discussed earlier.

The equivalent 12-hr leaf water potential was utilized in the model in tabular form and read directly from values shown in Fig. 5. Plant resistance was calculated from equation [19]. Leaf area was read directly from the experimental values shown in Fig. 6. Since root radius was not determined in the experiments, a constant root radius of 0.05 cm was assumed based on the results of NaNagara (1974). His determination were made for corn plants grown under conditions very similar to those in this experiment. To provide

TABLE 1. SUMMARY OF "EQUIVALENT" LEAF WATER POTENTIAL AND AMBIENT CONDITIONS

| Days after emergence	Equivalent leaf water potential (bars)	Leaf temp., (°C) max.	min.	Ambient relative humidity, % min.	max.
14	−15.3	35.0	19.4	36	72
15	−31.5	34.4	19.0	38	70
16	−53.2	38.1	19.4	40	73
17	−12.1	25.0	20.1	60	78
18	−20.9	37.4	18.9	40	80
19	−53.3	32.2	18.5	40	68
20	− 4.3	32.9	19.2	40	66
21	− 3.4	32.2	19.0	44	68
22	−33.8	32.0	19.8	65	80
23	−17.1	26.6	21.7	62	80
24	− 0.5	39.6	20.0	35	80
25	− 1.7	39.3	18.9	34	70
26	− 2.8	36.4	20.0	44	76
27	−12.7	36.9	19.7	40	76
28	−26.6	39.6	19.6	36	72
29	−33.3	39.6	19.9	40	80
30	−21.0	44.2	19.9	40	75
31	−45.4	44.7	25.6	36	80
32	−66.9	42.9	20.6	37	76
33	−54.5	43.9	21.1	38	78
34	−64.3	42.2	21.4	40	80
35	−78.9	41.7	21.1	No data	
36	−36.3	40.3	21.3	No data	
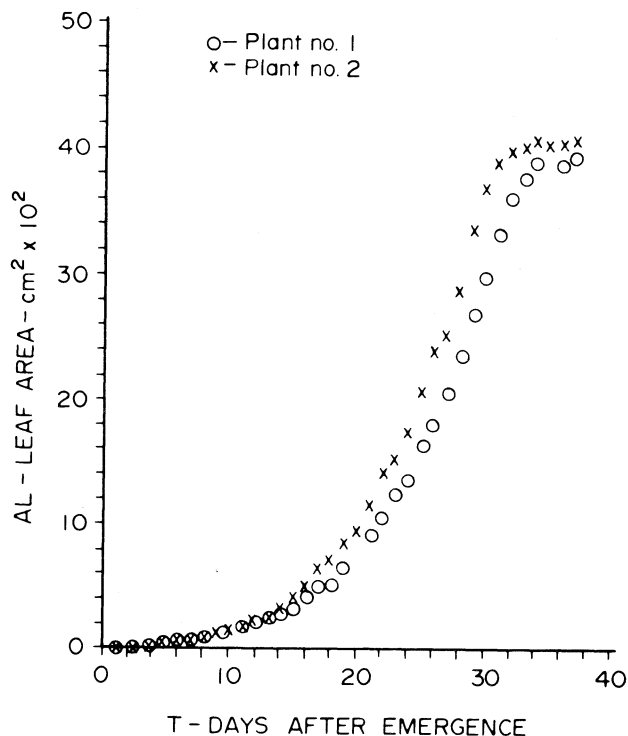
FIG. 6 Leaf area versus days after emergency for plants 1 and 2.

a comparison of daily experimental and model transpiration values, experimental transpiration was estimated from soil water content profiles for selected days for pot No. 1. The resulting experimental values of transpiration are shown in Fig. 7 together with model results. Curve A in Fig. 7 shows results of the model operation with plant resistance defined by equation [19]. In this instance the model considerably underestimates both daily and total transpiration.

From curve A it appears that the resistance values calculated from equation [19] are high by about a factor of 5. A possible explanation of these high resistance values is that the soil volumes in the resistance experiments were extremely small even when compared to the pot experiments. Thus root growth was severely restricted as leaf area increased. This reduced root length for a plant of fairly large leaf area would have required a greater soil-root gradient than normal to satisfy the evaporative demand. Thus the assumption that the water potential as determined by the tensiometer represented the value at the soil-root interface may have resulted in an over-estimation of the water potential at the soil-root interface. Such an error would have caused a corresponding over-estimation of plant resistance as can be seen from equation [12] since a larger root-leaf gradient was assumed than actually occurred. A reduction of plant resistance would result in increased transpiration providing soil hydraulic conductivity was not limiting and other factors remained unchanged. Therefore, to provide an estimate of what plant resistance would be necessary for the model to predict the total transpiration observed in the 23-day period modeled, equation [19] was multiplied by the ratio of the model to experimental transpiration for this period. The resulting relationship is

$$ RP = 14.6 \left| \psi_L \right|^{1.09} \qquad [21] $$
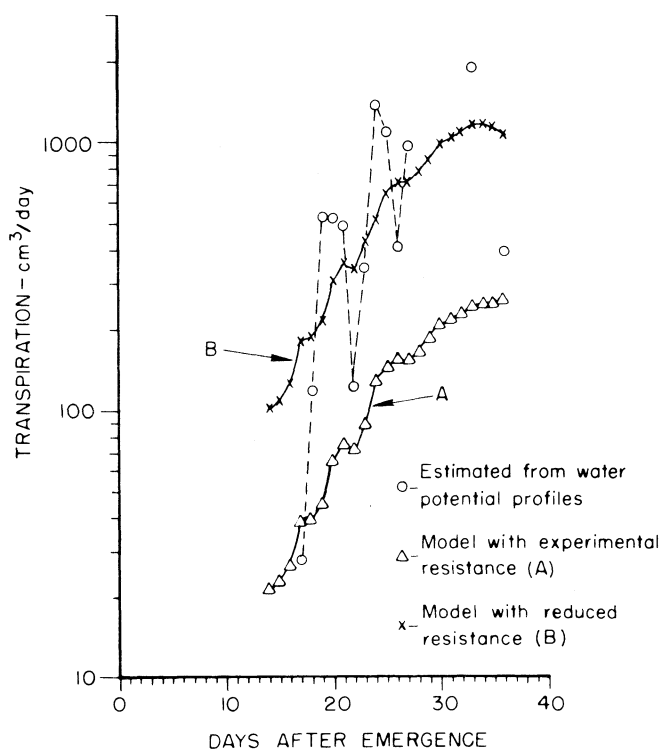

FIG. 7 Comparison of daily transpiration from experimental and model results for plant No. 1.

The model was again operated for the 14-23 day period using equation [21] to describe plant resistance with other inputs unchanged. Results of this operation are shown as curve B in Fig. 7.

The experimental values of daily transpiration show considerably more variation than is indicated by the model results using reduced resistance. A comparison of the daily transpiration from day 17 through 27 with equivalent leaf water potentials shown in Fig. 5 for those same dates shows a very marked relationship between the two. For days of low leaf water potential (i.e. large negative values) transpiration is low and for days of high leaf water potential (i.e. near zero) transpiration is high. This implies that plant resistance is even more sensitive to leaf water potential than equation [19] indicates.

The total transpiration for the period modeled was estimated using initial and final water content profiles and found to be 14514.5 cm³. The model with modified resistance gave a total volume of transpiration of 14169.0 cm³. The difference between these values represents a predictive error of 2.4 percent which is not surprising since the plant resistance was modified to better predict cumulative transpiration. The ratio of daily transpiration predicted by the model to that determined experimentally ranges from 0.38 to 6.7 with a mean of 1.6.

A comparison of curves A and B in Fig. 7 reveals some interesting information regarding the effect of soil-water depletion on transpiration. In curve A the plant resistance was so large that it dominates and transpiration continues to increase throughout the period modeled. However, with lower plant resistance and the fact that much more water is removed from the soil, the rate of transpiration increase begins to decline on the 33rd day in curve B. Transpiration actually declines on the 35th and 36th day even though there is a decrease in plant resistance from the 35th to the 36th day. Thus in the model, the transpiration rate becomes limited by soil water availability on the 33rd day.

In addition to the model output presented in this paper the model is also capable of producing:

1 Water potential or water content distributions in the bulk soil as a function of time.

2 Water potential or water content distribution within the radius of influence of a model root as a function of time.

3 Transpiration as a function of time, radius, and depth.

Additional output may also be selected. Those noted above are values which would normally be chosen.

SUMMARY AND CONCLUSIONS

A mathematical model was developed which describes water uptake by a plant as a function of leaf water potential, initial soil water potential and other soil and plant parameters. The model utilizes two non-linear partial differential equations for which there are no known analytical solutions. Therefore, to operate the model it was necessry to develop a numerical procedure employing finite difference techniques for the solution of the equations. A computer program, MULTROOT, was developed to solve the numerical model on a digital computer.

Operation of the model with experimental data

from plant No. 1 yielded values of daily transpiration which were considerably less than the experimental values. It was found that by reducing plant resistance, model results were significantly improved. With reduced resistance, the model predicted experimental transpiration over a 23-day period within 2.4 percent.

This study showed that the model developed herein predicted daily transpiration quite well for a corn plant from 14-36 days after emergence as the soil dried from near saturation to a soil-water potential of -22 bars. The model shows the effects of the interaction of plant growth and soil drying on transpiration.

The model appears to be limited by the difficulty of defining plant resistance, soil hydraulic conductivity in a very dry soil and the soil water characteristics in a very dry soil.

Some of the experimentally determined plant and soil parameters are possibly the factors limiting the model at the present time. Future work should initially concentrate on determining plant resistance over a wide range of plant age, size, and leaf water potential. To operate the model at soil water potentials less than -20 bars, it would also be desirable to evaluate the soil properties in this range.

The following conclusions were drawn from this study:

1 The model developed in this study illustrates the dynamic and complex interactions between the soil and plant and its atmospheric environment in determining the rate of transpiration.

2 The model is capable of predicting transpiration provided the proper plant resistance is utilized.

3 Plant resistance appears to be primarily a function of leaf water potential.

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