

Nutritional Physiology of Trees

P Smethurst, CSIRO Forestry and Forest Products and Cooperative Research Centre for Sustainable Production, Hobart, Tasmania, Australia

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Introduction

Healthy trees require balanced nutrition to support metabolism and growth. Nutritional physiology is the field of knowledge pertaining to the uptake, utilization, storage, and internal transport and recycling of mineral nutrients. Here, nutritional physiology is described where possible with particular reference to trees and forests. First, a brief historical perspective of major developments in this field is followed by a description of essential nutrients. Finally, some aspects that pertain more to trees than other plant forms are outlined, i.e., nutrient pools and cycling. Trees have somewhat unique nutritional aspects related to their longevity, size and, in common with some other plant forms, the generally heterogeneous and low-nutrient-availability conditions to which some trees are adapted.

History and Key Contributors

The early history of tree physiology is that of plant physiology in general (Table 1). As long ago as 2500 BC, writings mentioned the fertility of the land, e.g., in Mesopotamia. Since those times, and up until about the end of the sixteenth century, interest developed in the effect of soil amendments on plant growth. By the end of this period, it was recognized that each soil type provided a different sort of nourishment and that it was affected by amendments and related to the ash content of plants. The next century and a half was characterized by the search for this nourishment, which was referred to as the 'principle vegetation.' This period was accompanied by advances in chemistry that enabled analysis of plant and animal materials. It was not until 1775 that Francis Home's analyses and experiments indicated that there was more than one 'principle.' Field plot experimentation commenced in the nineteenth century around the period when Liebig and Sprengel arrived at the law of minimum, i.e., yield was in direct relation to the single most limiting nutrient and unrelated to the level of others. With further advances in chemical analysis and experimental techniques, the importance of nutrients present in ever lower concentrations became evident from about the midnineteenth century. During the twentieth century, much work was done on the precise role played by each nutrient using

ever more sophisticated techniques, e.g., histology, microscopy, chemical purifications and analysis, and isotopic tracers.

Trees were included in some of these earlier studies, e.g., van Helmont studied the growth of a small willow, but specific studies of trees as distinct from other plant forms were not initiated until much later. During the twentieth century, some unique aspects of trees were elucidated, i.e., physiology of woody tissues, nutrient retranslocation, hydraulic properties, and nutrient budgets.

In recent decades, notable developments have occurred in understanding: (1) the processes delivering nutrients to roots; (2) the transport processes across plant membranes (e.g., during uptake by cells in roots and leaves); (3) the detailed biochemistry of nutrients; (4) the genetic and hormonal controls of a plant's response to its nutritional environment; and (5) nutritional effects on photosynthesis and assimilate partitioning.

Nutritional physiology has now reached the stage where individual or small numbers of genes have been identified that control specific nutritional process, e.g., nutrient transport across membranes. There is a remarkable degree of similarity in genetic make-up across the plant kingdom. Hence, processes studied in plants in general are also likely to be applicable to trees, but it appears that subtle differences in the control of genetic expression lead to the main differences in nutritional physiology between trees and other forms of plants.

Nutrients and Their Functional Roles

Carbon, hydrogen, and oxygen are essential for plant growth and are taken up as either CO₂ or water. Other elements essential or beneficial to growth are called mineral nutrients. Each mineral nutrient has one or more specific functions (Table 2). Essential nutrients are generally divided into groups based on concentration; macronutrients have concentrations greater than about 10 μmol g⁻¹ dry weight, and micronutrients less than this concentration. Other nutrients considered essential or beneficial for some higher plants are sodium (Na), silicon (Si), and cobalt (Co). There is also interest in selenium (Se), aluminum (Al), iodine (I), and vanadium (V), but further research is needed to clarify their status.

The concentration of ions in cytoplasm is maintained within limits imposed by the conditions required to maintain the integrity of organelles and cellular processes. An abundance of any particular ion will cause more of that ion to be stored at high concentrations in vacuoles or in other relatively nonreactive forms or locations. The distribution of

Table 1 Significant events in the development of tree nutritional physiology

<i>Date or period</i>	<i>Author(s)^a</i>	<i>Significance</i>
2500 BC	Various	Fertility of land recognized
900–0 BC	Various	Amendments promoted fertility
1563	Palissy	Ash content of plants represented material removed from soil
1561–1624	Bacon	Unique nourishment in soil
1577–1644	von Helmont	Water was the only nourishment
1627–1691	Boyle	Chemical analysis indicated that plants contained salts, spirits, earth, and oil, which were all formed from water
1604–1668	Glauber	Salt peter (KNO ₃), not water, was the main component of vegetation
1643–1679	Mayow	Seasonal niter variations in soil implied uptake by plants
1700	Woodward	Growth dependent on impurities in water
1741–1820	Young	Pot experiments showed that substances added to soil could promote or retard growth
1775	Home de Saussure	More than one principle in vegetation O ₂ uptake and CO ₂ released by plants, but the opposite occurred under light and CO ₂ was essential for growth; soil supplied ash and N; roots were selectively permeable to water and salts; plant composition varied with soil and age
1802–1882	Boussingault	Field plot experimentation
1787–1873	Sprengel and von Liebig	C came from the atmosphere, and H from water; alkaline metals needed to neutralize acids formed by plants as a result of metabolic activities; P necessary for seed production; toxicities related to excessive uptake and inadequate excretion; plant analysis led to fertilizer recommendations; law of the minimum
1843–c. 1890	Laws and Gilbert	N needed to be added to nonlegumes; soil fertility could be maintained by chemical fertilizers
1860–present	Various	Identification of essential and beneficial nutrients required in very low concentrations
1920	Hoagland	Composition of soil solution related to plant growth
1970–1991	Asher, Ingestad	Concepts and methods linking relative rates of growth, nutrient supply, and uptake
1977, 1984	Nye and Tinker, Barber	Mass-flow and diffusion theory in relation to nutrient supply and uptake
1950–1980	Passiourra	Soil–plant water relations
1970–1990	Jarvis	Forest water relations
1970–1992	Marschner, Mengel and Kirkby	Plant mineral nutrition
1960–1990	Various	Nutrient budgets of forest ecosystems; descriptions of tree root systems
1970–1993	Epstein, Clarkson	Kinetics of nutrient uptake
1991	Nambiar and Fife	Nutrient retranslocation in trees
1990s	Various	Genetic control of nutrition in several simple or agriculturally important plants

^aSince 1900, it has been increasingly difficult to attribute significant advances to individuals, but some key examples are indicated; significant advances tend now to be marked more by key syntheses of an accumulation of many incremental advances than by major new discoveries.

nutrients within a cell is therefore not uniform but localized into zones of either storage or use. Forms, utilization, and storage of the essential nutrients are summarized as follows.

Nitrogen

Because of the importance of N in plant metabolism, leaf area development, greenness (chlorophyll amount and function), and overall plant growth and yield are strongly dependent on an adequate N supply. Most forest tree species grow well with either NH₄⁺ or NO₃⁻ as their main N source, but a few have a preference for one or the other form. Nitrate is usually reduced to ammonia in the roots, but, with high levels of supply, reduction can be delayed until it reaches the leaves. Ammonia, which damages cellu-

lar processes, is rapidly incorporated into amino acids and its equilibrium with NH₄⁺ is highly pH-dependent. In leaves, a complex and incompletely understood set of interactions between vacuolar, cytoplasmic, and apoplastic NH₃ and NH₄⁺ concentrations occurs such that acceptable concentrations of NH₃ are maintained in the cytoplasm and these processes are mediated by ion-transporters in the membranes between these compartments.

Potassium

Potassium does not bond with C and is present in plant tissues (organic matter) as inorganic K⁺. The main role of K is in water relations (turgor control) and in the neutralization of weak acids in the cytosol and chloroplast; enzyme activation is another

Table 2 Mineral nutrients essential for healthy growth of higher plants, including trees

<i>Nutrient</i>	<i>Adequate foliar concentration for many species ($\mu\text{mol g}^{-1}$ DW)</i>	<i>Function</i>
Nitrogen (N)	1000	Amino acids, proteins, nucleotides, nucleic acids, chlorophyll, and coenzymes
Potassium (K)	250	Osmosis and ionic balance; stomata control; activates many enzymes; phloem loading; plant movement
Calcium (Ca)	125	Cell walls; enzyme cofactor; membrane permeability; regulates membrane and enzyme activities; secondary messenger
Magnesium (Mg)	80	Chlorophyll; activates many enzymes
Phosphorus (P)	60	Energy transport; nucleic acids, several coenzymes, phospholipids
Sulfur (S)	30	Some amino acids and proteins; coenzyme A
Chlorine (Cl)	3	Osmosis and ionic balance; probably photosynthesis reactions producing O
Iron (Fe)	2	Chlorophyll synthesis; cytochromes and nitrogenase
Boron (B)	2	Ca utilization; nucleic acid synthesis; membrane integrity
Manganese (Mn)	1	Some enzymes; chloroplast membrane integrity; O release during photosynthesis
Zinc (Zn)	0.3	Many enzymes
Copper (Cu)	0.1	Enzymatic oxidation and reduction
Nickel (Ni)	0.001	Enzyme function in N metabolism
Molybdenum (Mo)	0.001	N fixation and N reduction

important role. To some extent K can be substituted by other cations (Na, Mg, and Ca) or organic solutes.

Calcium

Calcium in plants is mostly in vacuoles and in cell walls; there is very little in cytoplasm. In vacuoles, Ca is commonly precipitated as insoluble crystals of oxalates, and in some species as insoluble carbonate, phosphate, or sulfate. Apart from storage, and by interaction with cytosolic Ca across vacuolar membranes, vacuolar Ca serves in osmoregulation and as a secondary messenger. In cell walls, Ca is bound to pectate polysaccharides. Very low concentrations of free Ca^{2+} (*c.* 100 nmol L^{-1}) are maintained in cytoplasm, apparently to avoid precipitation with organic phosphates such as adenosine triphosphate (ATP), and to avoid inhibition of many enzyme systems. The role of Ca in enzyme activation seems to be regulated through reversible binding to small proteins such as calmodulin. Ca is also very important to membrane stability, thereby regulating the leakage of cytoplasmic solutes and maintaining compartmentation of cells.

Magnesium

Magnesium is an essential part of chlorophyll, and up to half of total Mg may be in this form. It also combines with ATP to allow it to function in many reactions, and it activates many enzymes needed in photosynthesis, respiration, and nucleic acid synthesis. A substantial proportion of Mg is also involved

in the regulation of cellular pH and the cation–anion balance. The concentration of Mg in the cytoplasm is strictly controlled so as not to inhibit photosynthesis and storage is mainly in vacuoles.

Phosphorus

Phosphorus is taken up largely as inorganic phosphate (P_i). The form of P_i in both the plant and soil, is highly pH-dependent such that the degree of protonation ranges from none (PO_4^{3-}) in alkaline solutions to three (H_3PO_4) in strongly acid solutions. Inorganic P is rapidly incorporated into organic compounds, e.g., sugar phosphates, phospholipids, nucleic acids, and phosphate esters. As P supply increases beyond sufficiency, P_i accumulates in vacuoles and as polyphosphate and phytate.

Sulfur

Sulfur is taken up by roots as SO_4^{2-} , which either accumulates or is reduced to $-\text{S}_2$ or $-\text{SH}$ forms. Sulfur is an essential component of many metabolic compounds, e.g., some amino acids, enzymes, coenzymes, and cofactors, and the S–S bond is responsible for maintaining many of the folds in proteins. Sulfur is particularly important for photosynthesis and oil production.

Chlorine

Chlorine seems to be important in charge-balance and osmotic functions, and it is concentrated in chloroplasts but does not occur as a metabolite.

Iron

Iron acts as a structural component and cofactor for enzymatic reactions, and it is absorbed and utilized in the Fe^{2+} form.

Boron

Boron uptake is mainly passive as boric acid (H_3BO_3). Boron is involved in development and growth of meristems, but it is poorly retranslocated from older shoots to more actively growing shoots. Boron has a strong affinity for OH^- groups and is thereby mainly involved in cell walls, sugar translocation, membrane transport, carbohydrate metabolism, RNA metabolism, and photohormonal activity. Boron can accumulate in the ends of needles of conifers to very high concentrations, which reflects unidirectional transport during transpiration.

Other Micronutrients

Further details of Mn, Zn, Cu, Ni, and Mo are given in the further reading list; although these nutrients occur at very low concentrations, they are essential for plant growth.

Nutrient Supply

Nutrient uptake by roots accounts for nearly all nutrient uptake under natural and cultivated conditions, but foliar uptake is important under some circumstances, e.g., in densely populated areas where NH_3 gas and other nutrients in dust are significant, in nurseries where nutrients are applied as foliar sprays, and in forest plantations where foliar sprays are used to correct some micronutrient deficiencies.

Nutrients are taken up by roots mainly as inorganic ions from soil solution. The rate of uptake depends primarily on the concentration in the soil solution immediately adjacent to the root. The rate of nutrient uptake is independent of the rate of water uptake, but the concentrations of nutrients at root surfaces depend strongly on soil water content. Soil water content is important because it affects root growth and nutrient transport to the root surface in both the water flux created by transpiration (called mass flow), and the diffusive flux towards or away from the root. The forms of ions taken up by roots differ somewhat with plant species and growing conditions, and they are regulated by a combination of soil processes, the importance of which depends on the nutrient in question. These processes include organic matter mineralization/immobilization, mineral dissolution/precipitation, solid/liquid equilibria, oxidation/reduction reactions, and solid, liquid, and gaseous inputs and outputs (*see Soil Development and Properties: Nutrient Cycling*).

Uptake and Translocation

Nutrients move passively between, but external to, cells in the root cortex (apoplastic transport). Uptake, i.e., nutrient movement across the plasmalemma of root cells, can be a passive process, but it is more often an active process requiring energy, because the ion movement is usually against a gradient in electrochemical potential. A variety of mechanisms specific and nonspecific to individual ions are involved in uptake, some of which are well understood, but most of which are only postulated or poorly defined. Some of these mechanisms are restricted to certain groups of related plants but most occur widely across the plant kingdom, including trees.

Some nutrients are transformed soon after uptake, e.g., NO_3^- is often reduced to NH_4^+ and incorporated into amino acids in roots prior to transport to the shoot. Nutrients generally diffuse radially inwards in roots from one cell to the next by crossing plasmodesmata (**Figure 1**). Water can also pass from cell to cell via a transcellular path, but this is unlikely to be an important path for nutrients. Via plasmodesmata, nutrients pass the casparian strip, which largely blocks apoplastic transport at the endodermis, and they continue on to the cytoplasm of the xylem parenchyma cells. A mainly active process then releases nutrients into xylem vessels for passive transport towards the shoot. Transport in xylem sap involves exchange with cell walls and surrounding living cells. Coniferous trees lack continuous vessels but instead have tracheids which somewhat impede the flow upwards. However, they allow intensive transfer of solutes between xylem and phloem. Xylem-to-phloem transfer is important because water transport is directed mainly towards zones of high transpiration; these are not the zones of high nutrient demand because their main growth phase has passed. Phloem-to-xylem transfer occurs but its importance is largely unknown. The proportions of xylem and phloem transport depend on the ion of interest and other conditions.

Nutrients diffuse from the xylem into the apoplasm of the target tissue, which is usually a leaf. Transfer into the cytoplasm is analogous to uptake in roots and hence it is usually active. The uptake of foliar-applied nutrients is by the same mechanism if the nutrient has been able to pass the cuticle which is waxy and poorly pervious in some species.

Nutrient Pools and Internal and External Cycling

One key difference between trees and most other plant forms is their lifespan. The oldest trees are

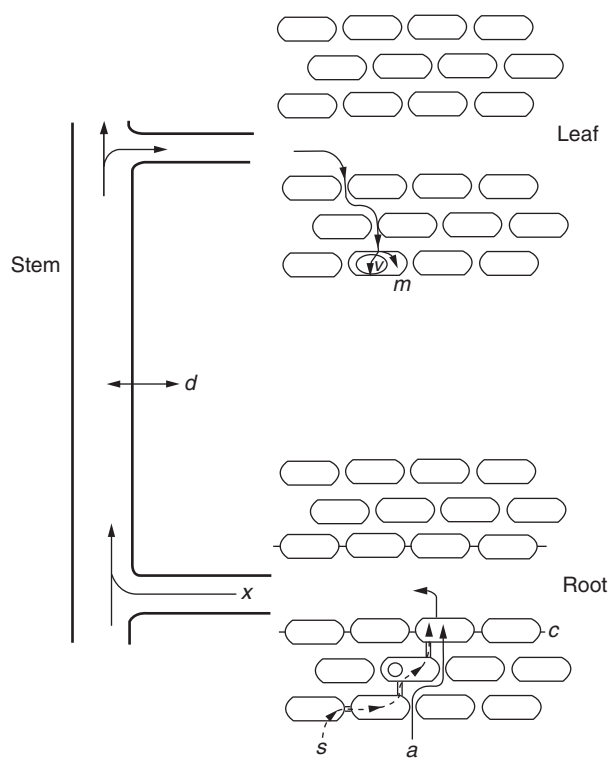


Figure 1 Simplified diagram of the path of nutrients from soil solution to utilization and storage in leaves. Nutrients move through roots external to the plasmalemma of cells, i.e., apoplastic (a) pathway, or are taken up across these membranes and transfer to adjacent cells via plasmodesmata, i.e., symplastic (s) pathway. Symplastic transport may include transformation and intermediate storage, e.g., in vacuoles (v). Apoplastic passage to the xylem is largely blocked by an impermeable casparian band (c) and suberized cell walls. Once released to the xylem stream (x), nutrients are transported towards the shoot, but during transport they may diffuse (d) reversibly into adjacent tissues, e.g., phloem and sapwood. In leaves, nutrients continue to be carried in veins and into cell walls via diffusion and mass flow of the transpiration stream. Uptake into leaf cells then occurs across the plasmalemma, followed by metabolic use (m) or storage, e.g., in vacuoles (v). Some nutrients are involved in symplastic–apoplastic exchange during the life of a leaf, and withdrawn to other tissues before or during senescence.

several thousand years old, and even most production forests are one or more decades old when harvested. In contrast, most of our knowledge about nutritional physiology has been developed from studies of species that live for only a year or two. Because of the longevity of trees, some aspects of nutrition develop that are not as obvious in ecosystems based on shorter-lived species. Of particular note are the low concentrations of nutrients in wood compared to other tissues, the large pools of nutrients potentially held in trees, the large proportion of annual nutrient supply that can be satisfied by internal nutrient recycling, and the importance of external nutrient cycling in older forests. Some of

these points are illustrated by an examination of the budgets of various nutrients for a typical 50-year-old, high-productivity eucalypt forest (Table 3) and a typical 16-year-old loblolly pine (*Pinus elliotii*) plantation (Table 4), and for K in 10- and 40-year-old black pine (*P. nigra*) plantations (Figure 2).

In recent decades, substantial knowledge has accrued on nutrient budgets for a variety of forest ecosystems and the processes controlling the rates of transfer of nutrients between pools has been greatly clarified. For example, it used to be thought that nutrient retranslocation from nonsenescing foliage was a response to low nutrient availability, i.e., under nutrient-stressed conditions the proportion of nutrients retranslocated would be increased, even if the total amount was less when compared to less nutrient-limited conditions. However, in many species, it seems retranslocation is driven by the rate of growth, such that the total amounts and proportions of nutrients (on a whole-tree basis) required for new growth that are met by nutrient retranslocation increases with growth rate, which in turn is often positively correlated with external nutrient supply. Relatively fertile conditions can stimulate growth to such an extent that external nutrient supply cannot meet the demand of an expanding canopy. Nutrients are then withdrawn from leaves or needles lower in the canopy that remain alive and retranslocated to zones of higher demand. Hence, retranslocation is demand-driven. A separate mechanism drives nutrient withdrawal from senescing leaves such that the proportion of nutrients in individual leaves (or needles) withdrawn prior to senescence will depend on genotype, nutrient status, and other environmental factors. This process is most pronounced in deciduous trees, but it is also significant in evergreens. Leaf senescence is triggered by seasonal and microclimatic effects related to reduced light availability or temperature, and in some cases is under hormonal control (e.g., auxins and cytokinins). Leaf senescence and nutrient withdrawal to various degrees can also be triggered by water or nutrient limitations or toxicities (e.g., of salt or Al) or shading.

In contrast to non-woody species, sapwood provides trees with a transient store of some nutrients under some conditions. For example, N can move into sapwood during periods when uptake greatly exceeds the requirement for new growth, and later be withdrawn when nutrient supply–demand conditions are reversed.

Conclusions

Interest in soil fertility and plant nutrition can be traced back several millennia, and several centuries

Table 3 Mass of organic matter and amounts of nutrients in pools and transfers in a typical eucalypt forest of high productivity aged 50 years

	Organic matter ($t\ ha^{-1}$)	N	P	Ca ($kg\ ha^{-1}$)	Mg	K
Pools						
Above-ground stand	500	500	50	500	250	400
Litter layer	30	150	10	110	30	25
Return from plant to soil per year						
Litterfall	8	60	2	60	20	10
Leaching	0.05	5	<0.1	5	2	15
Inputs and outputs per year						
Rainfall	0.01	5	<0.1	5	5	2
Streamflow		5	0.01	0.2	3	2
Total cycle per year^a		105	6	75	32	53
Return, plant to soil		65	2	65	22	35
Internal redistribution		30	3	0	5	10
Inputs–outputs		7	<0.1	5	2	0
Net supply from soil reserves per year		10	1	5	3	8
Other inputs per year						
N ₂ -fixation, asymbiotic + symbiotic		7				
Rock weathering		0	0.1	3	1	8

^aTotal cycle is the sum of all of the fluxes between plant and soil plus that needed for new growth.

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Table 4 Transfer rates of nutrients in a typical 16-year-old loblolly pine plantation

Component	N	P	K	Ca	Mg
	($kg\ ha^{-1}\ year^{-1}$)				
Requirement of trees					
New needles	55.0	6.3	31.9	8.1	4.8
1-year-old needles	0	0	0	8.1	0
Initiated branches	4.3	0.7	5.2	1.7	0.7
1-year-old branches	2.3	0.3	–0.6	2.5	0.4
Stem	5.3	0.6	4.4	3.0	1.2
Roots < 1 cm in diameter	48.7	12.3	20.0	34.4	9.2
Roots > 1 cm in diameter	1.5	0.4	2.4	0.7	0.7
Total requirements	117.1	20.6	64.5	58.5	17.0
Transfer within trees					
From 2-year-old needles	17.0	0	18.0	0	0
Transfer to forest floor					
Litterfall	58.2	7.8	16.0	29.2	6.9
Throughfall + steamflow	9.6	0.5	12.3	6.0	2.0
Total to forest floor	67.8	8.3	28.3	35.2	8.9
Transfer to mineral soil					
Forest floor to mineral soil	25.2	4.0	20.6	24.1	4.7
Roots < 1 cm in diameter to soil	48.7	12.3	20.0	34.4	9.2
Total to mineral soil	73.9	16.3	40.6	58.5	13.9
Additional transfer					
Requirements in excess to transfer to mineral soil	26.2	4.3	4.7	0	3.1
Soil depletion	38	0.34	48	35	10
Loss in ground water	0.70	0.03	1.56	1.26	0.88

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for trees *per se*, but the rate of improvement in our scientific understanding of nutritional physiology has increased markedly in recent decades. The growth, maintenance, and reproduction of plants requires 14 nutrients supplied mainly from the soil through a variety of uptake mechanisms in roots.

Transport from the roots, via xylem to leaves, involves a variety of passive and active mechanisms to move nutrients between zones of different concentration. Ultimately, nutrients are utilized in specific metabolic roles, or, if in excess, are generally reversibly stored in particular zones of the cell or less

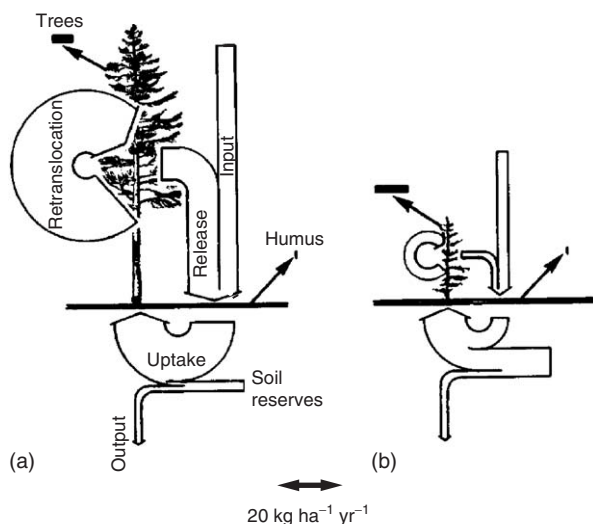


Figure 2 Patterns of K cycling in (a) 40-year-old and (b) 10-year-old *Pinus nigra* plantations. This diagram illustrates the change in sources and sinks of nutrients as a tree grows. The older trees here had about half the annual requirement for K as the younger trees. Most of this requirement was met by retranslocation and cycling through the litter layer, in contrast to a younger tree that relied heavily on soil reserves. Reproduced with permission from Miller H (1984) Dynamics of nutrient cycling in plantation ecosystems. In: Bowen GD and Nambiar EKS (eds) *Nutrition of Plantation Forests*, pp. 53–78. London: Academic Press.

reactive forms. Nutrient retranslocation occurs to meet the demands of an expanding canopy and some nutrients are conserved by withdrawal from leaves during senescence; these processes are quite pronounced in trees. Numerous physiological mechanisms are under some degree of genetic control, the elucidation of which will be a major focus of investigation for the next few decades. In contrast to non-woody plants, trees can to some extent store nutrients in sapwood under very high nutrient supply regimes and later withdraw these nutrients during periods of insufficient supply from soil.

See also: **Soil Biology and Tree Growth:** Soil Organic Matter Forms and Functions; Tree Roots and their Interaction with Soil. **Soil Development and Properties:** Nutrient Cycling; Nutrient Limitations and Fertilization. **Tree Physiology:** A Whole Tree Perspective; Physiology and Silviculture; Root System Physiology; Shoot Growth and Canopy Development; Stress; Xylem Physiology.

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Canopy Processes

R O Teskey, University of Georgia, Athens, GA, USA

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Introduction

A forest canopy is the aggregate of the leaves of trees that typically forms a layer overhead. It may also include the leaves of vines, epiphytes, and parasitic plants when they are present. A canopy can have large gaps, allowing plentiful light to reach the forest floor, or be closed and dense, with almost no light penetrating below it. The primary purpose of the forest canopy is to capture solar energy needed for photosynthesis. A number of factors can reduce the potential carbon gain of forests by preventing the