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REVIEW OF NITROGEN DISTRIBUTION AND CYCLING IN FOREST ECOYSTEMS

by

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CONTENTS

1 INTRODUCTION

Sustained productivity of forests depends on the maintenance of soil fertility. In order to assess the long term impacts of forest management practices on soil fertility, it is not sufficient merely to examine the balances between the nutrient gains from various natural and fertilizer inputs and the losses resulting from soil leaching or tree crop removal. It is also important to understand the functioning and the rates of biological cycling within the forest ecosystem, as the processes governing the cycling may affect the condition of the nutrient capital within the soil and hence soil fertility.

The productivity of forests in many countries throughout the world is primarily limited by nitrogen deficiency, despite the fact that the soils may contain substantial quantities of nitrogen. In north-eastern China, nitrogen deficiency is thought to be the main nutrient deficiency limiting the growth of plantation forests, and it may also govern the pattern of forest succession in natural forest ecosystems, such as those at Changbai mountain.

As a contribution to studies of nutrient cycling in forests in north-eastern China, this review of literature on nitrogen cycling has been compiled.

2 NITROGEN IN THE FOREST ECOSYSTEM

The subject of nitrogen in the forest is a complex one, so it is useful to consider it at four levels, though of course these are interrelated. Firstly, how much nitrogen capital is there present in the forest and how is it distributed among the components of the ecosystem? Secondly, in what quantities is nitrogen gained and lost from the ecosystem and in what quantities or at what rates is nitrogen transferred between the ecosystem components? Thirdly, what are the main factors governing the key nitrogen transfers and what are the mechanisms operating those transfers? Fourthly, how does forest management and exploitation influence the amounts of capital, the transfers and the key processes.

A diagrammatic representation of these aspects is given by Figure 1 (Bolin and Arrhenius, 1977).

3 NITROGEN CONTENT AND DISTRIBUTION

3.1 Trees, shrubs and ground flora

The nitrogen content and its distribution in the vegetation biomass of some natural and plantation forest ecosystems of a wide range of ages are given in Tables 1 and 2. There is generally about 200-300 kg N ha^{-1} in the above-ground biomass, with rather less, 70-200 in the below-ground biomass. The majority of the biomass nitrogen is contained within the tree component, with only some 2-6% in the understory and ground vegetation. Most of the nitrogen within the trees is usually contained within the foliage and bark, although the branch and stem components often contain as much.

It is clear that there is considerable variation in N content of forest stands, between sites, species and with stand age. Other factors such as stand management history, the research methods in estimating stand biomass and chemical analysis, may also contribute to some of the variation of data in Tables 1 and 2.

The site effect can be illustrated by the data of Wood et al (1977) for two 3-year old plantations of the American plane tree (Platanus occidentalis), where the nitrogen content of stands varied by 72% (Table 2). Similarly, Ovington's (1962) data for two 47-year old plantations of Norway spruce (Picea abies) indicate site variations of 113% for nitrogen content of stands (Table 2).

Within particular sites, different species of tree may also vary greatly with respect to growth rates and nitrogen contents. This aspect is illustrated by the data of Alban et al (1978), who compared the N contents of adjacent, 40-year old plantations of aspen, spruce, red pine and jack pine growing on a fine sandy loam soil in Minnesota, USA (Table 1). Between the species, nitrogen contents of the stands varied from 276-383 kg ha^{-1}. When differences in site quality, tree growth rate and stage of development are taken into account, the differences in nitrogen content of stands, even between coniferous and deciduous species, may be small (Miller, H.G. pers. comm; 1984).

The third factor, which strongly influences the N content of forests is stand age which, in plantation forestry, can range from only one year on some sites, to hundreds of years at the time of harvest. Generally speaking, in the early stages of growth, the N content of the stand increases with tree age, but with time the rates of N accumulation decline. These decreases in accumulation with age are illustrated by the data of Ovington (1959), who examined differences in N contents of nine plantations of Scots pine (Pinus sylvestris), varying in age from 7-55 years (Figure 2).

The patterns of accumulation of nitrogen in the different parts of the tree may be rather different however, and these are illustrated (Figure 3) for Corsican pine (Pinus nigra var. maritima) by the data of Miller (1984).

3.2 Forest floor and soil

Data for the nitrogen content of the forest floor (ie litter, fermentation layer and surface humus) and the mineral soil are given in Table 1. The amounts of nitrogen in the forest floor are usually in the range 100-1000kg N ha^{-1}, but values in excess up to 3000 kg N ha^{-1} can occur. These amounts can often equal or exceed those in the above-ground tree component itself (Table 1). In general, the amount of nitrogen in the forest floor components are related to the weight and thickness of the material itself (Table 3), there being often a highly significant correlation between content and weight across a range of sites (Carey et al., 1982).

The organic matter accumulates in the forest floor because its rate of production usually exceeds that of decomposition. Several factors affect the amount accumulated, the climate, the productivity and density of trees, the stage of development of the stand and the nature of the litter material itself.

Site climate is important through the effects of temperature and moisture on decomposition. Increasing elevation (reducing site temperature) and winter rainfall can cause decreasing amounts of accumulated organic matter, whereas increasing summer rainfall is associated with increases in amount of organic matter (Carey et al, 1982); both of these effects may be related to their influence on litter production rate, as litter fall in turn is closely related to tree productivity (Miller, 1984).

Amounts of organic matter in the forest floor can also be related to site aspect and slope, interacting through differences in soil temperature (degree days) and forest species composition (Van Cleve, 1979; Figure 4). The amount of organic matter accumulated and its nitrogen content are also correlated with the density of the forest stand, ie the number of stems per hectare (Carey et al, 1982). After planting, the amount of forest floor increases to a maximum about two-thirds of the way through a rotation and then stabilizes, later to fall as litter input declines (Miller, 1984). If litter and the humus derived from it, have a high C:N ratio, there might be a continuing accretion of N long after the organic matter accumulation has stabilized (Foster & Morrison, 1976). The quantities of forest floor and the amounts of nitrogen contained are also dependent on the tree species. Smaller amounts may be found under tree species such as alder and poplar, whilst higher amounts may occur under spruces and pines (Tables 1 and 3; Freedman, 1981; Brown, A.H.F. pers. comm.; Van Cleve, et al. 1971; Van Cleve, 1979).

The nitrogen content of the mineral soil is often considerable being some 5-10 times that in the above-ground biomass of the trees; sometimes the amounts can be several thousand kg N.ha^{-1} (Table 1; Freedman, 1981). Again, the nitrogen content of the mineral soil is related to soil organic matter content.

Within and between forest sites, there is always considerable variation in the quantities of forest floor and soil and its nitrogen content (Gessel et al, 1973). The variability encountered "within" sites may be so great as to mask "between" site differences (Stutzbach et al, 1972).

4 BASIC STRUCTURE OF THE N CYCLE

The basic structure and processes involved in the N cycle in a forest ecosystem, or any terrestrial ecosystem, are represented in Figure 1 (Bolin & Arrhenius, 1977). The relative amounts of N in the various global compartments vary widely but are in the ratio of approximately 1:30:30:600 for microorganisms:plant biomass:soil inorganic nitrogen: soil organic matter (Soderlund & Svensson, 1976).

In a mature forest ecosystem, the N cycle is balanced and almost closed (Bolin & Arrhenius, 1977). The main processes, whereby N enters it, are biological N fixation and deposition from the atmosphere. The processes, by which N is lost, are leaching, denitrification, soil erosion, surface runoff and ammonia volatilization, which in total often closely balance the fixation and atmospheric deposition. An estimated average of 95% of the total N is recycled within the terrestrial system, only 5% being transferred to and from it in one cycle (Bolin & Arrhenius, 1977). The system is driven by the input of solar energy to the plant biomass, which allows it to incorporate N from the soluble inorganic fraction in the soil. The turnover of this pool is maintained by microorganisms which decompose litter and soil organic matter, and by an equilibration between it and the exchangeable fraction of N adsorbed to clay minerals and organic colloids.

Two examples of detailed forest nitrogen cycles, given in Figures 5 and 6, are respectively those for a non-fertilized N-deficient 50-year old Corsican pine (*Pinus nigra var. maritima*) stand on aeolian coastal sand (Miller *et al*, 1979) and for a P-limited mixed deciduous oak (*Quercus petraea*), ash (*Fraxinus exelsior*), birch (*Betula pendula*) woodland, with a hazel understory situated on an acid brown earth soil (White & Harrison, in prep).

Many other studies of forest nitrogen cycles have also been carried out (Foster & Morrison, 1976; Duvigneaud & Denaeyer de-Smet, 1970; Bringmark, 1977, Switzer & Nelson, 1972; Johnson & Risser, 1974).

5 INPUTS TO THE FOREST ECOSYSTEM

N input to forest occurs mainly via three routes. These are precipitation, aerosols and N fixation. Because N is not a constituent of soil parent minerals, it is not released in significant quantities by rock weathering processes.

5.1 Precipitation

Table 4 illustrates data for N input to forest with precipitation and aerosols. Precipitation provides a variable amount of N to the forest ecosystem. Additions range from 1.1 to 8.7 kg $ha^{-1}yr^{-1}$. However, Stewart (1968), suggests that a more general figure would be between 4 and 10 kg $ha^{-1}yr^{-1}$. Freedman (1981) calculated "typical" values for the array of north temperate sites and indicated mean precipitation input of about 6 kg $ha^{-1}yr^{-1}$.

Not only does the amount of N in precipitation vary, but the form varies and may depend upon numerous factors. In general, high precipitation sites have higher N input via this route than do low precipitation sites (although this may be offset by more rapid rates of leaching). In addition, forested sites near large urban areas frequently receive relatively large precipitation inputs of NO_3-N, NH_4-N and organic N.

5.2 Aerosols

Aerosols, ie dry deposition, represent input of atmospheric particulates or gases, but occurring in the absence of precipitation. Included in this category would be the filtering of atmospheric particulates by forest canopies, the absorption of water-soluble gases onto moist surfaces, or direct gaseous uptake via leaf stomata. Unfortunately, there are almost no quantitative measurements of N input via aerosols, although its process is significant. For example, Likens et al (1977) calculated aerosols of fixed N at Hubbard Brook to be 14.9 kg $ha^{-1}yr^{-1}$ compared with 5.8 kg $ha^{-1}yr^{-1}$ via deposition with precipitation.

Soil absorption of NH_3 from the atmosphere has been suggested as another mechanism for N accretion (Malo & Purvis, 1964). The absorption was reported to be directly dependent upon partial pressures of NH_3 above the soil (Coffee & Bartholomew, 1964). In addition, it was suggested that clayey soils and acidic soils were more efficient than sandy soils and high pH soils in absorbing NH_3.

5.3 N fixation

The fixation of atmospheric N_2 is a biological process, occurring by the action of various microorganisms via the enzyme nitrogenase. They include bacteria, actinomycetes, blue-green algae, or other microorganisms. Some are free living, and others live in associations with higher plants that range from loose rhizosphere association, to symbiotic occurrences in root nodules (Wollum & Davey, 1973).

Data of N fixation are summarized in Table 4. Free living N_2 fixing agents are unlikely to be important on forest floors, and even although heterotrophic N_2-fixing agents may associate with decaying wood, they fix N_2 inefficiently relative to the fixed C which they consume. Wollum and Davey (1973) reported that for a variety of conditions from the USA, Canada, Japan and Sweden, the equivalent fixation rate would be in the order of 1 to 5kg N $ha^{-1}yr^{-1}$. Photosynthetic systems such as cyanobacteria, lichens and nodulated plants could play more important roles but only when the canopy is open to allow good light penetration. Some forests, dominated by trees or shrubs having symbiotic associations with N_2-fixing microorganisms, have very high rates of fixation. For example, rates of fixation of up to 320 kg $ha^{-1}yr^{-1}$ have been measured in an Alnus rubra stand in the pacific northwest of the USA (Wollum & Davey, 1973).

According to the estimate of N_2 fixation (40×10^9 kg N yr^{-1}) in the world's forests (Soderland and Svensson, 1976) and forest area (39×10^6 km^2) on earth (Odum, 1971), Freedman (1981) calculated a global mean rate of forest N_2 fixation of about 10 kg N $ha^{-1}yr^{-1}$ and indicated that some of this fixation of atmospheric N_2 may be offset by N_2 losses by the denitrification of nitrate by microbiological processes, which produce gaseous NO_x or N_2.

6 LOSSES FROM THE FOREST ECOSYSTEM

N losses from undisturbed forest soil occur mainly via three routes. These are soil leaching, denitrification and NH_3 volatilization. Disturbance of forested watersheds is a key factor that influences N losses via soil leaching into streamwater. This is dealt with in section 10.

6.1 Soil leaching

Due to the anionic nature of the nitrate ion, it is relatively mobile within the soil matrix. Consequently, it is subject to leaching when excess water from precipitation or irrigation is present. Under leaching conditions, the nitrate may become a constituent of streams and groundwater.

It is well shown from Table 5 that N losses from soil leaching is a variable amount, ranging from 0 to 40 kg $ha^{-1}yr^{-1}$. It is influenced by the amounts of precipitation, topography, soil type, vegetation coverage and tree removal.

6.2 Denitrification

Denitrification is the process whereby nitrogenous compounds are reduced by microbial action to produce gaseous nitrogen. The main products are N_2O and N_2 and the substrates are nitrate and nitrite.

There are only a few quantitative data on the rates of denitrification in forest and woodlands. Losses of N due to denitrification may range from 9 to more than 50 kg $ha^{-1}yr^{-1}$ and its losses may reach 84% of added fertilizer N (Melillo et al, 1983).

6.3 Ammonia volatilization

The hydrolysis of urea to ammonia is an important pathway for the conversion of the organic N to inorganic N, particularly in those soils receiving either urea-based fertilizers or animal wastes. The amounts of ammonia lost by volatilization can be significant and values ranging from 18 to 70% loss of added N are not uncommon (Volk, 1959). Ammonia volatilization is not restricted to urea compounds, as any ammonium material can be volatilized if appropriate conditions exist.

The extent of volatilization depends upon a number of factors including air movement, temperature and soil acidity (Watkins et al. 1972). Under acid to neutral conditions, the ammonia-ammonium equilibrium is towards the ionized form. At pH 6.0, about 0.1% occurs as non-ionized ammonia, but at pH 7.0, 8.0 and 9.0 the non-ionised ammonia is 1.0, 10, and 50% respectively (Warren, 1962).

7 NET BALANCE OF INPUTS AND LOSSES

The net balance of N in a forest ecosystem is total N inputs minus total N losses. If the net N balance value is positive, then the forest ecosystem is accumulating N over time. Conversely, if it is negative, then the N capital in the forest ecosystem is being depleted. In general, there is a positive net N gain in the forest ecosystems (Freedman, 1981). For example, the wooded non-calcareous site gained 23 kg N $ha^{-1}yr^{-1}$ over a period of 82 years (15 kg in the soil to a depth of 68.6 cm, plus an estimated 8 kg in the trees) and the wooded calcareous site 65 kg N over a period of 81 years (53 kg in the soil plus an estimated 12 kg in the trees) (Jenkinson, 1971).

8 TRANSFERS IN TEMPERATE FOREST STANDS

8.1 Quantities required for annual tree growth

Between 20 and 160 kg ha^{-1} of N are incorporated annually into tree biomass (Table 6). The upper estimates are probably closer to reality since these also include root biomass incorporation. However, most of this N is recycled by litterfall, throughfall, and internal redistribution within the vegetation, so that the net uptake (increase in biomass N) is in the order of 5 to 25 kg $ha^{-1}yr^{-1}$. Such averages may be misleading since N requirements vary with stand age (Figure 7), being low at initiation, maximum at the pole stage, and declining somewhat as the crop reaches maturity (Kimmins 1977; Miller 1981, 1984).

The time and magnitude of maximum N demands vary with the species (Remezov et al., 1955). However, within limits, a given species grown on various soil will have about the same nutrient content with large differences found only under conditions of luxury consumption or acute deficiency (Remezov et al., 1955). It was estimated by Remezov (1956) that a coniferous forest has a maximum annual uptake per hectare of 50-60 kg N. Pines express their greatest need for N prior to age 30 (Remezov et al. 1955, Smith et al., 1963). The latter authors reported that 77% of the N contained in a 60-year old stand of loblolly pine was accumulated within the first 23 years. Similar patterns were observed on both fertile and infertile sites, although the quantities of N contained in the stands differed considerably (Switzer et al.,1966). As the forest stand matures, the rate of nutrient return to the soil matches nutrient uptake and in ageing stands, return exceeds uptake (Remezov et al. 1955).

8.2 Amounts returned to soil in litter and canopy leaching

The rate of nutrient cycling can be estimated in part through the collection of litter produced under different forest stands and subsequent chemical analysis. Such collections in various locations have yielded estimates of annual litter production ranging from about 3000 to 6000 kg ha^{-1} in both warm temperate and cool temperate climates (Wollum & Davey, 1973).

Data relevant to N amount returned to soil in forest litter are summarized in Table 6. They range from about 10 to 90 kg ha^{-1} yr^{-1} in temperate forests. It has been noted that N amount returned to soil in forest litter under mixed hardwood stands is usually more than under conifers growing under similar climatic conditions. Metz (1952) reported twice as much N ha^{-1} was returned by hardwoods compared to pinces and Wells et al., (1972) also showed 57.7% as much N ha^{-1} in the litter under their pine stand as from the hardwood litter in an adjacent stand. It is noteworthy that, even in their pine stand, the hardwood understory provided 36.4% of the N returned to the soil in litter.

Apart from litterfall, throughfall (canopy wash) and stemflow are also two component parts of N return from the trees to the forest floor. The N return by throughfall is usually adjusted to take into consideration elemental addition from the atmosphere during periods of precipitation. Cole et al (1967) reported that 10% of N is returned in the leaf and litter wash.

In addition, recent studies indicate that the growth and death of fine roots (5 mm) can provide a much greater input of N to the forest floor and soil than occurs through above-ground litter (Henderson & Harris, 1975; Switzer & Nelson, 1972; Wells & Jorgensen, 1975; Agren et al. 1980; Melillo, 1981; Persson, 1980; Staaf & Berg, 1977; Heal et al., 1982).

9 TURNOVER IN SOIL

9.1 Mineralization - microbial immobilization processes

In its normal complexes, N in and on the soil is almost entirely in organic forms unavailable to most plant roots, with the possible exception of a few amino acids (Miller & Schmidt, 1965). Therefore, before the bulk of the soil N can be utilized, it must undergo a series of chemical and physical changes as a result of biological process. When most nitrogenous substances are degraded, the N in the substrate is eventually released as ammonium ions. The process is generally referred to as mineralization. At the same time, the active populations of micro organisms is placing demands on the available N supply by incorporating N into their own biomass. This microbial N uptake has been referred to as immobilization. In the soil the opposite processes of mineralization and immobilization often occur simultaneously.

Overrein (1969) found, when he applied 100ppm N as urea to Norway spruce and Scots pine, he could partition 16% of the added N to plant uptake and 60% to microbial immobilization. The amounts of nitrogen immobilized in forest litter layers by microorganisms can be up to 44% of that present in litter and can exceed or equal the amount extractable from the litter (Ausmus et al., 1976; Flanagan & Van Cleve, 1977). The absolute amounts involved can be around 15 Kg ha^{-1} for the litter and up to 55 kg ha^{-1} in the top 10 cm of the mineral soil (Ausmus et al., 1976).

Indirect estimates based on population dynamics of the microflora and fauna indicate that gross mobilization of N by decomposers is equal to or greater than estimated uptake by the vegetation. For example, in the mixed deciduous woodland at Coweet, USA, annual decomposer turnover accounts for 591 kg N ha^{-1} compared to plant uptake of 142 kg N ha^{-1} (Mitchell et al., 1975). Annual net mineralization can be calculated from N budget data. It is estimated that in deciduous woodland a microbial biomass containing 1.5 to 7.5 kg N ha^{-1} mineralizes 65 to 458 kg N ha^{-1} annually. The microbial mobilization of N is much greater than plant uptake and may represent a turnover equivalent to 10-20% of the total soil N each year (Heal et al., 1982). The annual rate of mineralization in a Corsican pine plantation is calculated to be 25-75 kg N ha^{-1} (Miller, 1984) and in a deciduous woodland as 130-170 kg N ha^{-1} (see Figure 6). Shorter term mineralization rates can be obtained by incubation techniques (Popovic, 1980).

There are a number of factors which influence the mineralization-immobilization reactions in soil. In general, those factors which influence organic matter decomposition will also govern the extent of mineralization-immobilization. The most important factors are the nature of the substrate, soil moisture, temperature, soil animals, and microbial populations (Witkamp & Van der Drift, 1961). With respect to substrate, it has been noted that there is a definite species variation, as the litter of some tree species is more readily decomposed than that of others (Daubenmire & Prusso, 1963). Some investigators have noted greatest mineralization occurring under alternating wetting and drying cycles (Birch, 1964).

9.2 Soil animals

Numerous organisms are involved in the mineralization process, including soil animals. Invertebrate animals play important roles in i) reducing the size of organic materials and making them more easily invaded by other organisms, ii) selectively decomposing and changing portions of the organic residues, iii) transforming residues into humic substances, iv) forming aggregates of organic matter with the mineral soil, v) and mixing the organic materials with the upper mineral soil horizons (Edwards et al., 1970). Soil invertebrates also appear to be extremely important in the release of nitrogen from the microbial biomass in litters and soils (Baath et al., 1981, Ineson, et al., 1982; Anderson & Ineson, 1983; Anderson & Ineson, 1984).

9.3 Nitrification

Nitrification, the microbial process converting ammonia to nitrate, is important, as nitrate available in soil can influence tree nutrition (see below). Nitrifying bacteria are invariably present in forest soils but nitrification rates generally are lower than in good agricultural soils. This is because nitrifying bacteria function poorly in acid soils, and forests (particularly coniferous forests) are generally established in acid areas, with the soils becoming even more acid as the forests mature. Several workers have noted little or no nitrification in incubated samples of non-N-treated forest floors and soils (Roberge & Knowles, 1966; Geist, 1977) or in limed or unlimed humus samples (Nommik, 1978). Nitrification may not occur in the forest floor, but may do so in the mineral soil, even in the BC horizon; mineralization and nitrification in the mineral soil should not be overlooked (Federer, 1983).

Nitrification can be stimulated by liming (Tamm, 1982). Little nitrification occurs with addition of an acid forming fertilizer such as ammonium sulphate (Overrein, 1967). Populations of nitrifying bacteria also increase following clear-felling, leading to a 10-40 fold increase in nitrate production (Tamm, 1982; Gordon & Van Cleve, 1983). Lowering of the water-table in wet soils, also results in nitrification; soils wet to near the soil surface do not nitrify (Levy, 1981).

Citing a lack of evidence that nitrification is an important process in forest soils, some authors (Bormann & Likens, 1979; Cole, 1981) have concluded that most temperate forest trees are supplied with NH_4^+-N rather than NO_3^--N. In contrast, others (Melillo, 1977; Robertson, 1982) have shown that soils collected from temperate forests often show a high nitrification potential. Nitrification is considered to decrease through the forest succession to be inhibited in the climax stage (Rice and Pancoly, 1972), but whilst this may be true of the forest floor, it may not be true of the mineral soil (Federer, 1983). Studies of N nutrition of some important forest tree species have shown that growth is sometimes greater, when N is supplied as nitrate rather than as ammonium (Krajina et al, 1973). In a tree mixture experiment, in which Norway spruce was grown alone or in mixture with Scots pine and alder, the improvement in growth of the spruce when grown in mixture was partially associated with increased nitrate formation in the soil; no fertilizers had been applied (Brown & Harrison, 1983).

9.4 Decomposition of soil organic matter and N release

The importance of the pool of organic N within the litter and soil derive not only from the large proportion of the N capital that it represents, but also because the mobilization of this N is essential for the functioning of the forest ecosystem. Plant production depends on the availability of N, which is largely determined by the processes of mineralization of plant litter and soil humus, mediated by the decomposer organisms.

The C/N ratio of the litter in most forest floors is relatively high (in the range of 40 to 60:1) (Roberge & Knowles, 1966; Williams, 1972) corresponding to total N concentration of 0.6 to 1.4% (ash-free basis). The C/N ratio may be higher in conifers than deciduous tree litter (Ausmus et al. 1976; Metz, 1952).

As plant litter decomposes, carbon is released by respiration, N is retained by the microorganisms and the N concentration rises, while the C/N ratio decreases, ie N immobilization dominates over mineralization. This process continues until C:N reaches 25-35. For example, Gosz et al (1973), using the nylon meshbag technique, found that during 12 months on the forest floor, the N% of yellow birch leaves increased from 0.85 to 2.31% (C/N decreased from 62:1 to 23:1).

Rates of organic matter decomposition are controlled by:

a. The composition of the sources of carbon and energy.

b. The availability of nutrients.

c. The concentration of inhibitory compounds, such as polyphenols Handley, 1954).

d. Climate and edaphic factors (Heal, 1979).

Mineralization of N bound in organic matter and its recirculation through the microbial, faunal and plant populations, normally retains N within the ecosystem, and it is only when the organic matter supply becomes limiting that N is released from the ecosystem. Such conditions can occur when: (a) the C:N falls below about 20:1, through addition of inorganic N as fertilizer to a system with low organic matter content; (b) inorganic N is in excess of the rate at which it can be utilized by the microflora, eg through addition of large concentrations at one time or when decomposition of organic matter is inhibited by temperature or moisture conditions, or by limitations of nutrients other than N (Heal, 1979).

9.5 Immobilization in soil organic matter

The vast majority of the soil N is in organic form. During the early stages of succession of forest ecosystems, N fixation results in an increase of N capital, which is retained in the soil as accumulating dead organic matter. There are few documented examples of changes in N capital during succession but in the development after deglaciation, through pioneer Dryas and Alnus stages and transition to spruce forest (Figure 8), Crocker and Major (1955) showed that the annual N accumulation over about

100 years was approximately 28 kg ha^{-1}, with fastest rates probably at about 50 kg ha^{-1}. From the peak of 2800 kg N ha^{-1}, N was apparently lost during the spruce stage at about 10 kg ha^{-1} annually, possibly stabilizing after about 200 years. Jenkinson (1971) has also shown that in the conversion of agricultural land to woodland through natural development of scrub, nitrogen accumulated in the soil organic matter at a rate between 13-49 kg N $ha^{-1}yr^{-1}$.

As forest stands immobilize nitrogen in the soil litter and soil organic matter, the rate of cycling of the nitrogen in the ecosystem may decline. Thus previously healthy trees become progressively nitrogen deficient during stand development, particularly on poor soils which contain limited amounts of nitrogen capital in them (Miller _et al_. 1979; Miller, 1984). As trees become increasingly deficient, tree growth declines or even ceases altogether.

9.6 Seasonal variation in available N

Seasonal levels of extractable ammonium and nitrate in the surface soil are strongly influenced by specific climate, vegetation, and other environmental factors. In general, the highest rates of net N mineralization, as measured using _in situ_ soil incubations in temperate forests, typically occur in spring or early summer with a secondary peak present late in the growing season (Melillo, 1977; Weaver & Forcella, 1979; Nadelhoffer _et al_. 1983; Pastor _et al_. 1984). Monthly net N mineralization rates and pools of ammonium-N in soil fluctuated during the growing season. Nitrate-N pools in soil were generally smaller than ammonium-N pools and monthly nitrification rates were less variable than net N mineralization rates (Figures 9 and 10, Nadelhoffer _et al_., 1984) but this may be because nitrate may be the dominant form of nitrogen taken up in forests (Nadelhoffer _et al_. 1984). In addition, another example of the influence of stand and season on the nitrogen transformation in F and A11 horizons are given in Figure 11 (Bollen 1974). Seasonal changes in nitrogen mineralization and nitrification rates can become more marked following clear felling of the forest trees (Gordon & Van Cleve, 1983; Likens, 1985)..

10 EFFECTS OF FOREST MANAGEMENT FACTORS

10.1 Water management

From the biological aspects of forest management, the drainage of wet sites or the creation of elevated planting microsites through bedding or similar operations, really involves soil oxygen management (Wollum & Davey, 1973). Drainage or bedding improves the aeration of the surface soil. This in turn will decrease denitrification and increase mineralization and nitrification. Thus, the availability of N will increase and so will the possibility of leaching, especially if beds are improperly oriented (Troedsson & Utbult, 1972).

Water management on dry sites usually involves operations calculated to conserve available moisture through increasing infiltration. This can be done by contour furrowing. The objective of water management on dry sites should be to increase the moisture supply for both seedlings and N-mineralizing microflora (Wollum & Davey, 1973).

With spruces, on waterlogged soils, plants may assimilate nitrogen only when the water-table has been lowered to at least 6 cm below the soil surface (Levy, 1981). The nitrogen nutrition of the trees appears to improve as the water-table declines, and as nitrate-N is formed in the soil; nitrification begins only a considerable period after reduction in the water-table (Levy, 1981). Drainage of waterlogged sites appears therefore to be an important factor in the nitrogen nutrition of spruces in particular.

10.2 Forest fire

A silvicultural tool which can have an influence on the soil N economy is the prescribed use of fire. In this case, oxidation of organic matter is rapidly accelerated, and the opportunity exists for N loss from the site and for N transformations on the site.

The burning of forests can lead to N losses via three principal mechanisms. These are: volatilization losses to the atmosphere, and stream-water losses via accelerated rates of soil erosion, or leaching.

Losses of N to the atmosphere occur via the volatilization of organically bound N in either soils or vegetation, with the process being particularly rapid at higher combustion temperatures (Raison, 1979). The actual percentage loss to the atmosphere of the total N in the fuel depends on the characteristics of the burn, including moisture content of the fuel (De Bano _et al._, 1979) and the temperature of the combustion (Knight, 1966). Under moderate burn conditions, N losses as low as 10% are reported, while high temperature burns of dry fuels cause N losses of up to 67% (Table 7). Thus, fire can cause very large losses of N from forested sites, especially if the forest floor burns in addition to the above-ground vegetation. The burning of forests also leads to accelerated rates of N loss from watersheds by the erosion of suspended soil particulates, or by the leaching of soluble ions. The relative degree of effect depends on many factors, including the intensity of the burn, and various site factors, such as slope, soil type, etc (Table 7).

Interestingly, the study of Wells (1971) points out rather conclusively that proper use of fire does not appear to reduce the amount or availability of N on the sites. After 20 years of burning at different frequencies and different times of the year and comparing these results with non-burned plots, the greatest total N (in the residual organic layers plus the top 10 cm of mineral soil) was found in those plots which had been burned annually during the winter. Others have also indicated no significant loss of N from the site due to the prescribed use of fire (Klemmedson _et al._, 1962); and some have reported a stimulation of N fixation following prescribed fire (Jorgensen and Wells, 1971).

10.3 Effects of forest harvest on soil leaching losses

In general, the harvesting of forests causes soil disturbance leading to significant losses of soil and N from watersheds by erosion and leaching. Besides sediment losses from watersheds, of particular concern are the losses of nitrogen, mainly as soluble nitrate (Table 8). In a much quoted study at Hubbard Brook, New Hampshire, USA, a small catchment was felled and subsequently maintained devoid of vegetation for 3 years by regular herbicide application (Likens _et al._, 1978). As a result, the stream nitrate-N concentration, which in the first year in an untreated catchment was 0.7 mg l^{-1}, rose to 38.4 mg l^{-1} in the felled site. In the second year, the respective values were 1.3 mg l^{-1} and 52 mg l^{-1}. The N losses from the felled area were 104 kg ha^{-1} in the first year and 147 kg ha^{-1} in the second year. At a Hubbard Brook site where herbicide was not applied, and in several more recent studies (Haveraaen, 1981; Krause, 1982), where the vegetation was allowed to recolonize the clear-felled site, nitrate losses were many times less, although usually above those in the control catchment. The magnitude of leaching varies greatly with location, soil type, weather, tree species, cutting pattern, and in particular the rate of revegetation (Vitousek & Melillo, 1979).

10.4 N removal by forest harvesting

It has never been disputed that forest harvesting removes some N from the site. First, the advent of whole-tree logging, and, more recently, of in-woods chipping have increased the amount of N removed from the site (White, 1974). Whole-tree logging of Scots pine in Finland has been reported to remove approximately twice as much N from the site as conventional short-wood harvesting and in-woods, whole-tree chipping removes about three times as much (Malkonen, 1972). A second change in forest management in many areas has been the significant reduction in rotation age. As noted above (Smith et al. 1963) 77% of the N contained in a 60-year old stand of loblolly pine had accumulated by age 23. Using these data, it can be calculated that rotation of 20 to 25 years, rather than 60 years, would almost exactly double the N drain from the site.

Table 9 summarizes data relevant to calculated N removals for selected stands of various rotation lengths and harvest methods (Freedman, 1981).

i) Short-rotation plantations

The data for a consecutive 1-year rotation of a hybrid *Populus* plantation indicate that, removal of N would be about 5.6 times the total atmospheric input over the 100-year period. The N removal would exceed the initially positive net flux by 12 times. In addition, the pre-existing soil pool of total N would be depleted by about 63% and the "available" soil pool would be depleted by much larger factors, ie by factor of 108 for N.

The data calculated relevant to a 7-year rotation of *Populus deltoides* indicate that N removal by the whole-tree harvest would exceed the calculated total atmospheric inputs by a factor of 1.9, while the calculated pre-existing positive net fluxes for N would be exceeded by factor of 4.3. Whole-tree harvest N removal would also deplete the 22% of total soil N. It appears likely that these short-rotation harvests would require substantial N restoration by fertilization.

ii) Medium length rotations

With the 29-year rotation of an intolerant hardwood stand, N removal with whole-tree harvested biomass would be 51% of the total N atmospheric input and only 1.2 times the calculated pre-existing net N flux. Moderate depletion of the total soil N pool would occur, amounting to about 9% of the total N. It appears unlikely that N restoration by fertilization would be required, except perhaps over time periods of the order of centuries.

iii) Longer rotations

With an aproximately 100-year rotation of the *Picea rubens-Abies balsamea* stand, N removal with whole-tree harvested biomass would be only 15% of the total calculated N input and only 34% of the calculated positive net N flux over the 100-year period. In addition, only small depletion of the total soil N pool, amounting to about 6.4% of the total N. It appears unlikely that N restoration via fertilization or other treatments would be required, except perhaps over long time periods. In such calculations it is essential that soil erosion or leaching losses are also taken into consideration in relation to atmospheric inputs, but they rarely are.

10.5 Tree mixtures and addition of lime

In many forest ecosystems, tree growth can be seriously limited by nutrient deficiencies, particularly of N and P because they are immobilized in humified organic matter.

Currently, there is increasing interest in mixing other species with commercial forest trees as a possible means of ameliorating these conditions. Admixed lodgepole pine (*Pinus contorta*) and larch (*Larix* Kaempferi) have been shown to improve the N status and growth of Sitka spruce (*Picea sitchensis*) (O'Carroll, 1978; McIntosh & Tabbush, 1981). It has also been reported that mixing Scots pine (*Pinus sylvestris*) and alder (*Alnus glutinosa*) with Norway spruce (*Picea abies*) has encouraged a marked increase in earthworm populations, the activities of which have contributed to increased mineralization of both N and P (Figure 12) (Brown & Harrison, 1983).

Some N-fixing species, such as broom and tree lupin can be mixed with Sitka spruce to improve its N status. Legumes may, however, require low rate applications of phosphorus and potassium fertilizer to enable them to become established on infertile forest soils (Jorgensen, 1978). In addition, use of ground limestone also increases N level in foliage (Table 10 and Table 11) (O'Carroll, 1982) but it may also decrease it (Adams & Dickson, 1973). Nitrification can be stimulated by liming, which thus may result in enhanced nitrate production at risk of soil leaching (Tamm, 1982).

Liming of conifer species on acid soils without additional treatments frequently leads to a decrease in tree production (Popovic and Andersson, 1984) and it is thought that a mechanism for this is increased microbial immobilization of nitrogen in soil caused by lime.

10.6 Use of N-fertilizer

Because of its amphoteric nature, N can be offered to the plant in various forms, from the most oxidized nitrate, through the non-ionized urea to the most reduced ammonium. Various tree species seem to respond more favourably to the anionic nitrate, while others respond to the reduced form of urea or the cationic ammonium. In general, conifers do best with either all reduced N or a mixture of ammonium and nitrate (Van den Driessche, 1971; McFee & Stone, 1968).

Different sources of N are subject to various transformations and ease of transport in the forest ecosystem. These reactions in turn influence the efficiency of any given N source under a set of ecological conditions. Non-ionic urea has been quite popular as a source of N for forest fertilization, particularly in cool climates. In many instances, urea appears to be a favourable N source (Pharis et al., 1964; Roberge & Knowles, 1965) whereas, in other cases, its use must be carefully considered because of possible losses (Overrein, 1972; Watkins et al. 1972).

Table 12 presents data on the responses, which occurred when fertilizer N was applied over a 3-year period to a 36 to 39 year old N-limited plantation of Corsican pine growing on the Culbin Sands in Morayshire (Miller, 1981). The addition of fertilizer N increased the N content and yield of trees as well as the soil organic N, but there was no net increase in the mineral N content of the soil or in the N present in the ground vegetation. The figures in Table 12 indicate that substantial amounts of N have been lost, either through soil leaching or denitrification, when higher levels of nitrogen fertilizer was applied.

In Scandinavia and boreal forests, N deficiency is more common (Tamm, 1982; Miller, 1981; Freedman et at., 1981; Heilman, 1966). In the UK, deficiencies of P and K are more usual and enhanced tree growth sometimes depends on the addition of two or more nutrients (McIntosh, 1981).

Recovery of N and P from fertilizers applied to forest stands (Table 13) is generally well below that reported for agricultural crops, which is usually in the range 30-80% (Black, 1968). However, most of the values shown in Table 13 are probably conservative since most were determined over periods shorter than the normal response period observed in forest stands and values did not include N in root systems. In general, N recovery values are better on more N-responsive sites and for lower and more frequent rates of application (Ballard, 1980). The high recovery value shown for K fertilization can be attributed to the substantial volume response to the fertilization, and the mobility and efficient cycling of K in forest ecosystems (Stone & Kszystyniak, 1977). Percentage recovery of N fertilizer in trees is no better than the % recovery of P fertilizer (Table 13).

The season of the year, as such, does not itself influence the effectiveness of soluble N fertilizers, but it is perhaps rather the associated climatic conditions (Ballard, 1984). Poor performance of both urea and ammonium nitrate can be expected if intensive leaching conditions occur after application; tree responses to summer applications of these N forms can be 23-92% lower than for applications in spring or autumn (Ballard, 1981). Urea effectiveness will be low if applied under conditions favouring high volatilization: dry litter and soil conditions, high temperature and windy conditions (Heilman et al. 1981). Ideal conditions for applications of soluble N fertilizers are periods of high root activity, moderate temperatures, moist litter and soil conditions and a high probability of moderate rainfall within a few days of application. The greatest probability of these conditions occurring is in spring or autummn, for when greatest responses are reported (Morrison et al. 1976; Ballard, 1981).

Experience with broadcast N fertilization of forest stands shows that their response is only short-lived. Response trends for conifers typically show a peak 2-6 years after fertilization followed by a decline to growth rates of unfertilized stands in 5-10 years (Figure 13) (Miller et al. 1976; Jonsson, 1977; Mead & Gadgil, 1978; Ballard, 1981). Rapid immobilization of fertilizer in organic forms, reducing extractable NH_4-N levels to background levels sometimes within a year of fertilization, may explain the short-term tree response (Johnson et al. 1980). Frequent applications of smaller amounts of N fertilizer may provide greater longer term tree response than single large applications, because of the relatively low efficiency with which forest stands use single applications, but surprisingly little research has been carried out in these comparisons (Ballard, 1984).

The age or stage of development of the forest also governs the degree of response of trees to fertilizer. Generally, young trees to an age of 30-40 years are the most likely to respond, with a declining likelihood of response later as the tree demand on the soil declines (Miller, 1981; Moller, 1983).

Site latitude and altitude are also important factors tied in with the degree of N fertilizer responses in forest stands (Moller, 1983). These effects are undoubtedly due to direct effects of climate (moisture and temperature) on the growth and nutrient uptake by trees, and also indirect effects on nitrogen recycling through decomposition of the forest floor litter (Carey et al. 1982; Tsutsumi, 1971; Bray & Gorham, 1964) and nitrogen immobilization in soil organic matter.

11 INTEGRATION OF N-CYCLING DATA BY MODELLING

With the cycling of nitrogen in the forest ecosystem being influenced by many differing processes and external environmental factors, it is essential, particularly when attempting to deduce the effects of management practices, to try to integrate data using mathematical modelling. Through the use of an appropriate model, the key factors and processes in the cycling of nitrogen can be ascertained. Further, if management practices are monitored for their influences on nitrogen cycling at the begining of a forest rotation, the model may be able to predict the duration of the effects into the later stages of forest development thus giving early indications of probable economic benefits. Various management options can also be tested against each other, using the simulation potential of a model.

It is beyond the scope of this review to discuss the various mathematical models available. However, one such model for use on uneven-aged, multiple tree-species forest (up to 6 species) stands is that published by Aber and Mellilo, (1982). This offers many opportunities to examine both the internal consistency of nitrogen cycle data and forest management options. Clearly integrating nitrogen cycling data in relation to forest productivity and development should be an essential part of future research programmes.

Table 1. Nitrogen distribution in temperate forest stands (kg ha^{-1})

Forest type	Age (yrs)	N in total aboveground biomass	N in belowground biomass	N in forest floor	N in soil profile	depth (cm)	References
Sub-alpine coniferous forest (*Abies amabilis*) USA	175	372		650	3555 15855	26 60	Turner & Singer, (1976)
Sitka spruce stand Ireland	35	1374	130.9	1174			Carey & O'Brien, (1979)
Aspen	40	383	89	667	2058	36	Alban *et al*., (1978)
Spruce	40	383	67	752	2542	36	
Red pine	40	373	75	538	2750	36	
Jack pine USA	40	276	37	689	2312	36	
Douglas fir USA	36	294	32	175	1677 2809	30 60	Cole *et al*., (1967)
Boreal forest (Ave 8 forest types)		252		699	1556	root zone	Krause *et al*., (1979)
Loblolly pine forest USA	16	321		307	1753	root zone	Wells *et al*., (1972)
Pinus nigra plantation UK	40	198		183	722		Miller *et al*., (1979)
Mixed deciduous woodland UK		934		165	5550		Heal *et al*., (1982)
Birch forest Finland		36	13				Kjelvik & Karenlampi (1975)

Table 1. Nitrogen distribution in temperate forest stands (kg ha^{-1}) (continued)

Forest type	Age (yrs)	N in total aboveground biomass	N in belowground biomass	N in forest floor	N in soil profile	depth (cm)	References
Birch forest USA		222	131	846	2879	54	Rosswall *et al.* (1975)
Aspen forest USA		497	188	761	3067	54	Van Cleve (1979)
Spruce forest USA		279	71	640	2362	54	Van Cleve (1979)
Birch forest Norway		106	94		11000	45	Kjelvik & Karenlampi (1975)
Temperate deciduous forest Belgium		947	313	35	13800	30	Duvigneaud & Denaeyer de Smet (1970)
Temperate deciduous forest USA		351	181	1100	3600	45	Bormann *et al.* (1977)
Populus simonii China	9	176			4300		Lu Qi-qiong *et al.* (1981)
Korean pine China	120			429	11500	60	Shao Duning *et al.* (1980)
Hardwoods USA		375	186	1104			Whittaker *et al.* (1979)
Scots pine Sweden	120-150	92	13	75			Bringmark (1977)

Table 2. Nitrogen distribution in vegetation (kg ha^{-1})

Forest type	Age (yrs)	Overstory vegetation Foliage	Branch	Bark	Live-tree wood	Dead tree wood	Total	Lichen	Understory vegetation Root and stump	Herbs	shrubs	roots	References
Sub-alpine coniferous forest (*Abies amabilis*) USA	175	173	18	13	116	25	345	13			14.7		Turner & Singer (1976)
Aspen	40	87	82	115	84		370		89	1.8	13		Alban *et al.* (1978)
Spruce	40	153	127	43	59		382		67	0.3	1		
Red pine	40	131	60	42	113		346		75	0.5	26		Alban *et al.* (1978)
Jack pine	40	65	76	33	85		259		37	0.8	16		
USA													
Douglas fir USA	36	102	61	48	77		288		32		6		Cole *et al.* (1967)
Hardwoods USA		70	132	52	82		337		181	1.7	2	5.3	Whittaker *et al.* (1979)
Scots pine Sweden	120-150	19	14	3	14	0.6	51	8	18	4.4	3.4	2.2	Bringmark (1977)
plane tree													
(*Platanus* site a	3						52						Wood *et al.* (1977)
occidentalis) b	3						90						
Norway spruce b	47						331						
(*Picea abies*) a	47						705						Ovington (1962)

Table 3. Comparative range of thickness, weights and nitrogen in forest floor studies*.

Investigator/ location	Species or humus type	Thickness (cm)	Weight (kg/ha)	Total nitrogen	
				(kg/ha)	(%)
Gessel and Balci					
Washington	Mor	12.8	157,880	2040	1.10/1.46
	Mull	7.6	103,350	1393	
Balci					
Eastern	Douglas-fir				
Washington	Mor	ND	28,540	327	1.15
Balci					
Western	Douglas-fir				
Washington	Mull	ND	14,300	192	1.35
Tarrant and Miller					
Western	Alder-fir	ND	32,140	254	0.79
Washington	Fir	ND	27,500	96	0.35
Youngberg					
Western	Douglas-fir	ND	38,620	389	0.94
Oregon	Douglas-fir	ND	22,950/85,930	169/1306	0.63/1.95
McFee and Stone					
New York	Birch-spruce	16	238,300	3000	1.31
			128,000/260,000	ND	ND
Williams and Dryness					
Washington	Felty mor	4.3	68,850	665	0.95
and Oregon		2.3	34,290	651	1.01
		1.3/13.0	19,040/170,790	176/1810	0.70/1.40
Woolridge					
Eastern		5.4	71,530	641	0.75
Washington		1.8/11.6	18,190/223,150	123/1607	0.41/1.39

ND - Not determined

* From Gessel et al. 1973

Table 4. Nitrogen inputs in rainfall and aerosols and N-fixation (kg $ha^{-1}yr^{-1}$)

Forest type	Age (yrs)	N input (1) in rainfall	N input (2) in aerosols	N input in N-fixation	References
Pinus nigra plantation UK	40	5 (1) + (2)			Miller *et al*. (1979)
Mixed deciduous woodland UK		6 (1) + (2)		40-100?	Heal *et al*. (1982)
Northern hardwood forest USA	2	6.5 (1) + (2)		1.2	Melillo *et al*. (1983)
	50	6.5 (1) + (2)		0.3	
Pine hardwood USA		6 (1) + throughfall 9 (1) + throughfall			Aber *et al*. (1983)
Hardwoods USA		5.8		14.2	Whittaker *et al*. (1979)
Scots pine Sweden	120-150	3.6			Bringmark (1977)
Alnus rubra USA				320	Wollum & Davey (1973)
Sub-alpine coniferous forest (Abies amabilis) USA	175	1.3 (1) + (2)			Turner & Singer (1976)
Douglas fir USA	36	1.1			Cole *et al*. (1967)

Table 4. Nitrogen inputs in rainfall and aerosols and N-fixation (kg $ha^{-1}yr^{-1}$) (continued)

Forest type	Age (yrs)	N input (1) in rainfall	N input (2) in aerosols	N input in N-fixation	References
Pine forest Finland		2.45 (1) + (2)		3.49	Alexander (1974)
Birch forest Finland		2.45 (1) + (2)		1.39	Alexander (1974)
Birch forest USA		2.00 (1) + (2)		17.00	Alexander (1974)
Aspen forest USA		2.00 (1) + (2)		17.00	Van Cleve & Noonan (1975)
Spruce forest USA		1.30 (1) + (2)		0.07	Van Cleve & Noonan (1975)
Birch forest Norway		1.26 (1) + (2)		1.65	Alexander (1974)
Temperate deciduous forest Belgium		8.70 (1) + (2)			Duvigneaud & Denaeyer de Smet (1970)
Douglas fir forest USA		1.10 (1) + (2)			Gessel _et_ _al_. (1973)
Temperate deciduous forest USA		6.50 (1) + (2)		14.20	Bormann _et_ _al_. (1977)

Table 5. Nitrogen losses in soil leaching and denitrification (kg $ha^{-1}yr^{-1}$)

Forest type	Age (yrs)	N losses in soil leaching		N losses in denitrification	NH_3 volatilization	References
		from forest floor	from rooting zone			
Sub-alpine coniferous forest (*Abies amabilis*) USA	175	10.3	2.7			Turner & Singer (1976)
Douglas fir forest USA	36	4.8	0.6			Cole *et al*. (1967)
Birch forest USA			< 0.0001			Alexander (1974)
Aspen forest USA			< 0.0001			Van Cleve & Noonan (1975)
Spruce forest USA						Van Cleve & Noonan (1975)
Douglas fir forest USA			0.6			Gessel *et al*. (1973)
Temperate deciduous forest USA			4.0			Bormann *et al*. (1977)
Pinus nigra plantation UK	40		0			Miller *et al*. (1979)
Mixed deciduous woodland UK			13			Heal *et al*. (1982)

Table 5. Nitrogen losses in soil leaching and denitrification (kg $ha^{-1}yr^{-1}$) (continued)

Forest type	Age (yrs)	N losses in soil leaching		N losses in denitrification	NH_3 volatilization	References
		from forest floor	from rooting zone			
Northern hardwood forest	2		43.0	51.6		Melillo *et al.* (1983)
USA	50		4.0	9.0		
Pine hardwood			6	22		Aber *et al.* (1983)
hardwood			6	10		
USA						
Beech forest	125	72.8 (from humus layer)	6.0 (50cm)			Heinrichs & Mayer (1977)
Spruce forest Germany	88	76.3 (from humus layer)	14.9 (50cm)			

Table 6. N transfers in temperate forest stands (kg ha^{-1} yr^{-1})

Forest type	Age (yrs)	Uptake		Return				References
		Total^a	Net	Throughfall (1)	Stemflow (2)	Litterfall	Root decomposition	
Douglas fir USA	36	38.8	23	1.5	0.2	13.6		Cole *et al.* (1967)
Abies amabilis USA	175	23.1	11.9	1.3		16.3		Turner & Singer (1976)
Pinus nigra plantation UK	40	21	6			12.0	4	Miller *et al.* (1979)
Mixed deciduous woodland UK		169	24			97.0		Heal *et al.* (1982)
Birch forest Finland		63				12.3		Kjelvik & Kärenlampi (1975) Alexander, (1974)
Birch forest USA		84		2.02 (1) +	(2)	18.0		Rosswall *et al.* (1975) Alexander, (1974)
Aspen forest USA		111		2.46 (1) +	(2)	22.3		Van Cleve & Noonan (1975)
Spruce forest USA		20		1.60 (1) +	(2)	4.0		Van Cleve & Noonan (1975)
Birch forest Norway		81				81.0		Kjelvik & Kärenlampi (1975) Alexander, (1974)
Temperate deciduous forest Belgium		123				79.0		Duvigneaud & Denaeyer (1970) de Smet

Table 6. N transfers in temperate forest stands (kg ha^{-1} yr^{-1}) (continued)

Forest type	Age (yrs)	Uptake[a]		Throughfall (1)	Stemflow (2)	Litterfall	Root decomposition	References
		Total	Net					
Temperate deciduous forest		80	9.0	9.30 (1)	+ (2)	54.2	7.1	Bormann et al. (1977)
USA								
Red alder stands	23-30					81.9		Radwan et al. (1984)
USA								
Beech forest	125			21.1	2.7			Heinrichs & Mayer (1977)
Spruce forest	85			28.3				
Germany								
Scots pine	120-150			2.3		5.3		Bringmark (1977)
Sweden								
Eastern deciduous		124	14.5	4.4		34	70.1	Henderson & Harris (1975)
Loblolly pine		69.2	11.1	3.3		27.9	26.9	Switzer & Nelson (1972)
Loblolly pine		117.1	5.6	4.6		58.2	48.7	Wells & Jorgensen (1975)
Black spruce			18.5					Roberge et al. (1970)
Ponderosa pine			8.5					Klemmedson (1975)
Douglas fir			9-12			7-15		Heilman & Gessel (1963)
USA								
Birch spruce forest						18.6		Cheng Borong & Xu Guangshan (1984)
Larch forest						18.9		
Korean pine spruce						22.7		
Broad leaved Korean pine						66.2		
China								

[a] Includes redistribution

Table 7 Summary of literature relevant to losses of N to the atmosphere and from watersheds by the soil erosion, as a result of burning.

Community	Location	Burn	N loss or post-fire watershed effects	Reference
Chaparral	SW United States	simulated	lost 67% of total N by intense burn of dry soil, <25% when soil and litter were moist.	De Bano *et al*. 1979
Tsuga-Pseudotsuga	NW United States	simulated	at 300°C, lost 25% of total fuel N, or 167 kg N/ha; at 700°C, lost 64% of total fuel N, or 411 kg N/ha.	Knight, 1966
Pine	-	simulated	volatile losses of 25% of total N in forest floor fuel.	Hosking, 1938
Calluna vulgaris	England	simulated	at 310-580°C lost 43% of N at 590-750°C lost 57% of N	Evans & Allen, 1971
Coniferous	NW Europe	wildfire	atmospheric losses of 10% of total site N, ca. 320 kg/ha.	Viro, 1974
Montane coniferous	n.c. Washington	wildfire	losses via volatilization and convection were 855 kg N/ha.	Grier, 1975
Populus tremuloides	S Ontario		after prescribed fire, N was retained within surface soils. Soil organic matter with high CEC.	Smith & James, 1978
Picea-Pinus	NW Ontario		two naturally-burned watersheds. Total N losses from watersheds were $(\bar{x})$ 2.6 kg ha^{-1}yr^{-1}. c.f. 0.9 for unburned watershed.	Schindler *et al*. 1980
Pseudotsuga menziesii	Oregon		watershed clear-cut and slash burned, streamwater NO_3-N losses in first year were 15.7 kg ha^{-1}yr^{-1} up from pre-impact of 4.9. Returned to baseline after 6 years.	Brown *et al*. 1973

Table 8 Nitrate concentration and total nitrate losses reported in studies on the effect of clear-cutting on N losses from forest ecosystems.

Site	Disturbance	Nitrate losses ($mg\ NO_3\text{-}N\ l^{-1}$)		Nitrate losses ($kg\ NO_3\text{-}N\ ha^{-1}$)		References
		Control	Disturbed	Control	Disturbed	
Hubbard Brook, New Hampshire	devegetation	0.22	10.5	2.0	125.5	Likens _et_ _al_. 1970
Hubbard Brook	clear-cutting	0.44	5.1			Pierce _et_ _al_. 1972
Hubbard Brook	strip-cutting	0.26	1.27	0.5	10.7	Hornbeck _et_ _al_. 1975
Alsea River, Oregon	clear-cutting slash burning	0.16	0.44	0.9	15.4	Brown _et_ _al_. 1973
Thompson Forest, Washington	clear-cutting			0.48	0.87	Cole & Gessel, 1965
Maimai catchment, New Zealand	clear-cutting slash burning			0.43	1.0	Neary _et_ _al_. 1978
Southern and middle Sweden						
Low quality site	clear-cutting	0.2	0.4			Tamm _et_ _al_. 1974
Intermediate quality site	clear-cutting	0.1-1.0	1.1			
High quality site	clear-cutting	0.4-0.6	1.4			

Table 9. N removal with harvested biomass by intensive harvest techniques (kg ha^{-1} 100 yr^{-1})

Rotation Age (yrs)	Forest type	Harvesting type	N removal	% of total inputs	% of net flux	% of total soil	% of available soil	References
1	hybrid *populus*	whole tree clear-cut	8600	538	1230	63	10800	Hansen & Baker, 1979
7	*Populus deltoides*	(a) conventional clear-cut	1343	84	192	10	1562	White, 1974
		(b) whole tree clear-cut	2986	187	427	22	3472	
29	mixed intolerant hardwoods	(a) conventional clear-cut	593	37	85	6.8	791	Ribe, 1974
		(b) whole tree clear-cut	817	51	117	9.4	1089	
50	Red pine plantation	(a) conventional clear-cut	388	24	55	6.7	554	Alban *et al*. 1978
		(b) whole tree clear-cut	865	54	124	15	1330	
		(c) complete tree clear-cut	1053	66	150	18	1500	
55	tolerant northern hardwoods	(a) conventional clear-cut	244	15	35	2.8	325	Whittaker *et al*. 1979
		(b) whole tree clear-cut	675	42	96	7.8	900	
		(c) complete tree clear-cut	1004	63	143	11.5	1339	
100	Red spruce-balsam fir	(a) conventional clear-cut	120	8	17	3.2	255	Freedman *et al*. 1981
		(b) whole tree clear-cut	239	15	34	6.4	509	

Table 10 Effects of legumes (broom and lupin) and ground limestone on mean height (cm) and foliar nitrogen (% d.m.) of Sitka spruce after 3 years*.

	Mean height	Foliar N
Without legumes	66	1.92
With legumes	77	2.17
Significance	$P < 0.01$	$P < 0.01$
Without limestone	67	1.93
With limestone	76	2.15
Significance	$P < 0.05$	$P < 0.05$

* From O'Carroll, 1982

Table 11 Two-way tables showing mean height (cm) and foliar N (% d.m.) after three years with and without legumes and limestone.

	Without legumes		With legumes	
	Height	N	Height	N
Without limestone	62	1.78	71	2.09
With limestone	69	2.06	83	2.25

* From O'Carroll, 1982

Table 12. Distribution of N and recovery of fertilizer N in 36 to 39-year old Corsican pine (Pinus nigra) growing on sand dunes (kg ha^{-1}).*

	N in unfertilized stands	additional N following application of fertilizer N totalling[a]			
		252	504	1008	1512
trees	198	129	224	355	496
ground vegetation	3	7	4	11	-1
soil organic layers	183	122	103	178	200
mineral soil layers	701	0	0	0	0
total	1085	258	331	544	695
N-fertilizer recovered in trees %		51	44	35	32
N- fertilizer lost %		0	34	46	54
N-fertilizer in organic layers %		48	20	18	13

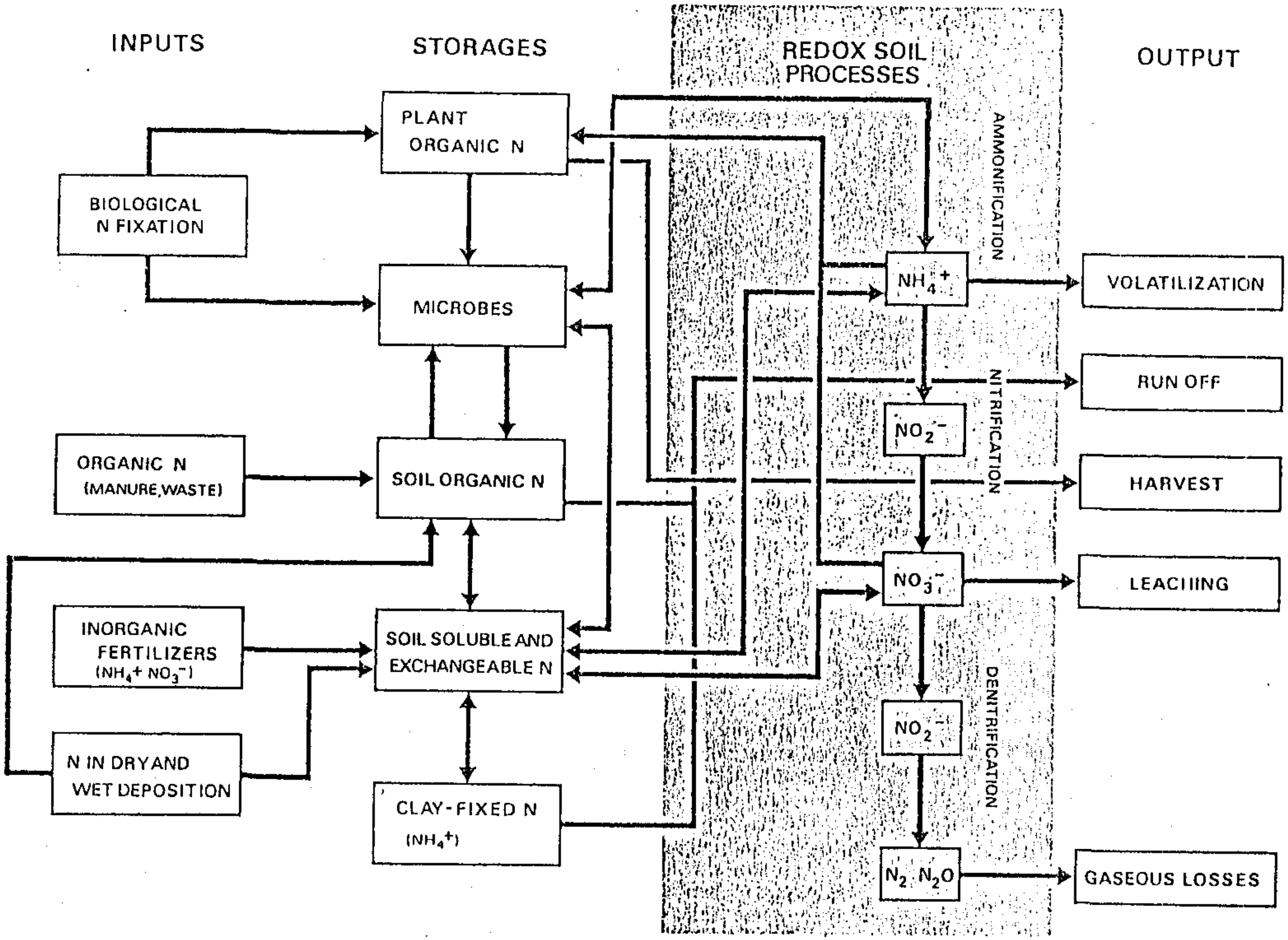
[a] Total application given over three years, equal amounts being applied in each year.

* From Miller, 1981

Table 13 Recovery in trees of N, P and K from fertilizers applied to forests.

Species	Country	Age (yr)	N, P or K applied kg ha^{-1}	Duration (yr)	Recovery in trees (%)	Reference
Pinus taeda	USA	5	N112	2	14	Baker *et al*. 1974
			N224	2	9	
P. elliottii	USA	13	N224	1.5	26	Mead and Pritchett, 1957
P. nigra	UK	36	N252	3	49	Miller *et al*. 1976
			N504	3	44^a	Miller *et al*. 1976
P. sylvestris	Sweden	15	N60	1	12	Bjorkman *et al*. 1967
	Sweden	39	N200	5	12	Tamm, 1963
Picea mariana	Canada	5	N56	0.5	8^a	Knowles and Lefevbre, 1972
P. abies	Sweden	12	N100	1.5	23	Nommik, 1966
Platanus occidentalis	USA	5	N845	5	11-14	Wittwer *et al*. 1980
Pinus elliottii	USA	15	P118	15	23^a	Pritchett and Smith, 1974
	USA	5	P78	5	15^a	White and Pritchett, 1970
P. radiata	NZ	33	P224	8	11^a	Will, 1965
	NZ	3	P34	3	3	Ballard, 1978
P. resinosa	USA	32	K90	12	53	Leaf and Berglund, 1969

[a] Includes roots



From Bolin and Arrhenius. 1977.

Figure 1. The basic inputs, storages and outputs of nitrogen in terrestrial systems. The vertical arrows in the shadowed part indicate the soil processes involved in the redox transformations of nitrogen.

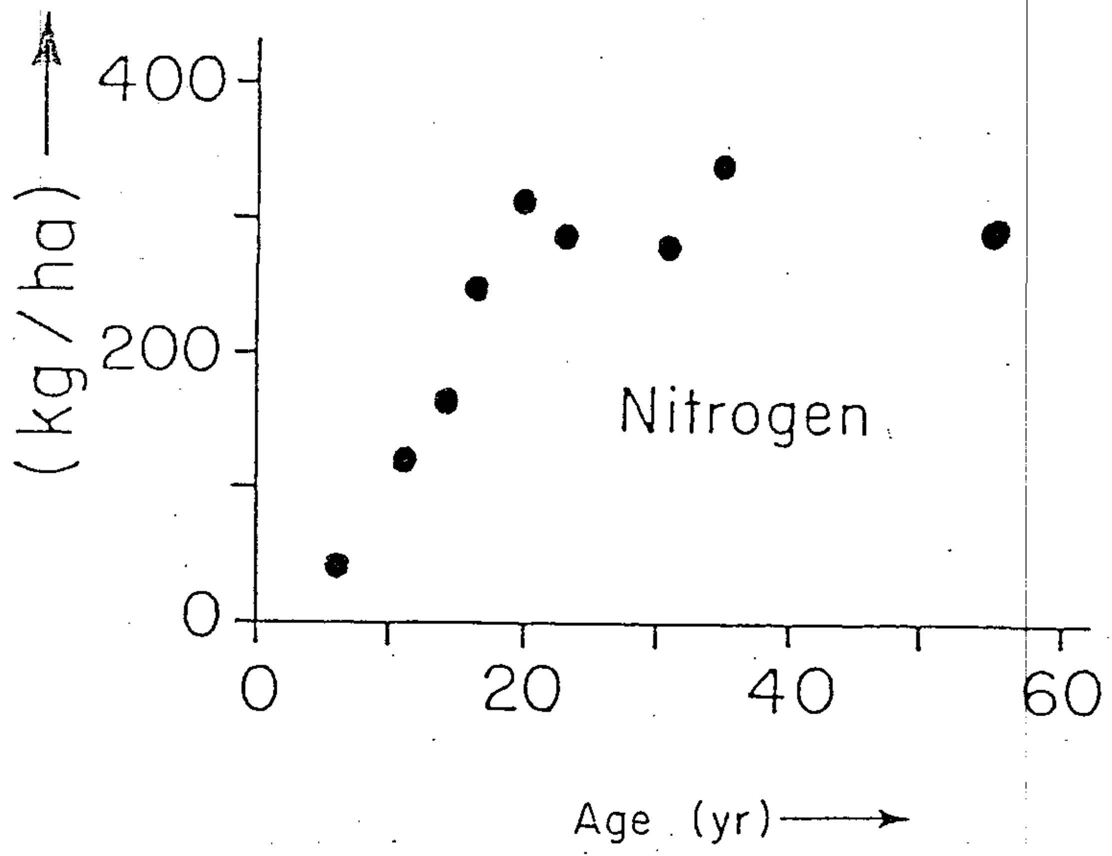


Fig. 2. The effects of stand age on the above-ground standing crops of nutrients in Pinus sylvestris plantations (after Ovington 1959).

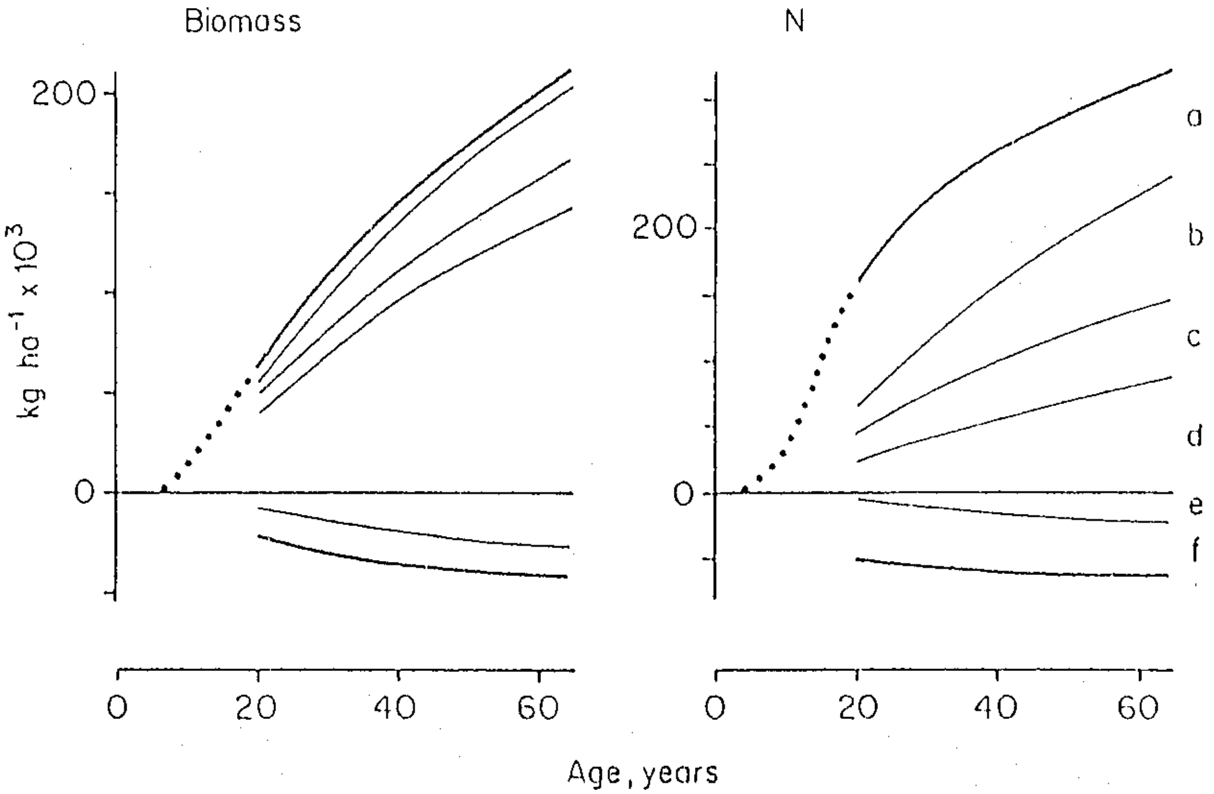


Fig. 3. Patterns of accumulation (kg ha^{-1}) of biomass and nitrogen in (a) foliage, (b) branches, (c) stem bark, (d) stem wood, (e) stump and (f) lateral roots for a managed plantation of *Pinus nigra* var. *maritima*. Data for ages 20 to end of economic rotation from Miller *et al.* (1980a, b), extrapolated back to time of planting by analogy with the pattern published by Madgwick *et al.* (1977). Stand height is 10 m at age 24 and 20 m at age 51 years.

From Miller, 1984.

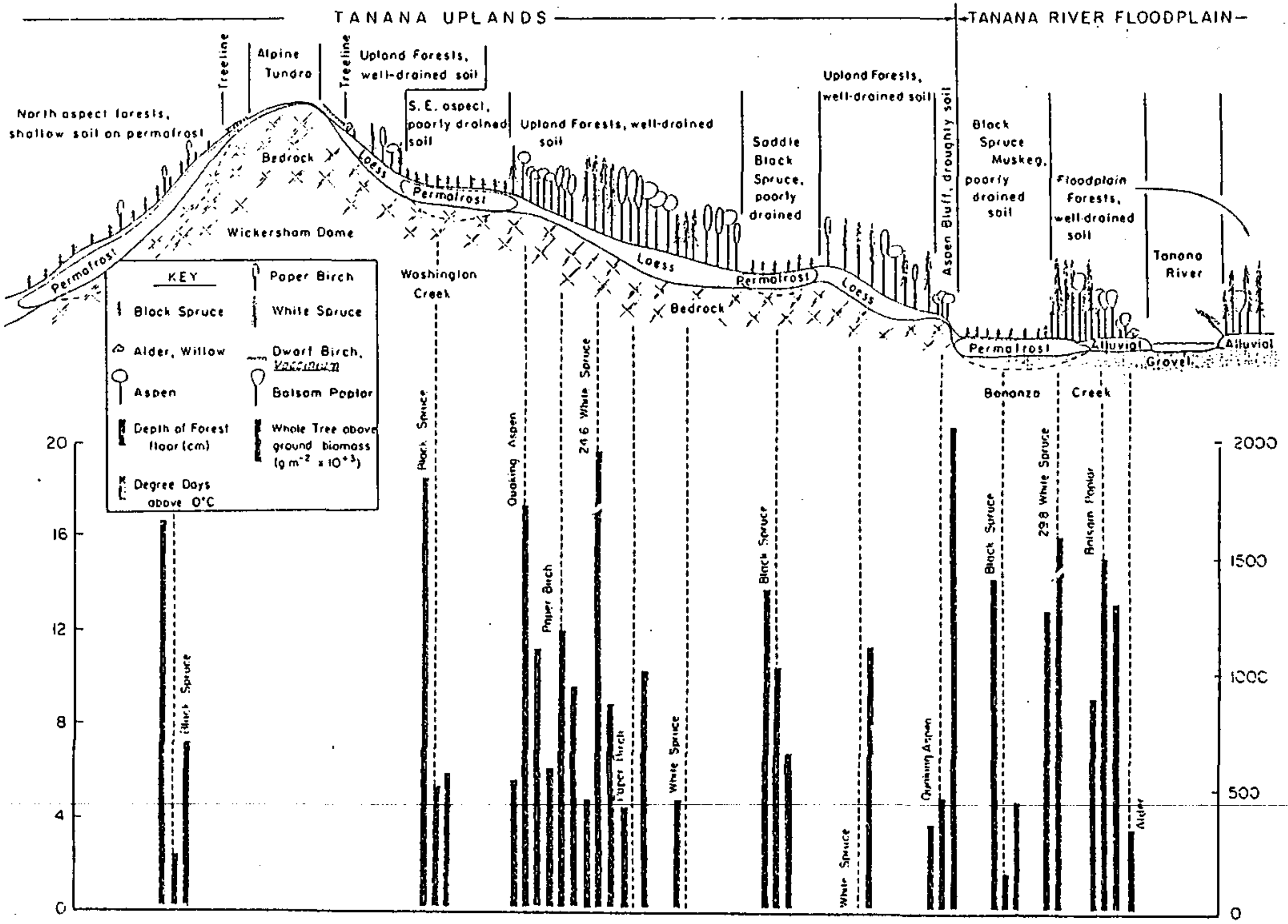


Figure 4: Composite cross-section showing distribution of forest vegetation types with topography in the Tanana uplands and lowlands in the vicinity of Fairbanks. Tree productivity, depth of forest floor, and soil temperature are presented for selected vegetation types.

From Van Cleve, 1979.

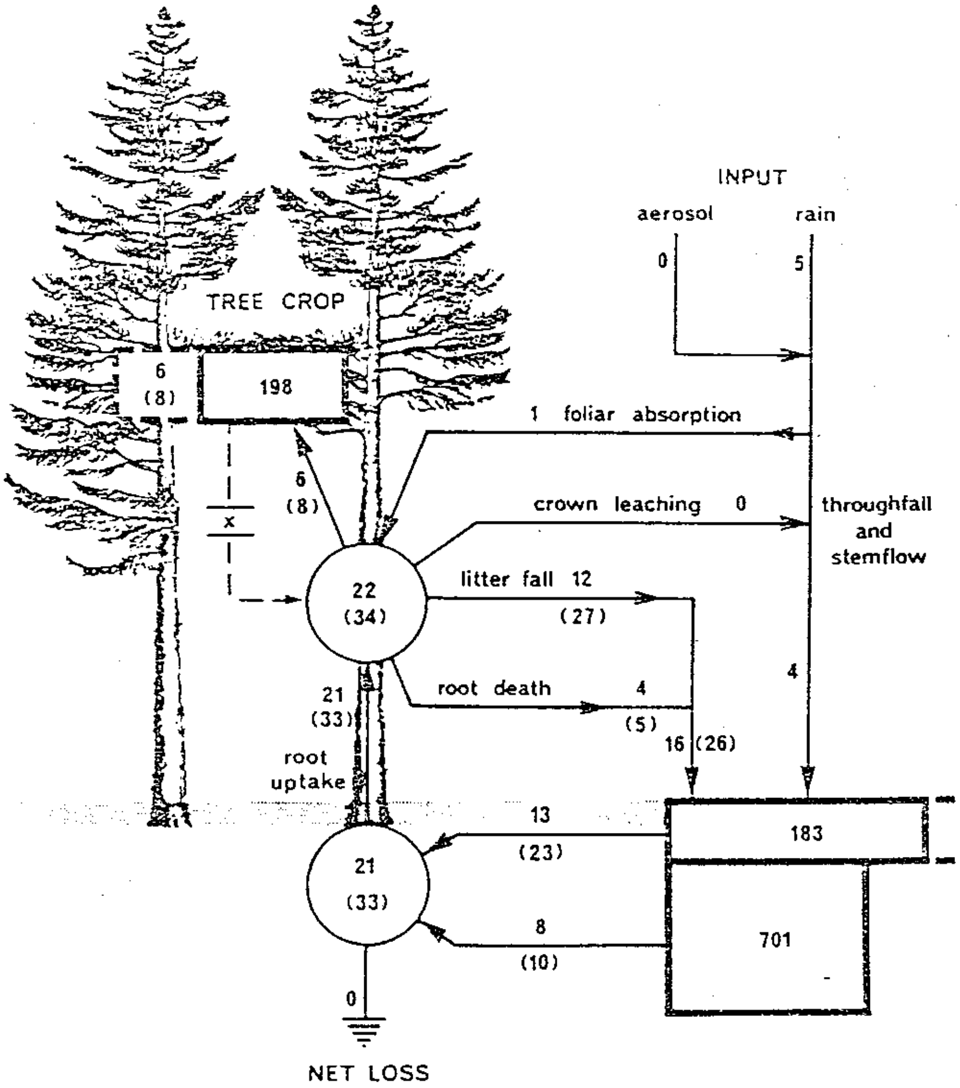


FIG. 5 Annual nitrogen budget in unfertilized trees. Nitrogen concentration in top-whorl foliage was 0.88%, basal area growth was 0.75 m² ha⁻¹ year⁻¹, and volume growth was 7.2 m³ ha⁻¹ year⁻¹. Zones of accumulation are shown by rectangles, the annual rate of new accumulation being represented by the dashed portion. Mobile pools are depicted by circles. *Link x between* accumulation and mobile pool in the tree represents potential mobilization from second-level sources (see text). Values for accumulation are expressed in kilograms per hectare (*kg ha⁻¹*) and rates of accumulation and fluxes are in kilograms per hectare per year (kg ha⁻¹ year⁻¹). Growth of these trees was declining progressively; the fluxes estimated from the model as being necessary to sustain a steady growth rate are shown in parentheses.

Miller et al., 1979.

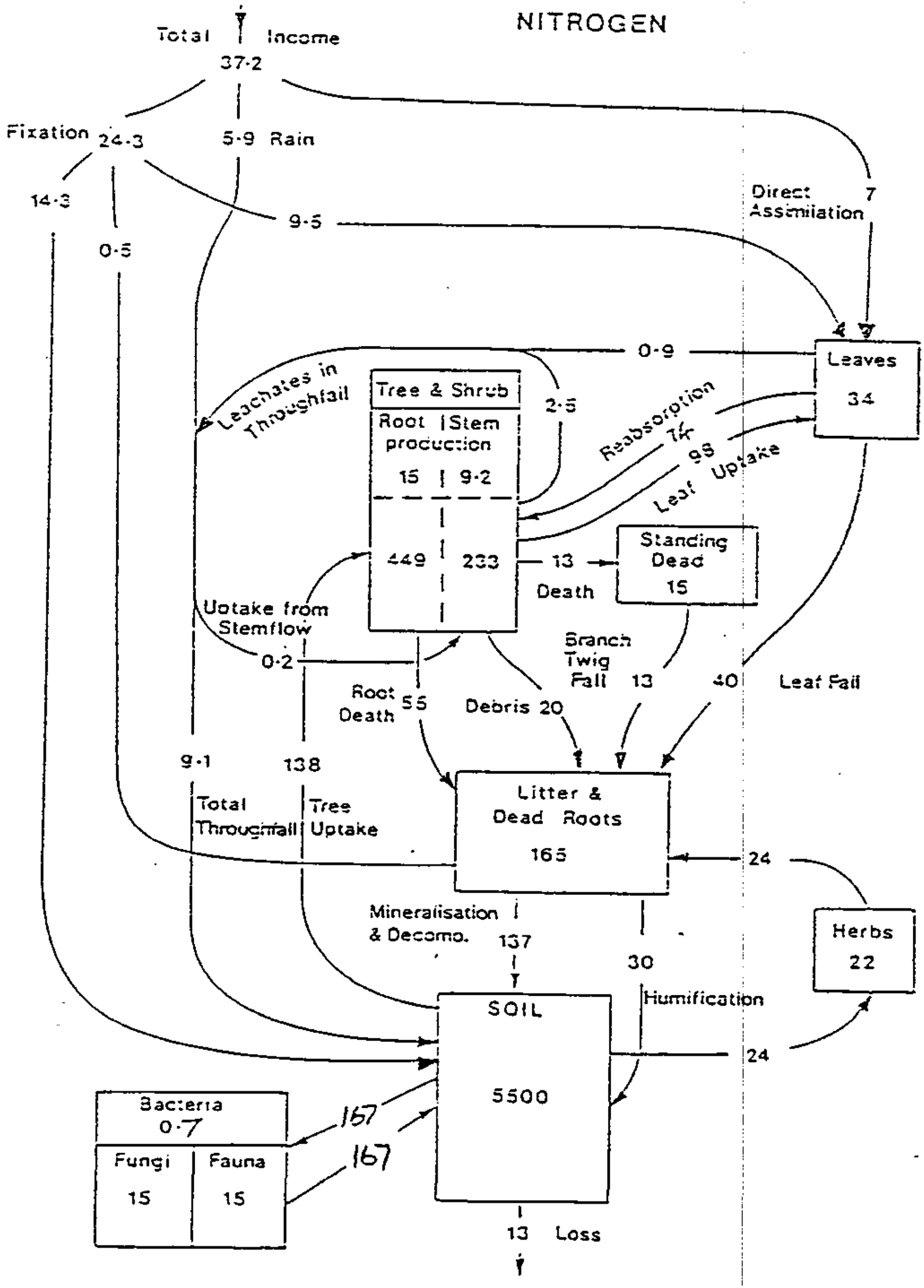


Fig. 6. Nitrogen cycle of a mixed-deciduous woodland. (Meathop Wood), Cumbria, UK. Contents in kg ha^{-1}, transfers in kg ha^{-1} yr^{-1}.

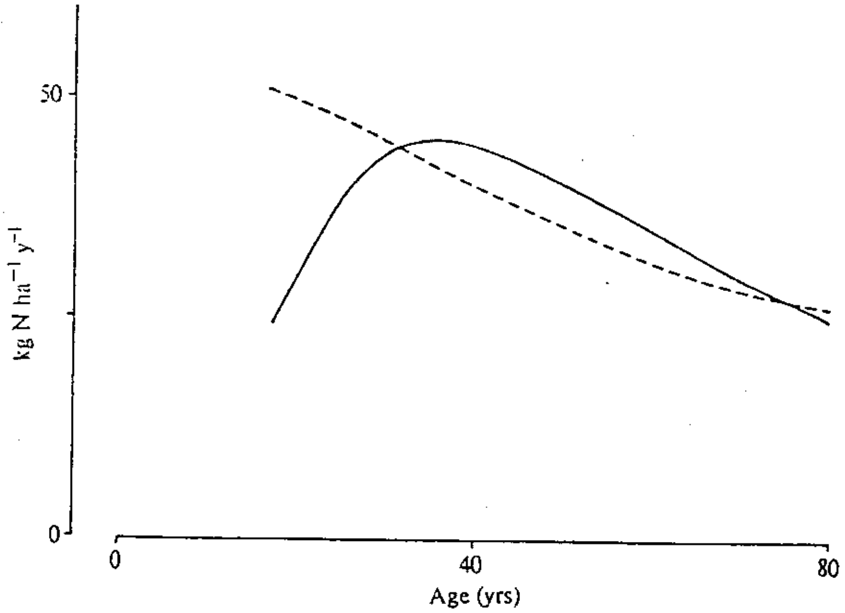


Fig. 7 Models of rate of uptake of nitrogen by slow growing (Yield Class 6) Corsican pine (——) and rate of supply of available nitrogen (- - -), assuming a rainwater input of 5 kg nitrogen ha^{-1} y^{-1}, an initial nitrogen capital of 1200 kg ha^{-1}, and mineralization rates of 1 per cent for half the nitrogen in litter fall and 4 per cent for the remaining litter fraction plus soil organic nitrogen, having first subtracted the amounts accumulated in tree biomass or removed in thinnings (data from Miller *et al.*, 1979; Miller, Miller and Cooper, 1980a and b).

From Miller, 1981.

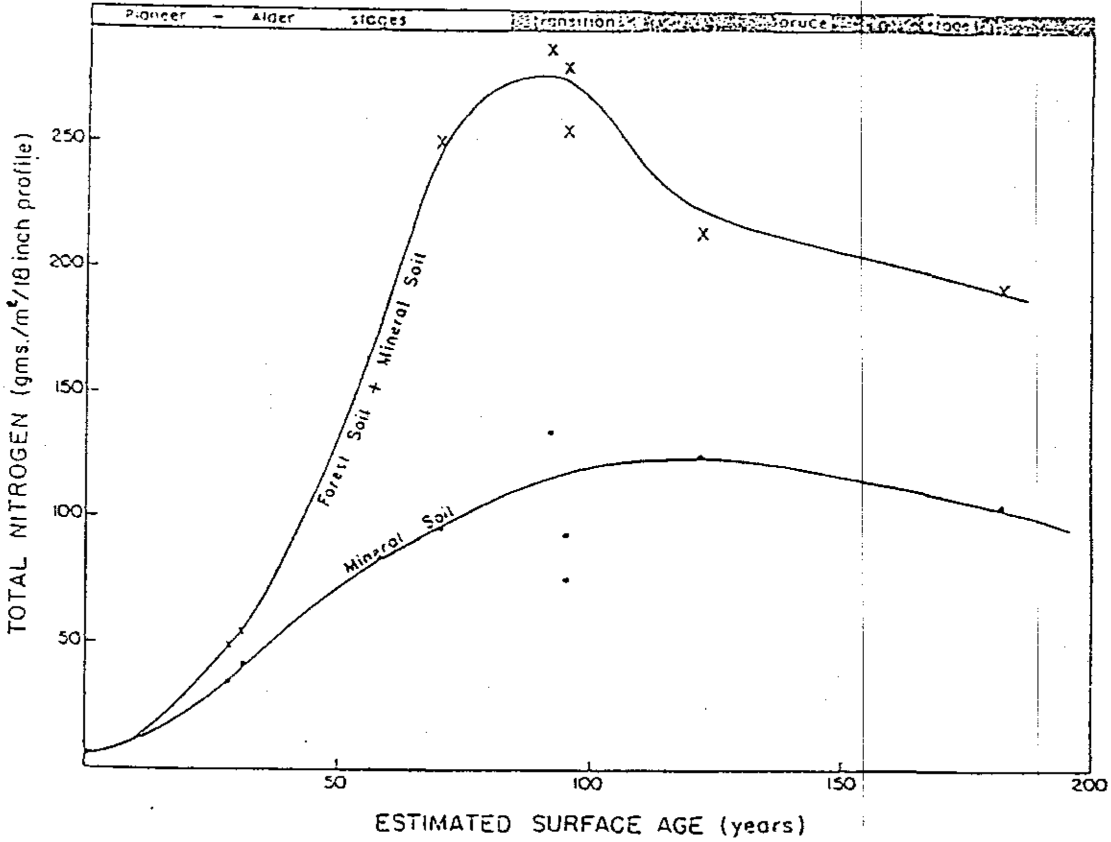


Fig. 8. Differences in the total nitrogen content of soils on surfaces of varying ages.

From Crocker and Major, 1955.

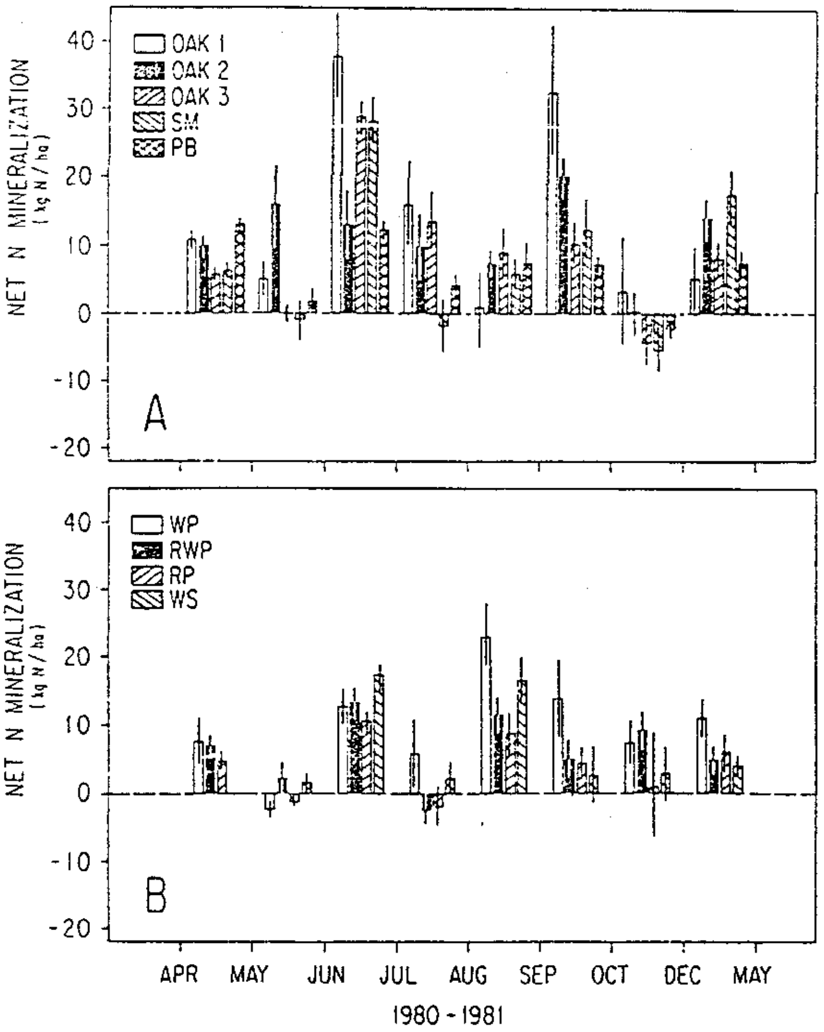


Fig. 9 Seasonal net N mineralization in: a) deciduous sites; b) conifer sites. Vertical lines are ± 1 standard error of means.

From Nadelhoffer et al., 1984.

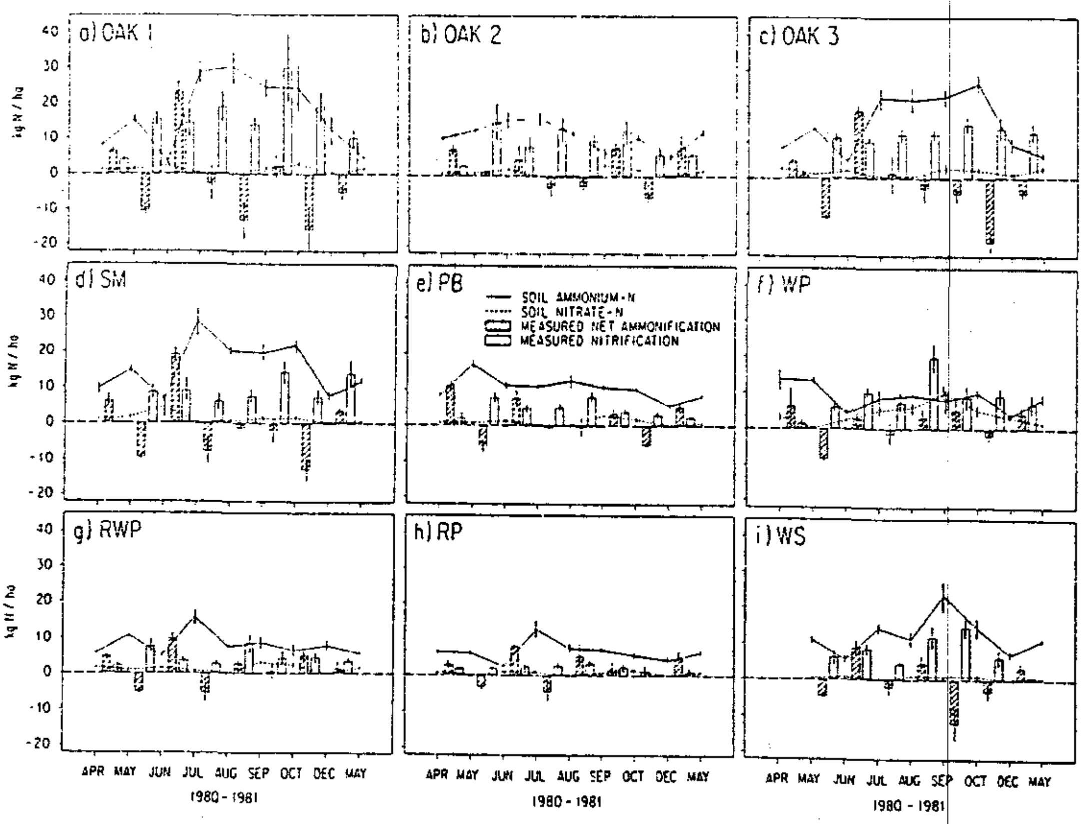


Fig. 10 Seasonal patterns of net ammonification and nitrification in nine temperate forest sites. Vertical lines are ± 1 standard error. Soil pools (0–10 cm) of ammonium- and nitrate-N at the start of each incubation interval are shown for comparison.

From Nadelhoffer et al., 1984.

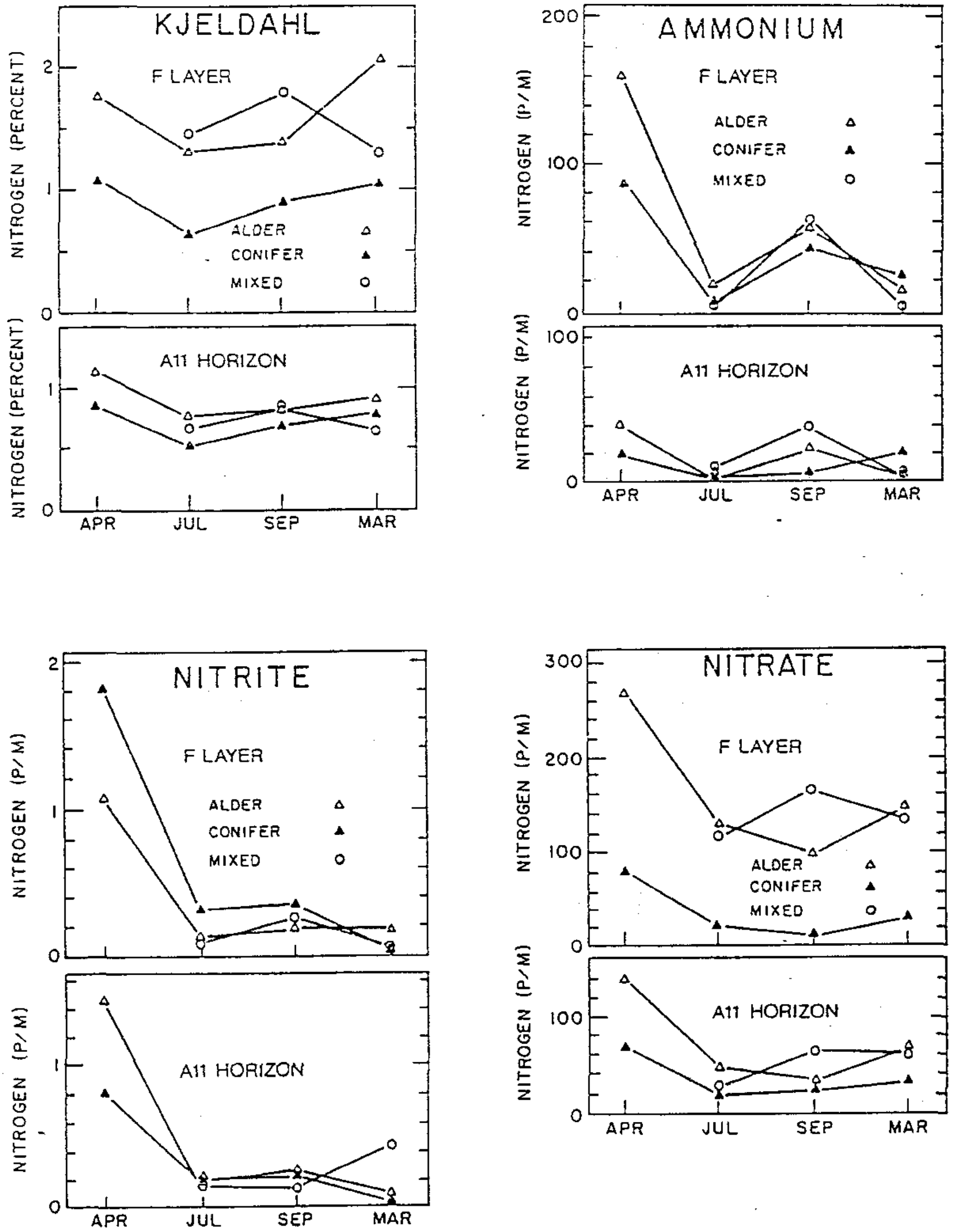


Figure 11--*Seasonal changes in nitrogen status in F and A11 horizons under three different stands on Astoria silty clay soil.*

From Bollen, 1974.

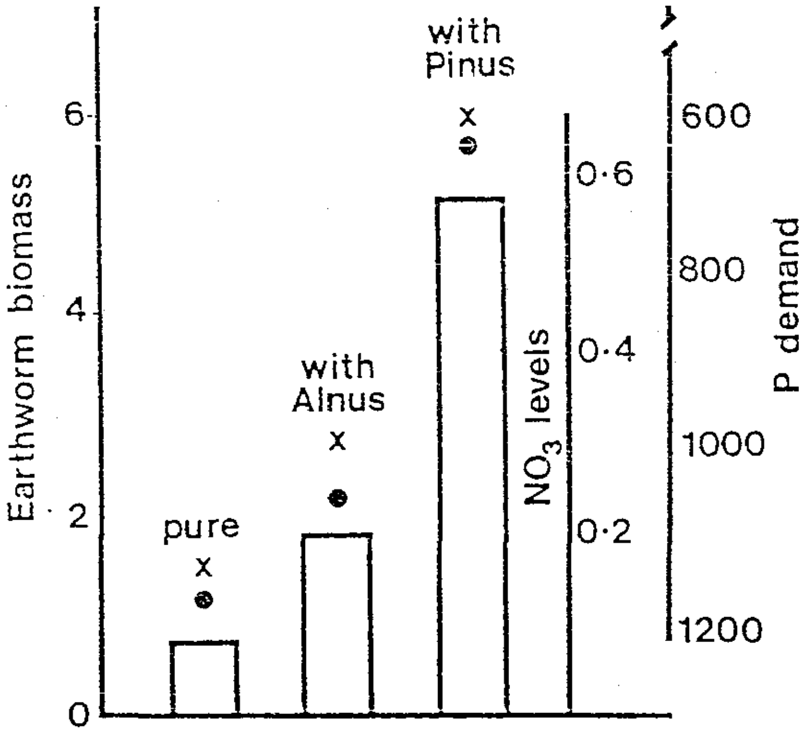


Figure 12a Mean weight of earthworms per trap (g) — vertical bars, extractable soil NO$_3$ (mg/l CaCl$_2$ extractant) — x, and root P deficiency (uptake, pgP/mg root/15 min) — • under *Picea abies* in pure and mixed stands at Gisburn (see text for explanation of inverted P scale).

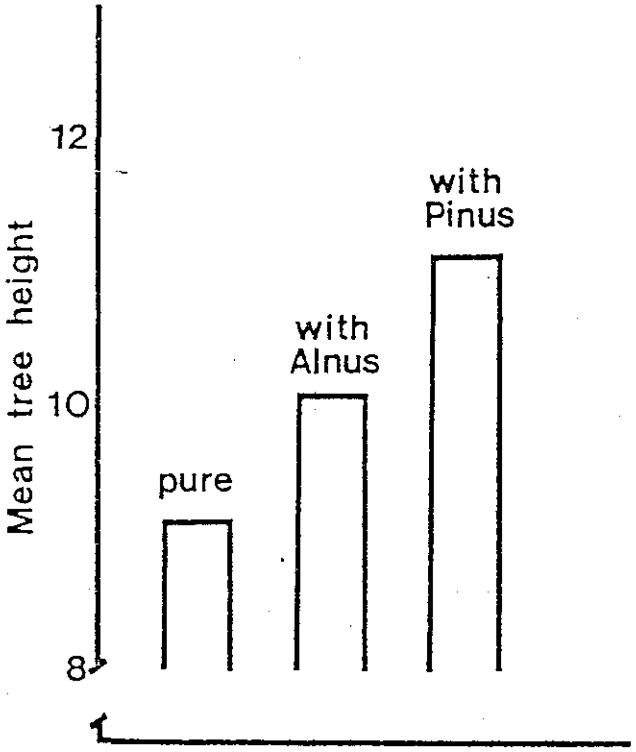


Figure 12b Mean height (m) of *Picea abies* in pure and mixed stands at Gisburn.

From Brown and Harrison, 1983.

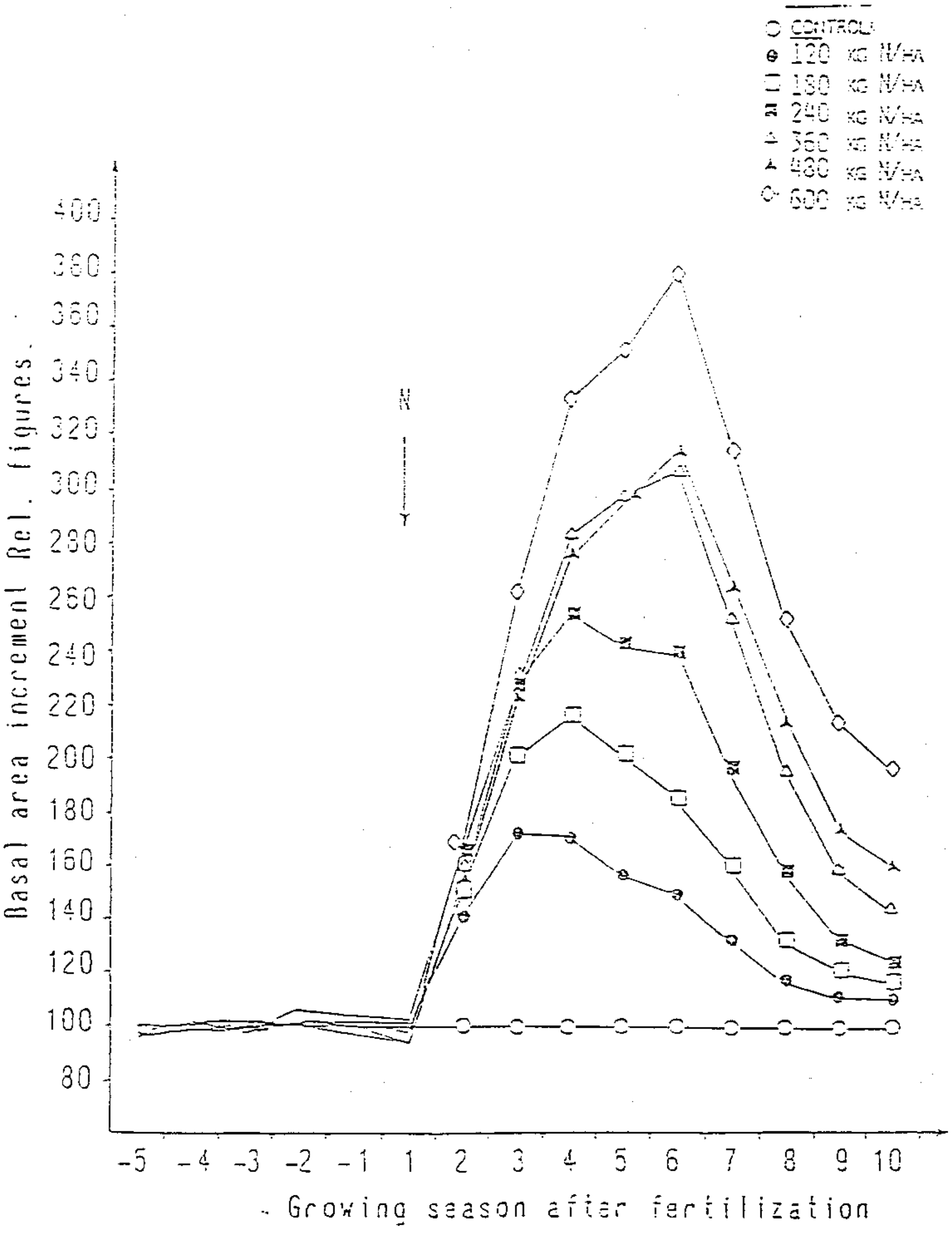


Figure 13. Mean basal area growth response in relative figures for 4 pine trials with one fertilization. 600 kg N/ha mean for 3 trials. (redrawn from Jonsson. 1977

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