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Professor G.W. Leeper Memorial Lecture

Forest soils: cycles, sustainability and sequestration

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INTRODUCTION

I would first like to thank the Soil Science Society of Australia for their invitation to me to present the 8th Professor G.W. Leeper Memorial Lecture. I have been greatly influenced by Geoff Leeper throughout my university career, as an undergraduate, as a post-graduate, and especially during the years we worked together on our book, Forest Soils and Nutrient Cycles (Attiwill and Leeper, 1987).

Soil science is dominated by studies of agricultural soils. While the study of forest soils has developed as a discipline in its own right, we are mostly dependent on methods that have been developed for agricultural soils. In this lecture, I aim to show that, because of fundamental differences between agricultural and forest soils as outlined by Attiwill and Leeper (1987), many of the methods that have been developed for the study of agricultural soils are limited in their application to forest soils.

Early research on forest soils was largely driven by trial-and-error field trials, with little analytical basis. Current problems of the sustainability of forest growth and of the sequestration of C in forest soils will only be resolved by basic research aimed at developing new methodologies. In developing these themes for this written paper, I have drawn heavily on, and quoted freely from, my previous reviews of these themes (Attiwill and Leeper, 1987; Attiwill and Adams, 1993; Attiwill, 1995; Attiwill *et al.*, 1996; Attiwill and Weston, in press).

THE AVAILABILITY OF NUTRIENTS IN AGRICULTURAL AND FOREST SOILS

The study of soil chemistry has, by and large, concentrated on agricultural soils. The immediate, practical questions to be answered have centered on the availability of plant

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nutrients, on the need to develop chemical tests to define those soils that are suitable for particular crops and on the prescription of the quantity of fertilizer that must be added to increase the productivity of the crop. With the exclusion of N (the availability of which is driven by biological processes in all soils), we might summarize the essential difference between availability of plant nutrients in agricultural and forest soils:

- the availability of nutrients in agricultural soils is an immediate concern that mostly addresses inorganic equilibria over weeks or months
- the availability of nutrients in forest soils is a long-term concern that should address biological processes and inorganic equilibria over years and centuries

The growth of forests is a long-term process in which nutrients are cycled from plant to soil in litterfall and root turnover (Fig. 1). Nutrients are withdrawn from tissues as they age and are translocated to actively growing tissues. Timber harvesting takes away the aged tissues with relatively low nutrient concentrations, leaving the tissues with relatively high nutrient concentrations on site.

In contrast, all of the nutrient supply for an annual crop is taken up from the soil within the few months taken for the crop to reach maturity. There is little cycling of nutrients from plant to soil. At maturity, the most nutrient-rich parts of the crop (seeds, leaves, storage organs) are harvested, leaving only the tissues with relatively low nutrient concentrations behind.

Stone (1979) commented on the very great difficulty of defining nutrient supply and nutrient availability: "there is no such thing as 'nutrient supply' for tree growth in the same useful sense that there is 'moisture supply'. Each of the elements essential for plant growth has its unique chemistry in the soil, its particular relationships to lithology and atmospheric inputs, and its own rate and magnitude of circulation through vegetation. No rule of thumb about 'nutrient supply' is useful beyond the grossest generalization, though fortunately the number of nutrients warranting our first consideration is few."

A simple example illustrates the point. We use a variety of weak reagents, dilute acid or dilute alkali, to extract some fraction of total P that we call 'available' P. We then assess the

usefulness of this fraction by correlation with growth of the crop or forest. With repeated extractions, more P comes into solution as new surfaces are exposed (Fig. 2), so that the definition of 'availability' is arbitrary, and thus the value of any test depends on its interpretation.

With this brief introduction, I now want to address two current problems for forests world-wide:

1. Is the rate of nutrient supply from forest soils sufficient to sustain productivity and diversity of our forests in the face of major disturbances such as bushfires and timber harvesting?
2. What role can forests play in storing C that is being released into the atmosphere through increasing rates of use of fossil fuels? Carbon dioxide is, of course, fixed by plants in the process of photosynthesis. It is stored as organic matter both in the trees and in the soil.

I think that we have to admit that the current status of research in forest soils makes it difficult to give quantitative, unambiguous answer to these questions, and I shall try to demonstrate why this is so. In my view it comes down to too little basic research, and too little research on our native forests, and I would first like to show why we are in that position through a brief historical perspective of research in forest soils.

HISTORICAL OVERVIEW OF THE SCIENCE OF FOREST SOILS

It is generally accepted (e.g. Stone, 1979; Tamm, 1979) that the first major work on nutrient cycles in forests was that of Ebermayer (1876) - *Comprehensive study of forest litter, with regard to the chemical statics of silviculture*. Ebermayer was concerned with the removal from the forest floor of the fine materials shed from the trees. This material was used as bedding - 'litter' - for animals in the barns over winter; after the winter, the litter, now enriched with animal droppings, was spread over the arable fields.

Following Ebermayer (1876), and up to the turn of the century, there were many detailed studies of the distribution of nutrients in forests of central Europe. The results of these studies were brought together in a landmark paper by Rennie (1955). Conventional wisdom at the time was that there are 'soil degraders' (the conifers, and spruce in particular) and 'soil

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improvers' (some of the hardwoods such as birch). Following the World Wars, Britain was aiming to become self-sufficient in timber. If birch is a soil improver, then it could be planted on soils of low fertility such as those supporting *Calluna* heath and, in the words of the Forest Policy (quoted in Rennie, 1957) 'there need be no misgivings regarding the maintenance of the rates of growth of timber'. But if, as Rennie (1955) showed, demand for nutrients by the growing forest exceeds the nutrient supply available from the soil, then the forest will fail. While this now seems obvious, the conventional wisdom was so strongly held that Rennie (1957) found it necessary to challenge the Forestry Commissioners of the United Kingdom to prove him wrong.

The correction of a nutrient deficiency by the addition of an appropriate fertilizer is a simple and relatively economic business. Compared with agriculture, however, the use of fertilizers in forestry is relatively recent. White and Leaf's (1956) comprehensive bibliography of fertilizer research in forestry contained a mere 700 entries. About 25% of the papers were concerned with nurseries and nursery practice, and some 10% gave attention to 'degraded' forests (also described as 'stunted', 'degenerated', 'impoverished' etc.) in Middle Europe (particularly Germany and Czechoslovakia) and to the reclamation or 'improvement' of 'useless' land (swamps, bogs, peats, heathlands, moorlands, *Calluna* soils) in the United Kingdom, Sweden, Norway, Denmark and Finland and the subsequent establishment of tree plantations. All of that is simply a reflection of the view of the time – that it was good to develop the land.

The 1960s saw the start of extensive use of fertilizers in forests. Tamm's (1968) historical view of the development of the use of fertilizers in Europe is worth recalling:

- 1865-1900 - the recognition, starting with Ebermayer (1876), of nutrient cycling and nutrient demand in forests; almost no experimentation;
- 1900-1925 - trial-and-error field trials, with little analytical basis;
- 1925-1960 - scientific foundation for tree nutrition established; many experiments, but limited practical application;
- 1960 onward - the start of large-scale application of fertilizers in forests.

And indeed, this was a large-scale expansion. For example, the area of fertilized coniferous forest in north-western and south-eastern United States increased from nothing in 1967 to 850,000 hectares in 1978 (Bengtson, 1979). Baule (1973) estimated that the world-wide area of forest to which fertilizer had been applied doubled from 2 million hectares in 1970 to 4 million hectares in 1973.

While these areas are impressive, we should remember that they are less than 0.1% of the world's forested land (Baule, 1973). In short, fertilizers are not used on most of the world's forests. The traditional view of tree nutrition in silviculture of natural forests has always been that: 'the loss of nutrient elements through the exploitation of timber is not very serious if the leaves and twigs are left behind in the forest' (Köstler, 1956); and that 'while mineral nutrients are as indispensable for trees as for agricultural crops, the cycle (of nutrients) rarely breaks down under rational forest management, and so mineral elements "take care of themselves"' (Baker, 1934).

Ebermayer's (1876) study set the scene for early, largely practical, studies of nutrient cycling. What is the mass of nutrients in a forest, and how are the nutrients distributed? How and at what rates are nutrients transferred between plant and soil? What is the balance - inputs minus outputs - of nutrients, and what are the factors which determine this balance? How are soil properties affected by the cycle of nutrients between plant and soil? How will harvesting of forest products (removal of timber, removal of litter, intensive harvesting of all materials) and silvicultural operations (e.g. burning, fertilizing, thinning) affect soil properties and sustained productivity of the ecosystem? Thus, from the pioneering work of Ebermayer (1876) more than a century ago, much of the work on forest soils has been directed toward nutrient cycling (Fig. 1), in particular to:

- quantifying the cycle of nutrients (uptake and return between plant and soil and retranslocation within the plant)
- quantifying inputs and outputs, including nutrient removals in harvested timber.

While all of this is obvious, the science that is required is not obvious. Twenty years ago Stone (1979) concluded that, despite a wealth of data on nutrient cycling processes for many

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forests, we do not have a sound experimental basis on which to assess the sustained productivity of forest ecosystems.

A major impetus for research in forest soils in the Northern Hemisphere was 'acid rain' and its effects on the growth of forests and on processes in forest soils. Sulphur emissions have increased since the start of the industrial revolution to the extent that 75% of total, global emissions of S (total about 105 Mt year⁻¹ of S) come from anthropogenic sources (Fig. 3, from Ayers and Granek, 1995). While emissions from natural sources are about evenly distributed between Northern and Southern Hemispheres, 90% of anthropogenic emissions come from sources in the Northern Hemisphere (Fig. 3; about 70 Mt year⁻¹ of S in the Northern Hemisphere and 7.7 Mt year⁻¹ of S in the Southern Hemisphere).

Because of the increasing acidity of rain through much of the Northern Hemisphere, we saw in the 1980s the widespread prediction of a general decline of European forests (the concept of 'Waldsterben'). By the 1990s this view was greatly modified, particularly by evidence (Kauppi *et al.*, 1992; Kauppi *et al.*, 1995) that the growing stock of European forests increased between 1971 and 1990 by 25% and that growth of the forests increased by 30%. Skelly and Innes (1994) concluded that 'the concept of a general forest decline is untenable', and that the evidence for air pollution causing forest decline 'away from known sources of pollution is extremely limited'.

Within Australia, the expansion of plantations of softwoods (*Pinus radiata* in the southern states, *Pinus elliottii* and *Araucaria* in Queensland, resulted in a great deal of research as limitations to growth by both major and micro-elements became obvious. With the rise of environmental concerns in the 1960s and 1970s, the rate of establishment of new pine plantations decreased. As a consequence of changing technologies and of the outcomes of Regional Forest Agreements throughout Australia, the establishment of hardwood plantations (principally of *Eucalyptus globulus* and *E. nitens*) now exceeds the rate of establishment of softwoods (National Forest Inventory Australia, 1999). Much of the research on forest soils in Australia is now driven by problems encountered with these new hardwood plantations.

I will not attempt in this lecture to deal with this vast area of plantation research. I have no doubt that our knowledge of soils of pine and eucalypt plantations exceeds our knowledge of

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soils of our native forests, and that is cause for concern. For example, the meeting earlier this month of Research Working Group 3 – Soils and Nutrition in New Zealand.(Anon., 1999) was entirely devoted to plantations.

THE SUSTAINABILITY OF FOREST GROWTH

Measuring the rate of supply of N and P

Nitrogen and P in organic forms in soil are mineralized to inorganic forms by soil microorganisms. Transformations of N during mineralization (Fig. 4) are well understood; heterotrophic organisms convert organic N to ammonium-N which may be oxidized by autotrophic organisms to nitrite-N which never accumulates but is further oxidized to nitrate-N. Depending on conditions, however, the demand for N by the heterotrophs in response to the supply of C may be so great that little ammonium-N escapes out of an 'internal cycle' of mineralization followed by immobilization of the ammonium-N in microbial biomass (Jansson, 1958; Paul and Juma, 1981; Attiwill and Leeper, 1987). Rather less is known of the detail of mineralization of P, but models similar to those used for the mineralization of N have been proposed (Halm *et al.*, 1972; Ghoshal and Jansson, 1975) and it is assumed that much of the demand for P by trees in the mature forest is supplied by the cycling of P in organic residues (Attiwill, 1980; Miller, 1981).

Measuring the rate of mineralization of N or P requires measuring either the rate of depletion of organic forms or the rate of accumulation of inorganic forms. For N, some 95% or more of the total in a forest soil is organic so that measuring a small depletion against a large background is impossible. Nor can we identify that smaller, discrete fraction of organic N which is most biologically susceptible. Most studies measure the rate of accumulation of the ammonium-N and nitrate-N produced by mineralization during a given period. Both forms are taken up by plants and nitrate-N is highly mobile in the soil, moving freely in solution. The soil must be contained during the period of measurement so that both uptake and leaching are prevented; this is done by incubating a sample of the soil either under specified conditions in the laboratory or under *in situ* conditions in the forest. The *in situ* methods which have been used in our laboratory and elsewhere (Adams and Attiwill, 1986; Raison *et al.*, 1987; Adams *et al.*, 1989) were developed from the pioneering work of Lemee (1967), Ellenberg

(1977), Rapp *et al.* (1979) and others. We have used these methods extensively over a range of eucalypt forests in south-eastern Australia and in closed-forest (or cool temperate rainforest) dominated by *Nothofagus cunninghamii* Hook. and *Atherosperma moschatum* Labill, and we have shown that rates of mineralization of N measured by *in situ* methods are closely related to rates of turnover of N in litterfall over (Fig. 5, from Attiwill *et al.*, 1996).

Measurement of the rate of mineralization of P is far more difficult. Total P in the surface soil may be more or less equally distributed between inorganic and organic forms. While only a small fraction of the inorganic P is labile, this fraction is in equilibrium with surfaces which remove H_2PO_4^- from solution. Ion-exchange resins will trap both H_2PO_4^- produced by mineralization and H_2PO_4^- coming from the altered equilibrium with solid-phase phosphates. This competitiveness between biological and chemical sinks for P remains a priority area of research in quantifying the long-term sustainability of P-supply for forests. Indices of the potential for mineralization of P such as the concentration of microbial P, the concentration of labile organic P (soluble in NaHCO_3) and acid phosphomonoesterase activity are highly correlated with each other (e.g. Fig. 6) and with indices of the potential for N mineralization such as organic and total labile N extracted with hot KCl (Adams *et al.*, 1989; Polglase *et al.*, 1992). The measurement of phosphatase activity or labile organic P may give the best index of mineralization potential (Fig. 6), and should be further investigated. Finally, while Adams (1990) showed that a large proportion of labile organic P in soils of *E. regnans* forests is in diester form, the activity of acid phosphodiesterase is much less than that of phosphomonoesterase (Watt, 1992).

Replacing the losses of N and P due to timber harvesting

In our example of harvesting a eucalypt forest of high productivity on a rotation of 100 years (Table 1), N-balance is restored if the rate of symbiotic N_2 -fixation is $3.6 \text{ kg ha}^{-1}\text{year}^{-1}$, depending on the intensity of harvesting. *Acacia* species are a natural component of both understorey and shrub layers in eucalypt forests, and where they grow densely, rates of N_2 -fixation of $20 - 30 \text{ kg ha}^{-1}\text{year}^{-1}$ have been recorded (Adams and Attiwill, 1984b; Adams and Attiwill, 1984a; Turvey *et al.*, 1984). For most forests, however, the distribution of N_2 -fixing

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species is irregular, and that makes the estimation of an areal rate of N₂-fixation very difficult. If we are to replace N-losses by managing N₂-fixing species, we need much more research on managing the rate of N₂-fixation by these species relative to the long-term economic value of their N-input. This is a most difficult area of research because the available methodologies (e.g. studies based on ¹⁵N) are difficult to apply in forests (May, 1999).

Resolution of the decrease in P in surface soil of 0.05 ppm per year due to harvesting our eucalypt forest on a 100-year rotation (Table 1) is a futile quantitative exercise. Apart from analytical uncertainties in assessing the pool of plant-available P and the rate at which it is sustained over 100 years, there are basic questions that remain unanswered: (i) the rate of rock weathering is a 'ball-park' estimate; how can it be improved? (ii) does P move from lower-class (or less available) reserves, in both surface soil and subsoil, to higher class at the rate of 0.05 ppm year⁻¹? (iii) are tree roots chemically active in obtaining P from lower class reserves? For example, the roots of some forest tree species exude low-molecular-weight organic acids that may play a role in solubilizing P (Smith, 1976; Fox and Comerford, 1990; Fox *et al.*, 1990).

The Britannia Creek Ecosystem Experiment - a field study of disturbance and sustainability

Some of the best mountain ash (*Eucalyptus regnans*) forest in Victoria grows in the Britannia Range, roughly between Warburton and Powelltown. Mountain ash does not regenerate in nature unless there is a disturbance of stand-replacing magnitude, such as bushfire.

In February, 1983, the Ash Wednesday bushfire burned through much of the Britannia Range, including a logging coupe of some 40 ha that had been logged by clear-felling over the 1982/83 summer (this area had previously been logged in 1932, so the forest was 50 years old). There was a very large amount of debris (non-merchantable stems, branches, leaves and understorey) from the logging operations, and the bushfire burned through the coupe with great intensity. The regeneration of mountain ash following clear-felling and the bushfire was prolific, and the rate of growth has been impressive. Sixteen years after the fire, the largest trees are 40 cm in diameter, with a maximum height of 35 m.

This clear-felled and burnt logging coupe provided the basis for the Britannia Creek Ecosystem Experiment, one aspect of which was to determine whether or not the loss of nutrients caused by clear-felling and burning causes a decrease in the rate of growth. A fully-replicated, 'reverse depletion' experiment was set up in the logging coupe. The reverse-depletion argument is that, if the addition of nutrients does not cause an increase in the rate of growth, then a loss of the same or lesser amount of nutrients will not decrease the rate of growth. Up to 500 kg ha⁻¹ of P and 1000 kg ha⁻¹ of N was added, the N and P being added alone, together and in combination with all other essential elements.

The Britannia Creek Ecosystem Experiment has provided the opportunities for a wide range of studies of forest processes including the effects of nutrients and environment on growth, on mineralization of N and P, and on decomposition, and for a wide range of studies of structure, including effects of nutrients on floral diversity. Sixteen years after clear-felling and bushfire, there is no significant effect of the addition of nutrients on growth of the forest (Fig. 7).. The effect of adding N on the concentration of N in the leaves of trees has not been significant, but the concentration of total P in leaves has increased significantly where P has been added alone (but not where P and N were added together; Fig. 8), and so there have been significant differences in the ratio concentration of P:concentration of N in leaves (Fig. 9). The increase in concentration of total P is due to the accumulation of inorganic P (Fig. 8), with no significant differences in the concentration of organic P. We conclude that the rate of growth is not nutrient-limited, and that the loss of nutrients caused by clear-felling, removal of timber and fire has not caused a decrease in productivity. Thus for the mountain ash forests of Britannia Creek, we conclude that the current harvesting system of clear-felling and burning is nutritionally sustainable. To understand why this is so demands the knowledge of inputs to the system - that is, of the input of N by N₂-fixation and of the input of P from lower-class sources, including weathering parent materials, as identified earlier in this paper.

CARBON SEQUESTRATION: THE STORAGE OF CARBON IN FOREST SOILS

The concentration of CO₂ in the world's atmosphere has increased steadily since the industrial revolution due to the burning of fossil fuels and the clearing and burning of vegetation. The longest-term, precise record is from Mauna Loa, Hawaii, where there has been a 16.1%

increase in mean annual concentration from 315.83 ppmv in 1959 to 366.70 ppmv in 1998 (Keeling and Whorf, 1999). This increase is about one-half the amount of CO₂ released into the atmosphere from emissions. In round terms for the year 1996, CO₂ emissions as C from fossil fuels are about 6.5 Gt year⁻¹ and 1.5 Gt year⁻¹ from land-use change (the latter being quite debatable), giving total emissions of C of 8 Gt year⁻¹. The amount of C entering the oceans is about 2 Gt year⁻¹, leaving 2 Gt ha⁻¹ as the 'missing sink'. Is the missing sink explained by an increase in the rate of C-storage in forests? This is a global question, and I will not attempt to address it here. However, that question raises another: to what extent can we offset the increase in atmospheric CO₂ by planting trees? I will first discuss that topic in relation to Australia's CO₂ emissions, and then outline the importance of soil and soil organic matter in sequestering C in forests.

Australia's emissions of CO₂: can plantations make a difference?

Australia's emissions of CO₂ from the burning of fossil fuels, cement manufacture and gas flaring amount to 83.7 Mt year⁻¹ as C, a mere 1.3% of the world's emissions, 6.5 Gt year⁻¹ (Marland *et al.*, 1999). However, per capita emission of C in Australia is 4.63 t compared with 1.13 t per capita for the world; Australia is the fifth-highest per capita consumer of fossil fuels. To what extent can we offset Australia's CO₂ emissions by planting more trees? The question also has a financial aspect: should those who plant trees be offered a financial incentive - a 'carbon credit'?

- In the latter part of the 1900s, the rate of establishment of pine plantations to meet Australia's deficiency of softwood timber increased rapidly. Over the last 20 years, however, new manufacturing technologies have increased the demand for eucalypt plantations, and in the period 1995-98 the rate of establishment of eucalypt plantations more than doubled (Fig. 10). The rate of establishment of eucalypt plantations in 1998 was four time greater than the rate of establishment of softwood plantations (Fig. 10).
- The area of Australia's plantations in 1999 is 1.2 X 10⁶ ha (National Forest Inventory Australia, 1999). Suppose we almost treble the area of plantations over the next 20 years by establishing 100,000 ha per year (this is a substantial increase over the current rate of establishment of a little over 60,000 ha per year; Fig.10).

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- Suppose all of the land is productive to the extent that it will produce a mean annual increment of $10 \text{ t ha}^{-1}\text{year}^{-1}$ of dry matter, or $5 \text{ t ha}^{-1}\text{year}^{-1}$ of C
- After 20 years of planting, $100 \times 10^6 \text{ t}$ of C will be fixed. At current rates, $1.7 \times 10^9 \text{ t}$ of C will be emitted over this period. Carbon fixed in the above-ground parts of the plantations is about 6% of C emissions.

This analysis is, of course, simplistic for a number of reasons:

- it is most unlikely that 2 million hectares of productive land will be available for plantations over the next 20 years
- using the current rate of C emissions for the next 20 years is highly conservative, given that the increase in annual C emissions over the past 10 years (1986-1996) was 37% (Fig. 11). At the world scale, the Mauna Loa records show that the increase of 2.87 ppmv for 1997/98 is the largest annual increase since the Mauna Loa measurements began in 1958 (Keeling and Whorf, 1999).
- the rate of clearing of woody vegetation in Australia (Fig. 12, from Barson, 1999) far exceeds the current rate of plantation establishment (Fig. 13). The 340,000 ha cleared in Queensland for the year 1996/97 (Fig. 12 and 13) is 3.4 times the increased rate of plantation establishment of 100,000 ha per year used in this analysis.
- the analysis does not account for storage of C below ground, in both roots and soil organic matter.
- the analysis does not account for losses of C from soil organic matter during the establishment of the plantation (cultivation, mounding, herbicides, increased temperature and water content of the soils etc). Balancing this loss by C-fixation through plantation growth may take 10 or more years (Grierson *et al.*, 1991; Turner, in press).

Long-term sequestration of C depends on the movement of C from more-easily oxidizable forms to less-easily oxidizable forms, and we must account for this movement whether we are studying C-storage in plantations in terms of C-credits or longer-term C-storage in forests in response to increasing CO₂ concentrations in the atmosphere. Forms and turnover of C in

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forest soils are therefore central to accounting for C-sequestration in forest ecosystems, and I will spend the last part of this lecture discussing C in forest soils.

Forms and turnover of carbon in soil

Organic matter includes most of the litter and humic layer in forest soils and generally forms between 1 - 10% of surface mineral horizons (Attiwill and Leeper, 1987). The comminution and decomposition of above- and below-ground litter in forests releases CO₂, and nutrient elements are mineralized and immobilized. While all organic matter is ultimately oxidized in forest soils, compounds which decompose over centuries and millennia are synthesized in the process of humification, which involves processes of both degradation and synthesis. This humus is amorphous, and is intimately mixed with soil mineral components; it is difficult to describe in any precise chemical manner. The inert organic matter of forest soils is protected from decomposition in a number of ways, including association with mineral particles, which is the basis for longer turnover times for organic matter in clay-textured soils relative to sandy soils. Most of the organic matter in soils is very old, and decomposition to inorganic constituents will take centuries to millennia (Jenkinson and Rayner, 1977; Attiwill and Leeper, 1987; Schimel *et al.*, 1994).

Both chemical and physical methods have been used to fractionate soil organic matter; it has not been possible, however, to separate organic matter into discrete components of varying decomposability (Sanchez *et al.*, 1989). Traditional chemical methods date from the classical empirical fractionation based on sequential acid and alkali extractions; which recognizes fulvic acids (soluble both in acid and in alkali), humic acids (soluble in alkali and precipitated by acid), and humin (insoluble both in alkali and acid). The relationships between these various fractions are uncertain; a 'favoured' view is that organic matter is a mixture of polymers formed from polyphenols derived from lignin together with amino compounds. The polymers so-formed have a wide range of molecular weights and acidic functional groups (Fig. 14).

Physical methods based on density usually separate soil according to free particulate organic matter (macro-organic matter), occluded particulate organic matter (light fraction), and colloidal or clay-associated organic matter (heavy or humified fraction, e.g. Golchin *et al.*, 1994). Density fractionation, based on dispersal of soil in NaI solution has proved useful in

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separating organic matter into components that are physically and chemically distinct (Strickland and Sollins, 1987), and which are mineralized at different rates by soil microorganisms (Christensen, 1992; Boone, 1994). Generally the light fraction extracted in NaI is comprised of partially decomposed roots and litter and is relatively labile; it has been reported to represent between 25 and 53 % of total soil weight in second-growth forest of Western Oregon (Strickland and Sollins, 1987). By contrast the heavy fraction is regarded as more resistant humic material which is adsorbed onto mineral surfaces (Theodorou, 1990). The heavy fraction can be further separated into proximate fractions such as soluble fats and oils, celluloses and lignin, and phenolic compounds. Studies employing these density-fractionation techniques (Entry and Emmingham, 1998) have established that old-growth forests store more C than young-growth forests, and that soils of old-growth forest contain greater percentages of recalcitrant organic matter which is typically richer in lignin and tannic compounds. Further application of these methods, which identify the most biologically active forms of C in forest soils, are critical to developing a better understanding soil organic matter turnover under a range of influences.

As is apparent from the preceding discussion of C-storage in forest soils, much of the recent interest in forms of organic matter in forest soils and their turnover time is in relation to the impacts of climate change and forest management on pools and fluxes of C. Models of soil C-turnover have been used to predict the effects of climate change and of different land-uses, on soil C-fluxes (Kelly *et al.*, 1997; Bolker *et al.*, 1998; Peng and Apps, 1998; Peng *et al.*, 1998). While a number of models have been developed, the most popular models are those based on the CENTURY model (Parton *et al.*, 1988) and the ROTH-26.3 model (Coleman and Jenkinson, 1996). These models have been used to simulate changes in organic-C of arable and grassland soils with accuracy (Coleman and Jenkinson, 1996).

Studies in forest soils, however, must encompass organic matter with a wide range of decomposition constants (Fig. 15). Although the C-models were originally developed for agricultural soils (Jenkinson and Rayner, 1977; Oades, 1988), they have recently been adapted to model the more complex environment of forest soils by inclusion of modules to accommodate the forest floor and litter layer (Parton *et al.*, 1994; Vitousek *et al.*, 1994). An

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adapted CENTURY model predicted the pattern or ranking of decomposition of surface litter in a matrix of *Metrosideros* sites on Mauna Loa, Hawaii, but did not predict the magnitude of differences among sites (Vitousek, 1994). The refinement of the CENTURY model as it applies to forest soils will doubtless demand a better understanding of the reactivity of organic matter on the forest floor.

Studies of the proportion of the large store of soil-C that exchanges with the atmosphere within centennial and shorter time-scales (compared with time-scales of millennia) are critical to our understanding of the global C-cycle (Torn *et al.*, 1997). At the scale of landscapes and over geologic time, Torn *et al.* (1997) demonstrated that the turnover time for the large, passive pool of soil-C is controlled primarily by soil mineralogy.

A selection of research imperatives in assessing the quantity and quality of organic matter in tropical soils Stevenson *et al.* (1989) comprehensively summarizes the concerns of this lecture:

- develop reliable procedures for measurement of soil organic matter pools, including litter, light fraction, microbial biomass (C, N, P and S), and the labile and passive components of soil humus;
- reconcile differences among conceptual, mathematical and operational definitions of soil organic matter pools;
- improve chemical procedures for extractions and fractionation of soil organic matter (emphasis on biologically meaningful fractions);
- determine dynamics of soil organic matter transformations in terms of nutrient fluxes (rather than static pool sizes). Promote more extensive use of stable and radioactive isotopes.'

CONCLUDING COMMENTS

The genus *Eucalyptus* dominates the forests of Australia. Australia has 112 million hectares of woodland, 39 million hectares of open-forest and 4.6 million hectares of closed forest. The genus *Eucalyptus* dominates the canopies of 124 million hectares of open forest, woodland and mallee, and shares the canopy with other genera in a further 10 million hectares. Eucalypts are

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the most dominant species in 270 forest communities in Australia. All but four of the approximately 700 species of *Eucalyptus* are endemic to Australia (these figures are taken from the Bureau of Rural Sciences; <http://www.brs.gov.au/nfi/forestinfo/eucalypt.html>).

I have aimed in this talk to outline some topics in the ecology of eucalypt forests and forest soils that are critical to sustainable management, irrespective of whether or not that includes the harvesting of timber.

The processes involved with Regional Forest Agreements for Australia's forests initiated a flurry of fact-finding activities. One result of the Agreements is a general down-sizing of the dependence of the timber industry on native forests, and an increased emphasis on eucalypt plantations as a source of timber for the future.

These changing emphases have resulted in a marked change in research activities across Australia. Most of the research in trees and soils is now firmly centred on plantations, presumably because that is where the government money is available. Most of this research is highly applied and site-specific. Since the plantation area is less than 1% of Australia's treed area, Australia's investment in research on the ecology of forests and forest soils is seriously unbalanced. I will therefore continue to call for an increase in basic research in the eucalypt forests of Australia.

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REFERENCES

- Adams, M.A. and Attiwill, P.M. (1984a) Role of *Acacia* spp. in nutrient balance and cycling in regenerating *Eucalyptus regnans* F. Muell. forests. I. Temporal changes in biomass and nutrient content. *Australian Journal of Botany*, **32**, 205-15.
- Adams, M.A. and Attiwill, P.M. (1984b) Role of *Acacia* spp. in nutrient balance and cycling in regenerating *Eucalyptus regnans* F. Muell. forests. II. Field studies of acetylene reduction. *Australian Journal of Botany*, **32**, 217-23.
- Adams, M.A. and Attiwill, P.M. (1986) Nutrient cycling and nitrogen mineralization in eucalypt forests of south-eastern Australia. II. Indices of nitrogen mineralization. *Plant and Soil*, **92**, (341-362).
- Adams, M.A., Polglase, P.J., Attiwill, P.M. and Weston, C.J. (1989) *In situ* studies of nitrogen mineralization and uptake in forest soils; some comments on methodology. *Soil Biology and Biochemistry*, **21**, 423-9.
- Anon. (1999) Site Specific Management of Softwood and Hardwood Plantations, in *Research Working Group 3 - Soils and Nutrition*, Australian Forestry Council, Forest Research, Rotorua, New Zealand, Rotorua, New Zealand,.
- Attiwill, P.M. (1980) Nutrient cycling in a *Eucalyptus obliqua* (L'Herit.) forest. IV. Nutrient uptake and nutrient return. *Australian Journal of Botany*, **27**, 439-58.
- Attiwill, P.M. (1995) Forest nutrient cycling, in *Encyclopedia of Environmental Biology*, (ed. W. A. Nierenberg), Academic Press, San Diego, pp. 625-39.
- Attiwill, P.M. and Adams, M.A. (1993) Tansley Review No. 50: Nutrient cycling in forests. *New Phytologist*, **124**, 561-82.
- Attiwill, P.M. and Leeper, G.W. (1987) *Forest Soils and Nutrient Cycles*, Melbourne University Press, Melbourne.
- Attiwill, P.M., Polglase, P.J., Weston, C.J. and Adams, M.A. (1996) Nutrient cycling in forests of south-eastern Australia, in *Nutrition of Eucalypts*, (eds P. M. Attiwill and M. A. Adams), CSIRO, Melbourne, pp. 191-227.

Peter M. Attiwill; Outline of Professor G.W. Leeper Memorial Lecture presented at The University of Melbourne, November 26, 1999. This paper is not to be used or quoted without permission of the author.

- Attiwill, P.M. and Weston, C.J. (in press) Forest Soils, in *The Forests Handbook*, (ed. J. Evans), Blackwell Science, Oxford, pp. .
- Ayers, G.P. and Granek, H. (1995) Sulfur in the Australian atmosphere, in *Managing SO₂ in Australia. National Conference: Issues and Strategies*, Clean Air Society of Australia and New Zealand, Melbourne,.
- Baker, F.S. (1934) *Theory and Practice of Silviculture*, McGraw-Hill, New York.
- Barson, M. (1999) Greenhouse in agriculture - an overview of the scientific issues. *Climate Change Newsletter*, **11**, (3), 1-4.
- Baule, H. (1973) World-wide forest fertilization: its present state, and prospects for the near future. *Potash Review*, **6**, 23.
- Bengtson, G.W. (1979) Forest fertilization in the United States: progress and outlook. *Journal of Forestry*, **77**, 222-9.
- Bolker, B.M., Pacala, S.W. and Parton, W.J. (1998) Linear analysis of soil decomposition - insights from the Century model. *Ecological Applications*, **8**, (2), 425-39.
- Boone, R.D. (1994) Light fraction soil organic matter: origin and contribution to net nitrogen mineralization. *Soil Biology and Biochemistry*, **26**, 1459-68.
- Christensen, B.T. (1992) Physical fractionation of soil organic matter in primary particle size and density separates. *Advances in Soil Science*, **20**, 1-90.
- Coleman, K. and Jenkinson, D.S. (1996) RothC-26.3 - A model for turnover of carbon in soil, in *Evaluation of soil organic matter models*, (eds D. S. Powlson, P. Smith and J. U. Smith), Vol. 38, Springer, Berlin, pp. 237-46.
- Ebermayer, E. (1876) *Die gesammte Lehre der Waldstreu mit Rücksicht auf die chemische Statik des Waldbaues*, Springer, Berlin.
- Ellenberg, V.H. (1977) Stickstoff als standortsfactor, insbesondere für mitteleuropäische Pflanzengesellschaften. *Oecologia Plantarum*, **12**, 1-22.

Peter M. Attiwill; Outline of Professor G.W. Leeper Memorial Lecture presented at The University of Melbourne, November 26, 1999. This paper is not to be used or quoted without permission of the author.

- Entry, J.A. and Emmingham, W.H. (1998) Influence of forest age on forms of carbon in Douglas-fir soils in the Oregon coast range. *Canadian Journal of Forest Research*, **28**, 390-5.
- Fox, T.R. and Comerford, N.B. (1990) Low-molecular-weight organic acids in selected forest soils of the southeastern USA. *Soil Science Society of America Journal*, **54**, 1139-44.
- Fox, T.R., Comerford, N.B. and McFee, W.W. (1990) Phosphorus and aluminium release from a spodic horizon mediated by organic acids. *Soil Science Society of America Journal*, **54**, 1763-7.
- Ghoshal, S. and Jansson, S.L. (1975) Transformation of phosphorus in organic matter decomposition studies with special reference to the immobilization effect. *Swedish Journal of Agricultural Research*, **5**, 199-208.
- Golchin, A., Oades, J.M., Skjemstad, J.O. and Clarke, P. (1994) Soil structure and carbon cycling. *Australian Journal of Soil Research*, **32**, (5), 1043-68.
- Grierson, P.F., Adams, M.A. and Attiwill, P.M. (1991) *Carbon Storage in Soil and in Forest Products*, Report Commissioned for the State Electricity Commission, Victoria School of Botany, The University of Melbourne,.
- Halm, B.J., Stewart, J.W.B. and Halstead, R.L. (1972) The phosphorus cycle in a native grassland ecosystem, in *Isotopes and Radiation in Soil-Plant Relationships, Including Forestry*, International Atomic Energy Agency, Vienna, pp. 571-86.
- Jansson, S.L. (1958) Tracer studies on nitrogen transformations in soil with special attention to mineralisation-immobilisation relationships. *Kungl. Lantbrukshögskolans Annaler*, **24**, 101-361.
- Jenkinson, D.S. and Rayner, J.H. (1977) The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science*, **123**, 298-305.
- Kauppi, P.E., Mielikäinen and Kuusela, K. (1992) Biomass and carbon budget of European forests, 1971 to 1990. *Science*, **256**, 70-4.

Peter M. Attiwill; Outline of Professor G.W. Leeper Memorial Lecture presented at The University of Melbourne, November 26, 1999. This paper is not to be used or quoted without permission of the author.

Kauppi, P.E., Tomppo, E. and Ferm, A. (1995) C and N storage in living trees within Finland since 1950s. *Plant and Soil*, **168-169**, 633-8.

Keeling, C.D. and Whorf, T.P. (1999) *Atmospheric carbon dioxide record from Mauna Loa*, Web site: <http://cdiac.esd.ornl.gov/trends/co2/sio-mlo.htm> Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee.

Kelly, R.H., Parton, W.J., Crocker, G.J., Grace, P.R., Klir, J., Korschens, M., Poulton, P.R. and Richter, D.D. (1997) Simulating trends in soil organic carbon in long-term experiments using the Century model. *Geoderma*, **81**, (1-2), 75-90.

Köstler, J. (1956) *Silviculture (Translated by M.L. Anderson)*, Oliver and Boyd,.

Lemee, G. (1967) Investigations sur la mineralisation de l'azote et son evolution annuelle dans des humus forestiers *in situ*. *Oecologia Plantarum*, **2**, 285-324.

Marland, G., Boden, T., Brenkhert, A., Andres, B. and Johnston, C. (1999) *Global, Regional, and National CO2 Emissions. In Trends: A Compendium of Data on Global Change*, Web site: <http://cdiac.esd.ornl.gov/trends/emis/aus.htm> Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee.

May, B. (1999). Silver wattle (*Acacia dealbata*): Its role in the ecology of the mountain ash forest and the effect of alternative silvicultural systems on its regeneration. PhD, The University of Melbourne, Melbourne.

Miller, H.G. (1981) Forest fertilization: some guiding concepts. *Forestry*, **54**, 157-67.

National Forest Inventory Australia (1999) *National Plantation Inventory of Australia 1999 interim tables: Australia's National Plantation Inventory: An Annual Tabular Update - June 1999.*, Web Site: <http://www.brs.gov.au/nfi/activities/npi/interim.html> Fisheries and Forestry Sciences Division, Bureau of Rural Sciences, Kingston ACT.

Oades, J.M. (1988) The retention of organic matter in soils. *Biogeochemistry*, **5**, 35-70.

Peter M. Attiwill; Outline of Professor G.W. Leeper Memorial Lecture presented at The University of Melbourne, November 26, 1999. This paper is not to be used or quoted without permission of the author.

- Parton, W.J., Ojima, D.S., Cole, C.V. and Schimel, D.S. (1994) A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture, and management, in *Quantitative modeling of soil forming processes*, Vol. 39, Soil Science Society of America Special Publication, Madison, Wisconsin, USA, pp. 147-67.
- Parton, W.J., Stewart, J.W.B. and Cole, C.V. (1988) Dynamics of C, N, S and P in grassland soils: a model. *Biogeochemistry*, **2**, 109-32.
- Paul, E.A. and Juma, N.G. (1981) Mineralization and immobilization of soil nitrogen by microorganisms, in *Terrestrial Nitrogen Cycles. Processes, Ecosystem Strategies and Management Impacts. Ecological Bulletins (Stockholm) 33*, (eds F. E. Clark and T. Rosswall), pp. 179-95.
- Peng, C.H. and Apps, M.J. (1998) Simulating carbon dynamics along the boreal forest transect case study (BFTCS) in central Canada - 2- Sensitivity to climate change. *Global Biogeochemical Cycles*, **12**, (2), 393-402.
- Peng, C.H., Apps, M.J., Price, D.T., Nalder, I.A. and Halliwell, D.H. (1998) Simulating carbon dynamics along the boreal forest transect case study (BFTCS) in central Canada - 1- Model testing. *Global Biogeochemical Cycles*, **12**, (2), 381-92.
- Polglase, P.J., Attiwill, P.M. and Adams, M.A. (1992) Nitrogen and phosphorus cycling in relation to stand age of *Eucalyptus regnans* F. Muell. III. Phosphatase activity and pools of labile soil P. *Plant and Soil*, **142**, 177-85.
- Raison, R.J., Connell, M.J. and Khanna, P.K. (1987) Methodology for studying fluxes of soil mineral-N *in situ*. *Soil Biology and Biochemistry*, **19**, 521-30.
- Rapp, M., Leclerc, M.C. and Lossaint, P. (1979) The nitrogen economy in a *Pinus pinea* L. stand. *Forest Ecology and Management*, **2**, 221-31.
- Rennie, P.J. (1955) The uptake of nutrients by mature forest growth. *Plant and Soil*, **7**, 49-95.
- Rennie, P.J. (1957) The uptake of nutrients by timber forest and its importance to timber production in Britain. *Quarterly Journal of Forestry*, **51**, 101-15.

Peter M. Attiwill; Outline of Professor G.W. Leeper Memorial Lecture presented at The University of Melbourne, November 26, 1999. This paper is not to be used or quoted without permission of the author.

- Sanchez, P.A., Palm, C.A., Szott, L.T., Cuevas, E. and Lal, R. (1989) Organic input management in tropical agroecosystems, in *Dynamics of soil organic matter in tropical ecosystems*, (eds D. C. Coleman, J. M. Oades and G. Uehara), NifTAL Project and University of Hawaii Press, Hawaii, pp. .
- Schimel, D.S., Braswell, B.H., Holland, E.A., McKeown, R., Ojima, D.S., Painter, T.H., Parton, W.J. and Townsend, A.R. (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles*, **8**, (3), 279-93.
- Skelly, J.M. and Innes, J.L. (1994) Waldsterben in the forests of Central Europe and Eastern North America: Fantasy or reality? *Plant Disease*, **78**, 1021-32.
- Smith, W.H. (1976) Character and significance of forest tree root exudates. *Ecology*, **57**, 324-31.
- Stevenson, F.J., Elliott, E.T., Cole, C.V., Ingram, J., Oades, J.M., Preston, C. and Sollins, P.J. (1989) Methodologies for assessing the quantity and quality of soil organic matter, in *Dynamics of Soil Organic Matter in Tropical Ecosystems*, (eds D. C. Coleman, J. M. Oades and G. Uehara), University of Hawaii and NifTAL Project, Honolulu, Hawaii, pp. 173-99.
- Stewart, H.T.L., Hopmans, P., Flinn, D.W. and Croatto, G. (1990) Harvesting effects on phosphorus availability in a mixed eucalypt ecosystem in southeastern Australia. *Forest Ecology and Management*, **36**, 149-62.
- Stone, E.L. (1979) Nutrient removals by intensive harvest - some research gaps and opportunities, in *Proceedings, Impact of Intensive Harvesting on Forest Nutrient Cycling*, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, Syracuse, New York, pp. 366-86.
- Strickland, T. and Sollins, P. (1987) Improved method for separating light and heavy fraction organic matter from soil. *Soil Science Society of America Journal*, **51**, 1390-3.
- Tamm, C.O. (1968) The evolution of forest fertilization in European silviculture, in *Forest Fertilization: Theory and Practice. Papers presented at the Symposium on Forest*

Peter M. Attiwill; Outline of Professor G.W. Leeper Memorial Lecture presented at The University of Melbourne, November 26, 1999. This paper is not to be used or quoted without permission of the author.

Fertilization, (eds G. W. Bengston, R. H. Brendemuehl, W. L. Pritchett and W. H. Smith), Tennessee Valley Authority, Gainesville, Florida, pp. 242-7.

Tamm, C.O. (1979) .

Theodorou, C. (1990) Nitrogen transformations in particle size fractions from second rotation pine forest soil. *Communications in Soil Science and Plant Analysis*, **21**, 407-13.

Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M. and Hendricks, D.M. (1997) Mineral control of soil organic carbon storage and turnover. *Nature*, **389**, 170-3.

Turner, J. (in press) *Forest Ecology and Management*,.

Turvey, N.D., Attiwill, P.M., Cameron, J.N. and Smethurst, P.J. (1984) Growth of planted pine trees in response to variation in densities of naturally regenerated acacias. *Forest Ecology and Management*, **7**, 103-17.

Vitousek, P.M. (1994) Beyond global warming - ecology and global change. *Ecology*, **75**, (7), 1861-76.

Vitousek, P.M., Turner, D.R., Parton, W.J. and Sanford, R.L. (1994) Litter decomposition on the Mauna Loa environmental matrix, Hawaii - patterns, mechanisms, and models. *Ecology*, **75**, (2), 418-29.

Watt, C. (1992). Availability and forms of phosphorus in a Mountain Ash (*Eucalyptus regnans* F. Muell.) forest regenerating after disturbance. B.Sc. (Honours), The University of Melbourne,.

White, D.P. and Leaf, A.L. (1956) *Forest Fertilization. A Bibliography, with Abstracts, on the use of Fertilizers and Soil Amendments in Forestry*, Technical Publication Rep. No. 81, State University College of Forestry at Syracuse University, Syracuse, New York.

Table 1. Estimates of the pools of nutrients and of net inputs and outputs (including those due to timber harvesting) of nutrients for a eucalypt forest of high productivity (from Attiwill and Leeper 1987; Attiwill and Weston, in press)

Pool or process	N	P
Pools		
Above-ground, kg ha ⁻¹	500	50
Litter layers, kg ha ⁻¹	200	10
Soil (0-30 cm), kg ha ⁻¹	15000	900
Inputs - Outputs, kg ha ⁻¹ per 100 years	-360	-16
Inputs - Outputs, % of total pools	-2.3	-1.7
Inputs - Outputs, change in concentration (µg g ⁻¹ year ⁻¹) in surface 30 cm of soil	-1.2	-0.05

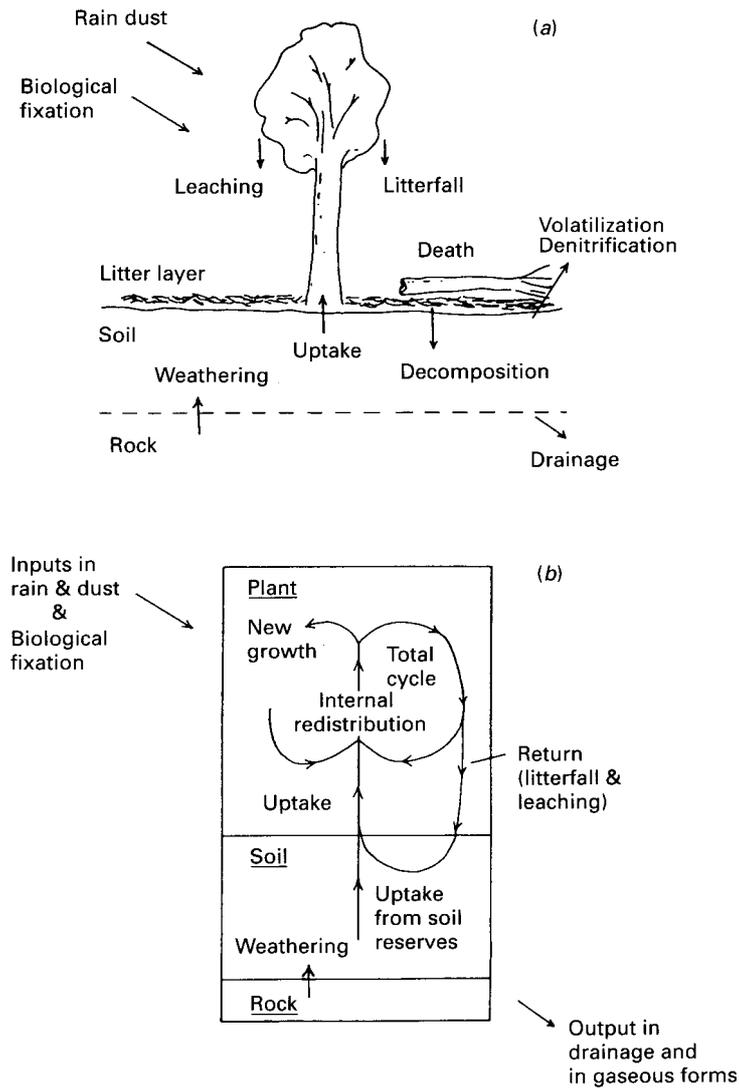


Figure 1. The cycle of elements in forests. From Attiwill (1993), after Attiwill (1987).

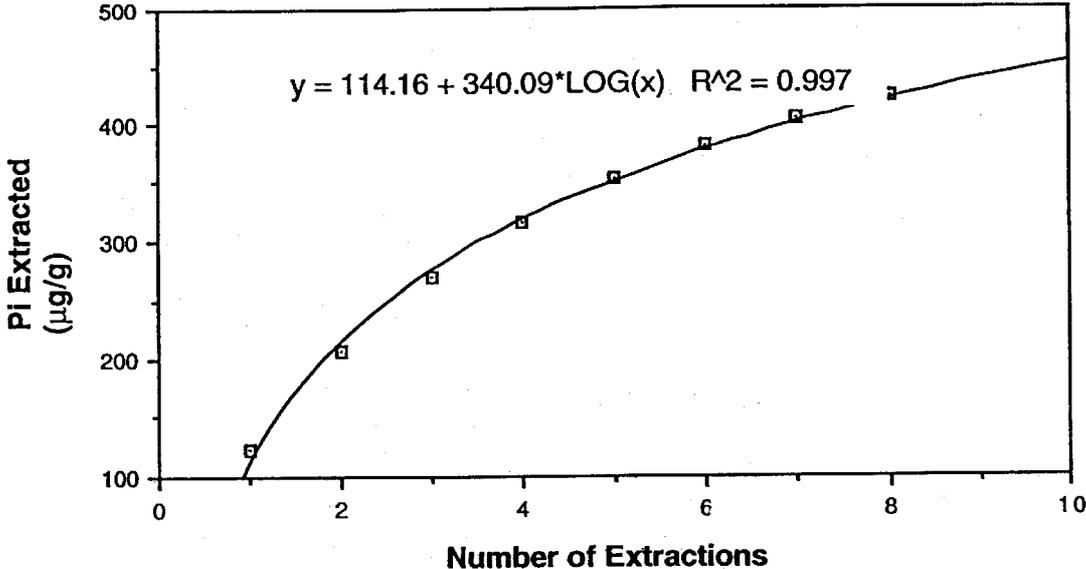


Figure 2. The amount of P extracted by repeated extractions from a mountain ash soil, Britannia Creek. From Watt (1992), based on the method of Stewart (1990).

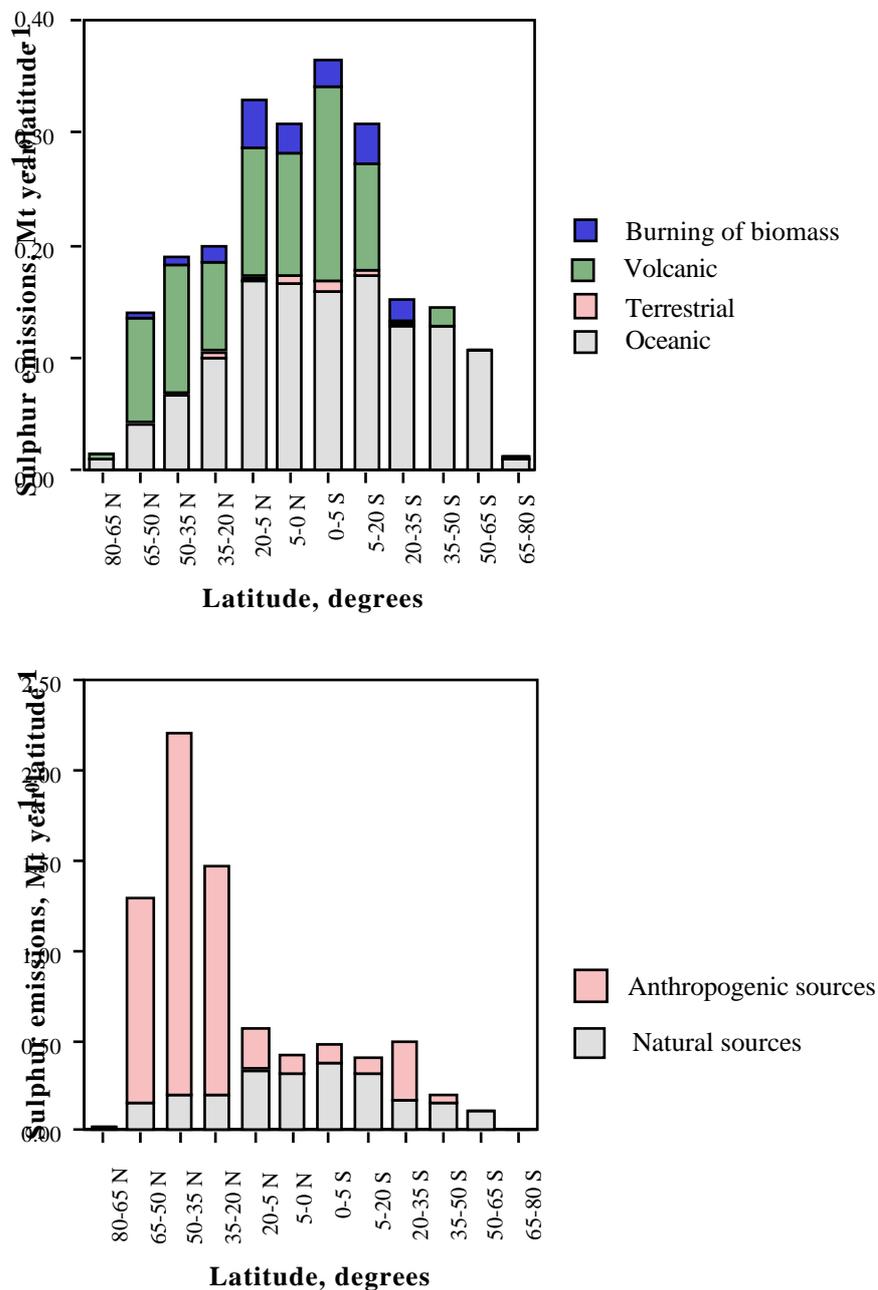


Figure 3. Global emissions of sulphur from natural sources (top), and a comparison of sulphur emissions from natural and anthropogenic sources (bottom). From Ayers (1995).

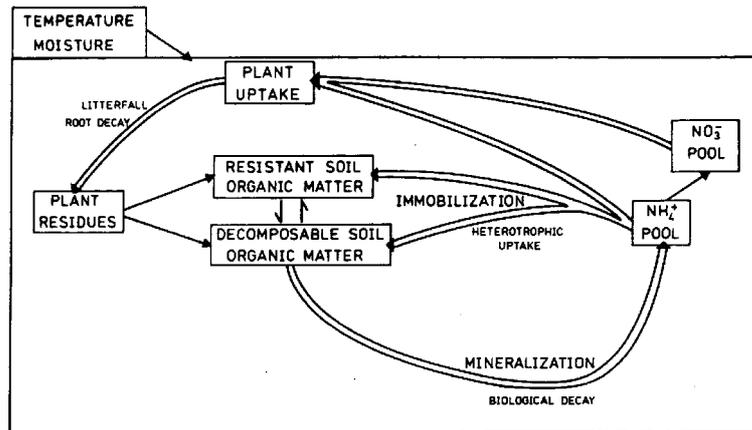


Figure 4. A model of nitrogen transformations in forests. From Adams (1989), adapted from Jansson (1958)

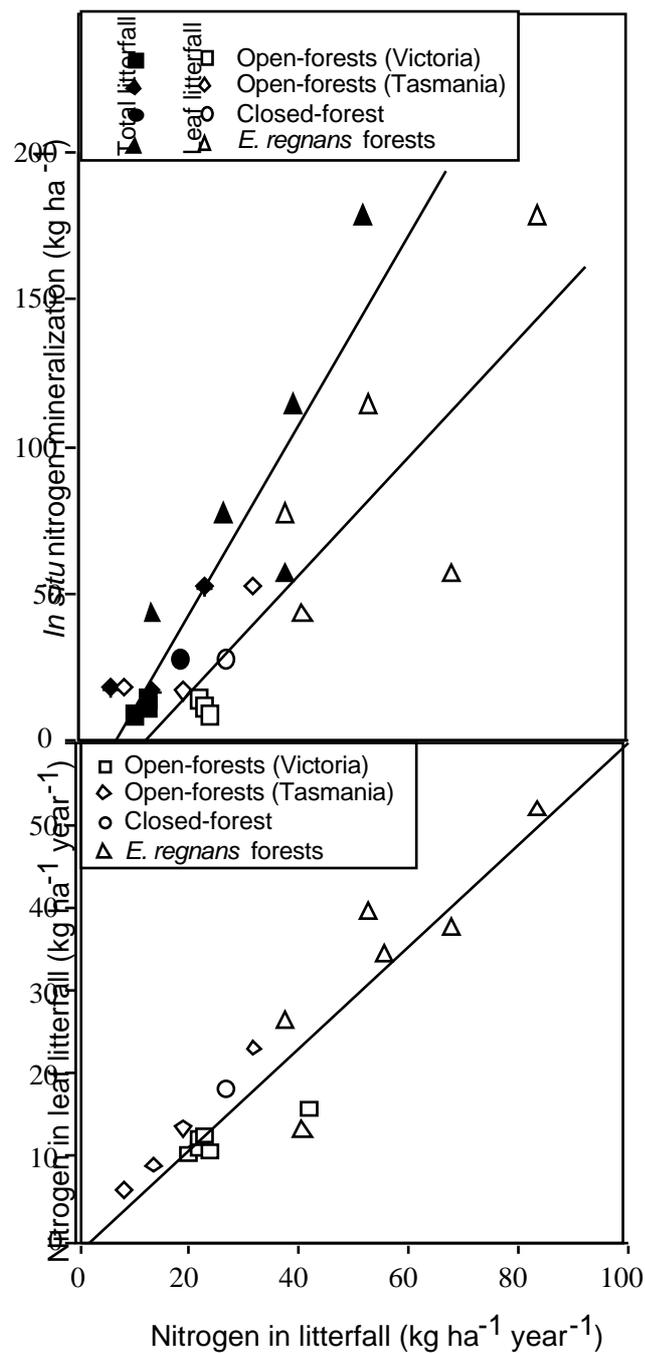


Figure 5. (Upper) The relationship between annual nitrogen mineralization *in situ* and the return of nitrogen in litterfall, and (lower) the return of nitrogen in leaf litterfall in relation to the return of nitrogen in total litterfall. The data cover a range of forest types in south-eastern Australia. (from Attiwill *et al.*, 1996)

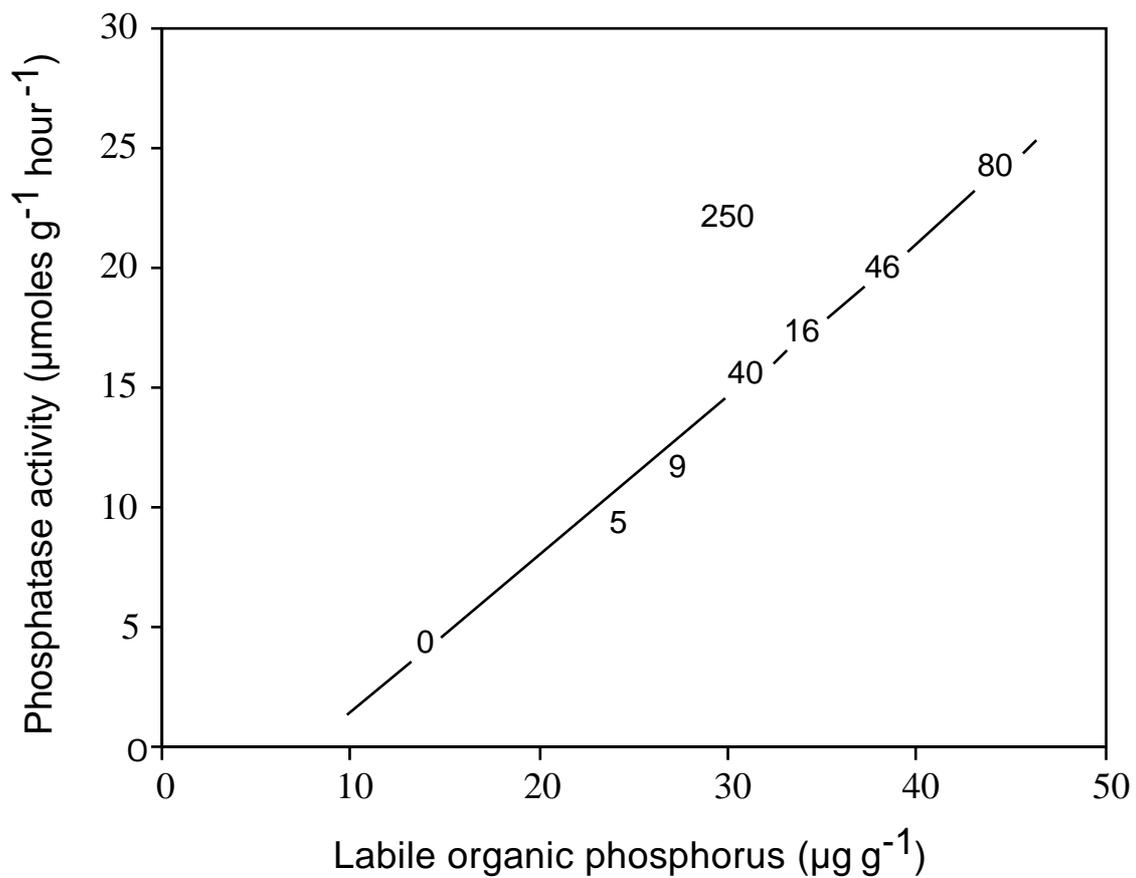


Figure 6. The relationship between the activity of phosphomonoesterase and labile organic phosphorus (extracted in 0.5 N NaHCO₃) in an age-sequence of *E. regnans* forests in Victoria (from Polglase *et al.*, 1992).

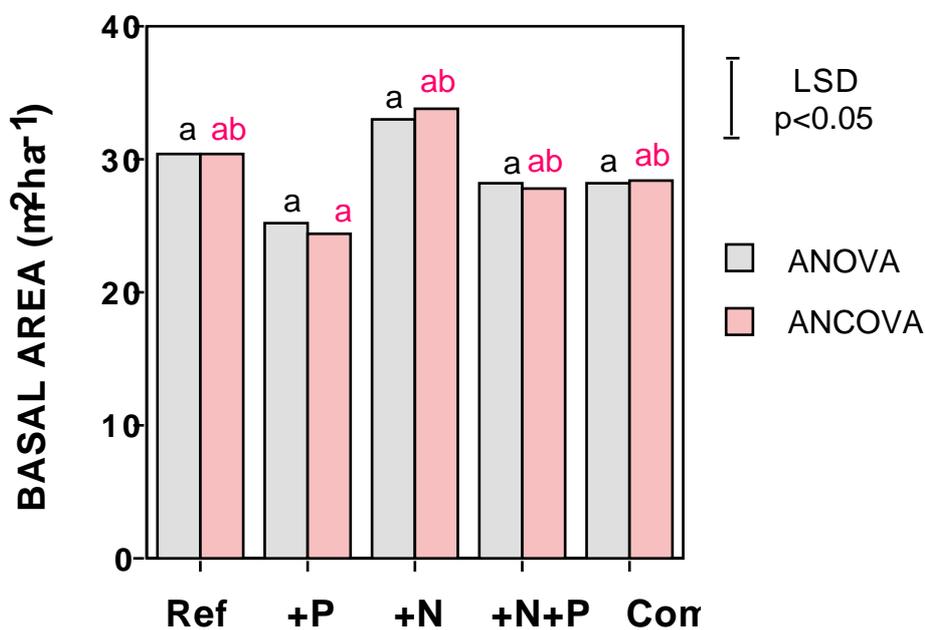


Figure 7. Analyses of variance and covariance of the response (as basal area of the trees at age 16 years) of a regenerating mountain ash forest at Britannia Creek, Victoria, to the application starting at age 3 years of P (up to 500 kg ha⁻¹), N (up to 1000 kg ha⁻¹), N+P, and all essential elements.

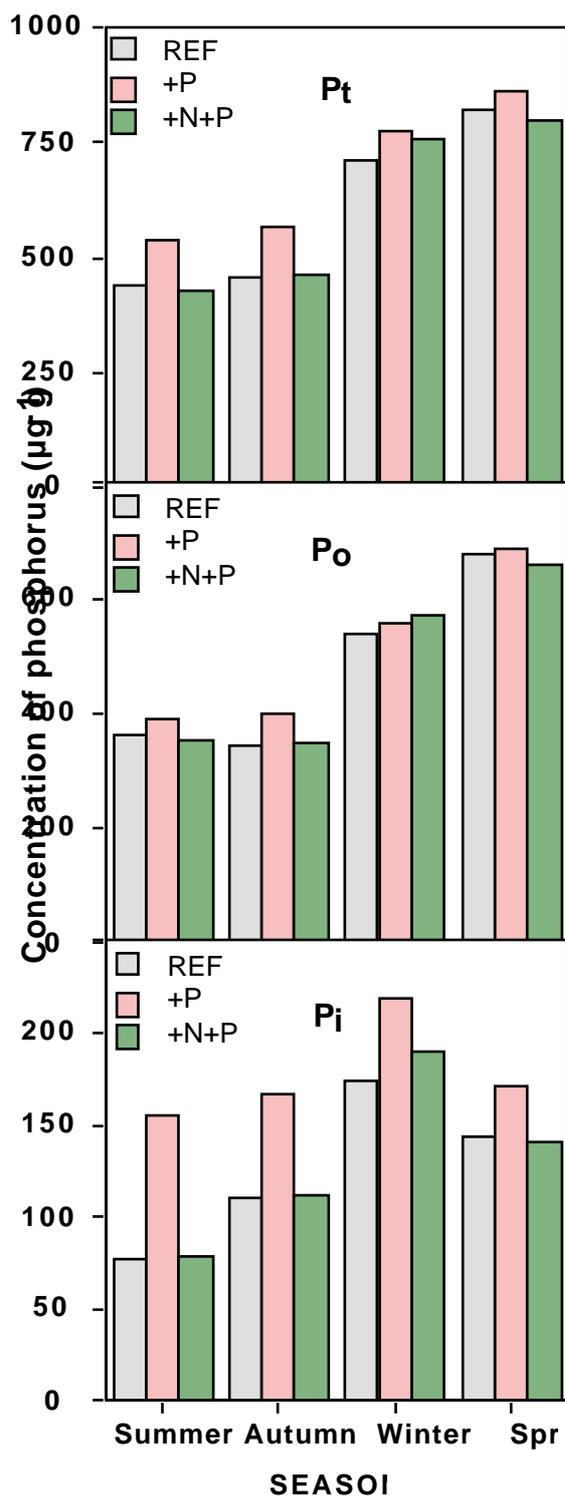


Figure 8. Changes in the concentration of total P, inorganic P and organic P in leaf litterfall of mountain ash forest at Britannia Creek, Victoria, with season, and with the addition of P (up to 500 kg ha⁻¹) and N (up to 1000 kg ha⁻¹). The fertilizers were added 1986-90, and this response was measured in 1992.

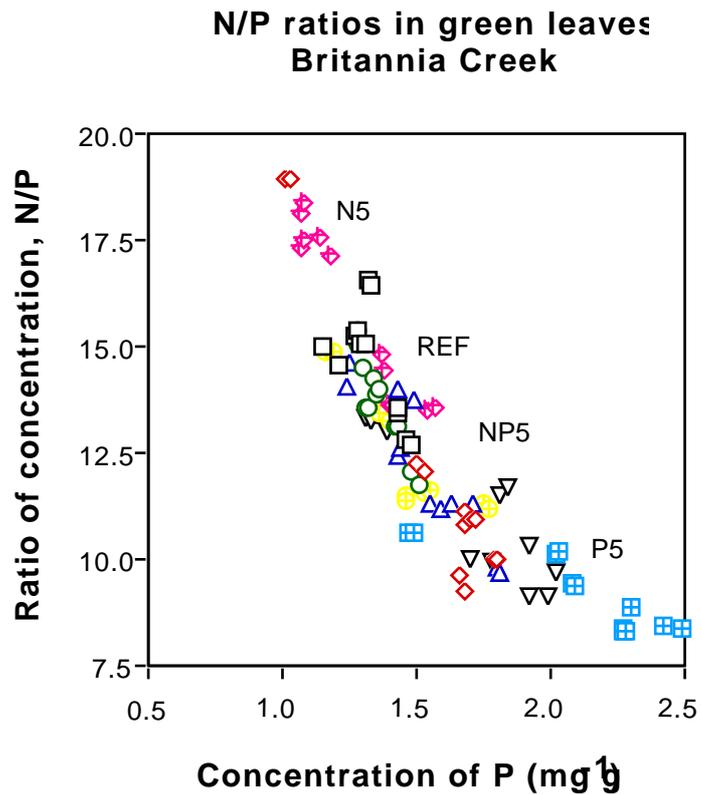


Figure 9. Changes in the concentration of P and N in leaves of mountain ash forest at Britannia Creek, Victoria, with season, and with the addition of P (500 kg ha⁻¹) and N (1000 kg ha⁻¹). The fertilizers were added 1986-90, and this response was measured in 1994.

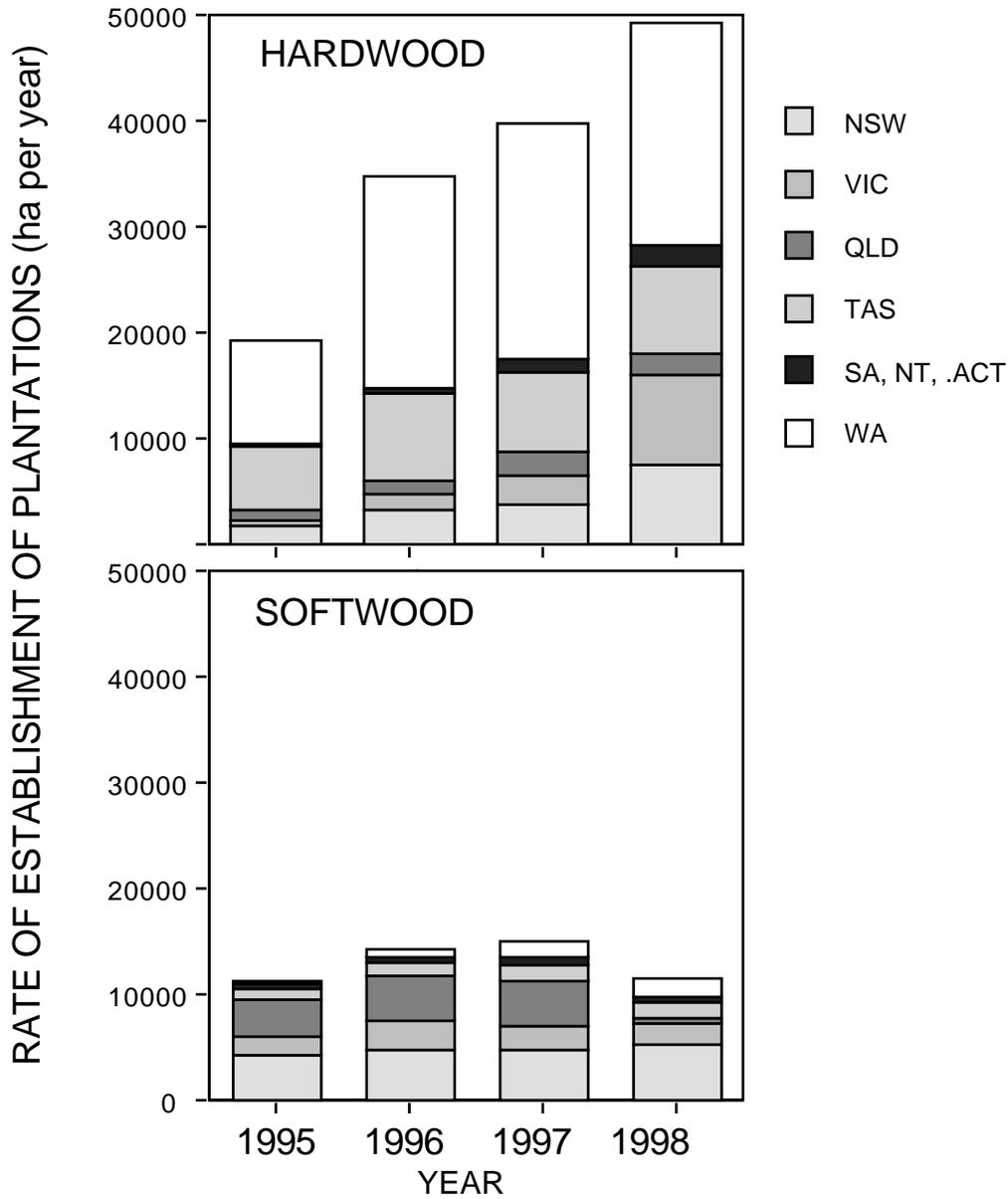


Figure 10. Annual rate of establishment of tree plantations in Australia. From National Forest Inventory Australia (1999).

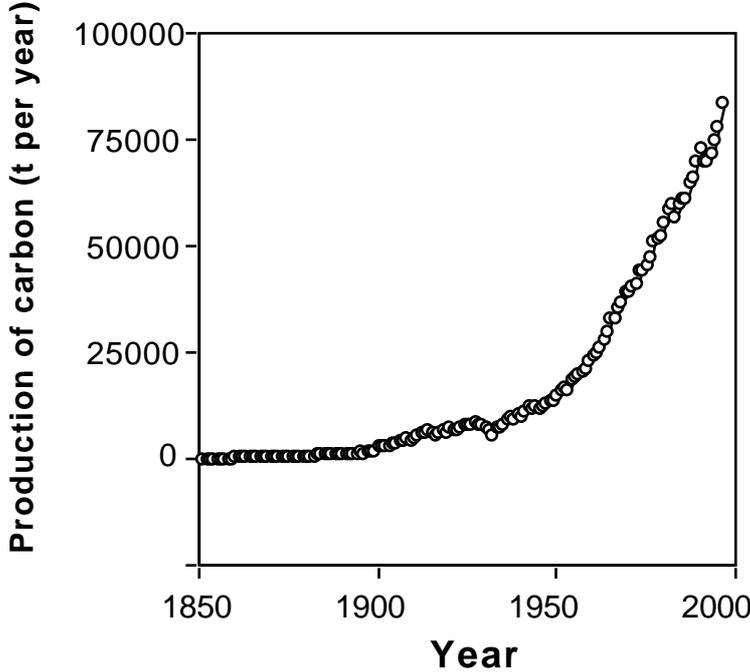


Figure 11. Total emissions of carbon from fossil-fuel burning, cement manufacture and gas flaring in Australia, 1851-1996. From Marland et al (1999).

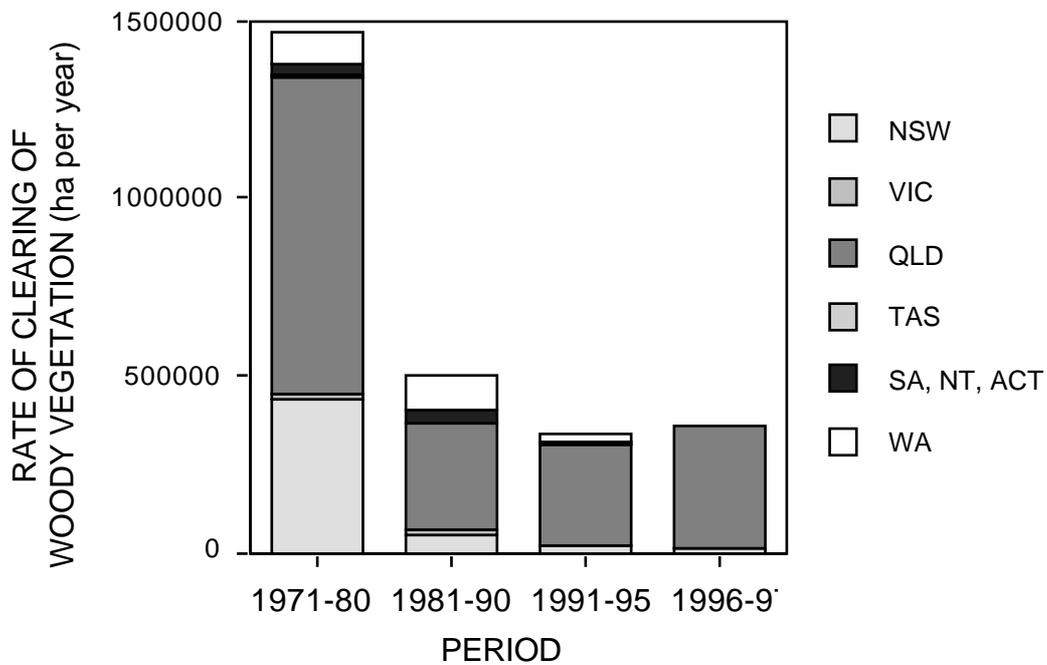


Figure 12. Annual rate of clearing of woody vegetation in Australia. From Barson (1999).

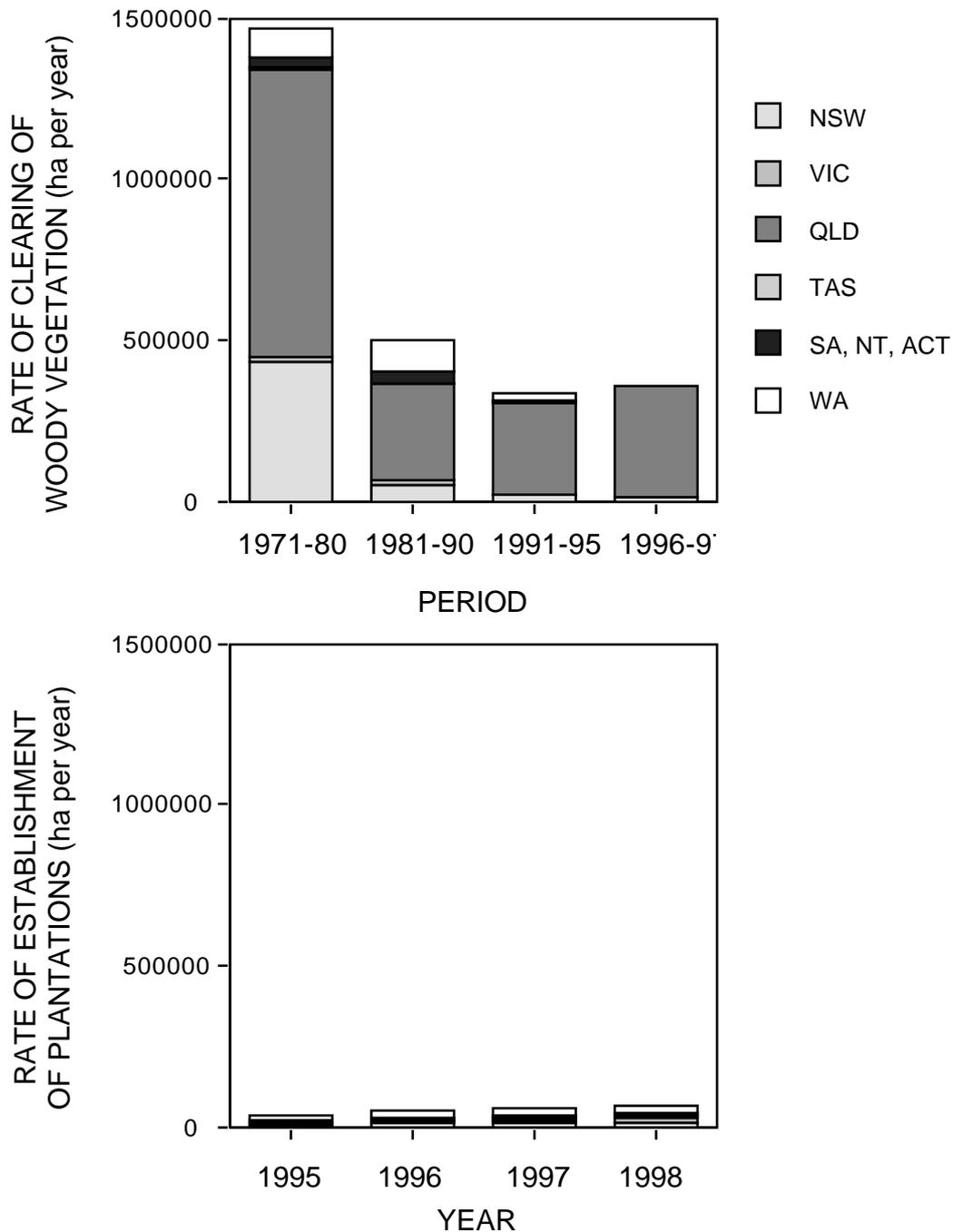


Figure 13. A comparison of the annual rate of clearing of woody vegetation in Australia (from Barson, 1999) with the annual rate of establishment of tree plantations. From National Forest Inventory Australia (1999).

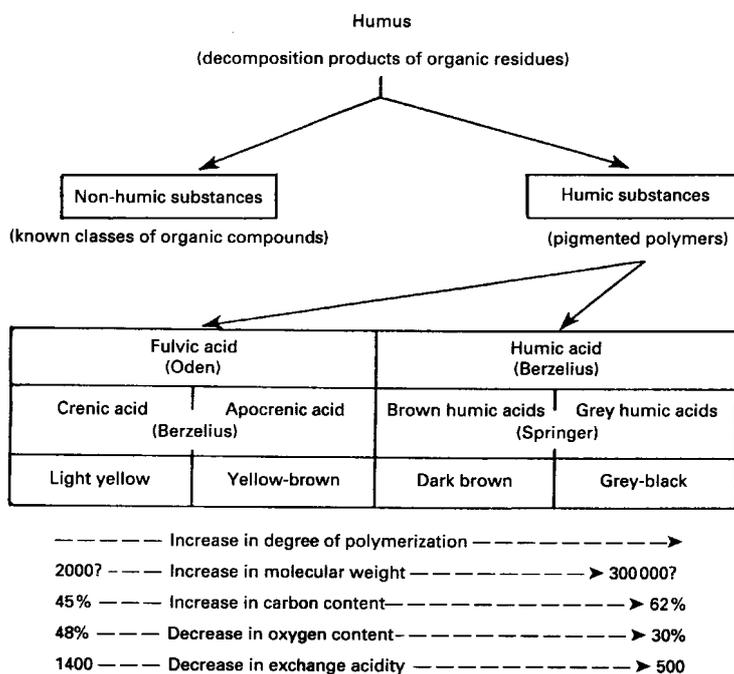
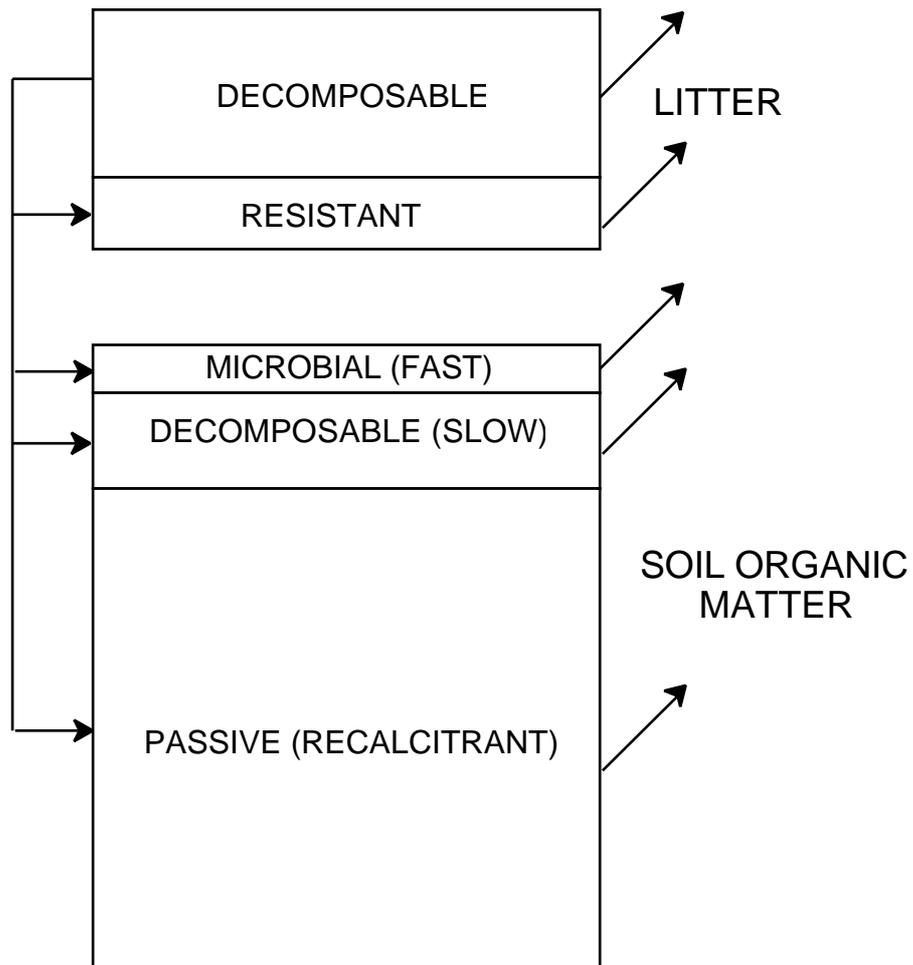


Figure 14. Classification and chemical properties of humic substances. Humin is not shown. From Stevenson (1989).



Models of changes in soil carbon (eg CENTURY, Parton *et al.*;
ROTHAMSTED, Jenkinson and Rayner)

Figure 15. A model of organic matter in the litter/soil system of forests (after Jenkinson and Rayner, 1977; Attiwill and Leeper, 1987; Parton *et al.*, 1994).