

MEASURED AND ESTIMATED PARAMETERS FOR A MODEL OF NUTRIENT UPTAKE BY TREES

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ABSTRACT

Quantitative mechanistic models, such as NUTRIENT UPTAKE, are useful tools in refining our understanding of the chemical, physical, and biological complex that controls plant nutrition. Previous work with woody species has raised important issues on how best to derive model input values and to set parameters on the model, given that many of these values change substantially over even one growing season. Data for this analysis were obtained by growing loblolly pine (*Pinus taeda* L.) seedlings from two families from seed in pots containing soil which had been amended with potassium, phosphorus+potassium, nitrogen+potassium, and nitrogen+phosphorus+potassium at rates equivalent to 67 kg K/ha, 28 kg P/ha, and 196 kg N/ha. Seedlings were harvested after each foliar growth flush over the course of one growing season, and information was collected on root growth and soil supply parameters. Solution depletion techniques were used to establish potassium and ammonium uptake kinetics values for both families. These data were then used to set parameters for the NUTRIENT UPTAKE model. Results indicate that such models should use values for root morphological characteristics that are more reflective of the seasonal average. Changes in soil supply parameters will need to be taken into consideration and, again, seasonal means appear more appropriate. Comparisons of model predictions with observed plant uptake of potassium and nitrogen indicated substantial over-estimates of uptake (1.1 to 10.0 times observed) by the model. Based on model runs and previous experience, this over-estimate was judged to be largely a function of the magnitude of the experimentally derived I_{\max} value. As an alternative, the model can be used to calculate theoretical I_{\max} values based on observed uptake in order to approximate growth interval or annual uptake more closely.

Keywords: I_{\max} ; buffer power; nutrient supply; modelling nutrient uptake; uptake kinetics; root growth rate; *Pinus taeda*.

INTRODUCTION

Improvements in our ability to model plant nutrient uptake are needed in order to assist the resource manager in evaluating plant response to a variety of existing and potential stresses. Previous work on *Pinus* spp. (Van Rees, Comerford, McFee 1990; Kelly & Barber

1991; Kelly *et al.* 1992; Smethurst & Comerford 1993) using the NUTRIENT UPTAKE model (Oates & Barber 1987) indicated that nutrient uptake is highly influenced by the amount of absorptive root surface and the kinetics of nutrient uptake. The degree of plant control over uptake kinetics is influenced by soil supply parameters, particularly the degree to which nutrient resupply at the root is dominated by mass flow *v.* diffusion (Rengel 1993; Darrah 1993). In high-fertility situations mass flow can dominate, while at low fertility levels or in high demand situations diffusion plays the dominant role.

To investigate the relative importance of root surface area, uptake kinetics, and soil supply parameters, seedlings from two loblolly pine families with previously observed differences in root *v.* shoot growth strategies (Crawford *et al.* 1991) were grown under four nutrient addition regimes. This data set and the NUTRIENT UPTAKE model were then used to: (i) document trends in root growth rates and soil supply parameters for potassium and ammonium over a growing season, and (ii) investigate potential differences in potassium and ammonium uptake kinetics as a function of family and time using the NUTRIENT UPTAKE model to integrate and evaluate key factors in the description of potassium and ammonium uptake.

MATERIAL AND METHODS

Data sets were developed that provided information on plant growth and nutrient content, soil nutrient supply, and nutrient uptake kinetics for the two families of loblolly pine being studied. Since the focus of this paper is on the NUTRIENT UPTAKE model, the methodology used to obtain each parameter will be described only briefly and references provided to direct the reader to more detailed descriptions of the methods used to develop the data sets.

Plant Culture Techniques

Seed from two half-sibling loblolly pine families were germinated in trays and then transplanted in early May to either 19- ℓ pots containing soil from the A horizon of a Cowarts (fine-loamy, silicious thermic Typic Kanhapludult) soil, or into 0.8- ℓ plastic tubules containing a potting mix consisting of sand, peat moss, and vermiculite. Each pot or tubule contained one seedling. In order to create four different fertility regimes, fertiliser was mixed with the pot soil prior to transplanting. The pots containing the Cowarts soil were amended with potassium (K), phosphorus+potassium (P+K), nitrogen+potassium (N+K), or nitrogen+phosphorus+potassium (N+P+K) at rates equivalent to 67 kg K/ha (potassium chloride), 28 kg P/ha (triple super phosphate), and 196 kg N/ha (ammonium nitrate). Potted seedlings were then placed in a shadehouse (\approx 40% light reduction) for the remainder of the growing season and watered to field capacity at least twice a week using a drip irrigation system. Seedlings transplanted into the potting mix were maintained in a similar manner but did not receive any supplemental fertiliser. Following the precedent of Crawford *et al.* (1991), the two families were identified using the code names "blue" and "green".

Plant Harvest

Ten seedlings from each family were harvested at the time of transplanting (4 May) to define initial root length and radius, plant weight, and plant nutrient concentrations for each

family. Subsequent harvests were made on 25 June, 30 July, 27 August, and 6 October after each foliar growth flush. At each harvest, 10 seedlings from each of the four nutrient regimes were taken at random (10 seedlings \times 4 nutrient regimes \times 4 harvests = 160 plants per family total harvest). The above-ground portion of the plant was removed and oven dried (60°C) for at least 72 h and then weighed.

Intact root systems were carefully separated from the soil, washed, patted dry, and the fresh weight was determined. Total root length (L_o) for each plant was estimated using an optical scanner technique combined with a computer algorithm (Krstansky & Henderson 1989). Root length and fresh weight values were then used to calculate average root radius (r_o), root growth rate (k), and root half distance (r_1) as described by Kelly *et al.* (1992). For each calculation of r_1 , the entire volume of soil in the pot was considered available for root occupancy.

After root length determinations were completed, roots were oven dried in the same manner as the shoot and weighed. Both shoot and root samples were analysed to determine potassium and nitrogen concentrations, using procedures described by Simmons & Kelly (1989).

Soil Analysis

In conjunction with each harvest, soil samples representative of the entire pot profile were collected from each pot, composited by treatment, and used to determine both the solid phase (c_s) and solution phase (c_1) concentrations of potassium and ammonium using methods described by Kelly *et al.* (1992). The buffer power (b) and diffusion coefficient (D_e) for potassium and ammonium in the pot soils were also determined using procedures and considerations as discussed by Van Rees, Comerford, Rao (1990), Kelly *et al.* (1992), and Kelly (1993).

Nutrient Uptake Kinetics

A nutrient solution depletion method (Claassen & Barber 1974) was used to obtain parameters needed to describe nutrient influx. Seedlings grown in the potting mix were removed from the mix and grown in solution culture as described by Kelly & Barber (1991). Seedlings were approximately 150 days post-germination and were in the midst of a foliar growth flush at the time of the uptake studies. Procedures used to determine the maximal rate of nutrient influx (I_{max}), solution concentration when influx is 0.5 I_{max} (K_m), concentration in solution where influx is zero (C_{min}), and the water uptake rate at the root surface (v_o) values for potassium and ammonium were the same as described by Kelly & Barber (1991).

Statistical

Analysis of variance combined with the Duncan's mean separation procedures available in SAS (SAS Institute 1985) were used to test for differences in biomass and root growth. The 0.05 probability level was used as the decision level for the acceptance or rejection of all null hypotheses.

RESULTS AND DISCUSSION

Plant Growth

Across all fertility regimes, the blue family had an average of 17% less root mass and 12% less root surface area than that of the green family at the final harvest. Total plant mass increased steadily over time in all seedlings. Highest biomass values were found in those plants growing in the soils amended with either phosphorus+potassium or potassium only (Table 1). At the final harvest, biomass values within the blue family ranged from 2.9 to 7.1 g with an average across nutrient regimes of 5.4 g. The green family exhibited slightly less variability at final harvest ranging from 4.8 to 8.2 g with an average of 5.7 g. Plants from both families were smaller in the presence of added nitrogen, possibly indicating a nutrient imbalance effect.

TABLE 1—Total plant biomass and potassium and nitrogen content at final harvest by family and nutrient regime.

Treatment	Biomass (g)		Potassium (g)		Nitrogen (g)	
	Blue	Green	Blue	Green	Blue	Green
K	7.1 ± 0.7*	5.0 ± 0.8	52.1 ± 5.5	42.8 ± 7.4	81.3 ± 8.8	60.6 ± 10.2
PK	6.6 ± 0.8	8.2 ± 1.2	47.5 ± 5.7	65.0 ± 10.0	85.4 ± 10.4	100.5 ± 15.4
NK	4.9 ± 0.8	4.8 ± 0.6	38.8 ± 6.9	40.5 ± 8.1	62.0 ± 11.0	61.2 ± 12.2
NP	2.9 ± 0.5	4.8 ± 0.6	18.9 ± 3.9	32.6 ± 4.4	23.9 ± 4.7	36.2 ± 4.9

*Standard error

Examination of the individual root growth responses within families indicates different patterns within particular nutrient regimes (Fig. 1). For example, blue family root growth rates for plants growing in the potassium and nitrogen+potassium nutrient regimes increased continually throughout the growth period, while green family plants growing under the same nutrient regimes peaked at the third harvest. Mean root growth rates for the growing season for the blue family ranged from 1.0E-4 to 1.4E-4 cm/s while green family mean values exhibited a much broader range (0.9E to 4.0E-4 cm/s).

Soil Nutrient Supply

Solid phase potassium values declined with time in both the blue and green family pots owing to dissolution and plant uptake (Fig. 2). On the other hand, solid phase ammonium-nitrogen values after an initial decline generally increased with time in the blue family pots. One can speculate that this trend was probably due to the combined effects of mineralisation and conversion of added nitrate to ammonium. This pattern was not expressed as consistently in the green pots, and in fact ammonium-nitrogen dropped substantially at the final harvest for the green pots (Fig. 2). The starting values of C_s for potassium should have been similar among the treatments. The solid phase value for potassium in the initial sampling (4 May) of the potassium-only regime was, however, approximately half the values observed for the other regimes. A possible reason for this difference will be discussed below. The observed differences in ammonium-nitrogen values for the N+K and N+P+K regimes are more difficult to explain (Fig. 2) other than as a co-incident variation due to random variability.

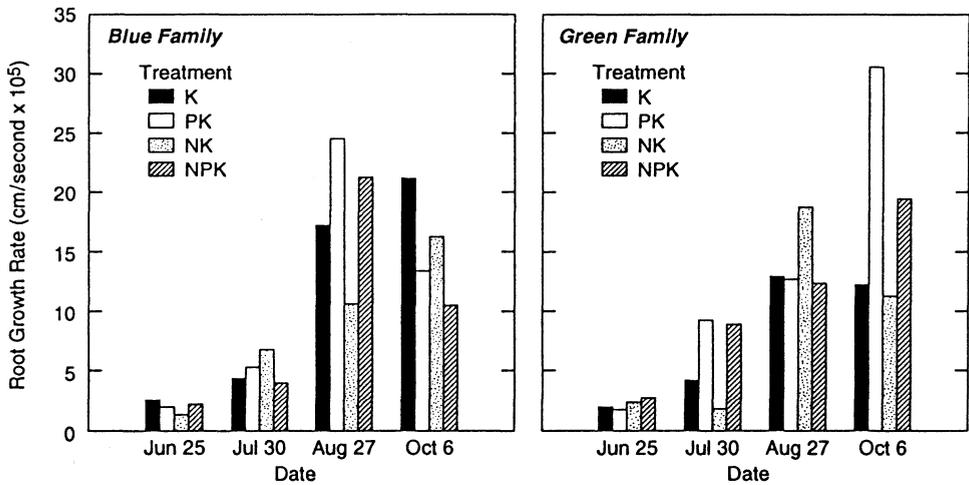


FIG. 1—Mean root growth rate (k) by interval for the blue and green families as a function of nutrient regime.

Solution phase concentrations of potassium declined in 2 months to approximately 10 to 12% of the starting concentrations (Fig. 3). Initial potassium concentrations were highest in the potassium-only addition, consistent with the differences in initial solid phase potassium concentrations. Comparing the data in Fig. 2 and 3 might lead one to speculate that more of the potassium may have been in a state where it was easily solubilised, but this is only conjecture and would imply phosphorus and/or nitrogen inhibition of potassium release to solution.

Solution phase ammonium-nitrogen decreased to very low concentrations before the second sampling (Fig. 3) and remained at extremely reduced levels for the balance of the growing season. As with potassium, there also appear to be offsetting differences between solid phase and solution phase ammonium-nitrogen.

Buffer power (b) is a calculated index that reflects the amount of solid phase ions available to move into solution to replace ions being removed by the root or lost to leaching (Barber 1984). The buffer power values plotted in Fig. 4 varied inversely in response to changes in both solid and solution phase concentration (Fig. 2 and 3). The general tendency for potassium is for the buffer power to increase initially and then decrease with time as illustrated by the potassium b values in Fig. 4. However, with ammonium-nitrogen since the C_1 values are relatively small and stable and the C_s values are increasing slowly, the b values also increase due to the fact that a relatively small and constant C_1 is being divided into a C_s value that is increasing in magnitude over time. This increase in the b value would seem to imply mobilisation of ammonium-nitrogen probably as a result of decomposition and/or the possible conversion of nitrate to ammonium.

Nutrient Uptake

The pattern of potassium and nitrogen content at final harvest in both families was similar, with a decrease in both elements in the presence of added nitrogen (Table 1). Average

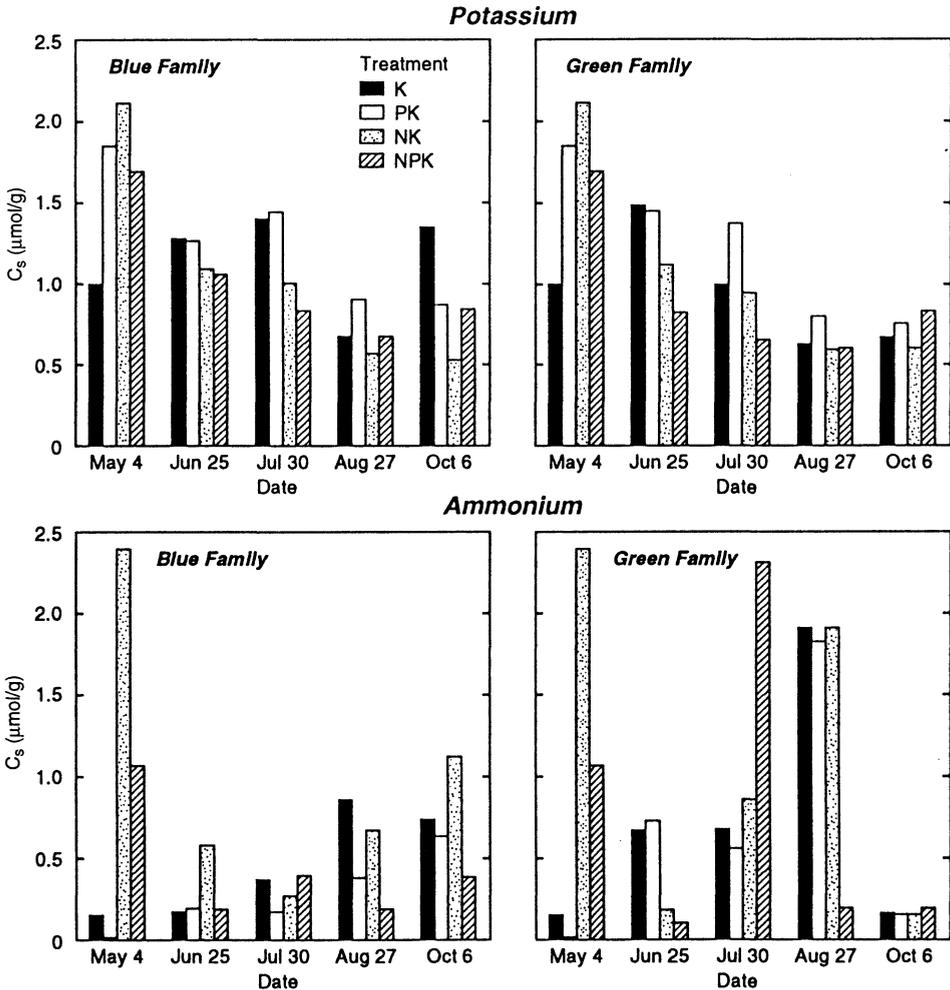


FIG. 2—Mean concentrations of potassium and ammonium in the solid phase (C_s) by harvest date and fertility regime for soils collected from blue and green family pots.

potassium uptake across all nutrient regimes was 12% higher in the green family than in the blue family plants (1158 v. 1019 $\mu\text{mol/plant}$) while average nitrogen uptake differed by 3% (4617 v. 4511 $\mu\text{mol/plant}$).

Solution culture work indicated a higher rate of uptake per unit root surface of both potassium and ammonium-nitrogen by the green family (Fig. 5). Attempts to establish nitrate-nitrogen uptake through solution kinetics studies indicated that the seedlings of both families did not take up nitrate-nitrogen, but instead released nitrate into solution. This is not surprising given the well-established preference of conifers for ammonium over nitrate (van den Driessche 1991). Consequently, uptake of nitrogen is assumed to be solely the result of ammonium uptake. Experimentally derived values for I_{max} , K_m , and C_{min} (Table 2) indicate differences between the two families in the magnitude of the I_{max} and K_m values while C_{min} values were essentially the same.

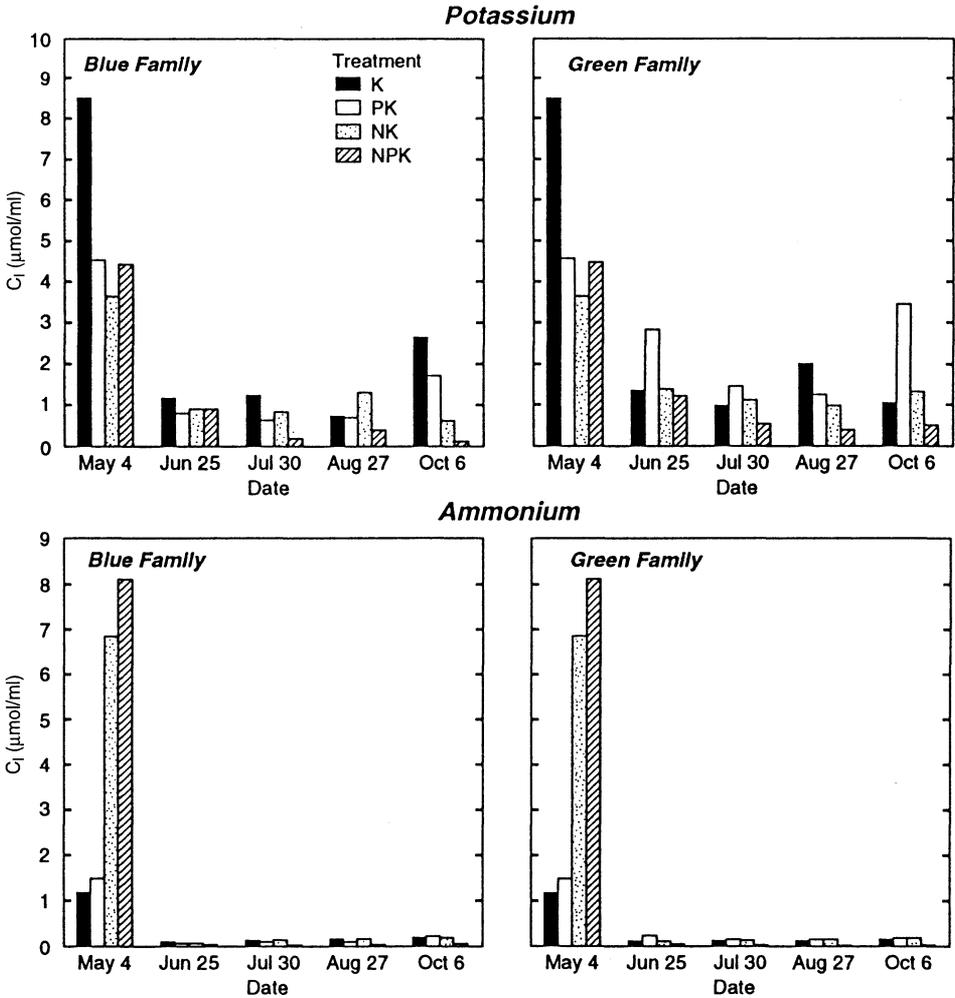


FIG. 3—Mean equilibrium solution phase concentrations (C_1) of potassium and ammonium by harvest date and fertility regime collected from soil taken from blue and green family pots.

Model Parameters

Using the green family as an example, values needed to set parameters in the NUTRIENT UPTAKE model for potassium uptake in the potassium-added treatment are presented in Table 3 by growth interval. In a typical application of the model, plants would be grown for a relatively short time (Barber 1984) in order to produce the values needed to set model parameters for a simulation. The values listed for the first growth interval (4 May–25 June) would be typical of the type of information collected in a short-term study. When the model was run for the green family using this data set, predicted potassium uptake exceeded observed uptake by a factor greater than 3 for three of the four treatments (Table 4). Comparison of other values in Table 4 indicate only once did the predicted potassium uptake value fall within $\pm 10\%$ of the observed value. Similar comparisons of predicted v. observed ammonium uptake revealed even greater discrepancies.

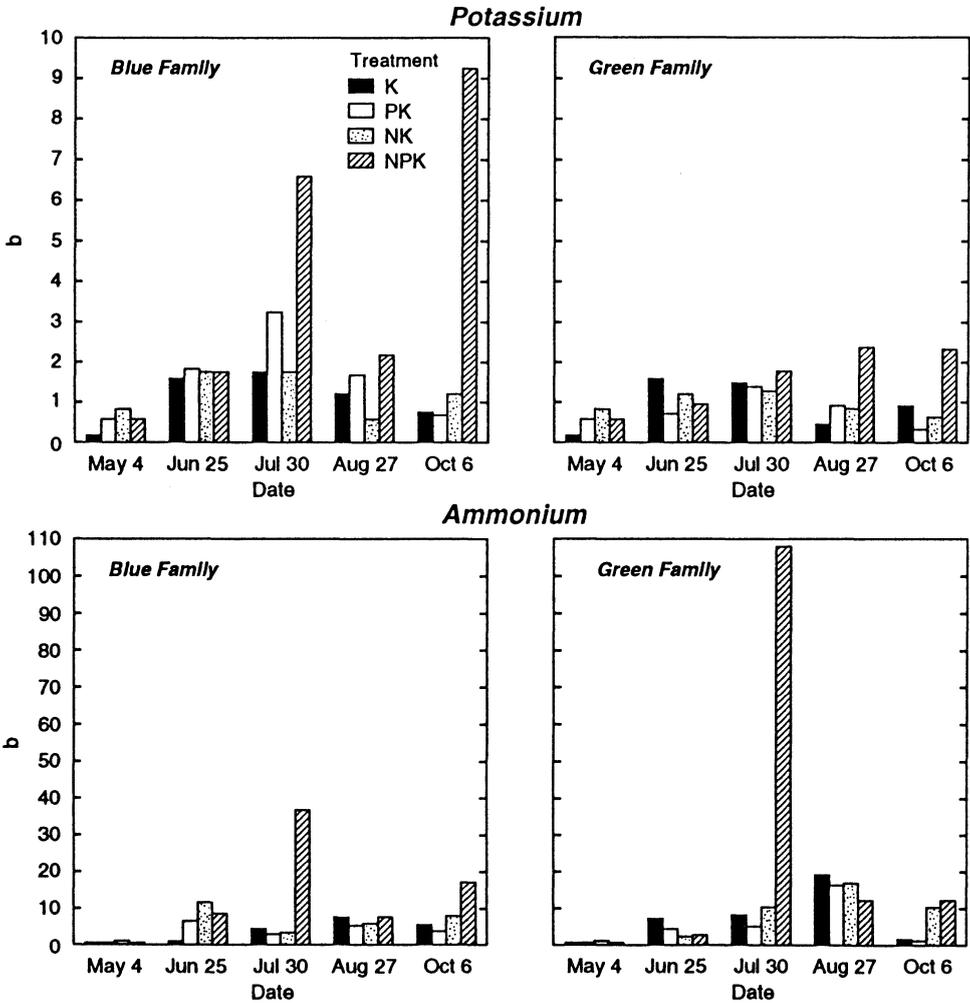


FIG. 4—Mean buffer power (b) values for potassium and ammonium for soil collected from the blue and green family pots by harvest date and fertility regime.

In an attempt to improve the agreement between observed and predicted uptake for the growing season, model parameters were set for appropriate soil supply and root morphological values for each growth interval (*see* Table 3). Since the values of these parameters change substantially over time, modelling by growth interval and summing for the season might give different values for predicted uptake. Previous sensitivity analyses of potassium uptake by loblolly pine indicated that the C_1 value could influence uptake estimates substantially (Kelly *et al.* 1992), and the use of initially higher solution levels might give a less accurate representation than the lower values actually observed during most of the growing season. Using an interval approach in the current study improved estimates only slightly, thus suggesting that, at least in this study, soil supply factors and root morphological characteristics were not contributing substantially to the over-estimates.

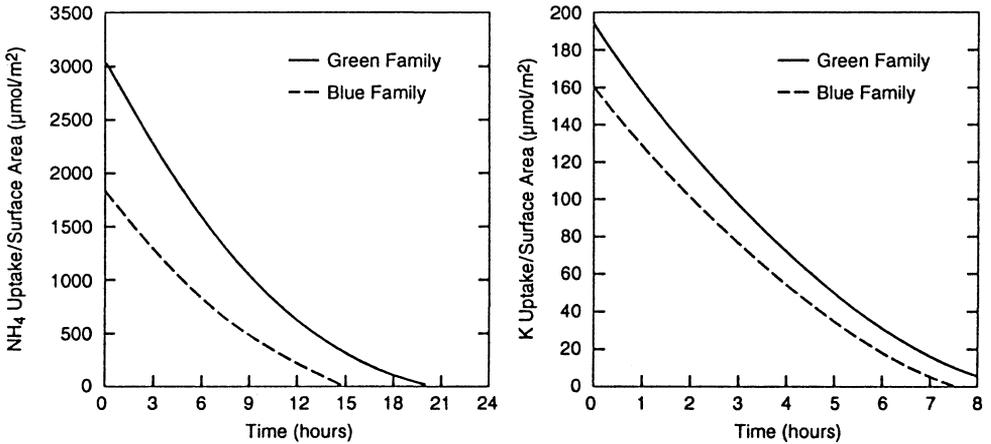


FIG. 5—Ammonium and potassium uptake per unit of root surface as a function of time for seedlings from the blue and green family.

TABLE 2— I_{max} , K_m , and C_{min} values for potassium and ammonium uptake, based on solution depletion determinations using 150-d seedlings.

Parameter	Units	Blue		Green	
		K	NH ₄	K	NH ₄
I_{max}	$\mu\text{mol}/\text{cm}^2/\text{s}$	1.37E-6	2.38E-5	3.65E-6	3.50E-5
K_m	$\mu\text{mol}/\text{cm}^3$	1.24E-2	3.25E-1	2.37E-2	1.97E-1
C_{min}	$\mu\text{mol}/\text{cm}^3$	2.0E-4	1.8E-3	2.0E-4	1.2E-3

The uptake kinetics values used in model simulations were the same for all growth intervals because uptake kinetics values were not determined for seedlings during each growth period. Instead, seedlings slightly older than those collected in the final harvest were used to establish the uptake kinetics values. Solution depletion approaches to the determination of uptake kinetics values require that a substantial amount of root material be present in the test solution to be able to detect measurable changes in solution concentration over relatively short time intervals. This need biases the experimental technique toward the use of older plants in order to have the requisite root surface area.

Earlier work by Kelly & Barber (1991) found that uptake kinetics values are higher during shoot growth-flush periods than during the intervening non-flush periods. Additionally, previous sensitivity analyses (Kelly *et al.* 1992) have suggested that, of the four values that define uptake kinetics in the model, the I_{max} value is by far the most influential when soil supply values are adequate to satisfy plant demand (Rengel 1993; Yanai 1994). Given these considerations, an alternative approach to determining I_{max} might have been to calculate a weighted average I_{max} value based on experimentally derived values for uptake during shoot growth and non-growth periods. However, this approach would require knowing the length of the shoot growth period for each interval to serve as weighting factors, and the acquisition of experimentally derived kinetics values for uptake during the shoot non-growth interval.

TABLE 3—Soil nutrient supply, root morphological characteristics, and root uptake kinetics values used in the NUTRIENT UPTAKE model by growth interval for the green family in the potassium-added nutrient regime.

Parameter	Name	Units	4 May– 25 June	25 June– 27 July	27 July– 27 Aug	27 Aug– 5 Oct
D_e	Diffusion coefficient for nutrient	cm^2/s	6.35E-6	6.64E-7	7.01E-7	2.29E-6
b	Buffer power	unitless	0.16	1.55	1.69	1.19
C_{li}	Initial concentration in solution	$\mu\text{mol}/\text{cm}^3$	8.54	1.35	0.99	2.03
r_1	Half-distance between roots	cm	6.02	6.02	3.89	2.47
r_o	Mean root radius	cm	0.043	0.043	0.049	0.052
L_o	Initial root length	cm	10	87.3	208.7	517.3
k	Root growth rate	cm/s	4.0E-5	4.0E-5	1.3E-4	1.2E-4
I_{\max}	Maximum influx at high concentration	$\mu\text{mol}/\text{cm}^2/\text{s}$	3.65E-6	3.65E-6	3.65E-6	3.65E-6
K_m	Nutrient concentration in solution where net influx is $0.5 I_{\max}$	$\mu\text{mol}/\text{cm}^3$	2.37E-2	2.37E-2	2.37E-2	2.37E-2
C_{\min}	Nutrient concentration where influx is zero	$\mu\text{mol}/\text{cm}^3$	0.0002	0.0002	0.0002	0.0002
V_o	Water uptake at root	cm/s	5.66E-7	5.66E-7	5.66E-7	5.66E-7
Time		s	4.49E+6	2.76E+6	2.67E+6	3.37E+6

TABLE 4—Comparison of observed and model predicted potassium uptake for the blue and green families for one growing season (180-d), using values obtained for the 4 May–25 June growth interval as parameters for the model.

Treatment	Blue			Green		
	Observed ($\mu\text{mol}/\text{plant}$)	Predicted	$\frac{\text{Predicted}}{\text{Observed}}$	Observed ($\mu\text{mol}/\text{plant}$)	Predicted	$\frac{\text{Predicted}}{\text{Observed}}$
K	1383	1309	0.95	1096	3583	3.27
PK	1216	2122	1.74	1664	1981	1.19
NK	993	1583	1.59	1038	8418	8.10
NPK	484	1369	2.82	835	8427	10.09

Alternatively, values for the shoot non-growth period could be estimated based on the relationship with the growth period value observed by Kelly & Barber (1991). These considerations point out that more attention needs to be given to how best to define

experimentally the uptake kinetics values for woody species since these species do not always share the same growth characteristics as the agronomic species (i.e., more or less continuous growth) more commonly evaluated with this model.

As an alternative to an experimental or weighted average approach, the model was used to calculate I_{\max} . Since we have a known uptake value as well as all other values needed to model nutrient uptake, it is possible to use the model to estimate an average value for I_{\max} that would be required to produce the observed uptake for each growth interval or for the entire growing season. This is accomplished by first ratioing the measured I_{\max} and the uptake value associated with that I_{\max} against the observed uptake. This I_{\max} is then inserted into the model and adjusted through a series of model runs until the observed uptake is approximated. For the model calculations of the growing season I_{\max} (Table 5), values for other model parameters were averaged for the growing season. Comparison of the model-derived I_{\max} with the experimentally produced values suggests that the experimentally derived values on average were at least an order of magnitude higher than the calculated value. Similar discrepancies between experimentally derived and model derived values were observed when I_{\max} was calculated for individual intervals (Table 6). This analysis suggests that if model derived values for I_{\max} are not used, it may be necessary to experimentally established uptake kinetics values for each growth phase and nutrient regime.

TABLE 5— I_{\max} values ($\mu\text{mol}/\text{cm}^2/\text{s}$) based on experimental (nutrient depletion) and model calculated approaches using mean values of all other parameters for the growing season.

	Potassium		Ammonium-nitrogen	
	Blue	Green	Blue	Green
<i>Experimentally derived</i>				
	1.37 E-6	3.65 E-6	2.38 E-5	3.50 E-5
<i>Model derived</i>				
K	3.76 E-7	7.70 E-8	3.35 E-6	2.07 E-6
PK	6.29 E-7	2.34 E-7	4.24 E-6	3.83 E-6
NK	2.70 E-7	5.86 E-7	1.44 E-6	1.26 E-6
NPK	1.47 E-7	4.69 E-7	6.10 E-7	8.82 E-7

TABLE 6—Model calculated I_{\max} values ($\mu\text{mol}/\text{cm}^2/\text{s}$) for potassium based on observed values for other parameters by growth interval, from the potassium-only nutrient regime.

Family	Growth period			
	4 May– 25 June	26 June– 27 July	27 July– 27 August	27 August– 5 October
Blue	7.09 E-7	1.15 E-6	1.26 E-6	6.52 E-7
Green	1.38 E-6	1.49 E-6	7.60 E-7	7.96 E-7

CONCLUSIONS

Although family differences in root growth parameters are possible and may need to be considered in certain situations, these differences appear to be of less concern for setting

model parameters than within-season changes in root growth. Consequently, model parameters should use values for root morphological characteristics that are more reflective of the average value for the season or growth interval rather than a value based on a relatively short growth interval as has been typically done in the agronomic context.

Changes in soil supply parameters will need to be taken into consideration if within-season nutrient uptake is modelled. As with root growth parameters, seasonal mean values appear more appropriate for longer-term simulations owing to the observed changes in these values across the growing season. Although changes in soil-supply parameters did not influence model predictions greatly under the circumstances used for these simulations, other work (Van Rees, Comerford, McFee 1990; Rengel 1993; Yanai 1994) has suggested that these parameters can become much more influential if the level of nutrient availability is low, as frequently happens in forest soils without added fertiliser.

This study also raises the question of whether the experimentally derived uptake kinetics values need to be determined under solution conditions more representative of the mean C_1 rather than initial conditions, or at solution levels more comparable to those within each growth interval. This raises questions about how concentration sensitive is the I_{\max} value, and could a plant potentially have a range of values? Alternatively, when all other data are available, model-derived estimates of I_{\max} can be substituted for experimentally derived values in order to approximate growth interval or annual uptake more closely with a reduced level of experimental work.

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