Effect of Temperature on Nutritional Requirements of Plants
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AUTHORS: Michael J. Ungs, a graduate student in forest science at Oregon State University when the report was written, is now a private consultant in environmental sciences. Larry Boersma is a professor in soil science at Oregon State University, and Suntaree Akratanakul is an assistant professor in soil science at Kasetsart University, Nakorn Pathom, Thailand.
Effect of Temperature on Nutritional Requirements of Plants

Michael J. Ungs, Larry Boersma, and Suntaree Akratanakul

ABSTRACT

Nutritional requirements of plants have traditionally been discussed in terms of results of specific experiments. These studies have established certain fundamental principles which explain observed responses. This report presents a mechanistic model based upon physical, chemical, and biological processes involved in nutrient uptake by plants with specific reference to temperature effects. The model consists of a set of equations which describe the steps involved. Explanations are offered for observed effects of temperature on active solute transport based on principles of thermodynamics and enzyme kinetics. The temperature effects follow from the change in the Gibbs free energy of transport processes and the changes in reaction rate constants of the Michaelis-Menten formulation for enzyme denaturation. The approach presented is not complete, but it provides an opportunity to focus on fundamental principles and allows experimentation based on a clear recognition of the dynamic and synergistic nature of the process.

Introduction

The nutrient requirements of plants are determined by the combined effects of all factors which regulate their growth and development. At the same time, mechanisms operate so the availability of nutrients regulates growth. The root depends on the shoot for carbohydrates, and the shoot depends on the root for water and mineral nutrients. As a consequence, growth and nutrient uptake are closely integrated (Fig. 1).

Temperature is one of the environmental factors that control plant growth. Temperature also affects the availability of nutrients in the soil. Nearly all the biochemical and physical processes involved in the growth of plants are temperature-dependent. Traditionally, nutritional requirements of plants have been discussed in terms of results of specific experiments. Numerous studies have been reviewed in great detail several times during the immediate past (Nielsen and Humphries, 1966; Hanna and Hutcheson, 1968; Nelson et al., 1968; Baumeister and Burghardt, 1969; Corey and Schulte, 1973; Walsh and Beaton, 1973; Carson, 1974; Nielsen, 1974). Much is known about the effect of temperature on nutrient uptake. Unfortunately, few of these studies have established fundamental principles that could explain the responses observed in experimental work. A recent review (Nielsen, 1974) concludes with: "It would be satisfying if this chapter could end with a comprehensive, point-by-point summary of the effects of root temperature on plants. Unfortunately this cannot be done. Our knowledge of the precise functions of the roots is inadequate; our understanding of the reactions that occur in the roots and how they are influenced by environmental conditions, stage of growth, and so on, is incomplete."
Figure 1. Accumulation of dry matter, nitrogen, potassium, and calcium as percent of maximum, plotted as a function of time (after Brouwer and Kuiper, 1972, Figure 4-18). The time scale shows sampling points during the growing season in a moderate climate.
This conclusion is not surprising if one recognizes the complexity of the problem. Mineralization processes and the movement of ions in the soil are temperature-dependent. Nutrients reach the root surface by being carried along in the transpiration stream or by diffusion. Both processes are temperature-dependent as a consequence of the change in the viscosity of water with temperature. Other nutrients become available to the root as a result of root extension. The rate of root growth depends on the soil temperature.

Essential to this review is detailed knowledge of the function of roots and their behavior in the soil. Lamenting the state of knowledge in this field, an editorial in Science (Epstein, 1972b) exclaimed: "The authors of biology textbooks conspire with nature to keep plant roots and their activities in the dark."

The uptake at the root surface is by surface absorption, by electro-diffusion along a potential gradient, and by ion exchange. The uptake of the nutrient ions by the protoplasm requires energy from respiration. Temperature exerts its effects here because of its influence on metabolic processes. Transport of the nutrients for distribution to the various components of the plant is temperature-sensitive. Viscosity effects as well as metabolic processes are important. One author (Canny, 1973) prefaced a chapter on the effects of temperature on phloem translocation with: "The classification of the constituents of a chaos, nothing less is here essayed." This exclamation, borrowed by the author from Moby Dick, applies to nearly all processes which combine to produce biomass.

Another problem in describing temperature effects is the dynamic nature of the temperature environment (van Wijk, 1966). Because of the daily course of the sun, the soil gains heat during the day and loses heat during the night. Similar changes occur in the air above the soil. There is a correlation between air temperature and soil temperature. However, changes during short periods of time may not be correlated. Furthermore, changes in the aerial environment are much more extreme than those in the root environment.

To describe the effect of temperature on nutritional requirements of plants, we developed a mechanistic model of the physical, chemical, and biological processes involved. The model consists of equations that describe separate steps involved in the uptake of nutrients by plants. This approach is not complete, but it provides an opportunity to focus on the fundamental principles. Experimentation should be based on a clear recognition of the dynamic and synergistic nature of the process.

The following components of the soil-plant-atmosphere continuum are discussed in terms of their contribution to the uptake of nutrients by plants: (1) heat transfer in the soil, (2) water flow in the soil, (3) distributions of solutes in the soil, (4) movement of water in the soil-plant-atmosphere continuum, and (5) movement of solutes from the soil to the plants. The review of these processes is followed by a discussion of temperature effects.
## List of Symbols

<table>
<thead>
<tr>
<th>Bracket notations</th>
<th>Physical unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>[1]</td>
<td>Unitless</td>
</tr>
<tr>
<td>[L]</td>
<td>Gross length (e.g., 1 cm of soil)</td>
</tr>
<tr>
<td>[L_p]</td>
<td>Potential (e.g., 1 millibar) [M/L/t²]</td>
</tr>
<tr>
<td>[L_r]</td>
<td>Root length (e.g., 1 cm of root)</td>
</tr>
<tr>
<td>[L_w]</td>
<td>Fluid length (e.g., 1 cm of water)</td>
</tr>
<tr>
<td>[M]</td>
<td>Mass (e.g., 1 gram)</td>
</tr>
<tr>
<td>[t]</td>
<td>Time (e.g., 1 second)</td>
</tr>
<tr>
<td>[T]</td>
<td>Temperature (e.g., 1 degree Celsius)</td>
</tr>
</tbody>
</table>

### English letter symbols

- \( A(z,t) \) Rate of water uptake by the root \([L^3/L^3/t]\)
- \( C(z,t) \) Concentration of solute in the soil water \([M/L^3]\)
- \( C_m \) Concentration of solute in the symplasm \([M/L^3]\)
- \( C_{Tu} \) Apparent thermal conductivity of soil \([ML/t^3/T]\)
- \( C_v \) Heat capacity of the soil \([M/L^2/T]\)
- \( C_x \) Concentration of solute in the xylem \([M/L^3]\)
- \( CNVRSN \) Conversion from the units of potential to those of hydraulic head \([L/L_p]\)
- \( D(\theta) \) Soil water diffusivity \([L^2/t]\)
- \( D_s(\theta) \) Apparent solute dispersion coefficient \([L^2/t]\)
- \( E_a \) Activation energy \([ML^2/t^2/mole]\)
- \( f \) Fluidity \([L^2/L^3/t]\)
- \( F \) Root density function is defined as length of active root per volume of soil at depth \( z \) and time \( t \) \([L_r/L^3]\)
- \( F_1 \) Root density function, used by Whisler et al. (1968) \([L_r/L^3]\)
- \( F_2 \) Root density function, used by Molz and Remson (1971) \([L^3_r/L^6]\)
- \( F_3 \) Root density function defined as the proportion of totally active roots in depth increment \( \Delta z \), used by Nimah and Hanks (1973) \([L_r/L^3]\)
- \( F_4 \) Empirical root effectiveness function, which includes the effect of root surface area, resistance, and density, used by Neuman et al. (1975) \([L_r/L^3]\)
- \( F_5 \) Root absorption function, used by Ungs et al. (1977) \([L_r/L^3]\)
- \( F_6 \) Root density, used by Farnum (1977) \([L_r/L^3]\)
- \( g \) Gravitational acceleration \([L/t^2]\)
- \( G(z,t) \) Rate of solute uptake by the root \([M/L^3/t]\)
- \( G_r \) Geometry factor for root system \([1]\)
- \( I_p \) Impedance to water flow in the plant \([L^3 L_p t/L^3]\)
- \( I_s \) Impedance to water flow in the soil \([L^3 L_p t/L^3]\)
- \( J_s \) Total solute flux into the root xylem \([M/L/t]\)
- \( J_s' \) The active component of solute flux into the root xylem \([M/L_r/t]\)
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$J_{s,max}(T)$</td>
<td>The maximum rate of active solute uptake by the root system, as a function of temperature</td>
<td>$[M/L_r/t]$</td>
</tr>
<tr>
<td>$J_v$</td>
<td>Total water flux into the root xylem</td>
<td>$[L^3/ L_r/t]$</td>
</tr>
<tr>
<td>$k$</td>
<td>Intrinsic permeability</td>
<td>$[L^6/L^4]$</td>
</tr>
<tr>
<td>$K$</td>
<td>Hydraulic conductivity of soil</td>
<td>$[L^2/L^2/t]$</td>
</tr>
<tr>
<td>$K_i$</td>
<td>Proportionality constants</td>
<td></td>
</tr>
<tr>
<td>$K_r$</td>
<td>Effective hydraulic conductivity of root cortex</td>
<td>$[L^2/L^2/t]$</td>
</tr>
<tr>
<td>$M_w$</td>
<td>Molecular weight of solute</td>
<td>$[M/mole]$</td>
</tr>
<tr>
<td>$n$</td>
<td>Sum of the cation and anion valencies of the completely dissociated salt being taken up by the root (e.g., $n = 1$ for nondissociated salts and $n = 2$ for Na$^+$ Cl$^-$)</td>
<td></td>
</tr>
<tr>
<td>$P$</td>
<td>Permeability of inner root membrane</td>
<td>$[L^2/L^2_t/p/L_r/t]$</td>
</tr>
<tr>
<td>$P_0$</td>
<td>Permeability of outer root membrane, in the three-compartment model</td>
<td>$[L^2/L^2_t/p/L_r/t]$</td>
</tr>
<tr>
<td>$q_w(z, t)$</td>
<td>Darcian flux of soil-water</td>
<td>$[L^3/L^2;L^2/p/L_r/t]$</td>
</tr>
<tr>
<td>$R$</td>
<td>Universal gas constant (.08205 liter·atm/mole/°K) or $[L^2/p/mole/T]$ or $[ML^2/t^2/mole/T]$</td>
<td></td>
</tr>
<tr>
<td>$R_a$</td>
<td>Effective surface area per unit root length involved in solute uptake</td>
<td>$[L_r]$</td>
</tr>
<tr>
<td>$RPF$</td>
<td>Longitudinal hydraulic resistance in the xylem</td>
<td>$[L]$</td>
</tr>
<tr>
<td>$RR'$</td>
<td>Radial hydraulic resistance in root</td>
<td>$[LL_p t/L^2_w]$</td>
</tr>
<tr>
<td>$RRES$</td>
<td>Longitudinal hydraulic resistance of root, per unit length of xylem</td>
<td>$[1]$</td>
</tr>
<tr>
<td>$S$</td>
<td>Solute concentration in the adsorbed phase</td>
<td>$[M/L^3]$</td>
</tr>
<tr>
<td>$t$</td>
<td>Time</td>
<td>$[t]$</td>
</tr>
<tr>
<td>$T$</td>
<td>Temperature</td>
<td>$[T]$</td>
</tr>
<tr>
<td>$\Delta x$</td>
<td>Horizontal distance between roots</td>
<td>$[L]$</td>
</tr>
<tr>
<td>$z$</td>
<td>Vertical space coordinate, positive downwards</td>
<td>$[L]$</td>
</tr>
</tbody>
</table>

**Greek letter symbols**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha, \beta$</td>
<td>Coefficients used to weight the effects of two different concentrations</td>
<td>$[1]$</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Volumetric water content of the soil</td>
<td>$[L^3/L^3]$</td>
</tr>
<tr>
<td>$\theta_r$</td>
<td>Root porosity, defined as the volume of solution per unit bulk volume of root tissue</td>
<td>$[L^3/L^3]$</td>
</tr>
<tr>
<td>$\nu$</td>
<td>Viscosity of water</td>
<td>$[M/L/t]$</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Density of water</td>
<td>$[M/L^3]$</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Reflection coefficient of the inner root membrane</td>
<td>$[1]$</td>
</tr>
<tr>
<td>$\sigma_0$</td>
<td>Reflection coefficient of the outer root membrane</td>
<td>$[1]$</td>
</tr>
<tr>
<td>$\psi$</td>
<td>Matric potential of soil water</td>
<td>$[L_p]$</td>
</tr>
<tr>
<td>$\psi_{rc}$</td>
<td>Water potential at the root collar (root at the soil surface)</td>
<td>$[L_p]$</td>
</tr>
<tr>
<td>$\psi_x$</td>
<td>Xylem water potential</td>
<td>$[L_p]$</td>
</tr>
</tbody>
</table>
List of Symbols (cont.)

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\psi$</td>
<td>Osmotic potential of soil water</td>
<td>$[L_P]$</td>
</tr>
<tr>
<td>$\omega$</td>
<td>Osmotic permeability of the inner root membrane</td>
<td>$[M/L_P/t/L^2]$</td>
</tr>
</tbody>
</table>

Special symbols

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\nabla$</td>
<td>Del operator</td>
<td></td>
</tr>
<tr>
<td>$\partial$</td>
<td>Partial derivative</td>
<td></td>
</tr>
</tbody>
</table>

Heat Transfer in Soil

Soils gain heat by absorbing short-wave radiation at the soil surface. Long-wave radiation emitted by clouds and sky is also important under certain conditions. At the same time, heat is lost from the soil by the emission of long-wave radiation. The net rate of heat exchange at the soil surface depends on the balance between incoming and outgoing radiation. This rate varies continuously throughout one day because of the changing intensity in short-wave radiation. During the day, the soil gains heat and the soil temperature near the surface rises. During the night, the soil loses heat and the soil temperature decreases (Fig. 2). These daily cycles in soil temperature are confined to the upper 20 to 40 cm. In addition to the daily cycle in soil temperature, there exists an annual cycle reflecting the progression of the sun from summer solstice to winter solstice. The annual temperature cycle is confined to about the upper 6 meters of soil.

Heat is transferred through soils by several mechanisms, including conduction across the solid particles, conduction through water, conduction through air in the soil pores, convective mass transfer of water, and by radiation. In addition, heat is transferred as latent heat which occurs when water evaporates at a warm location and condenses at a nearby location at a lower temperature. The conductivity is normally much higher for solid particles than for water and air. Heat transfer by convection of liquid water and by radiation is small. The most important contribution of water movement to the heat transfer arises from vapor distillation of temperature gradients (de Vries, 1958). The evaporation and condensation processes significantly increase the conductivity of the gaseous part of the porous medium. These two main mechanisms define the heat transfer equation (Philip and de Vries, 1957; Hillel, 1971) for soil as

$$ C_v \frac{\partial T}{\partial t} = \nabla (C_T \nabla T) - H_L \nabla (D_{W, vap} \nabla \theta) $$

where $C_v$ is the volumetric heat capacity of the soil $[M/L/t^2/T]$, $T$ is soil temperature $[T]$, $t$ is time $[t]$, $C_T$ is the apparent thermal conductivity of the soil $[ML/t^3/T]$, $H_L$ is the latent heat of vaporization of water $[ML^2/t^2/L^3]$, $D_{W, vap}$ is the water diffusivity in the vapor phase $[L^2/t]$, $\theta$ is volumetric water content $[L_3/L^3]$, and $\nabla$ is the del operator $[1/L]$.

Equation 1 can be solved by assuming that the temperature at the soil surface is a periodic function of time. This assumption allows an approximation of the fluctuations in the soil temperature caused by alternating periods of warming and cooling such as the succession of day and night or summer and winter (Fig. 2).
Figure 2. Daily and annual cycles of soil temperature. Measurements were made at Corvallis, Oregon (44°38'N; 123°12'W). Amplitude of cycles varies according to local climatic conditions.

Considering soil-temperature variations in the vertical direction only and ignoring the effect of moisture gradients, the solution to equation 1 is:

\[ T(z, t) = T_0 + A_0 e^{-z/d} \sin(wt - z/d) \]  

with

\[ d = \sqrt{\frac{2C_{Ta}}{C_w}} \]  

where \( T(z, t) \) is the soil temperature at depth \( z \) [L] and time \( t \) [t], \( T_0 \) is the average temperature at the soil surface [T], \( A_0 \) is the amplitude of the temperature cycle at
the soil surface \([T]\), \(w\) is the frequency of the temperature cycle \([1/t]\), and \(d\) is the damping depth \([L]\).

Equation 2 expresses the major features of the daily and annual cycles of soil temperature, namely the decrease of the amplitude, \(A_0e^{-z/d}\), with depth and the increase in phase lag, \(\sin(wt-z/d)\), with depth. Damping and phase lag of the temperature cycle with increasing depth are caused by the heat storage. The amplitude of the temperature cycle is only about 5 percent of that at the soil surface at \(z = 3d\). This means that daily temperature fluctuations are small at depths greater than 30 cm for a soil with \(d = 10\) cm. The value of \(d\) ranges from 8 to 15 cm for most soils. The value of the damping depth of the annual temperature cycle is \(\sqrt{365}\) or about 19 times larger than that of the daily cycle. The \(d_{\text{annual}}\) ranges, therefore, from 150 to 300 cm for most soils. For the soil with \(d_{\text{daily}} = 10\) cm, the \(d_{\text{annual}} = 190\) cm. Fluctuations of the annual cycle, therefore, are small at depths greater than 570 cm.

The graphs in Figure 2 are for a moderate climate. They indicate that the temperatures of most of the root zone remain low throughout the year. The warming of the soil in the spring lags behind the warming of the air. Root temperatures usually are lower than the air temperatures. Specific adaptations of plants to the temperature conditions of the root environment have occurred. However, agronomic and horticultural crops are now grown in climatic regions which usually are colder than those of their native habitat. As a consequence, plant growth is often limited by low soil temperatures.

Additional information concerning the thermal properties of soils and the variations in soil temperatures are in Baver et al. (1972).

**Water Flow in Soil**

The general equation (Hillel, 1971) describing water movement in porous materials as a result of gradients in the soil water potential and gradients in the soil temperature is:

\[
\frac{\partial \theta}{\partial t} = \nabla (D_T \nabla T) + \nabla (D \nabla \theta) - \frac{\partial K}{\partial z} + A \quad [L_w^3/L^3/t] \quad (4)
\]

where \(\theta\) is the volumetric water content \([L_w^3/L^3]\), \(t\) is the time \([t]\), \(T\) is the absolute temperature \([T]\), \(D_T\) is the thermal diffusivity \([L^2/T]\), \(D\) is the soil-water diffusivity \([L^2/T]\), \(K\) is the hydraulic conductivity of the soil \([L_w^3/L^2/T]\), \(z\) is the vertical space coordinate \([L]\), \(\nabla\) is the del operator \([1/L]\), and \(A\) is the volumetric uptake sink of water into the root (a negative quantity) \([L_w^3/L^3/t]\). This formulation is based on the assumption that the density of water in the liquid state does not significantly change with temperature. Equation 4 indicates that temperature influences the flow of water in the soil in at least two ways. The mean temperature affects the viscosity of the water, so that the hydraulic conductivity is a function of temperature. The hydraulic conductivity is proportional to the fluidity, \(f\), and to the intrinsic permeability, \(k\):

\[
K = k \cdot f \quad [L_w^3/L^2/t] \quad (5)
\]
The intrinsic permeability depends only on the soil structure and soil texture. The temperature dependence of the hydraulic conductivity, therefore, is described by the temperature dependence of fluidity:

\[ f = \frac{\rho g}{\nu} \quad [L^2/L^3V/t] \]  

where \( \nu \) is the viscosity \([M/L/t] \), \( \rho \) is the density of water \([M/L^3] \), and \( g \) is the gravitational acceleration \([L/t^2] \). The effect of temperature on viscosity and fluidity for pure water is shown in Table 1. The viscosity of water decreases about 3 percent for each one degree increase in temperature. The effect has dramatic consequences with respect to the uptake of water and nutrients by plants.

Table 1. Physical properties of water at different temperatures

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>Fluidity 1/cm/sec</th>
<th>Viscosity gm/cm/sec</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>5,483</td>
<td>.01787</td>
</tr>
<tr>
<td>4</td>
<td>6,254</td>
<td>.01567</td>
</tr>
<tr>
<td>5</td>
<td>6,452</td>
<td>.01519</td>
</tr>
<tr>
<td>10</td>
<td>7,496</td>
<td>.01307</td>
</tr>
<tr>
<td>15</td>
<td>8,597</td>
<td>.01139</td>
</tr>
<tr>
<td>20</td>
<td>9,715</td>
<td>.01002</td>
</tr>
<tr>
<td>25</td>
<td>10,979</td>
<td>.00890</td>
</tr>
<tr>
<td>30</td>
<td>12,136</td>
<td>.00798</td>
</tr>
<tr>
<td>35</td>
<td>13,290</td>
<td>.00719</td>
</tr>
<tr>
<td>40</td>
<td>14,711</td>
<td>.00653</td>
</tr>
<tr>
<td>45</td>
<td>15,935</td>
<td>.00596</td>
</tr>
<tr>
<td>50</td>
<td>17,416</td>
<td>.00547</td>
</tr>
</tbody>
</table>

Viscosity also is affected by the concentration and type of solute in the water. This effect is small for concentrations of ions encountered in the soil and usually is ignored. The effect is not small for transport problems in the plant itself, however.

The surface tension of water decreases with increasing temperature. As a consequence, the water potential in a soil with water contents below saturation increases with increasing temperature so that water flows from warm to cold regions. This is included in the second term on the right-hand side of equation 4. The magnitude of bulk flow of water caused by temperature gradients is small at water contents important for plant growth. Mass flow of water because of temperature gradients may be ignored.

Changes in the temperature of the soil occur according to daily as well as annual cycles. Effects of diurnal changes of the soil temperature on soil water movement were discussed by Philip and de Vries (1957), de Vries (1958), Cary (1965, 1966), Kay and Groenevelt (1974), and Aston and Gill (1976).

For one-dimensional, vertical flow, and isothermal conditions, equation 4 may be written as:

\[ \frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left\{ D \frac{\partial \theta}{\partial z} - K \right\} + A \quad [L^2/L^3V/t] \]  

Alternatively, the water flow equation in terms of matric potential can be written,
\[
\frac{\partial \psi}{\partial t} \left( \frac{\partial \theta}{\partial \psi} \right) = \frac{\partial}{\partial z} \left\{ K \frac{\partial \psi}{\partial z} \right\} \cdot CNVRSN - K \} + A \quad [L^3_w/L^3/t] \tag{8}
\]

where \( \psi \) is the matric potential \([L_p]\) and the coefficient \(CNVRSN\) converts the units of potential, e.g., bars, to the units of hydraulic head, e.g., cm of H\(_2\)O. For these units, \(CNVRSN = 1,020 \text{ cm H}_2\text{O/bar}\). The term \( (\partial \theta/\partial \psi) \) is defined as the specific water capacity of the soil.

The formulation of equations 7 and 8 requires the following conditions to be met: vapor movement does not occur, structural properties of the soil are constant in time and not altered by changes in water content, osmotic potentials do not contribute to flow, and there is no hysteresis in the relationship between hydraulic conductivity and water content or between water content and matric potential.

Equations 7 and 8 have been solved for many applications but most of these ignore the root uptake term, \( A \). From the literature, one can find applications which study the changes in water content of the soil because of infiltration of rain or irrigation water (Bresler et al., 1969; Gardner et al., 1970; Youngs and Poulavassilis, 1976), and changes in water content from evaporation (Gardner, 1958; Whisler et al., 1968; Hillel, 1975b). More detailed applications involve the extraction of water from the soil by plants. Freeze (1969) presents a rather complete review of the literature dealing with numerical solutions of the one-dimensional, vertical, unsaturated flow equation.

### Solute Transport in Soil

The displacement of solutes through the soil by mass flow of water has been the subject of a large number of investigations. The mathematical formulation most frequently used to describe solute transport for one-dimensional, vertical flow is:

\[
\frac{\partial (\theta C)}{\partial t} = \frac{\partial}{\partial x} \{ \theta D_s \frac{\partial C}{\partial z} \} - \frac{\partial}{\partial z} \{ q_w C \} - \frac{\partial S}{\partial t} + G \quad [M/L^3/t] \tag{9}
\]

where \( C \) is the solute concentration in the liquid phase \([M/L_w]\), \( S \) is the local solute concentration in the adsorbed or solid phase \([M/L^3]\), \( D_s \) is the apparent solute dispersion coefficient \([L^2/t]\), \( G \) is the solute root uptake term \([M/L^3/t]\), which is a negative quantity, and \( q_w \) is the volumetric or Darcian flux of soil-water \([L_w^3/L^2/t]\).

The first term on the right-hand side of equation 9 describes the solute flux caused by the diffusion-dispersion process. The apparent solute dispersion coefficient, \( D_s \), includes the effect of hydraulic dispersion and molecular diffusion. The second term represents the solute flux due to convective processes. The third term is an expression for the adsorption or desorption of the solute onto the soil particles. The last term represents root uptake.

The coupling process of water and solute distribution is readily apparent in equation 9. To solve equation 9, the soil-water flow equation first must be solved. Using either equation 7 or 8, \( \theta \) and \( q_w \) can be solved at a particular soil temperature where the Darcian flux is defined as:

\[
q_w = \{ -D \frac{\partial \theta}{\partial z} + K \} \quad [L_w^3/L^2/t] \tag{10}
\]
In addition to the flux term of equation 10, the soil sorption term, $S$, the solute concentration in the adsorbed phase, must be specified. The amount of solute in the adsorbed phase, in part, is controlled by the concentration in the liquid phase. If instantaneous exchange between the solid and liquid phases is assumed, the so-called equilibrium models result (Table 2). These mathematical descriptions show the sorbed phase as a function of the concentration in the liquid phase and several constants. The constants are functions of soil material involved, chemical species, and other factors. They are always empirically determined. The choice of model to use depends on personal preference and conditions to be described.

Non-equilibrium models (Table 3) result when allowance is made for the fact that the exchange between the liquid phase and the solid phase is not instantaneous but time-dependent.

<table>
<thead>
<tr>
<th>Table 2. Equilibrium models of isothermal soil sorption of solute†</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Name</strong></td>
</tr>
<tr>
<td>Linear</td>
</tr>
<tr>
<td>Langmuir</td>
</tr>
<tr>
<td>Freundlich</td>
</tr>
<tr>
<td>Nonlinear</td>
</tr>
</tbody>
</table>

† $K_1$ and $K_2$ are specified constants for each model; $Q$ is the cation exchange capacity per unit weight of soil and $C_0$ is the total concentration of all cations in the soil solution.

<table>
<thead>
<tr>
<th>Table 3. Non-equilibrium models of isothermal soil sorption of solute†</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Name</strong></td>
</tr>
<tr>
<td>Linear</td>
</tr>
<tr>
<td>Bilinear</td>
</tr>
<tr>
<td>Langmuir</td>
</tr>
<tr>
<td>Freundlich</td>
</tr>
<tr>
<td>Nonlinear</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>

† $K_1$, $K_2$, and $K_3$ are specified constants for each model; $S_0$ is the initial and $S_{max}$ is the maximum concentration of adsorbed solute.
The models listed in Tables 2 and 3 assume that adsorption and desorption are defined by the same equation. Most of these models are derived for saturation conditions and were reviewed by Boast (1973).

The presentation of equations 1, 4, and 9 gives a complete summary of energy and mass (water and solute) transfer for the soil-plant system. Since the transfer processes interact with one another (a coupled process), these equations must be solved simultaneously to obtain the distribution profiles of temperature, water, and solute in the soil. To solve these, all the empirical coefficients must be acquired and the initial conditions and the upper and lower boundary conditions for all three components must be specified.

Only a few studies have been reported where simultaneous transport of water and solute under transient flow conditions was analyzed. Warrick et al. (1971) analyzed and modeled the one-dimensional, vertical flow of solute, assuming a spatially homogeneous water content. Kirda et al. (1973) and Bresler (1973) show numerical solutions for the unsteady, simultaneous, solute and water transport in unsaturated soils but only for conservative, non-interacting solutes, i.e., no adsorption/desorption or other sources and sinks. Ungs et al. (1977) describe a numerical analysis which includes all the terms in equations 7 and 9 except for the $G$ term. They provide a numerical integration scheme to solve the equations.

Most of the functions causing change in temperature, water, and solute involve straightforward physical driving forces such as temperature, water, and solute concentration gradients. Two terms that need additional elucidation are the plant uptake terms, namely $A$ for water and $G$ for solute.

Both $A$ and $G$ functions cause flow of water and solute towards the root and thus decrease the water content and solute concentration in the soil. These two terms, however, are far from being constants. It will be shown later, in more detail, that the uptake functions depend on the demand functions of the plant as much as on the amount of water and solute available in the soil. It must be recognized that the soil and plant system is dynamic. The rate of uptake of nutrients is the result of a dynamic interaction between plant and soil and either can be the limiting factor.

**Water Uptake by the Roots**

Nearly all the water entering land plants, and most aquatic plants as well, comes from the soil via the roots. Water flows from the bulk soil to the root surfaces and enters the roots, passing through epidermis, cortex, and endodermis. The water then enters the xylem system and is conducted to other parts of the plant. Most of the water reaches the leaves and evaporates. The flow of water in this soil-plant-atmosphere continuum is initiated and maintained by differences in water potential between the water in the leaves and the water in the soil. The rate of the process is controlled by the evaporative demand at the leaf surface and the ability of the soil to satisfy the demand. This control is exercised by plant factors such as stomatal regulation, hydrodynamic resistance in the xylem vessel, hydraulic conductivity of the soil, and specific water capacity of the soil.

The rate at which water can be absorbed by the roots in response to the evaporative demand depends on the extent of the root system and the rate of uptake by each individual root segment.
The distribution of roots in the soil depends on plant species and varies widely. This distribution is controlled by soil type, amount of water in the soil, nutrient availability, soil temperature, and competition with roots from other plants. The distribution of the roots, even in mature plants, is not fixed. Roots grow in different directions at varying spacings, and at rates which depend on several environmental conditions.

Mathematical formulations of the spatial distribution of roots have been attempted (Slack, 1975). These also must account for differences in the ability to absorb water. The zone with the highest rate of water uptake is immediately behind the root tip. Such zones range from about 1 cm for slow-growing roots to more than 20 cm for rapidly growing roots.

In addition to the work of Slack (1975), other geometric approaches to the modeling of the temporal and spatial organization of root systems have been attempted by Hackett and Rose (1972), Lungley (1973), and Busscher (1976). For the most part, however, such extensive geometric models are not needed for the study of nutrient and water uptake. The natural variability in soil-root properties makes it impractical to try to develop precise models.

The problems posed by the complexity of the root distribution can be overcome by using a macroscopic rather than a microscopic approach. The microscopic model tries to account for each detail along the flow path, including, for example, movement from cell to cell when crossing from the root surface to the xylem. The macroscopic model summarizes precise mechanisms by making simplifying assumptions. The macroscopic approach has been used with good success to describe the flow of water through the soil-plant-atmosphere continuum.

An important part of this approach is to describe the root sink term, $A$, in equation 7. This can be done in several ways. One is to use a static formulation where $A$ is a specified rate which remains constant for each point in the soil. The second approach is to use a forced, dynamic model, where $A$ is defined by empirical functions which give its spatial and temporal variation:

$$ A = F(z,t) \quad [L^m/L^3/t] \quad (11) $$

A third approach is to use a dynamic, autonomous model. According to this approach, the flow of water to the root surface is controlled by gradients in the water potential. The root sink term $A$ is the water absorbed per unit volume of soil per unit time. Table 4 summarizes several mathematical representations of the root sink term which have been used recently. All these define $A$ as being proportional to the potential difference between the soil at depth $z$ and the root surface at the same depth and inversely proportional to a soil impedance or, conversely, proportional to the hydraulic conductivity. Upon inspection, these models will be found to be similar. Specifically, the models of Gardner (1964), Ungs et al. (1977), and Farnum (1977) are analogous in that all three identify the impedance of the soil and plant separately. Additional models of water uptake by roots were described by Newman (1963), Klute and Peters (1968), Feddes and Rijtema (1972), Hillel (1975a), Feddes et al. (1976a). Some of the models were evaluated by van Bavel et al. (1968), Feddes and Zaradny (1976), and Feddes et al. (1976b).
Table 4. Macroscopic models of root uptake of water

<table>
<thead>
<tr>
<th>Author</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gardner (1964)</td>
<td>$A = \frac{[\psi_x - \psi]}{I_p + I_s}$</td>
</tr>
<tr>
<td>Whisler et al. (1968)</td>
<td>$A = K(\psi)[\psi_x - \psi] \cdot CNVRSN \cdot F_1$</td>
</tr>
<tr>
<td>Molz and Remson (1971)</td>
<td>$A = D(\theta) \cdot F_2$</td>
</tr>
<tr>
<td>Nimah and Hanks (1973)</td>
<td>$A = \frac{\left{[\psi_{rc} - \psi - \psi_x] \cdot CNVRSN + RRES \cdot z\right}}{\Delta x \cdot \Delta z} \cdot K(\psi) \cdot F_3$</td>
</tr>
<tr>
<td>Neuman et al. (1975)</td>
<td>$A = K(\psi)[\psi_x - \psi] \cdot CNVRSN \cdot F_4$</td>
</tr>
<tr>
<td>Ungs et al. (1977)</td>
<td>$A = \frac{\left{(\psi_{rc} - \psi) \cdot CNVRSN + z + RPF\right}}{\left[\frac{1}{K(\psi)} + \frac{1}{K_r}\right]} \cdot F_5$</td>
</tr>
<tr>
<td>Farnum (1977)</td>
<td>$A = \frac{[\psi_{rc} - \psi - \psi_x + \rho g z]}{[\frac{Gr}{K(\psi)} + RR \cdot CNVRSN]} \cdot CNVRSN \cdot F_6$</td>
</tr>
</tbody>
</table>

Most authors specify the potential difference to be that between the soil $\psi$ and the root xylem $\psi_x$ at depth $z$. If the potential in the root at depth $z$ is extended to the potential in the xylem at the root collar $\psi_{rc}$ (root at soil surface), then corrections must be made for the potential drop caused by flow resistance in the root xylem. Under certain conditions, the osmotic potential of the soil $\psi_x$ may become important, but usually it is considered negligible. The most difficult part in using root uptake models (Table 4) is in defining the spatial distribution of the roots and the part of the roots that is actually active in water uptake. The term $F_i$, $i = 1, 2, 3 \ldots$ in Table 4 represents the root distribution-activity and is usually expressed in units of root length per unit volume of soil. The authors listed in Table 4 give more detailed expressions for $F_i$.

Solute Uptake by Roots

Depending on the nature of the ions and their relative concentrations, they can come in contact with the root surface by three separate mechanisms (Barber and Olson, 1968), namely, mass flow of the soil solution, diffusion through the soil solutions, and the extension of roots to previously unexplored regions of the soil profile. Table 5 lists several ions and the most effective means by which the root can come in contact with them. The mobility of these ions also is strongly influenced by the type of the soil.

A general statement of the preference in ion uptake of one element over another is very difficult. Interactions of ions in the uptake process can be inhibitory, stimulatory, or neutral, depending on ion concentrations and the time
The rate of nutrient uptake is mathematically expressed by the G term in equation 9. The task is to write an expression for G which relates it to the mechanisms involved in the uptake. The transport of solute from the soil to the xylem involves (Lauchli, 1976; Pitman, 1977) the uptake of ions at the root surface and the transport of the ions across the root in the apoplast or symplast. The uptake mechanisms are modified by interactions with the flow of water across the root, the age and development of the root cells, the rate of metabolism of the plant as a whole and the root in particular, and finally the temperature of the soil-plant-atmosphere continuum.

The number of papers devoted to the mathematical description of uptake of solute by roots is small in contrast to the number of papers devoted to the uptake of water by roots. Most models deal with a specific part of the pathway, usually at the cellular level of membrane transport, and do not offer a basis for analysis of the effects of environmental conditions on the process. Thus, available models are incomplete at the microscopic level. Needed are dynamic, autonomous models at the macroscopic level. This paucity of attempts to describe nutrient assimilation in mathematical terms is not from a lack of interest. It reflects the difficulty involved in constructing functional models that adequately represent the behavior of the plant. The large number of mechanisms and processes involved in the transport process seems to leave the development of a macroscopic model as the only alternative. The most direct approach is to obtain empirical expressions for G. The linear model and the Michaelis-Menten model shown in Table 6 were derived in this manner.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Amount needed for 8,000 kg/ha</th>
<th>Approximate amount supplied by</th>
<th>kg/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Root interception</td>
<td>Mass flow</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>190</td>
<td>2.2</td>
<td>188.2</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>39</td>
<td>1.1</td>
<td>2.2</td>
</tr>
<tr>
<td>Potassium</td>
<td>196</td>
<td>4.5</td>
<td>39.2</td>
</tr>
<tr>
<td>Calcium</td>
<td>39</td>
<td>67.2</td>
<td>168.0</td>
</tr>
<tr>
<td>Magnesium</td>
<td>45</td>
<td>16.8</td>
<td>112.0</td>
</tr>
<tr>
<td>Sulfur</td>
<td>22</td>
<td>1.1</td>
<td>21.3</td>
</tr>
<tr>
<td>Copper</td>
<td>0.11</td>
<td>0.01</td>
<td>0.45</td>
</tr>
<tr>
<td>Zinc</td>
<td>0.34</td>
<td>0.1</td>
<td>0.11</td>
</tr>
<tr>
<td>Boron</td>
<td>0.22</td>
<td>0.02</td>
<td>0.78</td>
</tr>
<tr>
<td>Iron</td>
<td>2.13</td>
<td>0.22</td>
<td>1.12</td>
</tr>
<tr>
<td>Manganese</td>
<td>0.34</td>
<td>0.11</td>
<td>0.45</td>
</tr>
<tr>
<td>Molybdenum</td>
<td>0.01</td>
<td>0.001</td>
<td>0.02</td>
</tr>
</tbody>
</table>

† These are average values for a silt loam soil (after Barber and Olson, 1968).
Table 6.  Macroscopic models of solute uptake by roots

Linear model. Nye (1968) and Tinker (1968)
\[ G = - C \cdot K_1 \cdot F \]

Michaelis-Menten model. Nye and Marriott (1969), Baldwin et al. (1972)
\[ G = \frac{- C \cdot K_1 \cdot F}{1 + K_2 C} \]

Two-compartment model

\[ A = - J_\ell \cdot F \]  \hspace{1cm} \text{water uptake}  \\
\[ G = - J_s \cdot F \]  \hspace{1cm} \text{solute uptake}  \\

where

i)  \[ J_s = J'_s + \omega K_3 (C - C_i) + (1 - \sigma) J_v (\alpha C + \beta C_s) \]
\[ K_3 = \frac{nRT}{M_w} \theta_r \cdot R_a \]
\[ \alpha = \beta = 1/2 \]  \hspace{1cm} \text{Fiscus (1975)}  \\
\[ \alpha = 1, \beta = 0 \]  \hspace{1cm} \text{Dalton et al. (1975)}  \\

ii)  \[ C_x = J_s/J_v \]

iii)  \[ J_v = - P(\psi_x - \psi - \sigma K_3 [C - C_i]) \]

Three-compartment model. (symplasmic theory) Ginsberg (1971)

\[ A = - J_\ell \cdot F \]  \hspace{1cm} \text{water uptake}  \\
\[ G = - J_s \cdot F \]  \hspace{1cm} \text{solute uptake}  \\

i)  \[ J_s = J'_s + \omega K_3 (C_m - C_x) + (1 - \sigma) J_v (\alpha C_m + \beta C_s) \]
\[ K_3 = \frac{nRT}{M_w} \theta_r \cdot R_a \]

ii)  \[ C_x = J_s/J_v \]

iii)  \[ J_v = \frac{-PP_0}{(P + P_0)} \psi_x - \psi + (\sigma_0 - \sigma) K_3 C_m - K_3 (C_{x0} - C_x) \]

where one would set \( \alpha = \beta = 1/2 \) for an average concentration.
The concept of a membrane model can be introduced into a macroscopic model for solute uptake by analogy with the model for water uptake as follows:

Water uptake

\[ A = -J_v \cdot F \quad [L_w/L^3/t] \]  
Solute uptake

\[ G = -J_s \cdot F \quad [M/L^3/t] \]  

(12)

where \( J_v \) is the flux of water per unit length of root \([L_w/L_r/t]\) and \( J_s \) is the flux of solute per unit length of root \([M/L_r/t]\). \( F \ [L_r/L^3] \) is a function which describes the length of active roots per unit volume of soil. The pathway includes all membranes to be passed. The flux terms, therefore, are functions of membrane permeability, soil water content, solute concentration, and temperature. The evaporative demand at the leaf surface and the demand for nutrients by the growing plant influence \( J_v \) and \( J_s \) in a manner which provides feedback controls. An example of feedback control occurs when the evaporative demand exceeds the ability of the soil to satisfy the demand. The response to this condition includes closure of the stomates and loss of turgor pressure. Both conditions reduce growth. Stomatal closure restricts entry of \( CO_2 \) and loss of turgor pressure limits leaf elongation. The result of decreased growth is decreased demand for nutrients. Another example of feedback control occurs when low air temperatures restrict translocation in the above-ground parts of the plant.

The fluxes \( J_v \) and \( J_s \) may be induced by several separate mechanisms which operate simultaneously (Slatyer, 1967). These fluxes, therefore, can be expressed as the sum of separate fluxes as follows:

\[ J_v \approx \left[ \text{matric potential gradient} \right] + \left[ \text{electromechanical gradient} \right] \quad [L_w/L_r/t] \]  

(13)

\[ J_s \approx \left[ \text{active uptake} \right] + \left[ \text{electrochemical gradient} \right] + \left[ \text{mass flow} \right] \quad [M/L_r/t] \]

This representation suggests that \( J_s \) may have a positive value, indicating that in the absence of active processes, passive drag may occur along concentration gradients of water and/or solute.

The schematic conceptualization of the solute uptake according to equation 13 leads to the so-called two-compartment and three-compartment models (Fig. 3). In Table 7, a Michaelis-Menten model of active solute uptake is given. The active uptake term is assumed to be a strong function of temperature. Many literature reports deal with the mechanism of active solute uptake, including the surveys by Leggett (1968), Laties (1969), and Baumeister and Burghardt (1969).

Tables 4, 6, and 7 provide several models to define the \( A \) and \( G \) terms. These can be used to evaluate equations 7 and 9. The resulting equations, 7 and 9, are nonlinear. Such equations can be solved and have been solved extensively by employing the finite difference or finite element techniques (von Rosenberg, 1969). The soil profile is divided mathematically into small layers, \( \Delta z_i \), and the energy and mass balance equations are solved for each layer by linear approximations for the nonlinear terms. The values for \( A_i \) and \( G_i \) terms are evaluated for each layer, \( i = 1, \ldots, N \). The summation of water uptake, \( \Sigma A_i \Delta z_i \), for all layers must equal the
Figure 3. Schematic diagrams of the two- and three-compartment models for the uptake of solute by roots.

rate of transpiration, assuming that the amount used for metabolic processes is negligible with respect to transpiration. Water that is taken up is lost to the atmosphere via transpiration. The atmosphere is the ultimate sink for water. Similarly, the summation of the nutrient uptake, $\sum G_i \Delta z_i$, must equal the increase
in the amount of that nutrient in the plant plus the amount lost from the plant by excretions. The growth of the plant, the process by which nutrients are incorporated into the structure and storage parts, determines the sink strength for nutrient uptake. At this point, the mass balances for water and solute are complete since both the source and the sink components are accounted for.

The temperature balance is not so obvious because there is no explicit demand for heat by the plant. For the temperature equation 1 to be comparable to water and solute equations 7 and 9, an additional function to account for the response of the plant to heat transfer would be expected. This function should be analogous to the $A$ and $G$ terms. This function must include the conduction of heat from the soil through plant structures. Most of the heat energy transferred to the plant from the soil is incorporated in the energy of water and solute that the plant takes up. Because of the high specific heat of water, a large quantity of heat can be transferred with little change in temperature. Heat energy that plants receive from the soil and at a greater extent from solar radiation is dissipated from the plant. The atmosphere becomes the ultimate sink for heat. Energy transfer through plant structures may be negligible, but plant temperature can have a profound effect on plant metabolic activity. The temperature change might be little as cells are immersed in solution, but the effect becomes critical when the functions and reactions of organelles are sensitive to temperature change. An important example is the denaturation of enzymes. The deformation of enzymes and organelles leads to disturbances in the uptake and utilization of solute and water. The interactions between heat, water, and nutrient movements in plants are more complicated than in the soil because the transport processes not only are affected by the gradients of temperature, water content, and concentrations but also by the biochemical processes.

**Effect of Solute Concentration on Active Uptake**

In many experiments on ion uptake (Hewitt and Smith, 1974), for example with $K^+$ and $Rb^+$, an empirical relationship in the form of a rectangular hyperbola was found between the external concentration and the rate of active solute uptake under isothermal conditions. Various explanations have been proposed to explain this concentration-dependent behavior of active transport. These include the dual model, the cooperative model, and the multiphase model. These models have recently been reviewed by Nissen (1977) and Bowen and Nissen (1977). All of them
are based on the Michaelis-Menten formulation given in Table 7. They differ in the number of Michaelis-Menten terms and the value of the coefficients.

The Michaelis-Menten constant $K_m$ and maximum active solute flux $J_{s,max}$ are determined from either a Lineweaver-Burk double reciprocal plot of $1/J_s$ versus $1/[s]$ or a Hofstier plot of $J_s$ versus $J_{s,max}/[s]$. Several examples of $K_m$ values for various tissues and ions can be found in Clarkson (1974).

**Temperature Effects**

Temperature affects the uptake of water and nutrients in many ways (Sutton, 1969; Precht et al., 1973; Nielsen, 1974; Kozlowski, 1976). Low temperature corresponds to decreased conductivity of the soil and plant tissue because of increased viscosity of water and increased activation energy for crossing membranes. The permeability of the root cells also is decreased. Kuiper (1964) showed two components of the temperature effect on water uptake: one with a $Q_{10} = 4.0$ at low temperature and one with a $Q_{10} = 1.2$ above certain critical temperatures. He suggested that at low temperatures probably only transient pore development occurs. Above the critical temperature, the activation energy would be such that water-filled pores are maintained. At these temperatures, conductivity is proportional to viscosity of water.

Temperature not only has an effect on rate of root growth but also affects structural configuration of the root. Kuiper (1964) showed that roots of plants grown at low temperature absorbed more water per unit potential gradient than similar plants grown at higher temperatures. This difference occurred at low temperature but not at high temperature where rate of uptake was controlled by viscosity. It was noted that the slopes of the temperature response curves were similar. This was interpreted to mean that a similar metabolic control over the transport process was exercised despite different growth conditions.

The effect of temperature on rate of root growth has already been mentioned. Under increasing temperature conditions there is increased mobility of soluble nutrients in the soil such as with phosphorus, increased permeability of cell membranes to water and solute, increased rate of root growth corresponding to more surface area available for absorption, and acceleration of the rate of chemical reactions, and, finally at high temperatures, inactivation of enzymes occurs.

Temperature has a long-term effect on the morphology and distribution of roots from a combination of the effects summarized above (Nielsen, 1974). At low temperatures, roots usually are whiter and have a larger diameter, the root system is less branched, maturation is delayed, and cell elongation is favored. At high temperatures, roots usually are more filamentous and rapid cell division occurs. The effect of root temperature is also influenced by the temperature of the above-ground plant parts (Sutton, 1969).

The temperature response of water uptake and solute uptake is conceptualized in Figure 4. Two distinct temperature responses are recognized with respect to both processes, namely a low temperature response for region A-B and a high temperature response for region B-C (Pisek et al., 1973).

The mathematical formulations presented earlier can be used to identify the mechanisms which are significantly influenced by temperature.
Flow of water

\[ \frac{\partial \theta}{\partial t} = - \frac{\partial q_w}{\partial z} + A \quad [L_w^3/L_3^3/t] \quad (14) \]

where \( A \), the uptake of water by the roots, is described by

\[ A = -F \cdot I_v \quad [L_3^3/L_3^3/t] \quad (15) \]

so that the temperature effect is

\[ \frac{\partial \theta}{\partial t} \approx \begin{bmatrix} \text{viscosity effect} \\ \text{growth effects} \end{bmatrix} - \begin{bmatrix} \text{transpiration and permeability effects} \end{bmatrix}. \quad (16) \]
Nutrient uptake

\[
\frac{\partial (\theta C)}{\partial t} = \frac{\partial}{\partial z} \left( \frac{\partial C}{\partial z} - q_w C \right) - \frac{\partial S}{\partial t} + G \quad [M/L^3/t] \quad (17)
\]

\[
\frac{\partial (\theta C)}{\partial t} = \text{[viscosity]} - \left[ \text{sorption rates} \right] + \left[ \text{growth, permeability and active transport} \right] \quad (18)
\]

where \( G \), the function for solute uptake by the roots, is further described by

\[
G = -F \cdot [J^* + J_{\nu} (\Delta \psi, \Delta \psi, \omega, \sigma)] \quad [M/L^3/t] \quad (19)
\]

so that

\[
G \approx - \text{[growth]} \cdot \text{[active transport + permeability]}. \quad (20)
\]

We have noted the effect of temperature on the uptake of nutrients (Fig. 4). The shape of this curve is the combined effect of two processes, namely the increase in the reaction rate of chemical processes with temperature and the denaturation of proteins involved in active transport. A model to describe the process, consistent with experimental results, can be constructed, but the actual mechanisms have not been experimentally verified.

Active transport has been defined by several authors. A definition presented by Thornley (1976), stating that active transport is a process which sustains the flow of nutrients against an electrochemical potential gradient while requiring the expenditure of metabolic energy, will be used. Mechanisms involved in the active transport of nutrients across plant membranes were reviewed by Epstein (1972a), Anderson (1973), and Nissen (1974). Thornley proposed two general types of carrier-mediated transport. These are (1) a single mechanism consisting of an ATP-driven transport with either a slow or a fast diffusing carrier and (2) a dual mechanism consisting of two transport processes that can be described by a Michaelis-Menten type equation working either in parallel or in series. The hypothesis of a single mechanism does not exclude multiphase processes. Several processes involving ATP-driven transport may act in series with abrupt transitions from one mode of operation to another.

The effect of temperature on the reaction rate of chemical processes has been found empirically to vary inversely with the absolute temperature (Roberts, 1977).

\[
\ln K_a = \frac{1}{T}, \quad (21)
\]

where \( K_a \) is the rate constant for a given reaction and \( T \) is the absolute temperature. On the basis of classical thermodynamics, Arrhenius modified the van't Hoff equation to describe effects of temperature on the rate constant as

\[
\frac{d(\ln K_a)}{dT} = \frac{E_a}{RT^2}, \quad [1/T] \quad (22)
\]

where \( E_a \) is the activation energy of a reaction. Upon integration, the rate constant at temperature \( T \) can be expressed in terms of the rate constant at a reference temperature \( T_0 \) as:
the behavior in the high temperature region. At high temperatures, additional mechanisms are involved which reduce the efficiency of the uptake processes. These mechanisms most likely involve the denaturation of proteins above critical temperatures. The exact manner in which high temperature affects solute uptake, and in particular active transport, is not fully understood. It must involve loss of membrane integrity, disruption of electron-transport processes, and denaturation and conformation changes of enzyme complexes and other protein molecules.

Enzyme denaturation may be described mathematically by using a Michaelis-Menten formulation:

\[
\frac{[E_d]}{[E_n]} = e^{-\Delta G/RT} \tag{1} \label{eq:26}
\]

This formulation, where \([E_d]\) and \([E_n]\) are the concentrations of enzymes in the denatured and native forms, assumes that the enzyme is either in its native or in its denatured form and only the native form is active. All rates of reaction are temperature-dependent, but only the enzyme is denatured at high temperatures. The ratio of denatured to native enzymes on the membrane is, in analogy to the thermodynamics of proteins in solution (Roberts, 1977),

\[
\frac{[E_d]}{[E_n]} = e^{-\Delta G/RT} \tag{1} \label{eq:26}
\]

where \(\Delta H\) is the enthalpy, \(\Delta S\) is the entropy of the reaction, and \(\Delta G\) is the Gibbs free energy of the reaction. A typical response of \(\Delta G\) to temperature is shown in Figure 5.

For steady-state conditions, we can define the inverse equilibrium constant, \(K_s\), for the first step of equation 25, when enzyme combines with substrate to form \([E_n]\) complex as

\[
K_s(T) = \frac{E_a(T - T_0)}{RT_0} \tag{23} \label{eq:23}
\]

which is approximated by the van’t Hoff-Arrhenius equation as

\[
K_s(T) = A_a \exp \left\{ -\frac{E_a}{RT} \right\} \tag{24} \label{eq:24}
\]

where \(A_a\) is the frequency factor. Arrhenius defined the activation energy \(E_a\) as the minimum energy that must be acquired by the reactant molecules before a reaction can occur (Roberts, 1977).

The formulation expressed by equation 23 explains conceptually temperature effects in the low temperature region. The equation may be considered to apply to all processes involved in nutrient uptake.

The van’t Hoff formulation of chemical reaction, however, does not explain the behavior in the high temperature region. At high temperatures, additional mechanisms are involved which reduce the efficiency of the uptake processes. These mechanisms most likely involve the denaturation of proteins above critical temperatures. The exact manner in which high temperature affects solute uptake, and in particular active transport, is not fully understood. It must involve loss of membrane integrity, disruption of electron-transport processes, and denaturation and conformation changes of enzyme complexes and other protein molecules.
Figure 5. Schematic diagram of the change in Gibbs free energy as a function of temperature.

\[ K_s = \frac{k_1}{k_1} = \frac{[E_n][s]}{[E_n][s]} \quad [M/L^3] \quad (28) \]

and the conservation of enzyme species is

\[ [E_0] = [E_n] + [E_d] + [E_n][s] \quad [M/L^3] \quad (29) \]

where \([E_0]\) is the total number of sites whether free, bound with substrate, or in the denatured form. Upon substitution, the concentration of the enzyme complex becomes:

\[ [E_n][s] = \frac{[E_0][s]}{[K_s] \left[ 1 + e^{-\Delta G/RT} \right] + [s]} \quad [M/L^3] \quad (30) \]

For the second step shown in equation 25, where the enzyme complex releases the product and the native enzyme, the rate of reaction \(v\) is:

\[ v = k_2[E_n][s] \quad [M/L/t] \quad (31) \]

Substituting for \([E_n][s]\) from equation 30,

\[ v = \frac{k_2E_0[s]}{[K_s] \left[ 1 + e^{-\Delta G/RT} \right] + [s]} \quad [M/L/t] \quad (32) \]
When all of the enzyme is in the native form and is bound with substrate, there is maximum enzyme activity when \([E_0] = [E_nS]_{\text{max}}\). Then \(v_{\text{max}} = k_2[E_nS]_{\text{max}} = k_2[E_0]\).

If \(v\) and \(v_{\text{max}}\) are redefined as:

\[
v = J_s^* \quad [M/L_t/t] \quad (33)
\]

and

\[
v_{\text{max}} = J_{s,\text{max}}^* \quad [M/L_t/t] \quad (34)
\]

the rate of reaction (equation 32) can be rewritten analogous to the expression for active uptake in Table 7 as:

\[
J_s^* = \frac{J_{s,\text{max}}^*[s]}{K_m + [s]} \quad [M/L_t/t] \quad (35)
\]

where \(K_m\) is known as the Michaelis constant.

By analogy, we may consider the active uptake rate to proceed similarly to the enzyme reaction rate and the concentration of substrate \([s]\) to equal the solute concentration, i.e.,

\[
[s] = \alpha C + \beta C_x \quad [M/L_3^3] \quad (36)
\]

This seems to be acceptable if we describe the active uptake mechanism to be an ATP-driven transport with a diffusing carrier. The carrier is assumed to function in the same way an enzyme does. Furthermore, by comparing active uptake to that of an enzyme system it could be proposed that temperature affected the \(J_{s,\text{max}}^*\) and \(K_m\) terms in the active uptake process in the same manner as the denaturation of enzyme systems. Should this be the case, the effect of temperature on the rate of uptake is obvious. Not only is the Gibbs free energy, \(\Delta G\), of the transport process a function of temperature, but recall that the reaction rate constants \(k_1, k_{-1}\), and \(k_2\) are also Arrhenius temperature-dependent functions. Therefore, the maximum uptake rate \(J_{s,\text{max}}^*\) is temperature-dependent mediated via the rate of constant \((k_2)\). \(J_{s,\text{max}}^*\) will increase monotonically with temperature. As temperature increases further, the change in \(\Delta G\) becomes more rapid. This causes \(K_m\) to increase at a faster rate than \(J_{s,\text{max}}^*\). The general outcome would be that as temperature elevates initially, \(J_s^*\) increases as \(J_{s,\text{max}}^*\) increases up to a peak when \(K_m\) starts to increase causing a reduction in \(J_s^*\). At even higher temperatures, \(K_m\) dominates the reaction rate which, as a result, decreases the active uptake flux \(J_s^*\) because most of the carriers and associated enzymes will have undergone conformational changes that reduce their activities.

The explanations offered here for observed effects of temperature on active transport are based on principles of thermodynamics and enzyme kinetics. Christophersen (1973) used a similar approach to explain the influence of temperature on the growth of microorganisms. Roberts (1977) used an analogous approach to explain the effect of pH on the rate of reactions controlled by enzymes.

The concept of an enzyme-substrate reaction is instructive for the understanding of the effect of temperature on active transport. However, the actual
mechanism of active transport in solute uptake does not have to be restricted to enzyme systems.

The water and solute distribution in the soil as a function of time can be determined using the procedures outlined here. With this information, the rate of nutrient uptake can be obtained. First, the distribution of water in the soil is obtained with equation 9. The two equations must be solved by numerical integration (van Rosenberg, 1969). Solute adsorption models are in Tables 2 and 3 and root uptake models are in Tables 4, 6, and 7. The user must decide which models are most appropriate for a particular application. When there are substantial spatial or temporal variations in the temperature, the soil temperature also must be obtained and appropriate temperature corrections must be made in the coefficients in the adsorption and root uptake models.

Knowledge of the precise functions of the root remain uncertain. The concerns about lack of knowledge cited in the introduction to this bulletin are valid. We do submit, however, that a careful analysis of the processes involved in nutrient uptake by plants may guide our choices in experimentation so we can make progress in resolving some of these uncertainties.

References


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