NUTRIENT DYNAMICS AND REQUIREMENTS OF FOREST CROPS

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ABSTRACT

All species of trees share the same basic nutrient requirements. Proportions of mineral nutrients needed for unimpaired growth are similar among woody and herbaceous plants (at least under controlled laboratory conditions), although the quantities required per unit of time differ according to inherited potentials for growth. Availability of mineral elements has a large impact on dry matter partitioning between plant parts. Root growth can be favoured as well as suppressed in response to low nutrient availability. Both conifers and broadleaved species (deciduous and evergreen) can be very fast-growing under favourable soil conditions. Generally, conifers and broadleaved evergreens use less NPP for foliage production than deciduous species but the quantity of nutrients taken up and returned annually to the forest floor is generally lower in evergreen species. Nutrient-use efficiency, particularly of nitrogen, is slightly higher in conifers than in deciduous broadleaved species; it becomes higher when trees grow older and the processes associated with internal nutrient cycling are operating fully. Plantations managed for short rotations are the most nutrient-demanding, and cause the greatest losses of nutrients from the site at harvest.

Keywords: biochemical cycling; dry matter partitioning; growth rate; nutrient uptake; nutrient concentrations; nutrient retranslocation; nutrient use efficiency.

INTRODUCTION

Nutrient cycling in forest ecosystems has been studied since the end of the last century. Loss of nutrients through exploitation of timber was at that time generally believed to constitute a negligible threat to long-term forest productivity. However, a decrease in site quality was recognised in areas where timber production was combined with the practice of litter removal for use in cowsheds and stables (Köstler 1956; Rehfuess 1981). The establishment of large-scale plantation forests during past decades, in which rotation length has been considerably decreased through genetic improvement of planting stock and the introduction of modern silvicultural techniques, constitutes a new threat for the long-term productivity of the forest site (Bowen & Nambiar 1984). Intensified forest management, in combination with the recent use of harvesting residues as an alternative energy source, has increased the export of nutrients from the forest site. However, losses of nutrients may not be confined to those nutrients contained in the removed biomass. Certain silvicultural activities (e.g., prescribed burning, herbicide treatment, soil ploughing or ripping) may cause

substantial losses of scarce elements such as nitrogen and phosphorus (Attiwill 1981). Furthermore, leakage of base cations in areas with heavy acid deposition, as in central Europe and eastern North America, has allegedly imposed further nutritional stress to which trees are not accustomed. Other elements in these areas are beginning to take over the role played mainly by nitrogen as the growth-limiting nutrient. As a consequence, decreased tree growth and vitality are now common features in many industrialised countries (Cape *et al.* 1990; Hüttle 1993; Oren & Schulze 1989).

Basic knowledge of the processes regulating nutrient transfers (i) in the soil (the geochemical cycle), (ii) between tree and soil (the biogeochemical cycle), and (iii) inside the trees (the biochemical cycle) is decisive for the achievement of sustained forest growth. In this paper attention will be focused on nutrient transfer processes occurring inside the tree and from the tree back to the soil via litter formation, covering both the qualitative and quantitative aspects of mineral nutrition. By doing so I will try to answer such questions as: Do species or genotypes differ in their qualitative mineral requirements, in that they require essential minerals in different proportions? Do species vary in their absolute nutrient requirements for a given rate of biomass production? How do the age, nutritional status, and water status of the tree affect dry matter partitioning between roots, stem, and leaves? These topics will be illustrated with examples from laboratory investigations, natural forests (including plantations not treated with fertiliser), and stands managed (treated with fertiliser and sometimes irrigated) for short and long rotations. Broadleaved species as well as conifers will be included. The laboratory examples concerning the qualitative nutrient requirements of trees have been taken from studies in which the concept of steady state nutrition has been applied (Ingestad & Lund 1986). The advantage with this technique is that, during exponential growth, conclusions reached about growth dependence on environmental variables are largely independent of plant size and age.

The examples presented in this review include a number of field trials where the influence of both water and nutrients on growth, nutrient uptake, and dry matter partitioning, mainly between above-ground parts, has been extensively studied. These trials/projects are (i) SWECON (Swedish Coniferous project, *Pinus sylvestris* L.), (ii) Skogaby (south Sweden, *Picea abies* (L.) Karst.), (iii) Furadouro (Portugal, *Eucalyptus globulus* Labill.), and (iv) the Biology of Forest Growth experiment (BFG, Australia, *Pinus radiata* D. Don). My belief is that the results obtained from these controlled field trials are of general value, and may be applied to other tree species and to less intensively managed forest stands.

NUTRITION AND GROWTH—BASIC PRINCIPLES
Mineral Element Proportions

There are no major controversies with regard to the mineral elements needed to sustain plant development, although some debate exists whether elements such as silicon, sodium, and cobalt (nitrogen fixers) should be included in the list of essential elements. Of current concern is the amount needed of each element, i.e., the mineral nutrient proportions in the tissues, for unimpaired growth. The general opinion is that large species- and genotype-differences exist. This is not surprising considering the enormous range of climatic and edaphic conditions in which trees grow. Furthermore, the morphological and phenological differences between trees, or plants in general, are taken as evidence of large species-variations in nutrient demand. Considerable differences in growth response among families

of *Pinus radiata*, when grown under low soil-phosphorus conditions, have been reported (Nambiar 1985). Similar observations have been made for other nutrients and plant species. Such observations, however, do not necessarily imply that certain species/genotypes have lower physiological requirements of certain elements than others. Rather, the morphology of the root system, its distribution in the soil, and its ability to release hard bound nutrients such as phosphorus or iron via secretion of enzymes or organic acids, are characteristics more likely to play a key role in nutrient uptake and plant growth under harsh soil conditions (Attiwill & Adams 1993).

Tissue analyses on samples taken from field-grown plants reveal large variations in nutrient composition both within and between species. Basically, these variations mirror the soil composition at the particular site, and differences in the ability of species to accumulate or exclude excessive uptake of certain elements. However, laboratory investigations carried out by Ingestad and co-workers revealed surprisingly small differences in the proportions of minerals taken up under non-limiting nutrient conditions. A comparison of the macro-nutrient proportions by weight (N = 100) found under conditions of free access to all mineral nutrients for a number of deciduous and evergreen tree species, cereals, cucumber, lingonberry, and bilberry (Table 1) revealed more similarities than differences in young plants with

TABLE 1–Proportions by weight of some nutrient elements (N = 100) present in plants at optimum steady state nutrition and maximum growth

Species	Fraction	Proportion						Reference
		N	K	P	Ca	Mg	S	
Betula pendula	Plant	100	67	13	5	8	nm	Ingestad 1979a
	Leaf	100	53	14	6	10	nm	Ingestad 1979a
Salix viminalis	Plant	100	72	14	7	10	nm	Ericsson 1981
	Leaf	100	45	16	11	11	15	Ericsson unpubl. data
Populus simonii	Plant	100	70	14	7	7	nm	Jia & Ingestad 1984
	Leaf	100	48	11	7	7	nm	Jia & Ingestad unpubl. data
Alnus incana *	Plant	100	50	19	8	13	nm	Ingestad 1980
	Leaf	100	41	16	10	14	nm	Ingestad unpubl. data
Eucalyptus	Plant	100	64	13	9	9	8	Ericsson 1989
globulus	Leaf	100	37	10	10	9	6	Ericsson 1989
Pinus sylvestris	Plant	100	45	14	6	6	nm	Ingestad 1979b
Picea abies	Plant	100	50	16	5	5	nm	Ingestad 1979b
Cucumis sativus	Plant	100	75	13	9	9	9	Ingestad 1972
Vaccinium sp.	Plant	100	50	13	7	8	9	Ingestad 1973
Triticum aestivum, Secale cereale, Hordeum vulgare, Avena sativa	Plant	100	80	17	9	9	nm	Ingestad & Stoy 1982

nm = not measured
* = inoculated seedlings

respect to the mineral nutrient proportions taken up at growth maximum. The great similarity between species in nutrient requirements demonstrated in Table 1 is less surprising when it is considered that all plants share the same basic physiological processes, such as photosynthesis, respiration, cell division, and the production of associated enzymes.

Plants are opportunists and, when possible, take up more nutrients than actually required for growth of new tissues. The data presented in Table 1 have recently been shown to contain a certain fraction of "luxury" uptake except for nitrogen (e.g., Ericsson & Ingestad 1988; Ericsson & Kähr 1993). This behaviour may explain the major differences shown in Table 1. For example, the minimum proportion of phosphorus in relation to nitrogen required to sustain maximal growth was found to be 8 in juvenile leaves of *Eucalyptus globulus* (N = 100, Ericsson 1994b), i.e., the same as for birch (Ericsson & Ingestad 1988). When uptake of potassium and magnesium in excess of growth requirements was prevented in birch, the proportions of these nutrients in relation to nitrogen could be decreased to 25 (Ericsson & Kähr 1993) and 4.4 respectively (Ericsson & Kähr 1995), without affecting the relative growth rate of the seedlings.

Although the data presented clearly demonstrate that plants share the same basic mineral requirements, such data are sometimes questioned since they are obtained under laboratory conditions and with young plants. There is no reason, in my opinion, to believe that basic physiological processes on a cellular level, and thus mineral requirements for the production of new cells/tissues, should change when a plant becomes older or grows under field conditions. However, the amounts of nutrients that have to be met from root uptake, or internal recirculation, change during the life span of a tree.

The lack of constancy in tissue nutrient concentrations in field-grown plants is taken as evidence that the results obtained from the cited laboratory investigations are of low general value (*see* Nambiar 1985). However, cycling of nutrients within individual plant parts also occurs under steady state nutrition, although nutrient addition, nutrient uptake, and biomass increment proceed at the same rate. A pronounced gradient in leaf nutrients from the top to the bottom of the shoot is a normal feature in plants grown with the Ingestad technique, although the mean leaf/plant nutrient concentration remains constant during the phase of steady state growth (Ericsson & Kähr 1993, 1995; Ingestad 1979a). Obviously, basic plant properties (e.g., nutrient transfers from old to young developing leaves) do not change just because plants are grown under artificial conditions.

Tissue Nutrient Concentration and Growth

A linear relationship between tissue concentration of the limiting nutrient and plant growth has been demonstrated for a variety of species under laboratory conditions (Ericsson 1981, 1994b; Ingestad 1979a, 1980; Ingestad & Kähr 1985; Jia & Ingestad 1984). In Fig. 1, this relationship is exemplified for nitrogen and with the species *Alnus incana* (L.) Moench, *Eucalyptus globulus*, *Populus simonii*, and *Salix viminalis*. A linear relationship between tissue concentration and growth has been demonstrated also for phosphorus (Ericsson & Ingestad 1988), potassium (Ericsson & Kähr 1993), magnesium (Ericsson & Kähr 1995), sulphur (Ericsson & Kähr in prep.), iron (Göransson 1993), and manganese (Göransson 1994).

A positive correlation between the tissue content of minerals and plant growth is generally observed also under field conditions (Aronsson & Elowson 1980; Rytter & Ericsson 1993;
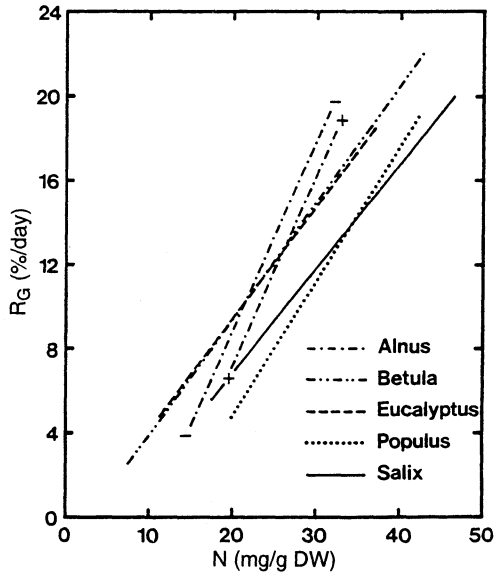
FIG. 1–Relationship between internal nitrogen concentration and growth (R_G) of *Alnus incana*, *Betula pendula*, *Eucalyptus globulus*, *Populus simonii*, *Salix viminalis* (from Ericsson *et al.* 1992).
+ = inoculated plants, − = uninoculated plants.

Nilsson & Wiklund 1994, 1995; Pereira *et al.* 1989; Snowdon & Benson 1992). However, deviations from this relationship are found, particularly when growth is also depressed by low water availability. Nutrients tend to accumulate in the tissues under such conditions, since growth of shoots is more sensitive to water stress than that of roots (Bongarten & Teskey 1987; Cannell 1985). Improved growth in eucalypts from fertiliser application is generally not associated with increased tissue nutrient concentrations (Cromer & Williams 1982). Sometimes even a negative correlation between nitrogen-status and growth of eucalypts has been demonstrated (Cromer *et al.* 1981). However, a clear and positive relationship between the leaf-nitrogen status and growth of *Eucalyptus globulus* has been demonstrated when the negative impact on growth from water shortage was minimised through daily irrigation of both control stands and those treated with fertiliser (Pereira *et al.* 1989). A positive relationship between growth and foliar concentrations has also been demonstrated in *Eucalyptus camaldulensis* Dehnh. (Bhimaya & Kaul 1966) *E. deglupta* Bl. (Lamb 1987), and *E. grandis* Maiden (Schönau 1981).

Nutrient Status and Dry Matter Partitioning

The genetic constitution of plants plays a superior role in determining the way assimilates are partitioned between roots, stem, and leaves. However, the growth environment plays an important role in its expression. The root fraction of the total biomass tends to decrease under low light conditions (Ingestad & McDonald 1989; Waring & Schlesinger 1985). The opposite occurs when water limits growth (Bongarten & Teskey 1987; Cannell 1985). An increased allocation of biomass to below-ground parts is generally associated with nutrient

deficiencies. Logically, such a growth response would enable plants to explore a larger soil volume at a time when the demand for nutrient uptake for shoot growth has decreased. However, recent investigations have shown that plants do not respond to nutrient shortage in a uniform way. Root growth is just as likely to be suppressed in response to decreased nutrient availability, as happened when birch seedlings were grown in the laboratory with limited potassium (Ericsson & Kähr 1993), magnesium (Ericsson & Kähr 1995), or manganese (Göransson 1994) (Fig. 2). An increased root fraction of the total biomass is obtained only when nitrogen (Ingestad 1979a), phosphorus (Ericsson & Ingestad 1988), or sulphur (Ericsson & Kähr in prep.) is in low supply. These contrasting patterns with regard to assimilate partitioning between above- and below-ground plant parts may be explained (Ericsson 1995) by the different physiological roles played by the individual elements. There is an increase in the shoot:root ratio when minerals closely associated with carbon fixation (potassium, magnesium, manganese) are in low supply (Marschner 1986). The opposite effect is obtained when the availability of minerals closely involved in the synthesis of new tissues (nitrogen, phosphorus, sulphur) limits growth (Marschner 1986). Thus, if the rate of carbon fixation cannot meet the demands set by growth, roots will suffer most because of their greater distance from the supply of assimilates. If, on the other hand, growth is limited by the availability of nutrients essential for the formation of new tissues, roots will constitute the greater sink (e.g., Brouwer 1962; Thornley 1972). This source-sink related allocation model may also be used to explain why root growth is reduced under growth-limiting light or carbon dioxide conditions, as well as why the opposite occurs when water limits growth. The asynchronous growth pattern of shoot and roots during the growing season (Bevington & Castle 1985; Hinckley et al. 1981) may also be explained by the suggested source-sink model, as well as why root production tends to decrease after canopy closure (Miller 1986). The latter phenomenon is probably a result of increased carbon costs for assimilate transport and maintenance respiration without a concomitant increase in carbon assimilation (Attiwill 1979).
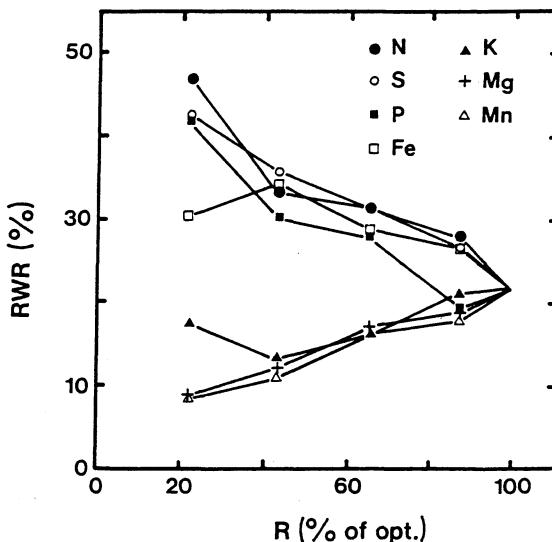

FIG. 2–Root weight ratio (RWR) as a percentage of total plant (*Betula pendula*) at stresses of different nutrients. The stresses were from 20% of optimum relative addition rate (R) of a certain nutrient to no stress at optimum (= 100%) (from Ericsson et al. 1992)

Besides the influence of nutrients, light, or carbon dioxide on the shoot:root ratio, the production and utilisation of carbohydrates are also affected by daily fluctuations in temperature above- and below-ground. As a consequence, the exact outcome from all these interactions on plant growth and development is difficult to predict. Plant growth on a yearly basis is, according to Luxmoore (1991), a result of 365.25 diurnal cycles with varying interactions between carbon source and sink strengths. Nevertheless, the presented data are useful in that they point out the likely direction of response to changes in the growth environment, as well as the probable mechanisms behind a changed biomass-allocation pattern.

An analysis of the mechanisms behind the large increase in productivity achieved through breeding and genetic selection among agricultural crops reveals no connection with the efficiency of the photosynthesis apparatus (Elmore 1980; McDonald 1984). Neither does the increase in the rate of photosynthesis per unit leaf area in response to an improved plant nitrogen status explain why internal nitrogen status (Fig. 1) has such a strong influence on plant growth rate (McDonald 1984). In fact, photosynthesis in birch grown at different nitrogen-availabilities, when expressed per unit leaf area and measured at the growth light level, proceeds with almost the same rate despite a four-fold difference in the relative growth rate of the plants (McDonald et al. 1991)

The large gain in productivity among agricultural crops has basically been obtained through a shift in the pattern of dry matter distribution within the plant (Gifford & Evans 1981; Gifford et al. 1984). The new high-yielding varieties use a larger fraction of the incoming photosynthetically active radiation during the growing season. Consequently, the amount of light collected by the leaves during the growing season is more important than the efficiency of the photosynthesis apparatus for the rate of biomass production. A strong linear relationship between intercepted light and yield (Fig. 3) has also been demonstrated for a
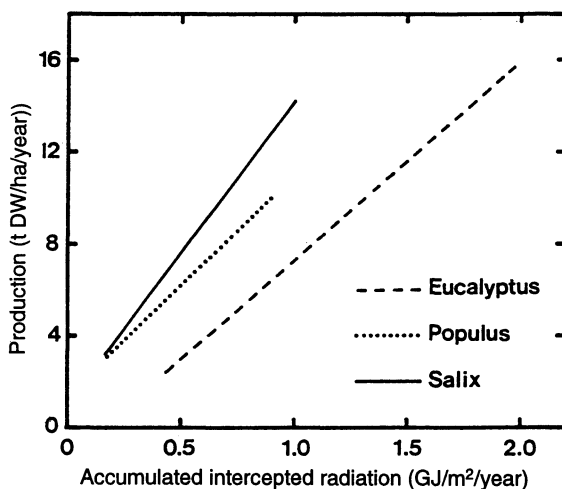

FIG. 3–Relationship between above-ground dry matter production and intercepted solar radiation for 1-year-old stands of *Salix viminalis* and *Populus trichocarpa* in Great Britain and for a 2- to 9-year-old stand of *Eucalyptus globulus* (from Ericsson et al. 1992)

large variety of plant species (Monteith 1977) including trees (Cannell *et al*. 1988; Linder 1985). The nutrient (nitrogen) status of plants affects growth mainly via light interception by strongly influencing the partitioning of assimilates between roots, stem, and leaves (Ågren & Ingestad 1987; Ingestad & Ågren 1988). The size of individual leaves (McDonald 1989) and their longevity and position in the canopy (Ford 1984; Linder & Rook 1984), as well as the start and termination of the growing season (Cannell 1989), are all factors closely linked to the nutrient status of the plant. Improved nutrition not only increases leaf area index (LAI), the shoot:root ratio, and the conversion efficiency of intercepted light (ε), but also decreases the fine root mortality and thereby the cost of fine root turnover (Linder & Axelsson 1982).

The interaction of water and nutrients on light interception and light use efficiency (ε) and hence biomass production under field conditions, is illustrated in Fig. 4. A non-closed forest stand operating at point A and with a $\varepsilon = \varepsilon_2$ is assumed. Under unchanged water and nutrient conditions the stand will move towards point B, where maximum LAI and hence biomass production under the given conditions are reached. During short-term water stress, ε will decrease, A ⇨ C, due to stomatal closure. If the stress persists for a long period, leaf shedding will occur and LAI decreases, C ⇨ D. When the water stress is released, ε increases, D ⇨ E. The growth rate of the stand will reach the initial value once the LAI has recovered. If the nutritional status of the stand is improved, ε will increase owing to reduced costs for fine root
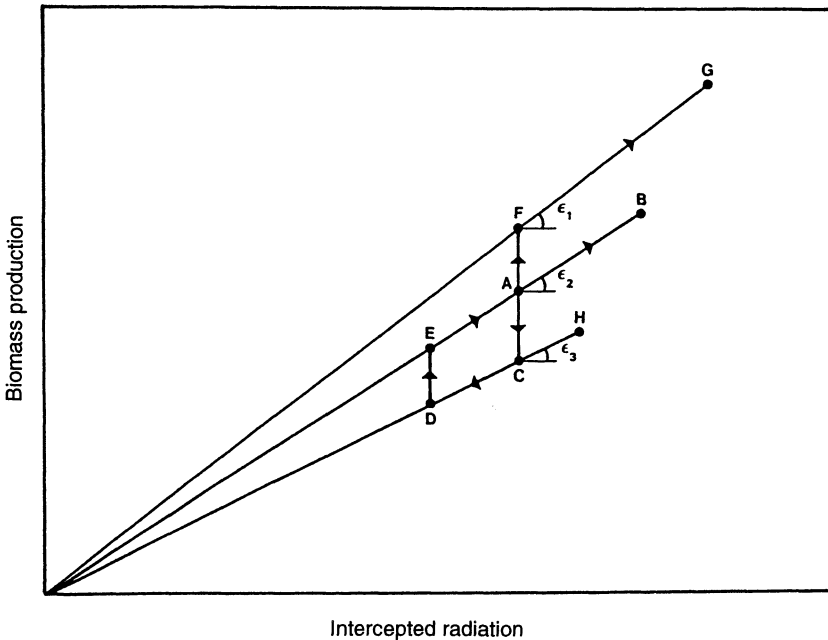
FIG. 4—Relationship between biomass production and intercepted photosynthetically active radiata in forest ecosystems. The slope of the lines, ε, represents the efficiency of conversion of intercepted light into biomass. The slope ε_1 represents the efficiency under optimum conditions in terms of water and nutrient availability, ε_2 moderate nutrient stress and non-limiting soil water conditions, and ε_3 nutrient stress and limiting soil water conditions. For further explanations *see* text. (From Linder 1987.)

turnover and improved ability of the plants to utilise high irradiance levels (Evans 1989), A ⇨ F. Simultaneously, LAI will increase, F ⇨ G, as a result of increased leaf size and numbers as well as decreased mortality (cf. Linder & Rook 1984). The point G may be regarded as the optimum LAI; its value is species-dependent and can be only reached under non-limiting water and nutrient conditions (cf. Grier & Running 1978; Jarvis & Leverenz 1983; Linder 1985).

GROWTH DYNAMICS AND ASSOCIATED NUTRIENT REQUIREMENTS IN FOREST STANDS
Growth Dynamics

Growth of trees, from establishment to maturity, follows a biphasic pattern. In the early stages of stand development a large amount of the assimilates is expended upon new foliage production. As a consequence, assimilate production (gross primary production, GPP), as well as the rate of biomass increment (GPP minus carbohydrates used for respiration = net primary production, NPP), increases and peaks at the time of canopy closure. Pioneer species, such as willows, generally develop more quickly and reach their maximum biomass production earlier in the life cycle than late-successional species, which often develop into tall and long-lived trees. Canopy closure and maximum current annual biomass increment (CAI) in *Salix viminalis* plantations occur as early as 4–6 years of age in Sweden (Willebrand *et al*. 1993), whereas NPP in a natural *Eucalyptus obliqua* L'Herit forest peaked at age 45 (Attiwill 1979).

Plant respiration continues to increase after canopy closure as living non-photosynthetic tissues in branches, bole, and large roots accumulate. As a consequence, NPP starts to decrease. Also, the length of this growth retardation phase varies considerably between species, and may last for periods from a few decades to several hundred years.

Stem Production and Associated Nutrient Requirements

The growth potential among tree species varies greatly. The edaphic and climatic conditions also strongly influence the rate of biomass production. Data on current and mean annual increments of dry stems (CAI and MAI) and, where possible, of above-ground net primary production (NPP) are presented in Table 2. The selected examples include conifers and deciduous and evergreen broadleaved species, grown under both natural and managed (irrigated and treated with liquid fertiliser) conditions. A close inspection of the data reveals that CAI and MAI of cold and warm temperate species rarely exceeds 10 tonnes/ha/year under natural conditions. However, the growth potential of most species is normally not realised under natural conditions. Daily irrigation and fertiliser application during the growing season of basket willow (Christersson 1987), *Picea abies* (Linder & Flower-Ellis 1992; Nilsson 1993), and *Pinus sylvestris* (Linder 1987) in Sweden, *P. radiata* in Australia (Snowdon & Benson 1992), and *Eucalyptus globulus* in Portugal (Pereira *et al*. 1989, 1994) have resulted in 100% to 300% increases in the rate of biomass production. The NPPs reached under such growth conditions are comparable to those reported for intensively managed agricultural crops such as potatoes and sugar cane (Odum 1971).

Interestingly, fast growth is a characteristic which is not confined to only one tree type. Evergreen trees, such as conifers (e.g., *Pinus radiata*) and eucalypts (e.g., *Eucalyptus*

TABLE 2–Current and mean annual increment (CAI and MAI) of stems and total above-ground biomass production (NPP) in natural and managed conifer and broadleaved (deciduous and evergreen) stands.

Species	Locality	Age years	CAI	MAI	NPP	Ref.
				tonnes/ha/year		
Conifers						
Natural stands						
Picea abies	South Sweden	38	5.8	–	8.2	1
P. abies	Central Sweden	27	2.2	–	–	2
P. abies	North Sweden	30	0.9	–	–	3
Pinus sylvestris	C. Sweden	20	0.9	–	3.5	4
P. radiata	Australia	14	7.6	7.5	17.0	5
P. radiata	New Zealand	12	11.5–26.5	3.7–8.8	20.9–48.5	6
Managed stands (irrigated and treated with liquid fertiliser)						
Picea abies	S. Sweden	38	13.2	–	20.6	1
P. abies	C. Sweden	27	8.5	–	–	2
P. abies	N. Sweden	30	3.5	–	–	3
Pinus sylvestris	C. Sweden	20	3.2	–	11.4	4
P. radiata	Australia	14	24.7	8.4	39	5
Broadleaved – deciduous						
Natural stands						
Alnus incana	Finland	–	10	7.5	–	7
A. rubra	N. America	–	14	12	–	8
Populus tremuloides	N. America	40	–	4.1	–	9
Managed stands (irrigated and treated with liquid fertiliser)						
A. incana	C. Sweden	7	11	5–6	–	10
Platanus spp.	Greece	5–6	–	7–15	–	11
Populus euramericana hybr.	Italy	–	–	13.0	–	12
P. euram. hybr.	Italy	13	–	13.4	20.5	13
P. deltoides	N. America	12	–	9.4	–	14
P. trichocarpa	Scotland	5	–	10–12	–	15
Salix viminalis	Scotland	1	–	9–10	–	16
S. viminalis	S. Sweden	2	13.3	11.4	21.5	17
S. viminalis	S. Sweden	3	12–18	12–14	18–24	18
Broadleaved – evergreen						
Natural stands						
Eucalyptus camaldulensis	Spain	10–15	–	8	–	19
E. globulus	Australia	6	3.6	2.0	7.2	20
E. globulus	Portugal	6	12.4	12.1	23.7	21
E. globulus	Spain	10–16	–	30	–	22
E. obliqua	Australia	66	9.0	5.4–5.7	14	23
E. grandis	Australia	27	–	12.2	–	24
Managed stands (irrigated and treated with liquid fertiliser)						
Eucalyptus archerii	England	4	–	10	–	19
E. globulus	Australia	6	10.0	6.2	15.4	20
E. globulus	Portugal	6	27.7	22.3	35.7	21

1 Nilsson 1993   9 Perala & Alban 1982   17 Nilsson & Ericsson 1986
2 Axelsson & Axelsson 1986   10 Rytter 1989   18 Christersson 1987
3 S.Linder pers.comm.   11 Panetsos 1981   19 Pearce 1985
4 Linder & Axelsson 1982   12 Frison 1968   20 Cromer &Williams 1982
5 Snowdon & Benson 1992   13 Rossi Marcelli *et al.* 1980 21 Pereira *et al.* 1989
6 Beets & Pollock 1987b   14 Switzer *et al.* 1976   22 San Miguel 1986
7 Paavilainen 1981   15 Cannell 1980   23 Attiwill 1979
8 Zavitkovski & Stevens1972   16 Cannell *et al.* 1987   24 Bradstock 1981.

globulus), seem to be just as productive as species which shed all their leaves annually (e.g., *Salix viminalis*). However, if the length of the growing season is taken into account, which in Sweden is about one-third the length of that in Portugal and Australia, it becomes evident that the growth performance of willow is outstanding. *Salix viminalis* is more efficient in producing biomass per amount of light intercepted than *Populus trichocarpa* Torrey et Gray and *Eucalyptus globulus* (Cannell *et al.* 1988; Linder *et al.* 1986). The high yields reported for *Pinus radiata* and certain eucalypt species are generally not an expression of extreme fast growth but, as indicated above, a consequence of a long growing season. A growth rate of 14.6 m^3/ha/year, as reported for the fertiliser-treated and irrigated *P. sylvestris* stands in central Sweden, is as fast as 44.6 m^3/ha/year for *P. radiata* grown in Australia, if the large differences in the amount of light intercepted during the growing season are taken into account (Linder 1987). According to Linder (1987) the growth efficiency, in terms of stem volume production per amount of light intercepted, is equal for both species, 16×10^{-4} m^3/ GJ. In comparisons of the maximum attainable relative growth rate under laboratory conditions, the growth rate of *Eucalyptus globulus* seedlings was surpassed by 25% of the *Betula pendula* seedlings (Ericsson 1994b).

An estimate of the amounts of nutrients associated with annual stem production (note that this does not necessarily imply nutrient uptake from the soil of the same magnitude—*see* section on "Nutrient Dynamics and Requirements During Stand Development") is obtained by combining the information given in Table 2 with data on stem nutrient concentrations (Table 3). Willows, when managed for short rotations, have extremely large nutrient requirements for stem growth (Table 4). About 62 kg N/ha are required annually at a production level of 14 tonnes/ha in a 3-year-old *Salix viminalis* plantation. This is about 2 to 6 times more nitrogen than is required for a similar rate of stem production in *Pinus radiata* and *Eucalyptus globulus* respectively. The corresponding quantities of the other macro-nutrients are also much higher in fast-growing willows. About 11 kg P, 41 kg K, 7 kg Mg, and 55 kg Ca are required at a stem production rate of 14 tonnes/ha. These quantities are about 2 to 5 times greater than required for the same rate of stem production in *P. radiata* and *E. globulus*.

Leaf Production and Associated Nutrient Requirements

Production of leaves constitutes a large part of the NPP, as can be seen in the annual leaf production and total standing leaf biomass (evergreens) of a number of tree species under different cultural as well as climatic conditions (Table 5). The chosen examples clearly demonstrate that the availability of water and nutrients has a strong impact on foliage production. On average, 5–6 tonnes/ha/year are produced in established warm and cold temperate deciduous forests (Cole & Rapp 1981). Intensively managed euramerican hybrid poplars may produce as much as 7 tonnes leaves/ha/year (Rossi Marcelli *et al.* 1980). Similar and even higher rates of leaf production have been measured in energy forest plantations of *Salix viminalis* (Nilsson & Ericsson 1986).

Generally, the annual growth of leaves is lower in evergreens than in deciduous species at comparable rates of woody biomass production. Stem production of 13 tonnes/ha/year in *Picea abies* and *Salix viminalis* was associated with an annual leaf production of 3.8 and 8.2 tonnes, respectively (cf. Tables 2 and 5). Under favourable water and nutrient conditions, needle production in *Pinus radiata* reached 8.5 tonnes/ha/year in Australia (Snowdon &

TABLE 3–Nutrient concentrations (mg/g) in stems of natural and managed conifer and broadleaved (deciduous and evergreen) stands.

Species	Age	N	P	K	Mg	Ca	Ref.
Conifers							
Natural stands							
Picea abies	38						
Wood		0.7	0.06	0.6	0.15	0.56	[1]
Bark		5.3	0.6	3.4	0.8	0.6	[1]
Pinus radiata	12–29						
Wood		0.28	0.05	0.6	0.18	0.33	[2]
Bark		1.7	0.2	1.7	0.7	1.3	[2]
Managed stands (irrigated and treated with liquid fertiliser)							
Picea abies	38						
Wood		0.8	0.1	0.6	0.15	0.56	[1]
Bark		6.7	0.8	4.0	0.9	6.0	[1]
Pinus radiata	15						
Wood		0.82	0.13	1.0	0.22	0.52	[2]
Bark		3.5	0.5	6.6	0.9	2.4	[2]
Broadleaved – deciduous							
Natural stands							
Populus tremuloides	49	1.7	0.2	1.2	0.4	5.8	[3]
Managed stands (irrigated and treated with liquid fertiliser)							
Populus euramericana	10	1.7	0.5	2.2	–	4.0	[4]
P. euram.	2	6.1	0.9	2.6	0.7	5.8	[5]
P. deltoides	20	1.8	0.3	1.9	0.5	4.2	[6]
P. deltoides	2	1.9	0.3	2.0	0.5	4.3	[6]
Salix viminalis	1	3.9–7.5	0.5–1.2	1.4–3.8	0.5–0.6	2.4–7.8	[7,8]
S. viminalis	3–4	3.3–4.4	0.8	2.9	0.4–0.5	3.5–3.9	[9,10]
Broadleaved – evergreen							
Natural stands							
Eucalypts in Australia							
Wood		0.4–2.3	0.02–0.2	0.1–1.1	0.03–1.1	0.3–1.5	[11]
Bark		1.7–9.2	0.1–0.5	0.7–16.0	0.4–3.2	3.8–32	[11]
Managed stands (irrigated and treated with liquid fertiliser)							
Eucalyptus regnans	4–17	0.7–1.3	0.1–0.2	0.9–2.0	0.2–0.5	0.9–2.0	[12]
E. grandis	9						
Sapwood		1.1	0.14	1.4	0.15	0.53	[13]
Heartwood		0.07	0.02	0.24	0.58	0.13	[13]
Bark		0.25	0.21	3.7	1.4	18.8	[13]
E. fastigata	4						
Wood		1.9	0.11	2.2	0.3	0.7	[14]
Bark		0.54	0.37	5.4	2.3	11.8	[14]
E. nitens	4						
Wood		1.9	0.12	2.3	0.3	0.7	[14]
Bark		5.3	0.45	6.7	2.5	16.0	[14]

[1] Nilsson & Wiklund 1994, 1995
[2] Stewart *et al.* 1981
[3] Perala & Alban 1982
[4] Giulimondi 1966
[5] Giulimondi & Duranti 1974
[6] Switzer *et al.* 1976
[7] Ericsson 1984
[8] Nilsson & Ericsson 1986
[9] Vigre & Ledin pers. comm.
[10] Törner 1988
[11] Feller 1980
[12] Frederick *et al.* 1985a
[13] Birk & Turner 1992
[14] Madgwick *et al.* 1981

TABLE 4–Annual nutrient requirements (kg/ha) associated with stem production in managed and natural conifer and broadleaved (deciduous and evergreen) stands.

Species	N	P	K	Mg	Ca	Ref.
Conifers						
Natural stands						
Picea abies	2.6	1.1	5.9	1.9	5.3	1,2,3
2 tonnes stem/ha/year						
Managed stands (irrigated and treated with liquid fertiliser)						
Pinus radiata	15.4	3.4	30.7	5.9	14.6	4,5
20 tonnes stem/ha/year						
Broadleaves – deciduous						
Natural stands						
Populus tremuloides	7.0	0.8	4.9	1.6	23.8	6
4 tonnes stem/ha/year						
Managed stands (irrigated and treated with liquid fertiliser)						
Populus euramericana	22.1	6.5	28.6	9.1	75.4	7,8
13 tonnes stem/ha/year						
Salix viminalis	61.6	11.2	40.6	6.6	54.6	9,10
14 tonnes stem/ha/year						
Broadleaved – evergreen						
Natural stands						
Eucalyptus obliqua	4.7	0.14	0.8	0.6	2.4	11,12
5 tonnes stem/ha/year						
Managed stands (irrigated and treated with liquid fertiliser)						
Eucalyptus globulus	20.5	0.6	3.6	2.6	10.7	12,13
22 tonnes stem/ha/year						

[1] Nilsson 1993
[2] Nilsson & Wiklund 1994
[3] Nilsson & Wiklund 1995
[4] Snowdon & Benson 1992
[5] Stewart *et al.* 1981

[6] Perala & Alban 1982
[7] Giulimondi 1966
[8] Rossi Marcelli *et al.* 1980
[9] Christersson 1987

[10] Vigre & Ledin pers. comm
[11] Attiwill 1979
[12] Feller 1980
[13] Pereira *et al.* 1994

Benson 1992). A slightly lower peak value has been obtained in young and intensively managed *Eucalyptus globulus* stands in Portugal (Pereira *et al.* 1989). However, due to the perennial nature of needles and leaves of evergreens, the total foliage biomass may reach substantially higher values than in deciduous species. Under favourable growth conditions *Pinus radiata* may hold 14 tonnes needles/ha at age 14 (Snowdon & Benson 1992), whereas the needle biomass in *Picea sitchensis* (Bong.) Carr. may reach 26.6 tonnes/ha in Scotland (Ford 1982).

The nutrient concentrations in leaves are higher than in any other plant part except fine roots. This is illustrated in Table 6, in which data on the normal range of macro-nutrient concentrations in foliage of conifers and deciduous and evergreen broadleaved species have been compiled. Foliage of conifers and eucalypts contains in general half as much nutrients as that of fast-growing deciduous trees such as poplars and willows. The high nutrient content of leaves implies that large amounts of nutrients are required annually for growth of this plant part. An estimate of the annual nutrient requirements for foliage production can be obtained by combining the data presented in Tables 5 and 6. The largest quantities of nutrients are associated with leaf production in intensively managed willow plantations (Table 7). As

TABLE 5–Annual foliage production and standing leaf biomass in natural and managed conifer and broadleaved (deciduous and evergreen) stands.

Species	Age (years)	Leaf production (tonnes/ha)	Leaf biomass (tonnes/ha)	Ref.
Conifers				
Natural stands				
Picea abies	15–27	1.3	4.0	1,2,3
P. sitchensis	16–18	–	26.6	4
Pinus sylvestris	20–29	1.2	4.2	1,5
P. radiata	14	4.0	11.2	6
Managed stands (irrigated and treated with liquid fertiliser)				
Picea abies	15–27	3.8	22.0	1,2,3
Pinus sylvestris	20–29	3.6	10.6	1,5
P. radiata	14	8.5	14.0	6
Broadleaved – deciduous				
Natural stands				
Alnus glutinosa	22	7.6		7
A. rubra	–	5.0		8
*Populus tremuloides**	10–120	1.6–2.5		9
Cold temp. average*		5.4		10
Warm temp. average*		5.5		11
Managed stands (irrigated and treated with liquid fertiliser)				
Alnus incana	5	2.5–3.9		12
Populus hybrids*	–	5.5–6.0		9
Salix viminalis	1–3	4.2–8.2		13
Broadleaved – evergreen				
Natural stands				
E. calophylla, E. diversicolor				
E. dives, E. grandis, E. muellerana,				
E. obliqua, E. regnans	–	2.6–2.7	2.6–8.9	14,15
Managed stands (irrigated and treated with liquid fertiliser)				
E. globulus	3–9.5	3.0–5.9	13.2	16,17
E. grandis	9	1.0	8.6	18

* Data based on leaf litter

[1] Axelsson & Axelsson 1986
[2] Nilsson 1993
[3] Tamm 1974
[4] Ford 1982
[5] Linder & Axelsson 1982
[6] Snowdon & Benson 1992
[7] Mitchell *et al.* 1981
[8] Zavitkovski & Newton 1971
[9] Bernier 1984
[10] Cole & Rapp 1981
[11] Bray & Gorham 1964
[12] Rytter 1988
[13] Nilsson & Ericsson 1986
[14] Bradstock 1981
[15] Cannell 1982
[16] Cromer & Williams 1982
[17] Pereira *et al.* 1989, 1994
[18] Birk & Turner 1992

much as 250–360 kg N are required to produce 8.2 tonnes leaves/ha in *Salix viminalis*. The corresponding peak values for *Pinus radiata* and *Eucalyptus globulus* are 75 and 136 kg/ha/year, respectively. On average 15–60 kg N/ha/year in conifers and eucalypts, and 60–120 kg N/ha/year in deciduous broadleaved species, are associated with annual leaf production under natural conditions and after canopy closure. The requirements for the other macronutrients in natural and intensively managed plantations are 2–30 kg P/ha, 5–160 kg K/ha, 1–30 kg Mg/ha, and 5–160 kg Ca/ha.

TABLE 6–Nutrient concentrations (mg/g) in foliage of natural and managed conifer and broadleaved (deciduous and evergreen) stands.

Species	N	P	K	Mg	Ca	Ref.
Conifers						
Natural stands						
Picea abies	12	1.6	3.9	1.0	3.9	1
Pinus sylvestris	12	1.5	6.0	0.8	1.7	2,3
P. radiata	9	0.9	6.6	1.8	4.0	4,5
Pseudotsuga menziesii	12	2.7	4.1	1.1	2.8	6
Managed stands (irrigated and treated with liquid fertiliser)						
Picea abies	19	1.9	5.0	1.2	4.7	1
Pinus sylvestris	16	1.6	6.0	1.0	3.2	2,3
P. radiata	16	0.9	6.6	1.8	4.0	4,5
Broadleaved – deciduous						
Natural stands						
Acer saccharum	22	1.8	10	1.2	6.0	7
Alnus glutinosa	34	2.0	7.7	3.7	8.1	8
A. rubra	26	1.1	10	1.9	9.2	9
Fagus sylvatica	17–27	1.5–2.2	5.2–8.0	0.7–1.9	3.6–11.4	6
Populus tremuloides	16–23	2.0	7–11	2.4–5.0	16–37	10
Managed stands (irrigated and treated with liquid fertiliser)						
Alnus incana	32–38	4.0–5.0	14–20	3.3–4.6	6.0–9.0	11
Populus euramericana	21–28	1.9–2.6	15–20	3.0–3.5	19–26	12
Salix viminalis	30–44	3.4–4.9	17–20	3.1–3.6	3.7–5.9	13
S. dasyclados	36–38	2.4–3.2	18–22	2.7–3.7	4.1–5.9	13
Broadleaved – evergreen						
Natural stands						
Eucalypts:						
wet sclerophyll forest	15	1.1	4.6	3.9	6.8	6
dry sclerophyll forest	12	0.7	3.4	3.1	4.5	6
E. muellerana	9	0.5	3.8	2.5	7.1	14
E. globulus	14	0.9	6.2	1.3	8.9	15
Nothofagus truncata	12	1.2	8.1	1.4	7.1	6
Managed stands (irrigated and treated with liquid fertiliser)						
E. globulus	15	1.1	6.6	1.6	9.3	15
E. grandis	16	1.3	7.2	2.2	5.1	16
E. fastigata	18	1.1	9.1	2.5	7.4	17
E. nitens	20	1.3	9.1	1.9	7.2	17
E. regnans	18	1.5	6.6	2.0	5.6	18
E. saligna	16	1.2	10	2.6	5.5	19

[1] Nilsson & Wiklund 1994, 1995

[2] Aronsson & Elowson 1980

[3] Tamm 1963

[4] Snowdon & Benson 1992

[5] Stewart *et al.* 1981

[6] Attiwill 1981

[7] Likens & Borman 1970

[8] Viro 1955

[9] Turner *et al.* 1976

[10] Alban 1985

[11] Elowson & Rytter 1988

[12] McColl 1980

[13] Christersson 1987

[14] Turner 1981

[15] Pereira *et al.* 1994

[16] Birk & Turner 1992

[17] Madgwick *et al.* 1981

[18] Frederick *et al.* 1985a

[19] Frederick *et al.* 1985b

TABLE 7–Annual nutrient requirements (kg/ha) associated with foliage production in natural and managed conifer and broadleaved (deciduous and evergreen) stands.

Species	N	P	K	Mg	Ca	Ref.
Conifers						
Natural stands						
Picea abies	16	2.5	5.1	1.3	5.0	1,2
1.3 tonnes leaves/ha/year						
Managed stands (irrigated and treated with liquid fertiliser)						
Pinus radiata	136	7.6	56.1	15.3	34.0	3,4
8.8 tonnes leaves/ha/year						
Broadleaved – deciduous						
Natural stands						
Populus tremuloides	57	5.0	27.5	12.5	92.5	5,6,7
2.5 tonnes leaves/ha/year						
Managed stands (irrigated and treated with liquid fertiliser)						
P. euramericana	168	15.6	120	21.0	156	5
6.0 tonnes leaves/ha/year						
Salix viminalis	250–360	33	164	29.5	48	8,9
8.2 tonnes leaves/ha/year						
Broadleaved – evergreen						
Natural stands						
Eucalyptus obliqua	31.2	1.9	8.8	8.0	11.7	10,11
2.6 tonnes leaves/ha/year						
Managed stands (irrigated and treated with liquid fertiliser)						
Eucalyptus globulus	75	5.5	33	8.0	46.5	11,12
5.9 tonnes leaves/ha/year						

[1] Nilsson 1993   [5] Bernier 1984   [9] Nilsson & Ericsson 1986
[2] Nilsson & Wiklund 1994, 1995   [6] Alban 1985   [10] Attiwill 1981
[3] Snowdon & Benson 1992   [7] McColl 1980   [11] Cannell 1982
[4] Stewart *et al.* 1981   [8] Christersson 1987   [12] Pereira *et al.* 1994

Root Production and Associated Nutrient Requirements

Root production may consume a considerable fraction of annual net photosynthesis, although the standing root biomass tends to stabilise at around 20% of the above-ground standing biomass (Harris *et al.* 1977) . Estimates of fine root production in temperate and boreal forests range from 1 to 12 tonnes/ha/year (Fogel 1985; Gholz *et al.* 1986; Santantonio & Herman 1985). Although usually constituting less than 5% of the total tree biomass, fine roots often account for a major proportion of the stand production. Estimates range from 5% in a fast-growing *Pinus radiata* plantation (Santantonio & Santantonio 1987) to 68% of the total net primary production in a sub-alpine forest (Grier *et al.* 1981). Irrigated and liquid-fertiliser-treated 20-year-old *P. sylvestris* used 31% of the net photosynthesis for root production (Linder & Axelsson 1982). This fraction of the net photosynthesis was doubled in the untreated control trees. In the annual carbon budget for *P. sylvestris* presented by Linder & Axelsson (1982), annual photosynthesis was double that of the control, but above-ground production more than tripled, indicating a major change in carbon allocation patterns. Although between 30% and 60% of the annual assimilate production in the irrigated/ fertiliser-treated and the untreated *P. sylvestris* stands, respectively, was used below-ground, the standing root biomass in general constitutes only about 20% of the total biomass

in trees (Harris *et al.* 1977). This indicates that the rate of fine root turnover, particularly under nutrient- and water-limiting conditions, was pronounced. Shoot growth favoured over roots after fertiliser application has also been demonstrated for *Pseudotsuga menziesii* (Mirb.) Franco (Brix & Ebell 1969) and other forest stands as well (Santantonio 1989).

As already mentioned, deficiency of potassium, magnesium, and manganese causes the root fraction of the total plant biomass to decrease in birch seedlings (Ericsson & Kähr 1993, 1995; Göransson 1994). A similar observation has been made in magnesium-deficient *P. abies* stands (Meyer *et al.* 1988). Results from laboratory experiments with birch seedlings indicate that the negative impact from magnesium shortage on root production is further aggravated under excessive nitrogen conditions (Ericsson unpubl. data). Nitrogen taken up in excess of growth requirements is generally stored as amino acids (Näsholm & McDonald 1990), and acts in this way as a sink for carbohydrates. It may therefore be concluded that magnesium deficiency under conditions with a high nitrogen deposition rate will more seriously affect root growth and hence the uptake of nutrients and water. Element deficiencies which negatively affect carbon assimilation will probably have a more negative impact on root growth after canopy closure. The fraction of assimilates used for maintenance respiration during this developmental stage continues to increase, while net photosynthesis does not (Attiwill 1979).

The nutrient requirement associated with fine root production may be pronounced, since the nutrient concentration of fine roots is relatively high (Table 8). Thus, for the range of observed fine root production (1–12 tonnes/ha/year), 10–120 kg N/ha, 1–20 kg P/ha, 1–15 kg K/ha, 0.8–10 kg Mg/ha, and 3–30 kg Ca/ha are required. Nutrient retranslocation from dying roots is generally small (Nambiar & Fife 1991) (Table 8), but the opposite trend has

TABLE 8–Nutrient concentrations (mg/g) in fine roots of conifer and broadleaved (deciduous and evergreen) species.

Species	Root diameter	N	P	K	Mg	Ca	Ref.
		Conifers					
Picea abies	<2 mm	13.1–13.5	1.5–1.9	0.3–2.2	0.4–0.9	1.5–5.0	1,2
P. abies	<2 mm	5.8–11.4	0.6–1.3	0.2–1.3	0.4–0.9	1.0–6.6	3,4
P. abies	<2 mm*	7.4–11.5	0.6–1.1	0.5–0.6	–	1.2–7.7	4,5
Pinus sylvestris	<2 mm	4.1–9.8	1.1–1.5	1.4–3.0	0.9–1.2	1.0–1.5	6,7
P. sylvestris‡	<2 mm	15.0	2.2	1.3	1.2	1.7	7
P. sylvestris‡	<2 mm*	14.8	–	–	–	–	7
Pseudotsuga menziesii	<2 mm	4.4	0.5	0.4	–	3.8	8
		Broadleaved – deciduous					
Alnus incana	<1 mm	22–25	–	–	–	–	9,10
Salix viminalis	<1 mm	15.9	1.4	2.4	1.7	15.5	11
		Broadleaved – evergreen					
Eucalyptus globulus	<2 mm	13.2‡–13.4†	2.8‡–3.9†	1.2†–1.4‡	–	1.3†–2.1‡	12

* Dead roots
† Untreated stands
‡ Irrigated and treated with liquid fertiliser

[1] Clementsson-Lindell & Persson 1992
[2] Persson & Ahlström 1994
[3] Majdi & Persson 1995
[4] Majdi & Persson 1993
[5] Majdi & Persson 1989
[6] Helmisaari 1991
[7] Ahlström *et al.* 1988
[8] Santantonio *et al.* 1977
[9] Rytter 1989
[10] Rytter *et al.* 1991
[11] R-M. Rytter pers. comm.
[12] Madeira *et al.* in prep.

been reported (Meier *et al.* 1985). Most of the nutrients needed for root growth must therefore be obtained by direct acquisition from the soil, or arrive via the phloem from the shoot. The retention time of nutrients bound in fine root litter is probably shorter than 1 year (Head 1973; Santantonio & Herman 1985). Part of the yearly nutrient demands set by root growth can therefore be met from decomposition of root litter produced the same year.

Nutrient Dynamics and Requirements During Stand Development

The amounts of nutrients required for the annual rates of root, stem, and leaf production have so far been regarded as the product of the amount of biomass produced (Tables 2 and 5) and its average nutrient concentrations (Tables 3, 7, and 8). However, such an estimate does not necessarily imply a nutrient uptake of the same magnitude from the soil. On the contrary, a large fraction of the nutrients required for growth of new tissues can be met by internal cycling of nutrients. The ability to use the same nutrients over and over again, before they are finally discarded in litter or immobilised in heartwood, is a characteristic which is particularly well developed in trees.

During early stages of stand establishment most of the nutrients required for growth are derived from soil uptake. The amount of nutrients retained from senescent plant parts, mainly leaves, constitutes only a small fraction of the total needs. However, the amount of the total nutrient requirement which comes from retranslocation within the plant gains more and more importance as the stand approaches canopy closure. By that stage and onwards, a substantial part of the yearly nutrient needs is covered by biochemical cycling. This is illustrated for *Alnus rubra* Bong. in Table 9 in which the nitrogen fluxes and accumulation modelled over 20 years for three different rotation lengths are shown. The fraction of the total nitrogen-requirement which is met by internal cycling decreases from 33% to 28% or 9% when the interval between harvests is reduced from 20 to 5 or 2 years, respectively. A similar or slightly larger fraction of the phosphorus, potassium, and magnesium requirements can be met by nutrient retranslocation if sufficient time is allowed for the nutrient cycles characteristic of forests to become fully effective (Miller 1983). According to estimates by Bernier (1984), 45–78% of the nitrogen, 31–65 % of the phosphorus, 62–67% of the potassium, 68–70% of

TABLE 9–Nitrogen, phosphorus, and potassium requirements and removal (kg/ha) over 20 years for three rotation lengths in *Alnus rubra* (from Miller 1983).

	Number of rotations × rotation length (years)								
	1 × 20	4 × 5	10 × 2	1 × 20	4 × 5	10 × 2	1 × 20	4 × 5	10 × 2
	N			P			K		
Requirements	3680	2890	1730	302	225	132	1045	835	507
Retranslocation	1140	810	170	135	87	19	539	338	76
Uptake	2540	2080	1560	167	138	113	506	497	431
Litterfall	2080	1600	240	108	84	12	405	322	49
Litter mineralisation	1180	970	150	70	54	8	369	290	47
Uptake from min. soil	1360	1110	1410	97	84	105	137	207	384
Removed in harvest	460	480	342	59	54	57	101	175	85
Harvested biomass (stems, tonnes)	156	80	57	156	80	57	156	80	57
Nutrient uptake from mineral soil per tonne harvested stem biomass									
	8.7	13.9	24.7	0.6	1.1	1.8	0.9	2.6	6.7

the magnesium, and 63–67% of the calcium required for above-ground production in poplars can come from nutrient cycling within the trees. It should be noted, however, that for most tree species calcium is not cycled internally; instead it accumulates with time (Waring & Schlesinger 1985). Miller (1984) has shown that the uptake of soil-nitrogen in *Pinus nigra* var *maritima* remained the same at ages 10 and 40, although annual foliage and stem production had doubled. This observation clearly illustrates the importance of internal nitrogen cycling for the nitrogen-economy of trees.

Nutrient withdrawal from senescent leaves to stems and roots is certainly an important mechanism by which plants make more efficient use of a limited nutrient resource. Between one-third and two-thirds of the leaf nitrogen and phosphorus contents can in this way be transported back to woody tissues and stored for use in the coming season (Bernier 1984; Ericsson 1984; Pereira *et al.* 1989; van den Driessche 1984). This nutrient conservation mechanism is demonstrated for a number of conifers and broadleaved species in Table 10. Generally, nitrogen-fixing tree species retranslocate a smaller fraction of the leaf nutrients before leaf fall (Dawson & Funk 1981; Elowson & Rytter 1988).

In conifers, nutrient retranslocation from older needle age-classes occurs long before they are shed (Miller 1984). This is illustrated for *Pinus nigra* var *maritima* in Table 11. The oldest cohort of needles had lost 21% of the initial nitrogen-content before they turned yellow. The corresponding percentages for phosphorus, potassium, and magnesium were 17, 16, and 20, respectively. Altogether, 67%, 67%, 84%, and 60% of the initial nitrogen, phosphorus,

TABLE 10–Nutrient withdrawal from foliage (percentage of initial content) before abscission in conifers and broadleaved species (deciduous and evergreen).

Species	N	P	K	Mg	Ca	Ref.
Conifers						
Picea abies	7.5†–22‡	35†–50‡	68‡–72†	9‡–26†	3†– -15‡*	[1]
P. exelsa	–	2	17	-35	-2	[2]
Pseudotsuga menziesii	61	58	58	79	-487	[2]
Pinus radiata	40	58	66–84	-12	-43–333	[2]
Broadleaved – deciduous						
Populus tremuloides	78	67	58	-14	23	[3]
P. deltoides	74	67	72	49	38	[3]
Alnus incana‡	20	14	10	40	-37	[4]
A. rubra	30	50	6	5	-22	[5]
Fagus sylvatica	41	77	52	14	13	[2]
Broadleaved – evergreen						
Eucalyptus						
wet sclerophyll forests	59	41	12	28	-20	[2]
dry sclerophyll forests	50	63	32	27	-36	[2]
E. grandis	44	66	74	21	--52*	[6]
E. regnans	50	58	80	40	3	[7]
Nothofagus truncata	45	63	81	-26	-38	[2]

* The negative sign indicates nutrient accumulation
† Untreated stands
‡ Irrigated and treated with liquid fertiliser

[1] Nilsson & Wiklund 1994, 1995   [4] Elowson & Rytter 1988   [6] Turner & Lambert 1983
[2] Attiwill 1981   [5] Miller 1983   [7] Frederick *et al.* 1985a
[3] Bernier 1984

TABLE 11–Nutrient concentrations and amounts in current, 3-year-old (the oldest age-class on the tree), and newly fallen needles in *Pinus nigra* var. *maritima* (from Miller 1984).

Plant part	N	P	K	Mg	Ca
			mg/g dry weight		
Current needles	15.4	1.5	7.3	1.1	2.3
3-year-old needles	12.5	1.2	6.3	1.0	4.5
Needle litter	7.6	0.7	1.7	0.8	4.9
			mg/100 needles		
Current needles	67	6	31	5	10
3-year-old needles	53	5	26	4	18
Needle litter	22	2	5	2	14
Nutrient retranslocation between year one and abscission					
	67%	67%	84%	60%	-40%*

* Nutrient accumulation

potassium, and magnesium content, respectively, was withdrawn before abscission. A considerable cycling of nitrogen between recently developed needles and developing ones has also been demonstrated in *P. radiata* (Nambiar & Fife 1991).

Nutrient retranslocation in stems at time of heartwood formation is another process which enables trees to make more efficient use of limited nutrient resources. This process has been associated particularly with eucalypts, but is clearly operating in other tree genera as well. A nine to 26 times lower phosphorus concentration in heartwood than in sapwood is commonly observed in eucalypts (Turner 1981). In conifers such as *Pinus nigra, P. radiata*, and *P. sylvestris* heartwood formation is associated with a 2- to 6-fold reduction in phosphorus concentration (Turner 1981; Wright & Will 1958). The concentration of potassium, but generally not of nitrogen and calcium, is significantly lower in heartwood than in sapwood in both eucalypts and conifers (Turner 1981; Wright & Will 1958).

A generally held idea is that nutrient retranslocation becomes a more important process for the nutrient economy of plants grown in soils poor in nutrients than in more fertile conditions. Although nutrient-starved plants often produce litter which contains lower nutrient concentrations, the absolute amount retranslocated prior to leaf abscission is lower than in well-fed plants. Furthermore, recent investigations have shown that nitrogen retranslocated from leaves constitutes a larger fraction of the total amount of nitrogen retranslocated in well-fed trees than in those grown under low soil nutrient availabilities. About 52% of the nitrogen derived from internal cycling in *P. radiata* at age 14 came from nitrogen withdrawn prior to needle fall when trees have a high nutrient status, whereas the corresponding fraction in water- and nutrient-limited trees constituted 21% (Snowdon & Benson 1992).

As already pointed out, the amounts of nutrients taken up from the soil vary during stand development. The quantities taken up are also a function of soil fertility and the growth capacity of the tree. Measured yearly uptake rates of macro-nutrients for a number of conifers and broadleaved species (Table 12) showed that the uptake of nitrogen rarely exceeds 100 kg/ha. Exceptions are young and intensively managed poplar and willow plantations. In highly productive *P. radiata* plantations uptake rates of the order of 100 kg N/ha have been reported (Beets & Pollock 1987a, b; Cellier *et al.* 1985; Crane & Banks 1992; Madgwick *et*

TABLE 12–Reported nutrient uptake rates (kg/ha/year) in natural and managed conifer and broadleaved (deciduous and evergreen) stands.

Genera/species	N	P	K	Mg	Ca	Ref.
Conifers						
Natural stands						
Picea						
Sweden	32	3	11	4	13	[1]
Pinus						
Australia	9	–	–	–	–	[2]
Finland	19–39	2–4	10–15	–	11–19	[3]
Ontario	26	2	15	3	19	[4]
Sweden	6	1	4	1	7	[5]
Temperate conifers, average 13 sites	46	5.5	28	4.6	20	[6]
Managed stands (irrigated and treated with liquid fertiliser)						
Picea						
Sweden	98	13	32	9	40	[1]
Pinus						
Australia	98	–	–	–	–	[2]
New Zealand	80–120	–	–	–	–	[7]
Scotland	69	6	28	11	34	[8]
Tanzania	145	13	78	32	109	[9]
Broadleaved – deciduous						
Natural stands						
Alnus						
Washington	83	6	64	18	86	[10]
South Korea	74	8	38	–	–	[11]
Betula						
Finland	78	6.5	33	–	39	[12]
Fagus						
Germany	72–107	5.0–6.7	38–46	3.0–3.4	28–33	[4,13]
Sweden	50–113	5–8	34–49	5–12	63–107	[14]
Quercus						
Belgium	92	7	69	19	201	[15]
England	44–85	3–6	30–60	–	40–111	[16]
Oklahoma	101	11	80	23	300	[17]
Missouri	54	6	29	7	82	[18]
Temperate deciduous, average 14 sites	98	7.2	48	10	56	[4]
Managed stands (irrigated and treated with liquid fertiliser)						
Populus						
Italy*	182–246	20–36	113–171	38	121–237	[19]
USA (age 4–6)	102	12	88	18	151	[20]
Salix viminalis						
Sweden (age 4–6)	165–191	28–34	131–155	18–27	53–84	[21]
Broadleaved – evergreen						
Natural stands						
Eucalyptus, Australia						
E. globulus	26	2.5	109	–	–	[22]
E. grandis (age 9.5)	37	2.2	36	11	73	[23]
E. grandis (age 27)	100	4.5	67	32	109	[24]
Managed stands (irrigated and treated with liquid fertiliser)						
Eucalyptus, Australia						
E. globulus (age 2)	26	2.5	–	–	–	[22]
E. globulus (age 3)	130	–	–	–	–	[25]
E. grandis (age 9.5)	52	5.1	47	14	96	[23]
E. regnans	75	10	–	18	74	[24]

* Hybrid poplars in nursery

[1] Nilsson & Wiklund 1994, 1995
[2] Crane & Banks 1992
[3] Mälkönen 1974a
[4] Foster & Morrison 1976
[5] Bringmark 1977
[6] Cole & Rapp 1981
[7] Beets & Pollock 1987b
[8] Miller et al. 1976b
[9] Lundgren 1978
[10] Turner et al. 1976
[11] Mun et al. 1977
[12] Mälkönen 1977b
[13] Ulrich & Mayer 1972
[14] Nilgård & Lindgren 1977
[15] Duvigneaud & Denaeyer-DeSmet 1970
[16] Brown 1974
[17] Johnson & Risser 1974
[18] Rochow 1975
[19] Frison 1969
[20] Shelton et al. 1982
[21] Nilsson & Ericsson 1986
[22] Cromer & Williams 1982
[23] Turner & Lambert 1983
[24] Birk & Turner 1992
[25] Pereira et al. 1994

al. 1977). Uptake rates of phosphorus and magnesium usually stay well below 30 kg/ha/year. Potassium, which next to nitrogen is required in the largest amounts by plants, is seldom taken up in quantities exceeding 50 kg/ha/year. The high uptake rates of calcium shown in Table 12 do not reflect a physiological requirement. This element is passively taken up by plants, and high tissue contents mirror the soil conditions. Accumulation of calcium in the bark tissue is particularly pronounced in bark-shedding eucalypt species such as *E. diversicolor* F. Muell. (Hingston *et al.* 1979).

Above-ground Biomass and Nutrient Content

Knowledge of the nutrient amounts in above-ground biomass is vital in evaluating the impact of different harvesting intensities (bole *v.* whole tree) on the long-term productivity of the forest site. There is a vast amount of information available on standing dry biomass of stems, branches, and leaves, and on above-ground net primary production. Cannell (1982) has compiled such data from all over the world. The mean and range of standing above-ground biomass and its nutrient content in a number of selected natural and managed forest stands are presented in Table 13. It may be concluded from this compilation that the standing

TABLE 13–Standing above-ground biomass and its nutrient content in natural and managed conifer and broadleaved (deciduous and evergreen) stands.

	Biomass (tonnes/ha)	N	P	K	Mg	Ca
		------------------------------(kg/ha)----------------------------				
Conifers						
Natural stands (16 stands, data from Bernier (1984) and Feller (1980))						
Average	225	415	48	306	69	408
Range	81–540	171–770	15–87	85–980	19–160	107–1046
Extreme (*Sequoia sempervirens*, California, Westman 1978)						
	3190	3846	1695	2412	569	2574
Broadleaved – deciduous						
Natural stands (11 stands, data from Bernier (1984) and Feller (1980))						
Average	141	384	40	222	68	467
Range	63–324	204–1050	20–84	76–452	35–114	151–881
Managed short-rotation stands						
Populus euramericana 2-year-old (Italy, Frison 1968)						
	24	133	21	83	–	126
P. euramericana 10- to 13-year-old (Italy, Frison 1978)						
	93	278	45	290	–	663
Salix viminalis 1-year-old (S. Sweden, Nilsson & Ericsson 1986)						
	14	155	28	130	17	53
S. viminalis 2-year-old (S. Sweden, Nilsson & Ericsson 1986)						
	32	230	–	–	–	–
S. viminalis 3-year-old (S. Sweden, Ericsson 1994a)						
	40	363	–	–	–	–
Broadleaved – evergreen						
Natural stands						
Eucalyptus marginata (Hingston *et al.* 1979), *E. obliqua* (Feller 1980; Attiwill 1964), *E. signata* (Westman & Rogers 1977 a,b), *E. regnans* (Feller 1980)						
Average	325	412	25	232	178	671
Range	104–601	282–473	17–31	98–424	67–344	251–1266
Managed stands (*Eucalyptus globulus* 3-year-old (Pereira *et al.* 1994))						
	73	229	45	236	47	323

above-ground biomass in natural forest stands averages between 150 and 325 tonnes/ha. The upper extreme in this Table is represented by a mature *Sequoia sempervirens* (D.Don) Endl. stand, in which the biomass has reached a little more than 3000 tonnes/ha (Westman 1978). Willow plantations managed for short rotations (4–6 years) constitute the other extreme. The total above-ground biomass (leaves included) removed with harvesting in such stands amounts to 53–77 tonnes/ha.

The amount of biomass is generally a good indicator of its nutrient content. However, although the standing biomass in intensively managed willow plantations is low in comparison with natural forests or plantations of other tree species, nitrogen content (300–400 kg/ha) in the above-ground biomass (leaves included) at time of harvest is close to that of an average-sized natural forest stand. This is a consequence of a low stem fraction in relation to total above-ground biomass in combination with the high bark content and extremely nutrient-rich leaves formed by fast-growing *Salix* species. A nitrogen content of almost 4000 kg/ha in the biomass of *Sequoia sempervirens* (Westman 1978) certainly represents the upper extreme. The phosphorus content in the above-ground biomass rarely exceeds 50 kg/ha, and in eucalypt forests the content of this element is particularly low in relation to the standing biomass. The other macro-nutrients are more variable in relationship to the biomass pool or its nitrogen content. Commonly, 200–300 kg K/ha, 70–180 kg Mg/ha, and 400–600 kg Ca/ha are bound in the woody and leafy biomass in natural and mature forest stands.

The bole or the total above-ground woody biomass, may constitute as much as 90% to 99% respectively of the total standing biomass in the examples given in Table 12. This implies that the major fraction of the above-ground nutrient pool is confined to the plant parts most frequently harvested. Even if only the stemwood is removed from the forest site, this biomass fraction in eucalypts may hold more than 30% and 50% of the above-ground phosphorus and nitrogen, respectively (Feller 1980). The nutrients bound in the above-ground tissues, particularly phosphorus, potassium, calcium, sodium, iron, and zinc, may in eucalypt stands growing on very poor soils be of the same magnitude as those present in available form in litter and the upper soil horizons (A and part of B1) (Westman & Rogers 1977).

The amounts of nutrients removed when harvesting the main woody biomass fraction, i.e., stems (wood + bark), vary between species, and particularly with the age of the tree. As already shown, the highest stem nutrient concentrations are found in intensively managed willow plantations, when harvested at 4 to 6 years (Table 3). The lowest concentrations of stem nutrients are associated with natural eucalypt forests grown in infertile soils. From this it follows that approximately 0.7–7.5 kg N, 0.1–1.2 kg P, 1.0–3.8 kg K, 0.2–0.7 kg Mg, and 0.9–7 kg Ca will be removed from the forest site per tonne harvested stem biomass (wood + bark), depending on the species and the length of the harvesting cycle (rotation).

Nutrient-use Efficiency

The data presented in Table 13 on above-ground standing biomass and nutrient contents are based on information gathered from 54 forest stands, mainly natural. This database has been utilised in order to compare the nutrient-use efficiency (dry matter production per amount of nutrient in biomass) among conifers and deciduous species (Table 14). The data presented in Table 14 reveal that eucalypts are outstanding in producing biomass from a

TABLE 14–Dilution of nutrients in above-ground biomass (nutrient-use efficiency, kg biomass/g nutrient) in conifer and broadleaved (deciduous and evergreen) stands

	N	P	K	Mg	Ca
	---------------(kg above-ground biomass/g nutrients in biomass)-------------				
Conifers					
Average (23 natural stands, data from Bernier (1984) and Feller (1980))					
	0.53	3.96	0.90	3.49	0.68
Range	0.24–1.4	0.98–11	0.47–2.0	0.31–5.6	0.21–1.6
Broadleaved – deciduous					
Average (24 natural stands, data from Bernier (1984) and Feller (1980))					
	0.37	4.1	0.68	2.3	0.34
Range	0.22–0.47	1.9–6.6	0.18–1.4	0.85–3.5	0.05–0.89
Broadleaved – evergreen					
Average (7 *Eucalyptus* stands, data from Cromer & Williams (1982) and Feller (1980))					
	0.78	10.5	0.77	1.69	0.50
Range	0.23–1.6	4.3–17.2	0.47–3.4	0.89–5.3	0.23–1.4
Managed (irrigated and treated with fertiliser) 3-year-old *E. globulus* (Pereira *et al.* 1994)					
	0.31	1.6	0.31	1.6	0.23

limited resource. This genus produces on average 0.9 and 24.4 tonnes above-ground biomass per kilogram of nitrogen and phosphorus, respectively, in the tissues. The corresponding values for conifers and deciduous trees are 0.47 and 0.35 tonnes/kg N and 3.0 and 3.7 tonnes/kg P, respectively.

Generally, trees become more efficient in producing biomass from a limited nutrient resource once the processes of internal nutrient cycling are fully operating. Nutrient-use efficiency increases when the fraction of nutrients cycling via the litterfall decreases. This implies that both the nutrient situation in the soil and the age of the trees, as well as the forest type (evergreen or deciduous), affect nutrient-use efficiency. In temperate regions, the annual circulation of nutrients in coniferous stands is lower than the circulation in deciduous stands, largely as a result of a lower leaf turnover in coniferous species (Cole & Rapp 1981). Leaching losses from the canopy are also lower in coniferous forests (Parker 1983). Nutrient withdrawal from needles appears to be more effective than reabsorption from deciduous forest leaves, at least when the amounts are expressed as a percentage of the annual nutrient requirements (Cole & Rapp 1981). These mechanisms result in greater nutrient-use efficiency, particularly for nitrogen, in conifers than in deciduous species, which may explain the frequent occurrence of coniferous vegetation on nutrient-poor sites and in boreal climates. These findings may also explain the occurrence of broadleaved evergreen vegetation in warm temperate climates with soils low in elements such as phosphorus (Monk 1966; Gray 1983; Goldberg 1982).

Nitrogen- and phosphorus-use efficiency varies within conifers and broadleaved trees as well. Part of this variation is due to stand age and soil fertility conditions. A high nutrient-use efficiency is a typical feature when plants are grown under low nutrient availabilities. The tissue concentration of nutrient-limited plants is generally lower than in plants grown under more fertile conditions. It should be noted, however, that a high nitrogen-use efficiency is often accompanied by low nitrogen-productivity, i.e., a low growth rate per unit nitrogen in the tissues (cf. Ingestad 1979a). Thus, when a plant makes more efficient use of the nutrients

taken up, its growth rate decreases (cf. Ingestad 1979a). This phenomenon is most pronounced in young plants, but is evident also in older trees (cf. Pereira *et al.* 1994; Snowdon & Benson 1992).

Litter Formation and Nutrient Contents

Although trees are very efficient at cycling nutrients from old to young tissues, sooner or later part of the nutrients contained in the living biomass will be lost in the litterfall. Logically, the amount of leaves shed annually must parallel the amount produced in the same year, at least in deciduous species. This also holds true in evergreens, once the tree crown is fully developed. However, part of the leaf biomass is already lost while the leaves are still attached to the trees. Herbivory, but also retranslocation of minerals and organic macro molecules before leaf abscission, may significantly reduce the amount of leaf litter formed in relation to the annual leaf production (Christersson *et al.* 1992; Woodwell 1974). Severe droughts, on the other hand, may cause the litterfall to substantially increase in evergreen tree species (Linder *et al.* 1987; Pook 1985, 1986). A reduced leaf biomass, and hence leaf area, may be decisive for plant survival in periods of severe drought.

The pattern of litterfall during stand development largely parallels the current annual increment of woody biomass. Before canopy closure, leaves constitute the major litter source. Later in stand development, litter composed of woody parts and reproductive organs gains importance.

As already discussed (Tables 10 and 11), one-third to two-thirds of the initial leaf nutrient content may be transported back to woody tissues prior to leaf fall. However, the efficiency with which nutrients are removed from the leaves at time of leaf fall may be significantly reduced when species have been moved from lower to higher latitudes. The main species used in energy forestry in Sweden, *Salix viminalis*, has its origin in central Europe. Major leaf fall in Swedish willow plantations starts late in the season, often as a result of exposure to sub-zero temperatures. As a consequence, leaves are often shed green and the efficiency of nutrient withdrawal is significantly reduced.

Examples of annual rates of litterfall and its nutrient content in coniferous and broadleaved tree species are given in Table 15. On average 3–5 tonnes litter/year, mainly in the form of leaves, are formed irrespective of forest type. This is in agreement with the rates of foliage production presented in Table 5. The amounts of nutrients per tonne of litter returned annually to the forest floor are 25–80 kg N, 2–6 kg P, 10–20 kg K, 3–6 kg Mg, and 20–40 kg Ca. Clearly, the input of nutrients from this process to the soil system is significant. It is also apparent that the turnover rates of litter will play an important part in the nutrient economy of forest stands, particularly after canopy closure, but that topic is beyond the scope of this paper.

NUTRITIONAL CONSEQUENCES OF INTENSIFIED FOREST MANAGEMENT

Undoubtedly, intensified forest management will have a negative impact on the long-term productivity of the forest site if the necessary counter measures are not taken (compensation fertiliser treatment). Shortened harvesting cycles in combination with increased tissue nutrient concentrations (associated with improved plant nutrient status, Fig. 1) increase

TABLE 15–Annual litterfall and nutrient content in conifer and broadleaved (deciduous and evergreen) forest stands.

Genera	Dry weight (tonnes/ha)	N	P	K	Mg	Ca	Ref.
				----(kg/ha)----			
Conifers							
Abies							
Washington	1.5–2.1	14–20	1–3	2–3	–	11–17	1
Picea							
Sweden	3.1*–5.6†	58*–83†	5.0*–5.6†	10.3*–10.6†	6.7*†	33.7	2,3,4
Germany	3.4	47	4.1	12.6	–	–	5
Pinus							
N. America	–	28	1.3	5.2	2.4	6.9	6
Scotland	3.7	25–51	2.5–3.9	7.2–11	4.3	21	7
Australia	1.6*–6.2†	9*–65†	–	–	–	–	8
Broadleaved – deciduous							
Alnus							
Washington	3.4	61	1.9	32	6.3	36	9
South Korea	3.5	46	6.4	29	–	–	10
Fagus							
Sweden	3.8–5.7	31–69	2.1–5.0	12–16	2.9–5.4	32–68	11
Germany	3.4	52	4.2	17	1.5	17	5
Populus							
P. tremuloides							
N. America	1.3–4.3	8–40	0.9–8.0	5–22	1.8–9.3	60–80	12
Populus hybrids							
Italy	2.7–7.1	2–125	2.8–18	2–128	0.6–25	7–248	12
Quercus							
Belgium	5.3	50	2.4	21	5.6	110	5
France	3.8	33	2.8	16	4.6	64	5
England	3.7	64	2.6	19	9.7	83	5
Temperate deciduous							
Europe, N. America	5.4	51	3.6	20	6.2	52	5
Broadleaved – evergreen							
Eucalyptus (data from 44 forest stands, low and high yielding, may include twig litter)							
Australia	0.15–10.0	7.9–8.2	–	–	–	–	13
Eucalyptus regnans (age 17)							
New Zealand	6.2	49.7	3.5	9.2	9.3	36.1	14

* Untreated stands
† Irrigated and treated with liquid fertiliser

1 Vogt *et al.* 1983
2 Nilsson 1993
3 Nilsson & Wiklund 1994, 1995
4 Nilgård 1972
5 Cole & Rapp 1981
6 Waring & Schlesinger 1985
7 Miller *et al.* 1979c
8 Snowdon & Benson 1992
9 Turner *at al.* 1976
10 Mun *et al.* 1977
11 Nilgård & Lindgren 1977
12 Bernier 1984
13 Baker & Attiwill 1981
14 Frederick *et al.* 1985a

nutrient losses from the site per unit of time and land area. The availability of elements such as calcium and magnesium, which often are taken up in excess of growth requirements (Tables 1, 7, and 13), could become a problem in future plantations if these nutrients are continually removed from the site. Debarking logs at the site, which helps to counterbalance this negative effect, is today beginning to be a common practice. Nutrient losses from leaching and soil erosion are becoming important threats to long-term productivity, when

forests are harvested more frequently. Nutrient losses associated with stand regeneration are also likely to increase in intensively managed plantations because soil-preparation methods (ploughing, removal of stumps and harvesting residues, herbicides, etc.) are more intensive than for conventional forestry. Canopy development is favoured over root development when the nutritional status of a forest stand is improved. As a consequence, the demand for water will be more pronounced in high-yielding plantations. Growth disturbances from water shortage (and in the worst case, tree mortality) are therefore likely to increase in importance in the future. Higher growth rates from intensive silviculture tend to increase water consumption, which may negatively affect water availability in surrounding agricultural areas. Consequently, increased forest production per land area and time is associated with a number of potential risks from both soil nutritional and hydrological points of view.

As forest management intensifies there will be a tendency for mixed forest stands to be replaced with monocultures, but this shift in species composition has a mainly negative impact on flora and wild life. However, there are advantages in using intensive management practices, other than the purely economic ones. In my opinion, one benefit from utilising the increase in forest production resulting from intensified management practices would be a reduction in the pressure on the remaining native forests.

CONCLUSION

The data presented in this review indicate that trees, whether they are conifers or broadleaved species, shed their leaves annually or are evergreen, share the same basic nutrient requirements. The mineral nutrient proportions in the tissues needed for unimpaired growth, are similar among woody and herbaceous plants (at least under controlled laboratory conditions). However, the quantities required per unit of time differ significantly between species owing to different inherited potentials for growth. The availability of mineral elements has a large impact on dry matter partitioning between the different plant parts. Root growth can be favoured as well as suppressed in response to low nutrient availability. Both conifers and broadleaved species (deciduous and evergreen) can be very fast-growing under favourable soil conditions, but in comparisons of the biomass produced per amount of light intercepted during the growing season, deciduous broadleaved *Salix* spp. are outstanding. Generally, conifers and broadleaved evergreens use less NPP for foliage production than deciduous species. The quantity of nutrients taken up and returned annually to the forest floor is generally lower in evergreen species. All three tree groups are effective with regard to nutrient withdrawal from foliage prior to leaf fall. Nutrient-use efficiency, particularly of nitrogen, is slightly higher in conifers than in deciduous broadleaved species. Evergreen broadleaved species such as eucalypts, however, are outstanding in producing biomass from a limited nutrient resource, particularly from phosphorus. Generally, nutrient-use efficiency becomes higher when trees grow older and the processes associated with internal nutrient cycling are operating fully. Plantations managed for short rotations are the most nutrient-demanding, and cause the greatest losses of nutrients from the site at harvest. The practice of debarking logs at site helps to reduce this problem.

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