Modelling potassium uptake by wheat


*Department of Soil and Water, Golestan Agricultural Research Center, Gorgan, Iran.
Division of Soil Science and Agricultural Chemistry, IARI, New Delhi-110 012, India.
* Corresponding author; Email: gh_roshani@yahoo.com

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Abstract

A model has been used to simulate potassium (K) uptake by wheat in a pot culture experiment. Three soils from India, namely Alfisol, Inceptisol and Vertisol, were differentially K exhausted by Sudan grass (Sorghum vulgare var. Sudanensis) for a period of 280 days and were used to simulate potassium uptake by wheat (Triticum aestivum) and also to predict the amounts of K released or fixed during cropping. Except in Alfisol all the predicted values of K uptake closely agreed with that of measured values. When predicted K uptake values were plotted against the observed values, \( r^2 \) values were found to be 0.927, 0.828 and 0.721 in Inceptisol, Alfisol, and Vertisol, respectively. There is a close relationship between observed and predicted values of K uptake as evident from the high \( r^2 \) values, but in case of Alfisol and Vertisol the model has over-predicted K uptake, which perhaps was due to over prediction of K release from non-exchangeable form. The model has been validated and has been applied to simulate response towards fertilizer application at different available K. It was showing that maximum response occurs at a particular value of available K, which shifts towards higher value as release threshold level (RTL) increases. Predicted K uptake was most sensitive to changes in root parameters such as root length density (RLD) and maximum influx rate (V\(_{\text{max}}\)), since changes in the time at which maximum root length density was attained (RLD-B) and the decay constant of V\(_{\text{max}}\) (V\(_{\text{max}}\)-B) gave the greatest changes in K uptake in almost all the soils except highly exhausted Alfisol in which predicted potassium uptake was more sensitive to changes in RLD-B and intercept (c) than to root uptake kinetics, as described by Michaelis-Menten constant (K\(_{\text{m}}\)) and V\(_{\text{max}}\). The predicted potassium uptake was least sensitive to changes in rate constants of release and fixation and fixation threshold level in Inceptisol and Vertisol, but was sensitive to release threshold level and rate constant of release in Alfisol.

Keywords: Potassium uptake; Simulation model; Potassium release and fixation.

Introduction

Early modeling of nutrient flux around the root was done by Bouldin (1961), Passioura (1963), Nye (1966), Olsen and Kemper (1968) and Nye and Marriot (1969). These models using varied assumptions provided a theoretical description of the nutrient concentration gradient perpendicular to root. Direct analytical measurement were attempted by Farr et al.
(1969) and Bagshaw et al., (1972), where a plane of roots was grown across a block of soil. These experiments indicated a gradient that was consistent with the size of the \( D_e \) (effective diffusion coefficient) value for the nutrient-soil combination. With development of the model to predict nutrient uptake, verification can be accomplished by comparing observed uptake and predicted uptake.

Brewster et al., (1976) and Claassen and Barber (1976) combined the theoretical model for the single root with an expression for the rate of root growth and predicted nutrient uptake over a period of growth. The Claassen-Barber and Cushman (Barber and Cushman, 1981) models have been validated with the series of pot experiments using a range of plant species and soils. Potassium uptake measured from plant analysis was compared with potassium uptake predicted from the model. They got a correlation of \( r^2 = 0.87 \), though predicted uptake was greater than the observed values. This may have been because of the assumption of no competition between roots and the same uptake rate for both day and night. The Claassen-Barber model does not account for root competition; the Cushman model accounts for root competition and a model developed by Itoh and Barber (1983) accounts for uptake by root hairs in addition to uptake by competing roots.

Claassen et al., (1986) developed a mathematical model to simulate nutrient uptake of plants from soil based on ion transport from the soil to the roots by mass flow and diffusion, on Michaelis-Menten kinetics of nutrient depends on soil solution concentration for by the choice of the boundary conditions.

Silberbush and Barber (1983) tested the Barber-Cushman model for prediction of K and P uptake by soybean grown in field on two soils with high and low level of P. The model accurately predicted K uptake in both soils and P uptake in soil with high P (52 µM in soil solution). In the soil with low P (7.8 µM in the soil solution) the predicted P uptake accounted for only 30 to 35% of measured uptake, even when the predicted uptake included the contribution of uptake by root hairs. The authors suggested that the poor prediction of P uptake in the low P soil was due to factors not included in the simulation model, such as VA mycorrhizae or the acidification of rhizosphere soil by root exudates.

Since the nutrient uptake predicted by the model may vary with nutrient, plant species, soil type and environmental condition, various validation experiments were conducted using a wide range of condition. Silva et al., (1991) used the Cushman-Barber simulation model to simulate potassium uptake by sweetcorn using a dark red Latosol alone or in a 1:1 Latosol: sand mixture. The following model parameters were determined: effective soil K diffusion coefficient; soil K buffering capacity; initial soil solution K; rate of root's water uptake; mean distance between root axes; mean root radius \( r_0 \); initial root length/pot; root growth rate \( k \); maximum root K uptake rate \( I_{max} \); Km (soil solution K concentration at which root K uptake rate was half that of maximum K uptake rate); and minimum soil solution K concentration \( C_{min} \). Sensitivity analysis indicated that K uptake increased rapidly with increasing \( r_0 \), \( k \) and \( I_{max} \) suggesting the importance of root surface area. K uptake was least affected by \( C_{min} \). Predicted K uptake values were greater than observed uptake on the Latosol but less than observed values on the Latosol/sand mixture.

Uptake of K was measured using a single onion root technique with four soil cylinder diameters, and measuring changes in exchangeable K in the soil. Bouldin’s model fitted the measured uptake when only exchangeable K was taken up, but that of Mitsios and Rowell (1987) allowed predictions of uptake of both exchangeable and non-exchangeable K \( (K_{free}) \)
after fitting the necessary parameters. Release of $K_{\text{net}}$ occurred in both 3 mm and 6 mm cells (root densities of 14 cm cm$^{-3}$) in 10 days. Predictions were made for longer times and differing soil water contents. After four weeks at a water content midway between field capacity and wilting point, the contribution of $K_{\text{net}}$ to total uptake was significant (up to 60%) for plants with high root densities.

Difficulties in modeling K uptake by plants are caused by the measurement of soil buffering capacity and measurements and prediction of root growth and morphology. A simplified diffusion model for determining K concentration in the soil solution for high crop yields was applied to wheat (*Triticum aestivum*) with an active rooting density of 3 cm cm$^{-3}$. The required K concentration ranged from 50-200 µM K (Barraclough, 1990).

**Materials and Methods**

A series of greenhouse and laboratory experiments were carried out with wheat (var. HD 2285) and Sudan grass (*Surghum vulgare* var. Sudanensis) in the greenhouse and laboratory of the Division of Soil Science and Agricultural Chemistry, Indian Agricultural Research Institute, New Delhi. Wheat crop (for root length density measurement) was grown in winter season of 2001-2002, and simultaneously sand culture experiment was also conducted with wheat to determine the kinetic parameters of potassium uptake. In first year, Sudan grass (*Surghum vulgare* var. Sudanensis) crop was grown in properly sealed 8-kg capacity clay pots containing 5 kg of three types of soils, namely Alfisol, Vertisol, and Inceptisol from India and placed randomly in greenhouse and seven cuttings of biomass were harvested periodically. Three bulk soil samples (about 500 kg each) with different properties belonging to Typic Haplustept (28º 04´ N and 77º 12´ E, Mehrauli series, plate 1a, IARI farm, New Delhi), Typic Haplustert (23º 20´ N and 77º 20´ E, Nabibagh-4 series, plot number 73 / 74, Indian Institute of Soil Science farm, village Nabibagh, Bhopal), and Typic Kandiustalf (13º 5´ 45” N and 77º 36´ 15” E, plot number 69 of Central Institute of Medicinal and Aromatic Plants farm, Allalasandra, Bangalore) were collected. These soils had wide variations in properties and used in all the experiments.

Measured quantity of deionized water was applied to the pots depending on the amount of evapo-transpiration, which was calculated by daily weighing method. A potted plant experiment on wheat was carried out during winter crop season. For this experiment, those soils that were subjected to exhaustive cropping with seven cuttings of Sudan grass for a period of 280 days were utilized. Soils were analyzed for various properties and the results are given in Table 1. Based on the assumption that nutrient flux from soil to root proceeds by mass flow and diffusion and influx into roots follows Michaelis-Menten kinetics, Nye and Marriot (1969) developed a mechanistic model for the transfer of nutrients from soil into plants. This model is based on conservation of solute and water in a series of small hollow cylindrical soil elements around the root. The flux into and out of such an element has to be equal to the change in concentration in it. This model has been modified and used by several authors. Modifications include allowance for root hairs (Itoh and Barber, 1983), inter-root competition (Cushman, 1979), and age-dependent parameters of root (Cushman, 1984).
Table 1. Characteristics of the soils under study.

<table>
<thead>
<tr>
<th>Soil order</th>
<th>pH</th>
<th>EC (dS m⁻¹)</th>
<th>OC (%)</th>
<th>CEC [cmol (p⁺) kg⁻¹]</th>
<th>Avail. P (mg kg⁻¹)</th>
<th>Sand (%)</th>
<th>Silt (%)</th>
<th>Clay (%)</th>
<th>Texture²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inceptisol</td>
<td>7.2</td>
<td>0.16</td>
<td>0.72</td>
<td>11.6</td>
<td>14.3</td>
<td>67.3</td>
<td>17.0</td>
<td>15.7</td>
<td>SL</td>
</tr>
<tr>
<td>Vertisol</td>
<td>7.8</td>
<td>0.30</td>
<td>0.96</td>
<td>34.2</td>
<td>9.4</td>
<td>7.2</td>
<td>37.3</td>
<td>55.5</td>
<td>C</td>
</tr>
<tr>
<td>Alfisol</td>
<td>6.9</td>
<td>0.14</td>
<td>0.61</td>
<td>7.2</td>
<td>6.8</td>
<td>48.5</td>
<td>14.0</td>
<td>37.5</td>
<td>SC</td>
</tr>
</tbody>
</table>

¹ For both pH and EC the soil : water suspension was 1 : 2.5.
² SL, C, and SC stand for Sandy Loam, Clay, and Sandy Clay soil texture.

Measurements on soils

In the present study the same model has been used with the modification that a source and a sink function for labile K have been added to the equation of continuity to account for fixation and release of K in the rhizosphere (Datta, 2001). According to this model the change of concentration of K with time around a root segment is described by the following equation:

\[
\frac{dC_l}{dt} = \frac{1}{r} \frac{d}{dr} \left( r D_e \frac{dC_l}{dr} + \frac{v_o r C_l}{b} \right) + \frac{\rho_b}{b} \left( \frac{dC_r}{dt} - \frac{dC_l}{dt} \right)
\]  

(Eq. 1)

Where, \( C_l \) = concentration of the soil solution (mg L⁻¹ solution), \( r \) = radial distance from the root axis (m), \( r_o \) = root radius (m), \( D_e \) = effective diffusion coefficient (m² s⁻¹) = \( D_l \cdot f \cdot b \theta \), and bulk density, \( \theta \) = volumetric moisture content, \( b \) = buffer power, \( \rho_b \) = bulk density (g m⁻³), \( v_o \) = rate of water uptake (m s⁻¹), \( t \) = time. The rate of K release, \( dC_r / dt \), and the rate of K fixation, \( dC_f / dt \) (µg g⁻¹ s⁻¹) are given as follows:

\[
\frac{dC_r}{dt} = \max \left[ 0, K_r (RTL - C) \right]
\]  

(Eq. 2)

\[
\frac{dC_f}{dt} = \max \left[ 0, K_f (C - FTL) \right]
\]  

(Eq. 3)

where, \( K_r \), \( K_f \), RTL and FTL are release rate constant, fixation rate constant, release threshold level and fixation threshold level, respectively. The “max.” function indicates rate of release is zero when labile K (C) is greater than RTL and rate of fixation is zero when C is less than FTL (Datta and Sastry, 1988; Datta 1996).

Release Threshold Level (desorption study)

To determine Release Threshold Level (RTL), K concentration in soil solution was lowered down to different levels by shaking 2 g soil samples for one hour in 0.01 M CaCl₂ solution containing no K and having different soil: solution ratio, viz. 1:400, 1:200, 1:150, 1:100, 1:50, 1:25, and 1:10. After this the suspensions were kept overnight for equilibration and supernatant solution was separated from solid by siphoning and centrifugation. The amount of K desorbed from solid phase to solution phase (ΔK) was calculated by...
multiplying K concentration of the equilibrated solution with volume of the solution (since initially no K was added) and the amount of K present on exchangeable (NH₄OAc-K) sites after equilibration which was determined by extracting the same sample with 1 N NH₄OAc (pH 7.0).

**Fixation Threshold Level (adsorption study)**

For determination of fixation threshold level, an adsorption equilibration was carried out in duplicate on 3 types of Indian soils used for exhaustive cropping with Sudan grass (Inceptisol, Vertisol, and Alfisol). For this, 2 g soil samples was shaken for one hour and kept undisturbed overnight with 0.01 M CaCl₂ having varying concentrations of K from 5 to 100 mg L⁻¹ in 1: 10 soil: solution ratio. As before, the solution was separated from the solid and the amount of K present on the exchangeable sites (NH₄OAc-K) after equilibration was extracted with 1 N NH₄OAc (pH 7.0) and the amount of K adsorbed from solution phase to solid phase (∆K) was calculated by multiplying decrease in concentration with volume of equilibrating solution.

**Buffer Capacity of Soil**

From the slope at any point of the curve illustrated in Figure 1 the buffer power \(\frac{dC}{dC_1}\), may be derived, where \(C\) is the concentration of labile K in the soil, and \(C_1\) is K concentration in the soil solution. It shows a combined desorption and adsorption curve depicting change in K in the adsorbed phase (∆K) as a function of equilibrium K concentration in solution. It is positive when K is adsorbed from solution and negative when desorbed to solution. It is similar to Q / I curve of Beckett (1964- a and 1964-b). The slope of this curve is assumed to represent the buffering capacity of soil. The buffering capacity determined in this way however can be in error when determined for very low or very high concentrations of K due to release of K from non-labile form or fixation to non-labile form.

![Figure 1. Relation between the equilibrium solution K (ESK) and potassium adsorbed or desorbed from soil (∆K).](image-url)
It also shows net amount of exchangeable K (NH₄OAc-K) or absolute values of K present on the adsorbed phase after desorption or adsorption had taken place as a function of equilibrium K concentration of solution (Figure 2). The slope of NH₄OAc-K curve is almost constant except at lower concentration where it has increased slightly due to increase in specificity for K at the edges of the layers, the ‘edge’ zone, and at partially opened layers, the ‘wedge’ zone. However, that change of slope was much less than that of the ΔK curves at the same concentration of solution. This indicates that some potassium has been released from the non-exchangeable position. Curve of Figure 3 is obtained by subtracting changes in adsorbed K (ΔK) from absolute values of exchangeable K (NH₄OAc-K) after equilibration which is a measure of initial amount of labile K (ILK). Plotting different values of ILK against corresponding values of solution K concentration gives a projection of original labile K when they are subjected to equilibration at different K concentration. A close look of this curve reveals that the ILK increases sharply below a concentration of 2.0 mg L⁻¹, which was termed as Release Threshold Level (RTL). At the other end of the curve, it bent downward beyond a concentration of 18.4 mg L⁻¹, which was termed as Fixation Threshold Level (FTL). Between these two threshold levels, curve remains nearly parallel to X-axis (Figure 3). Buffering capacity was taken as the slope of curve b and was calculated by fitting the data with a straight line equation, \( Y = bX + C \), with an intercept \( C \). This signifies that when concentration approaches infinitely dilute, the exchangeable K approaches a finite value but not zero due to release from non-exchangeable form.

![Figure 2. Calculating of buffer capacity (b) as slope of equilibrated solution K (ESK) versus ammonium acetate K (AAK).](image-url)
Figure 3. Determination of RTL and FTL by plotting equilibrated solution K (ESK) versus A.A.K-∆K.

The model has been simulated under the following initial and boundary conditions:

\[
t = 0, \quad r > r_o, \quad C_i = C_{li}
\]

\[
t > 0, \quad r = r_0, \quad D_v b \frac{dC_i}{dr} + v_o C_i = \frac{V_{\text{max}} (C_i - C_{\text{min}})}{K_m + (C_i - C_{\text{min}})}
\]

\[
t > 0, \quad r = r_i, \quad D_v b \frac{dC_i}{dr} + \frac{r_o}{r_i} v_o C_i = 0
\]

where, \(C_{li}\) = initial concentration of soil solution (mg L\(^{-1}\)), \(C_{\text{min}}\) = minimum concentration (mg L\(^{-1}\)) at which net influx=0, \(K_m\) = Michaelis-Menten constant (mg L\(^{-1}\) solution), \(V_{\text{max}}\) = maximum rate of net influx per unit of root volume (g m\(^{-2}\) s\(^{-1}\)), \(r_i\) = radius of the soil (m) cylinder which encloses 1 m of root along its axis and is given by \(1/\sqrt{(\pi \cdot \text{RLD})}\), where RLD being root length density in m m\(^{-3}\). This allows for inter-root competition between two neighboring roots each of which depletes soil from its own cylinder and can not take nutrient flowing from the adjacent cylinder, i.e., the flux at the boundary of two cylinders is zero.

Measurements on plants

Root influx parameters

In this experiment kinetic parameters of potassium uptake by wheat at different stages were studied and root influx parameters \(V_{\text{max}}\) and \(K_m\) were determined at different stages (CRIS-Crown Root Initiation Stage, MTS-Maximum Tiller Stage, FLS-Flag Leaf Stage and DFS-Dough Formation Stage). Wheat (var. HD-2285) was grown in sand medium with Hoagland nutrient solution (all nutrients except potassium, Table 2). Nutrient solution was drained out every day before fresh addition. Plants were taken out from sand culture at 22, 41, 69, and 87 days after germination and placed in a specially designed assembly of flowing solution in laboratory and greenhouse. The nutrient solution was allowed to flow into the culture vessel in a regulated manner by means of a separating funnel. The set-up was in the form of a U-tube, one arm of which in the shape of a large glass funnel where
plants were placed with proper support. Fresh Hoagland solution was added drop by drop and used up liquid was collected intermittently from the other end of the tube.

During day time, no special arrangement for bubbling of air or stirring the solution was made because the solution was continuously flowing which prevented the development of concentration gradient around the roots as well as depletion of oxygen in the nutrient media. That also removed some allelopathic compounds, if any, secreted by the roots. But in night time, an aquarium pump was used to make bubbling around the roots to avoid the above stated undesirable developments. Fresh Hoagland solutions having five different concentration of K (2, 6, 10, 13, and 16 mg L⁻¹) were added drop-wise on the funnels at the rate of about 3000 mL day⁻¹ and continuously supplied in five different assemblies. In laboratory an artificial light was provided to the plants for maintaining their normal photosynthesis rate but because of insufficient amount of light intensity, which has been measured by a Luxmeter, the set-up was transferred to the greenhouse.

### Table 2. Parameters of the modified model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>ME</th>
<th>MEA</th>
<th>HEA</th>
<th>B</th>
<th>MEB</th>
<th>HEB</th>
<th>R</th>
<th>MER</th>
<th>HER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Available potassium (mg kg⁻¹)</td>
<td>60.8</td>
<td>64.6</td>
<td>35.1</td>
<td>148</td>
<td>126</td>
<td>44.9</td>
<td>50.0</td>
<td>41.2</td>
<td>5.57</td>
</tr>
<tr>
<td>Buffering capacity (b)</td>
<td>2.79</td>
<td>2.91</td>
<td>6.35</td>
<td>10.3</td>
<td>19.8</td>
<td>20.2</td>
<td>0.74</td>
<td>1.15</td>
<td>1.53</td>
</tr>
<tr>
<td>Intercept of buffering curve (c)</td>
<td>30.5</td>
<td>28.9</td>
<td>28.9</td>
<td>99.8</td>
<td>58.7</td>
<td>56.6</td>
<td>20.2</td>
<td>20.0</td>
<td>26.5</td>
</tr>
<tr>
<td>Fixation Threshold Level (mg L⁻¹)</td>
<td>21.1</td>
<td>13.3</td>
<td>8.7</td>
<td>21.3</td>
<td>17.4</td>
<td>6.54</td>
<td>26.2</td>
<td>18.2</td>
<td>18.4</td>
</tr>
<tr>
<td>Release Threshold Level (mg L⁻¹)</td>
<td>6.25</td>
<td>4</td>
<td>1.63</td>
<td>12.4</td>
<td>8.15</td>
<td>1.38</td>
<td>7.24</td>
<td>5.61</td>
<td>1.98</td>
</tr>
<tr>
<td>Average moisture content (θ)</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
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</tr>
<tr>
<td>Fixation rate constant (d⁻¹)</td>
<td>0.098</td>
<td>0.086</td>
<td>0.077</td>
<td>0.078</td>
<td>0.076</td>
<td>0.074</td>
<td>0.088</td>
<td>0.088</td>
<td>0.06</td>
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<tr>
<td>Release rate constant (d⁻¹)</td>
<td>0.086</td>
<td>0.083</td>
<td>0.059</td>
<td>0.063</td>
<td>0.060</td>
<td>0.059</td>
<td>0.066</td>
<td>0.054</td>
<td>0.05</td>
</tr>
<tr>
<td>″ - B (d⁻¹)</td>
<td>-0.04</td>
<td>-0.04</td>
<td>-0.04</td>
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<td>-0.04</td>
<td>-0.04</td>
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<td>-0.04</td>
</tr>
<tr>
<td>Km – A (mg L⁻¹)</td>
<td>15.28</td>
<td>15.28</td>
<td>15.28</td>
<td>15.28</td>
<td>15.28</td>
<td>15.28</td>
<td>15.28</td>
<td>15.28</td>
<td>15.3</td>
</tr>
<tr>
<td>″ - B (d⁻¹)</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.01</td>
</tr>
<tr>
<td>RLDA - A (cm cm⁻³)</td>
<td>9.31</td>
<td>9.31</td>
<td>9.31</td>
<td>10.34</td>
<td>10.34</td>
<td>10.34</td>
<td>7.90</td>
<td>7.90</td>
<td>7.90</td>
</tr>
<tr>
<td>″ - B (d⁻¹)</td>
<td>75.5</td>
<td>75.5</td>
<td>75.5</td>
<td>68.4</td>
<td>68.4</td>
<td>68.4</td>
<td>80.77</td>
<td>80.77</td>
<td>80.7</td>
</tr>
<tr>
<td>″ - C</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Mean water uptake rate (cm d⁻¹)</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
</tr>
</tbody>
</table>

1 A, B, and R stands on Alluvial (Inceptisol), Black (Vertisol) and Red (Alfisol) soil.
2 ME and HE are stands on moderately and highly exhausted soil, respectively.

At different stages, after running the experiment for 24 h, outlet solution was collected and the rate of K absorption was determined from the difference in concentration at the inlet and outlet. At each stage the surface area of the absorbing roots was also calculated from its fresh root weight (Nye and Tinker, 1977). The values of $V_{max}$ and $K_m$ at each stage were calculated from the slope and intercepts of the linear equation fitted by plotting $C / V$ against $C$, where $V$ is the rate of K absorption when its concentration in solution is $C$. $V_{max}$
and $K_m$, values obtained at different stages were fitted to exponential equation of with coefficients $A$ and $B$ as shown below:

\[ V_{\text{max}} = A_V \exp (-B_V t) \quad (\text{Eq. 4}) \]

\[ K_m = A_K \exp (-B_K t) \quad (\text{Eq. 5}) \]

Where, $A_V$ and $A_K$ are the values of $V_{\text{max}}$ and $K_m$ at the start of simulation and $B_V$ and $B_K$ are constants analogous to decay constant of $V_{\text{max}}$ and $K_m$, respectively, with time, $t$, of growth.

**Root length density**

At different stages of wheat growth (22, 41, 69, and 87 days after germination), the shoot was harvested and the whole of the soil in the pot was screened carefully under moist condition to collect total roots which were then washed and measured for root volume by measuring cylinder, mean root diameter by counting the number of root per unit length on a grid transparent paper after blotting excess water. Using root volume and mean diameter of root, total root length was calculated, and then root length density was calculated by dividing total root length by total volume of the soil. This distribution of root length density with time was very closely fitted with a symmetric normal distribution curve. Thus the $RLD$ can be expressed as a function of time with the following equation:

\[ RLD = A \exp [-\frac{(B-t)^2}{C}] \quad (\text{Eq. 6}) \]

where, $A$ is a constant indicating maximum root length density attained during growth period, $B$ is the number of days after emergence at which the maximum root length density is attained, $C$ is a constant, and $t$ is time in days after emergence (Datta, 2001). Root length density, total dry matter weight and total K uptake by plants (shoot + root) and exchangeable K in soils were analyzed following the standard procedure. It was found that the root length density increased from an initial low value to maximum at 69 days after germination and then decreased gradually. The observed root length density is the net result of growth and decay processes. While initially growth rate was more than the decay rate, after attaining maximum decay rate was more than the growth rate. For field-grown crop this relation ship was applied for all the layers of rooted soil. In that case the constant, $A$, depicting the maximum value was assumed to decrease exponentially with depth of layer.

**Model parameters**

The mathematical model has the following 16 parameters:

1. $K_i$, Initial available K, mg kg$^{-1}$
2. $B$, buffer power of nutrient on the solid phase for nutrient in solution, dimensionless
3. $C$, intercept of buffering curve, mg K kg$^{-1}$ of soil
4. $FTL$, fixation threshold level, mg L$^{-1}$
5. $RTL$, release threshold level, mg L$^{-1}$
6. $\theta_m$, Average moisture content, %
7. $K_f$, fixation rate constant, s$^{-1}$
8. $K_r$, release rate constant, s$^{-1}$
9. $V_{\text{max}}$, maximum influx at high concentrations and at the start of simulation, g m$^{-2}$ s$^{-1}$
10. $V_{\text{max}} - B$, decay constant of $V_{\text{max}}$, s$^{-1}$
11. $K_{\text{max}} - A$, nutrient concentration in solution - $C_{\text{min}}$ where Influx = 1/2 $V_{\text{max}}$ at the start of simulation, mg L$^{-1}$
12. $K_{\text{max}} - B$, decay constant of $K_{\text{max}}$, s$^{-1}$
13. RLD- $A$, maximum root length density attained, cm cm$^{-3}$
14. RLD- $B$, the time at which maximum root length density was attained, s$^{-1}$
15. RLD- $C$, constant value
16. $V_{0}$, mean water influx, cm s$^{-1}$

Results

Simulation of K uptake model

A computer program has been written in Visual Basic following explicit finite difference forward integration method to simulate the changes in concentration of K in several thin cylindrical compartments of increasing thickness around one cm of root by applying the principle of conservation of solute and water in each compartment. In other words, the change in amount of solute in each compartment in a time step is equal to the difference between influx and outflux (both diffusive and convective) of the compartment plus any change in amount due to fixation or release. The change in concentration in each compartment is then calculated by dividing the amount of change with volume of the compartment, which is then added to the initial concentration at the beginning for updating this state variable. The time step ($\Delta t$) was kept small according to the following relationship between thickness of thinnest compartment and apparent diffusion coefficient to increase the accuracy and to get stable numerical solutions: $X = \sqrt{2D\Delta t}$ where, $X$ is thickness of thinnest compartment (first compartment near root surface) and $D$, apparent diffusion coefficient. The flux of solute out of the innermost compartment has been equated to the uptake by root in one time step as shown below:

$$\text{Uptake per unit volume of soil} = 2\pi r_0 \cdot \text{RLD} \times \frac{V_{\text{max}} (C_{la} - C_{\text{min}})}{K_{\text{max}} + (C_{la} - C_{\text{min}})} \times \Delta t \quad (\text{Eq. 7})$$

Where, $C_{la}$ is solution concentration in the innermost compartment and $\Delta t$ is a time step. Total uptake is obtained by summing up all these uptakes. Inter root competition has been simulated by equating flux to zero at $r = \frac{1}{\sqrt{((\pi \cdot \text{RLD})}$. A separate account has been maintained to sum up all the amounts for release or fixation (Datta, 2001).

Three Indian soils which have been exhausted by Sudan grass in the previous year were used to grow wheat crop for 87 days after germination. The total K uptake were recorded and compared with the simulated value. Single nutrient uptake by a growing root system is often estimated by Claassen and Barber (1976) model. The model solves the coupled equations of transport in the soil and absorption of nutrient by roots in fixed domains. In the present study the same model has been used with the modification that a source and a sink function for labile K have been added to the equation of continuity to account for fixation and release of K in the rhizosphere (Datta, 2001). The model was run to simulate K uptake in pot culture experiment. Except in Alfisol all the predicted values of K uptake agreed with
that of observed values. When predicted K uptake values were plotted against the observed values, \( r^2 \) values were found to be 0.927, 0.828 and 0.721 in Inceptisol, Alfisol, and Vertisol, respectively (Figure 4). There is a close relationship between observed and predicted values of K uptake as evident from the high \( r^2 \) values presented in Figure 4, but in case of Alfisol and Vertisol the model has over-predicted K uptake, which perhaps was due to over prediction of K release from NE-K.

**Figure 4.** Predicted and observed values of K uptake of wheat in different types of soils.
Sensitivity analysis

The Datta (2001) model was used with the parameters shown in Table 4 to predict potassium uptake, as each parameter was varied from 0.5 to 2.0 times the original value, while the other parameters remained at their initial levels. Results of the sensitivity analysis are shown in Figure 5.

![Inceptisol Sensitivity Analysis](image)

![Vertisol Sensitivity Analysis](image)

![Alfisol Sensitivity Analysis](image)

Figure 5. Sensitivity analysis of the effect separately changing mathematical-uptake model parameters on calculated K uptake in Inceptisol, Vertisol, and Alfisol.
Discussion

The release rate constants determined from the soils with high available K may not remain constant, rather decreased during K depletion from the soil by roots. Determination of rate constant as a function of available K may correct the over-prediction. Similarly, in this model a constant buffering capacity has been assumed, but in reality the buffering capacity increases as K deplete from a soil, so a concentration dependent buffer capacity may probably correct the over-estimation of K uptake.

Predicted K uptake was most sensitive to changes in root parameters \((RLD \, and \, V_{max})\), since changes in \(RLD-B\) and \(V_{max-B}\) gave the greatest changes in K uptake in almost all the soils except highly exhausted Alfisol in which predicted potassium uptake was more sensitive to changes in \(RLD-B\) and intercept \((c)\) than to root uptake kinetics, as described by \(V_{max}\) and \(K_m\). As evident from the Figure 5, the predicted potassium uptake was least sensitive to changes in rate constants of release and fixation and fixation threshold level in Inceptisol and Vertisol, but was sensitive to release threshold level and rate constant of release in Alfisol.

This model can be used to determine soil potential K supplying capacity to any crop, provided its root parameters are known. By knowing a crops maximum requirement, one will be able to recommend fertilizer dose and its efficiency and responses towards fertilizer application. This model is also helpful to estimate the utilizable potassium reserve of the soil of a country and the total potassium fertilizer requirement.

References