NUTRIENT UPTAKE BY WOODY ROOT SYSTEMS

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ABSTRACT

The fine-root system of perennial, dicot woody species can be dominated by brown roots. Although as much as 90% of the surface area of a root system can be in this category of roots, the nutrient uptake characteristics of brown roots are not well understood. If this part of the root system has active uptake, then its significance is obvious. If it does not then modelling predictions of nutrient uptake will need to account for this non-functional segment of the measured root system.

The topic of nutrient management strategies in forest systems is crucial to the understanding and predictive modelling of soil nutrient availability to species with these root characteristics.

Keywords: brown roots; short roots; white roots; uptake kinetics; root spatial patterns; Michaelis-Menten kinetics.

INTRODUCTION

Intensive forest harvesting and site preparation can change the nutrient capital and the availability of nutrients to the next rotation of trees (Morris & Miller 1994). Biomass removal, changes in soil physical properties, and removal of top soil are a few examples of activities that change the amount of nutrients present and the supply of nutrients in plant-available forms.

If nutrient availability is a limitation to productivity, then an understanding of nutrient uptake, allocation, and use by the plant is fundamental to predicting the consequences of harvesting, as well as to ameliorating negative harvesting effects. Predictions of nutrient uptake and demand by the plant at the root surface can be contrasted with the ability of the soil to supply nutrients. The result is a mechanistic evaluation of harvesting effects on nutrient supply.

Plant nutrient uptake can be described as a set of processes occurring simultaneously in three phases. The first phase is the cumulative effect of processes that release nutrients from their solid form to the soil solution. The second phase is nutrient movement through the soil solution to the absorbing surface of the plant (via mass flow and/or diffusion). The third phase is the uptake process at the absorbing surface of the plant. Once the nutrient is in the plant, questions on allocation and function can be addressed. In fact, nutrients in the plant can play a role in feedback mechanisms that control the uptake process.

This review addresses the nutrient uptake question and focuses on the root/hypha absorbing system of the plant. Clarkson *et al.* (1978) stated that the nutrient uptake effectiveness of a root system depends on:

(i) Relative amounts of different absorbing surfaces present,
(ii) Nutrient absorption rates of each type of surface,
(iii) Differential response of the absorbing surfaces to environmental variables, and
(iv) Contact of the absorbing surface with the surrounding soil.

We would add that it also depends on:

(v) Ability of the root to change the environment in which it grows, and
(vi) Spatial distribution of roots at the scale of inter-root competition.

We first consider the definition of the nutrient-absorbing surface of trees. There is no large body of information on trees, so examples from annual species will also be used. In turn we discuss the active uptake process in the context of Michaelis-Menten kinetics, the biofeedback between the plant and the uptake process, the effect of the root on its environment relative to its ability to acquire nutrients, and the effect of spatial distribution of roots on uptake efficiency. Lastly, we frame this information in the perspective of nutrient management strategies in forest systems.

NUTRIENT ABSORBING SURFACES OF TREES

Definition of Absorbing Surfaces

A perennial, dicot, woody root system is interesting because secondary xylem growth occurs, and this "woody" portion of the root system may be the major contributor to the fine-root population (where fine-roots are arbitrarily defined as roots <2 mm in diameter). As an illustration, mature stands of *Pinus elliottii* Engelm. var. *elliottii* (slash pine) had fine-roots accounting for about 90% of the total root length (Van Rees & Comerford 1986), while mature *Pinus taeda* L. (loblolly pine) had 67% of its root system surface area in roots with diameters less than 1.3 mm (Kramer & Bullock 1966).

A perennial dicot, woody, fine-root system can be described by considering the types of roots that constitute it. The following fine-root classification (Table 1) is based on the definitions of Sutton & Tinus (1983), the descriptions of Chung & Kramer (1975) and Kramer & Bullock (1966), as well as personal experience. Most studies of fine-root systems have generally not recognised nor included all these categories in their analyses.

TABLE 1–Categories of fine-roots in a perennial, dicot, woody root system.

Root category	Description
Lateral roots	
White roots	New primary lateral roots white in color
Brown roots	
Primary	Lateral roots, still having primary growth but the epidermis/cortex has turned brown from either suberin/ lignin deposition or cortical cell decay
Woody	Roots showing evidence of secondary growth by having secondary xylem
Short roots	A root of diminutive length (often less than 2 mm) arising from a lateral root. It may or may not be bifurcated and is considered incapable of further growth
Mycorrhizal	A short root infected with symbiotic fungi. May have a fungal mantle surrounding it if ectomycorrhizal
Non-mycorrhizal	A short root not infected with symbiotic fungi
Root hairs	A small tubular outgrowth from an epidermal cell.
Extramatrical hyphae	Hyphae and rhizomorphs emanating from the mycorrhiza and distributed in the soil.

Brown roots are the dominant fine-root category. Loblolly pine, growing in the Piedmont of North Carolina (Kramer & Bullock 1966), had the following surface area distribution:

(i) white roots	0.3%
(ii) mycorrhizas (not including extra-matrical hyphae)	2.7%
(iii) suberised roots	
<1.3 mm diameter	64.1%
>1.3 mm diameter	32.7%

In this case, as in most, it is unclear if the suberised root category is woody or just brown in colour with no secondary growth. White roots (representing less than 1% of the surface area) have been the major target of nutrient uptake research.

The surface area of extra-matrical mycorrhizas might very well dwarf the other root categories; however, with current methodology it is not possible to measure mycorrhizal hyphae length or surface area under field conditions.

Root hairs are part of the epidermis of the root. They are involved in water and ionic exchange between the plant and the growth medium. Therefore, when root hairs are present the root surface can be considerably enlarged depending on root hair length and density of hairs on the epidermis.

Although the location of the root hair zone is generally known (1 to 4 cm long and behind the zone of active root elongation—Jaunin & Hofer 1986), root hairs are not always present. Roots developing an ectomycorrhizal structure will not have root hairs (Mexal *et al.* 1979), but root hairs are common on some endomycorrhizal roots (Lyford 1975).

Root hair length varies between 80 and 1500 µm, with diameters of 5–20 µm, depending on species and cultivars (Dittmer 1949; Caradus 1979). Most studies of nutrient uptake by root hairs have been in relation to phosphorus uptake (Itoh & Barber 1983). Still, their contribution to the root system surface area of many plants is largely unknown.

Pathways of Nutrient Uptake for the Different Root Surfaces

The next question is whether all categories of roots have a nutrient uptake function. In any root there exist two pathways for nutrient uptake: the apoplastic and symplastic pathways. These pathways have been described by Dumbroff & Peirson (1971) and will not be repeated here.

A *white root* includes the area from the root tip to some point in the zone of primary tissues (Fig. 1). Therefore, a white root can have no endodermis, can have a developing endodermis, and can have a fully developed endodermis, depending on position along the root (Fig. 1). In the youngest white roots, the Casparian bands are absent and the xylem vessels are immature, so only very limited apoplastic entry to the xylem is possible. As the root matures the Casparian band becomes continuous and forms a barrier to apoplastic nutrient flow (Fig. 1).

In some cases a Casparian band can develop in the hypodermis, sometimes referred to as the exodermis (Peterson *et al.* 1981; Perumalla & Peterson 1986). In some plants this is an effective apoplastic flow barrier (Peterson *et al.* 1981). Yet, it is not clear if this strip is fully equivalent to that of the endodermis as proposed by Shone & Clarkson (1986). The presence and degree of development of suberin deposition is related to stress, with high water-stress causing it to form closer to the tip of the root.

In *brown roots* a fully developed endodermis can be compromised by short and lateral root development leaving a partial pathway for apoplastic water and nutrient flow where the roots exit the pericycle through the endodermis. If secondary xylem growth occurs, it can cause corruption of the endodermis, with the cortex progressively sloughing away (Troughton 1957). With time, cork tissue with a cork cambium develops, becoming another possible barrier to apoplastic flow.

Short roots are very often, but not always, mycorrhizal. In ectomycorrhizal plants, the fungal mantle becomes the surface area for absorption of both water and nutrients. Ectomycorrhizas may have a well-developed sheath which forms a tightly packed layer between the soil and root epidermis, extending around the root apex. The zone of maximum water and nutrient uptake of the root is separated from the soil by fungal tissue. Therefore all substances absorbed from the soil must pass through the fungal sheath or mantle before coming in contact with the outer cells of the root (Harley & Smith 1983). Like the root tissue, the fungal sheath is divided into symplastic and apoplastic compartments (Ashford *et al.* 1988, 1989).

Cellufluor has been used to test the apoplasmic permeability of the fungal sheath in *Pisonia* mycorrhizas. Ashford *et al.* (1988) documented the penetration of apoplastic tracers to the root epidermal cells in tip regions of the mycorrhizal root cap. Behind this area, where both the root and mycorrhizas are likely to be active, the sheath was impermeable to the tracer. Blockage of the apoplast was believed to be at the interface between fungus and root. It was concluded that the symplastic pathway within the fungus was very important at this stage. Short roots of endomycorrhizal species do not have the fungal mantle.

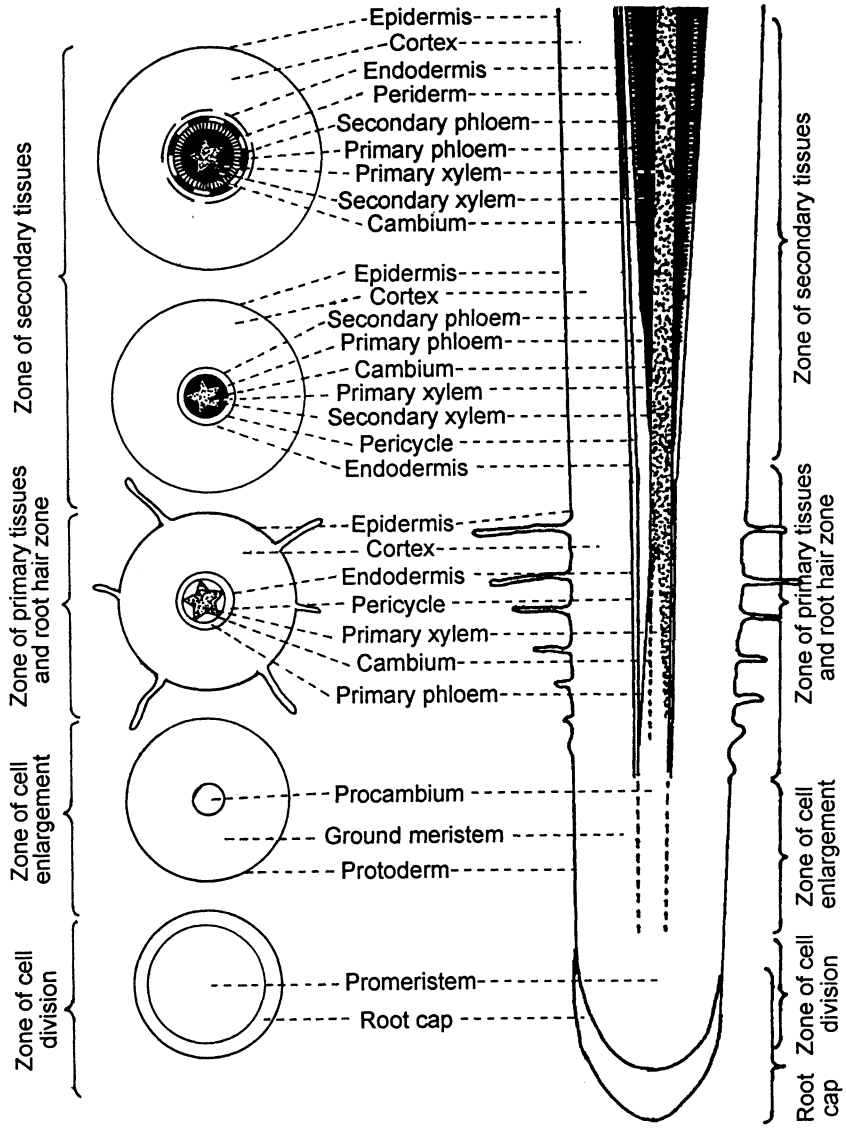

FIG. 1–A representation of a perennial root showing the anatomical changes along its length. Based on a figure by Richards & Considine (1981).

Root hairs generally arise from the epidermis. A root hair may increase the absorbing surface area and increase the ion and water absorption per unit length of root. When root hairs develop, a cuticle has been known to develop over them and the epidermis (Curl & Truelove 1986). The hydrophobic waxy components of the cuticle may increase resistance to water and nutrient flow, but the lack of experimental data makes definitive statements difficult. The relatively rapid deterioration of the cytoplasm of root hairs of maize roots suggests that root hairs may not function for very long (Fussender 1987).

Evidence of Uptake in Brown Roots

With annual plants it is well known that uptake rates of roots change with age (distance along the root axis) (Bowen 1969; Barber 1984; Marschner 1991) and that the important factor in zonality of ion uptake is the structural differences in walls of epidermal cells and in peripheral cells of the cortex, endodermis, and stele. There is no question that white roots, short roots, and mycorrhizal hyphae are active in nutrient uptake. The main question is whether brown roots function in uptake, and if so, is it active uptake? The question is significant because of the tremendous root length and surface area in this category.

The database for uptake by brown (woody?) roots is not extensive. *Citrus* and *Pinus taeda* both have brown (woody?) roots that absorb phosphate ($PO_{4}{-}$) (Crider 1933; Chung & Kramer 1975). The work by Chung & Kramer even suggested that an effective ion barrier existed, allowing selective ion absorption. Kramer (1946) suggested that the selective barrier was either the cork cambium, the vascular cambium, or both. Similar uptake rates for *Prunus* were subsequently reported (Atkinson & Wilson 1979). The same study by Crider (1933) also indicated active uptake of nitrate (NO_3) by woody (brown?) roots in *Citrus*, again with an effective ion selective barrier implicating active uptake.

The rate of potassium uptake by brown (woody?) roots of *Prunus* and *Malus* (Atkinson & Wilson 1980) and *Pinus elliottii* (Van Rees & Comerford 1990) was lower than or similar to the uptake rate of white roots. In the work on *P. elliottii* (Van Rees & Comerford 1990), potassium accumulated at a rate faster than that attributable to mass flow, suggesting an active uptake mechanism.

So, there is evidence that brown roots are capable of nutrient uptake. However, it is not clear if uptake is dominated by massflow or active uptake mechanisms. Nor, in most studies, is it clear exactly what category of brown roots was being investigated.

If uptake in brown roots is via apoplastic pathways, these pathways could include lenticels, wounds at the base of branch roots (Addoms 1946), and breaks in the endodermis (Dumbroff & Pierson 1971; Peterson *et al.* 1981). However, where active uptake is indicated it is not clear what is the barrier to apoplastic flow.

MICHAELIS-MENTEN KINETICS AS A DESCRIPTION OF ACTIVE UPTAKE

Appropriateness of the Equation for Real Conditions

Nutrient concentrations in the cytoplasm of soil-grown roots are usually much higher than in the soil solution at the root surface. Metabolic energy is required for nutrient uptake to occur against this chemical gradient. The transport of nutrients across cell membranes is enzymatically mediated and nutrient specific (Nye & Tinker 1977), but chemical details about transport to the enzyme carrier, the nature of the enzyme, movement via carrier, and release inside the cell remain largely matters of speculation.

Because active nutrient uptake at low concentrations (e.g., <1 mM) is enzymatic, the principles of enzyme kinetics have been applied to the mathematical description of nutrient uptake within the appropriate ranges of concentrations. In 1913, L.Michaelis and M.L.Menten developed a general theory of enzyme kinetics which was later extended by G.E.Briggs and J.B.S.Haldane (Lehninger 1970). The employment of simplifying assumptions resolved the theory mathematically to an asymptotic function between the velocity of the reaction and the concentration of the substrate, i.e., V = Vmax*S/(Km + S), where V is the velocity of the reaction, S is the concentration of the substrate, Vmax is the maximum velocity attainable, and Km is the S at half Vmax and is also related to the rate constants of the reactions and thereby the affinity of the enzyme for the substrate. The function is known as the Michaelis-Menten equation.

Claassen & Barber (1976) and Nielsen & Barber (1978) applied this function to nutrient uptake by roots, modified it by including a minimum concentration below which there was no further uptake, and substituted the terms I (inflow to a root) for V, and C (concentration) for S, i.e., I = Imax*(C–Cmin)/(Km + (C–Cmin)). Hence, this function is a description of nutrient uptake using Michaelis-Menten kinetics.

Although this function has fit observations of inflow *v.* concentration, there are several reasons why observations might deviate from this theoretical form. Nutrient uptake may be more complex than the simple enzyme system on which Michaelis-Menten kinetics are based. For instance, more than one enzyme or type of enzymes may be involved, diffusion to and from the carrier enzyme might be a limitation, energy supply to the enzyme may be a limitation, the rate constants may be nonlinear with substrate concentration (Lehninger 1970), and more than one uptake mechanism might be at work (Nye & Tinker 1977).

The phenomenon of multiphasic uptake (Epstein 1972; Hodges 1973; Nissen *et al.* 1980) is seen when Michaelis-Menten kinetics adequately describe uptake at normal soil solution concentrations, e.g., <1 mM, but at higher concentrations the process is not active and hence is unaffected if induction of the carrier enzyme is blocked (Omata *et al.* 1989; Oaks 1992). However, the high concentration at which this second mechanism dominates is much higher than the concentration of most nutrients under natural and most managed conditions. With the exception of nitrate under limited soil management conditions, multiphasic uptake is likely to be of no concern.

A further complication is that efflux of nutrients from roots may not be related to the activity of the uptake system because it is thought to be largely a diffusive process dependent upon internal and external nutrient concentrations and the integrity of the membrane.

Although Michaelis-Menten kinetics remain a useful description of nutrient uptake by roots, it is best thought of as an empirical description of nutrient uptake relative to solution concentration and not a theoretical approach.

Importance of Imax, Km, and Cmin Under Field Conditions

The importance of the Michaelis-Menten parameters under field conditions will depend mainly on the concentration of the nutrient in solution at the absorbing surface (C_{la}). The profile of nutrient concentration in solution relative to radial distance from the root can take three basic profiles. When plant uptake is equal to the supply by mass flow, C_{la} is equal to the bulk soil solution concentration. If demand at the root surface is greater than supply by mass flow in the soil, a depletion zone will develop and C_{la} will be less than the bulk soil solution. The higher the plant demand and the slower the rates of mass flow and diffusion supply, the lower will be C_{la}. However, if mass flow supply is more than the demand at the root surface, a surplus will build at the root surface and C_{la} will be greater than the bulk solution concentration.

The sensitivity of nutrient uptake to the Michaelis-Menten parameters depends on C_{la}. When mass flow is a dominant source of supply and is approaching or exceeding plant demand, then C_{la} is high. Uptake will be dependent on the value of Imax (Fig. 2). However, if mass flow does not contribute significantly to soil supply and supply by diffusion is significantly less than demand by the plant, C_{la} becomes very low. If C_{la} gets low enough, it gets to the point on the curves (Fig. 2) where they begin to converge and then plant uptake is not sensitive to Imax.

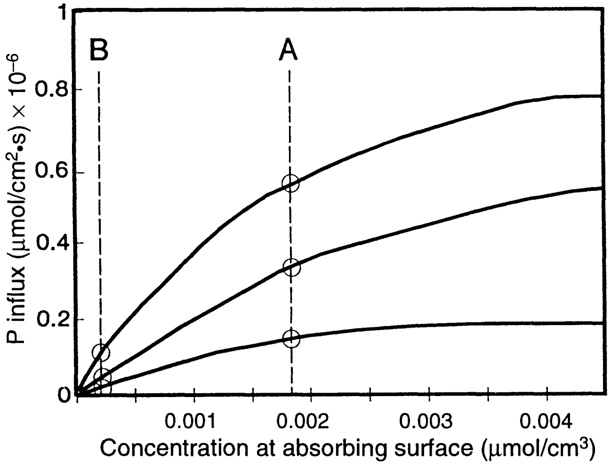

FIG. 2–A series of Michaelis-Menten curves. Case A represents the condition where the influx would be sensitive to the value of Imax while Case B represents the condition where the solution concentration is so low that sensitivity to Imax is unimportant.

There is a similar but reverse explanation to a plant's uptake sensitivity to Cmin. As C_{la} approaches the value of Cmin, plant nutrient uptake will be very sensitive to the value of Cmin. However, when C_{la} is much higher than Cmin (Cmin is very low relative to C_{la}), changes in Cmin will have little effect on plant uptake.

Although it is possible that these parameters could affect a plant's competitive ability, little is known about their genetic or environmental controls. Nevertheless, there is evidence that Km is under genetic and environmental control, and that plants continually presented with nutrients at concentrations approximating Km will grow at high relative growth rates in the absence of other limitations (Bloom *et al.* 1993).

It has been speculated that mycorrhizal hyphae may have lower Cmin values than the root with which they are associated, thereby enhancing phosphorus uptake. However, recent work by Li *et al.* (1991) indicated that this was not so for *Glomus mosseae* colonising *Trifolium repens* L. because both surfaces depleted phosphorus to similar concentrations.

The Imax parameter has received more attention than Km or Cmin, probably because Imax is more easily measured and it is quite responsive to imbalances between nutrient uptake rates and demand by the plant. For instance, Jungk *et al.* (1990) found that the Imax of soybean roots increased 376% owing to a decrease in pretreatment phosphorus concentrations from 30 to 0.03 μM, while Km values decreased by only 60%. Jackson &

Caldwell (1992) have shown for field-grown *Agropyron desertorum* roots that the phosphorus uptake capacity (i.e., Imax) can be increased by at least 73% in response to increases in phosphorus supply.

FEEDBACK MECHANISMS CONTROLLING UPTAKE KINETICS

Observed Temporal or Spatial Changes in Uptake Kinetics

Uptake kinetics of a root change as the root ages (i.e., with distance behind the root tip), and may vary temporally over short periods, e.g., 2 min (Ayling 1993), or spatially over small distances, e.g., 2 cm (Bowen 1969).

The potential significance of spatial and temporal variability of root uptake kinetics for nutrient competition between plants has been illustrated experimentally and theoretically by Jackson & Caldwell (1992) and Caldwell *et al.* (1992). They measured phosphorus uptake by excised roots of *A. desertorum* grown in microsites to which water or water with nutrients had been added. Plants were 0.5 m apart, and control and enriched microsites were located on opposite sides of individual plants. Four days after treatment with 1, 10, or 20 μM P, uptake rates of phosphorus by excised roots from enriched microsites were as much as 73% higher than those by roots from control sites. There was no comparable effect on nitrogen uptake in the range of 50–1000 μM. Model simulations indicated that this mechanism for enhanced phosphorus uptake from fertile microsites was more important than root proliferation.

Dighton & Harrison (1990) reported that, despite year-to-year variation in the phosphorus uptake capacity of fine roots of seven *Picea sitchensis* stands, increased growth rates after application of phosphorus fertiliser were accompanied by a decrease in the phosphorus uptake capacity by fine roots. The change in phosphorus uptake capacity after fertiliser application was considered a better indication of phosphorus deficiency in these stands than concentrations of phosphorus in foliage.

Feedback Mechanisms

The influx of potassium into barley roots was negatively correlated with the internal potassium concentration of the root ($r^2 = 0.71$; Siddiqi & Glass 1987). Similarly, the rate of ammonium influx into wheat roots was negatively correlated with the internal concentrations of ammonium and particular amino acids (Causin & Barneix 1993). Both of these studies indicated that high internal concentrations of a particular nutrient were associated with low rates of influx.

Although parameters in the Michaelis-Menten equation are strongly influenced by internal concentrations, the actual biochemical and physiological mechanisms of feedback control remain open to speculation. Hodges (1973), summarising the information available on ion uptake in the early 1970s, hypothesised a model of active cation and anion carriers located in the plasma membrane that transport nutrient ions into a cell in association with the transport of non-nutrient ions, e.g., hydroxide, hydrogen, and carbonate, and the regulation of a pH and charge gradient across the membrane. During the past two decades, some progress has been made on the specifics of this process for individual nutrients and plant or fungal species, but much is still speculative. For example, Siddiqi & Glass (1987) speculated that roots of low potassium concentration might be stimulated by the mediating effects of hormones to increase the synthesis of potassium transporters in the cell membranes. Causin

& Barneix (1993) speculated that glutamine or some product of transammination may be involved in the inhibition of net ammonium uptake. Genes have been identified that control the production of a nitrate carrier and its messenger RNA in *Aspergillus nidulans* (Unkles *et al.* 1991) and *Cyanobacterium synechococcus* (Omata *et al.* 1989). Although the biochemical mechanism responsible for phosphorus transport across root cell membranes is unknown, Clarkson & Grignon (1991) have clarified several aspects of pH and energetics control on the process.

Short-term feedback mechanisms may operate by regulating the energy supply to ion carriers in cell membranes or by altering the configuration of the membrane so that transport of the ion to, with, and from the carrier is retarded or enhanced. Longer term feedback on uptake kinetics probably involves regulation of the number of carriers.

EFFECTS OF ABSORBING SURFACES ON RHIZOSHPERE SOIL AND NUTRIENT SUPPLY

Absorbing surfaces take up nutrients predominantly in the liquid phase at a rate dependent upon the solution concentration of the nutrient. Absorbing surfaces can also influence these concentrations, modulate the supply of nutrients to the surface, and affect uptake rate. In this section we describe the main processes by which absorbing surfaces affect rhizosphere soil. Rhizosphere properties that are affected in both radial and longitudinal directions include: nutrient concentrations, pH, redox potential, root exudates, microbial populations, and their activity. Material for this section was drawn largely from Marschner (1991); additional sources are cited where appropriate.

Nutrient Concentrations and Micro-organism Activity

Nutrients are found in gradients from the root surface to the bulk soil solution. Nutrient concentrations along these gradients not only affect the direction of the diffusive flux but also probably influence solid-liquid phase equilibria and the rates of microbially mediated processes where these processes are nutrient dependent.

Partitioning of a nutrient between the solid and liquid phases is commonly non-linear and results in liquid concentrations that are more highly buffered at low than at high concentrations. As solution phase concentrations decrease in the depletion zone, the contribution of slowly available forms of nutrients can become important. For example, Jungk & Claassen (1986) found that within 2 mm of the surface of 7-day-old rape roots hydrochloric acid-extractable and ammonium-extractable potassium were both important sources of the nutrient, but within the rest of the depletion zone (2–10 mm) only ammonium-extractable potassium was depleted.

Rates of microbial processes that inter-convert nutrient forms may be limited by the concentration of substrates. Populations and activities of micro-organisms may be 5- to 50-fold higher in rhizosphere soil than in bulk soil owing to an enhanced supply of organic carbon. Non-infecting micro-organisms can affect nutrient supply to roots by (i) mineralising organic forms of nutrients, including those in dead cells of micro-organisms, (ii) immobilising inorganic forms of nutrients into new microbial biomass, (iii) affecting root morphology or physiology, and (iv) changing the chemical or physical forms of nutrients other than in mineralisation/ immobilisation reactions.

Processes that decrease nutrient concentrations include denitrification and immobilisation into microbial biomass of inorganic forms of many nutrients (e.g., ammonium, phosphate, and potassium). Microbial processes that increase nutrient concentrations include mineralisation by exo-enzymes such as proteinases (Paul & Clark 1989) and phosphatases (Dighton 1983; Tarafdar & Claasen 1988) that are induced by low concentrations of substrates, i.e., phosphate, ammonium, or nitrate-nitrogen. Additional organic nitrogen substrates for aminase enzymes in a depletion zone may be provided by asymbiotic nitrogen fixation, which is also stimulated by low concentrations of ammonium and nitrate (Dobereiner & Boddey 1981).

Inoculation of corn roots with *Azospirillum*, a non-symbiotic nitrogen-fixing bacterium, increased total root length per plant, the number of laterals per plant, the number of root hairs per millimetre of root, the length of root hairs, and shoot fresh weight (Martin *et al.* 1989). Hence, microbes in the rhizosphere have the potential to affect shoot and root growth, and root morphology.

There are many processes by which microbes change the form of nutrients beyond those in mineralisation/immobilisation reactions. Two examples will illustrate this potential. Some microbes produce chelators such as organic acids or siderophores that have a high affinity for specific trace elements such as iron and can release these nutrients near absorbing surfaces at rates commensurate with demand by the plant. Some microbes are much more effective at oxidising manganese than non-biological processes and thereby decrease manganese availability to absorbing surfaces.

Infecting micro-organisms that fix nitrogen (e.g., *Rhizobium* and *Frankia* species) or form mycorrhizas increase the nutrient supply to plants by converting atmospheric nitrogen into ammonium that is incorporated into plant tissues, and by increasing the extent and effectiveness of nutrient-absorbing surfaces. Mycorrhizal fungi can also produce many of the exudates that other microbes and plant roots produce which affect nutrient availability, e.g., organic acids, siderophores, and exo-enzymes.

pH and Organic Exudates

Absorbing surfaces affect rhizosphere pH by direct excretion or absorption of protons (H^+), hydroxyls (OH^-), or organic acids (protonated or deprotonated) in response to (i) a charge imbalance in cation *v.* anion uptake, or (ii) a specific nutrient deficiency. The effect is a net consumption or production of protons in the rhizosphere. These effects can result in pH values at the absorbing surface that are more than two units higher or lower than those in the bulk soil depending on the pH buffering capacity of the soil, the form of nitrogen supply, the plant species, and the nutritional status of the plant.

A variety of other compounds can be released in response to cell aging, root growth, specific nutrient deficiencies or toxicities, or other stresses. Sloughed-off cells and their lysates provide readily available forms of carbon and nutrients for microbial growth and activity in the rhizosphere and thereby affect nutrient availability by the means mentioned above. High molecular weight gelatinous exudates (mucilage) improve contact between the soil and the absorbing surface and are thought to enhance the transport of some nutrients, e.g., zinc (Nambiar 1976), to the surface in dry soils. These mucilages also inhibit the movement of aluminum to roots, reducing the risk of aluminum toxicity, and may have similar effects on copper, lead, and cadmium.

Several types of organic acids are excreted by roots and mycorrhizal hyphae in response to phosphorus deficiency. These acids, such as citrate and oxalate, improve phosphorus availability either by acting as an exchangeable ligand with iron- or aluminum-bound phosphorus,by dissolving metal-oxide surfaces that sorb phosphorus, or by complexing metals in solution and thereby reducing precipitation of metal phosphates. A good example of the importance of ligand exchange has been given by Ae *et al.* (1991) for pigeonpea. This species is very efficient at utilising iron-bound phosphorus because it produces piscidic acid that exchanges with bound phosphorus. Two other examples of the importance of these types of processes for phosphorus supply are given for *Pinus* by Fox *et al.* (1990) or Fox & Comerford (1990), and *Lupinus* by Gardner *et al.* (1982).

The supply of iron (and perhaps other trace elements such as manganese, zinc, and copper) to grasses is enhanced by the production of mugeneic acid (and its relatives) which binds with these nutrients and is transported as a complex into cells of the absorbing surface. This mechanism is apparently absent in non-grasses, but caffeic acid produced by non-grasses is thought to perform a similar function (Marshner 1991).

Redox Potential

High rates of oxygen consumption by microbes near absorbing surfaces can lead to lower redox potentials in the rhizosphere than in bulk soil, and thereby enhance denitrification, and the reduction of manganese, iron, and copper, which, depending on soil pH and availability of these trace elements, can promote or alleviate their toxicity or deficiency. The ability of many plant species to decrease the redox potential of the rhizopshere in response to iron deficiency is seen as a mechanism to increase iron availability and uptake.

Conversely, roots of some species growing in anaerobic conditions have been shown to oxidize their rhizosphere. For example, in *Pinus elliottii* oxygen (O_2) is moved from the aerated zone of the soil via porous roots and subsequently aerates its rhizosphere (Fisher & Stone 1990a, b, 1991). Such a mechanism allows active potassium uptake under what would appear to be anaerobic conditions.

SPATIAL PATTERN OF ROOTS AND ABSORBING EFFICIENCY

The effectiveness with which a root acquires nutrients from the soil solution is not just a matter of rate of supply from the soil balanced by the uptake potential at the root surface. It is also affected by competitive factors. Put simply, two roots that are each absorbing nutrients from an infinite volume of soil will be able to acquire more nutrients than two roots growing close enough to compete for nutrients. Competition between two roots will occur when depletion zones that develop around each root overlap (Nye & Tinker 1977). Therefore one would expect the degree of competition to be a function of the root density (or average inter-root distance) and the distribution pattern of roots in the soil (frequency distribution of the inter-root distance). Competition is also intimately related to the soil properties that define the size of the depletion zone around a root.

The spatial pattern of roots at the scale of inter-root competition has been the topic of very few studies (Litav & Harper 1967; Baldwin *et al.* 1971; Baldwin & Tinker 1972; Fusseder 1983; De Willingen & van Noordwijk 1987; Escamilla *et al.* 1991; Comerford *et al.* 1994), with only the latter two dealing with forest trees. The patterns have been described as random, uniform, or clumped spatial distributions. The early evaluations by Baldwin *et al.* (1971) sought to define the degree of inter-root competition based on spatial pattern and concluded that uniform patterns were the most efficient for nutrient uptake, while clumped patterns produced the most inefficient uptake. Under the test conditions, random patterns closely approximated the uptake efficiency of uniform patterns. This was further clarified by Escamilla *et al.* (1991) and Comerford *et al.* (1994) who showed that even random distributions of roots could lead to serious inter-root competition, even at relatively low root densities, if soil conditions allowed a wide depletion zone.

It seems reasonable to conclude that: (i) soils and nutrients which produce slow diffusion coefficients should result in minimal inter-root competition and the most efficient uptake per unit length of root, while (ii) soils and nutrients that allow high diffusion coefficients maximise the potential of overlapping depletion zones and inefficient uptake per unit length of root. This might be particularly significant in soils where nitrogen deficiencies (allowing depletion zones to rapidly develop and overlap) occur and nitrate is the dominant nitrogen form (since nitrate moves freely in most soils).

IMPLICATIONS FOR NUTRIENT MANAGEMENT IN FORESTS

Wood production is becoming increasingly specialised in the management of conditions for growth and the genotypes used to produce specific wood products. The nutrient supply and uptake concepts summarised above provide opportunities for forest managers and researchers, especially those in plantation forestry, to further refine nutrient management. In some places this knowledge could be used to identify potentially wasteful practices, such as too much fertiliser application, whereas in other places opportunities for an economic response to site amendments might be identified, e.g., the need for cultivation on particular sites. These theoretical predictions may complement and assist in the design of empirical experiments that investigate the manipulation of factors suspected of limiting tree growth. Some examples follow to illustrate this point.

Regulation of Nutrient Supply

Nutrient management in plantations is increasingly focused on matching nutrient supply from soil or added sources with nutrient demand by the crop (e.g., Smethurst & Nambiar 1990). The concepts presented above can be used in this context to predict rates of nutrient supply to absorbing surfaces without nutrient amendments and to predict the types of amendments needed to attain a desirable level of supply. For example, Barraclough (1989) used nutrient supply concepts to predict critical concentrations of soil solution nitrogen and phosphorus needed to sustain high growth rates of rape. Although the critical values depended on soil water content, and were 87 μM for nitrate-nitrogen and 10 μM for phosphate-phosphorus at a volumetric soil water content of 0.34, observed values were consistently higher. They concluded that nitrogen and phosphorus supply to the roots of this crop did not limit nutrient uptake. Predicting the effects of competing vegetation on nutrient uptake by crop trees is also possible. For example, simulated phosphorus and potassium uptake by *P. elliottii* growing with or without weeds was closely predicted over two 35-day periods by Smethurst *et al.* (1993). They also illustrated that simulated uptake under a variety of scenarios of weed control and fertiliser treatment qualitatively reflected observed differences in tree growth between the various scenarios. Such simulations could be used during the planning and interpretation stages of empirical experiments to increase the utility of these experiments and reduce the need for wide replication across the landscape and through time.

Diagnostic Techniques

The response of roots to increase their nutrient uptake capacity if rates of uptake are not adequate to satisfy the demands of the plant is under test as a diagnostic tool for predicting nitrogen, phosphorus, or potassium deficiencies in a range of crops including *Eucalyptus*, *Picea*, and *Pinus* species (Dighton & Jones 1992). Progress so far has confirmed that these forest genera exhibit the expected response, but the usefulness of this response as a diagnostic tool needs further evaluation against a background of variability in uptake capacity because of biological factors such as root age, seasonal and diurnal variations, temperature, and genotype. Several methodological factors also need investigation such as the type of root sampled, the period of delay between sampling and measurement, and the appropriate concentration of nutrient to expose the roots to during the uptake assay. A better understanding of uptake kinetics would contribute to the development of these diagnostic methods.

Selection of Genotypes

Plant genotypes differ in the value of soil solution phosphorus required to maximise growth. For example, Föhse *et al.* (1988) found that 80% of maximum yield of onion and tomato required 6.9 and 5.7 μM P, respectively, whereas wheat, ryegrass, and rape required only 1.4 μM P. Hence, it may be possible to refine for individual species the commonly cited critical value of 7 μM P in soil solution, although data presented by Skinner & Attiwill (1981) for *Pinus radiata* and by Tiarks (1982) for *P. taeda* suggest that this would remain an appropriate value. The extent and importance of within-species genotypic variability in nutrient uptake capacity and ability to acquire nutrients are largely unknown (Nambiar 1984). However, the increasing reliance on a restricted range of genotypes for high-growth-rate forest production and the increasing demands this will place on nutrient acquisition from commonly infertile soils suggest that nutrient acquisition traits should not be ignored. After reviewing this topic, Nambiar (1984) suggested that, "Breeding to enhance uptake has greater potential than breeding to improve nutrient utilisation" and that nutritional characteristics should be given more emphasis in breeding programmes than they currently receive.

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