12 Nutrient Cycling in Forests and Heathlands: an Ecosystem Perspective from the Water-Limited South

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12.1 Introduction

Nutrient cycling in forests and to a lesser extent, in heathlands, has been regularly and thoroughly reviewed, especially in the past 15 or so years. For example, there have been numerous major projects, conferences and meetings focused on nutrient cycling in forests since 1990 (e.g. Boyle and Powers 2001; Nilsson et al. 1995; Schultze et al. 2000). These compendia are complemented by nutrient cycling contributions to more broadly based meetings (e.g. to Press et al. 1999). Seminal texts on biogeochemistry such as that by Schlesinger (1997) are essential reading and deal with forests, woodlands, shrublands and heathlands in varying detail. More recent works by Melillo et al. (2003), Schultze et al. (2001) and Vitousek (2005) are focused on biogeochemistry and global change. Even encyclopaedic treatments of aspects of nutrient cycling in forests are now available (e.g. Burley et al. 2005; Evans 2001).

For heathlands, there are fewer syntheses. Much of the extensive work on wet heathlands in Europe has been summarised in papers by Aerts, Berendse and co-workers (e.g. Aerts 1990, 1999; Berendse et al. 1989, 1994). Similarly, the review by Aerts and Chapin (2000) drew heavily on studies of heath and taiga vegetation. Overwhelmingly, these works are written from a 'northern' perspective, or at best from a north and tropical perspective.

Attiwill and Leeper (1987) provided the first in-depth treatment of nutrient cycling in forests from a 'southern' perspective. More recently, the text on eucalypt nutrition by Attiwill and Adams (1996) provides several comprehensive treatments of nutrient cycling in a range of eucalypt forests.

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In 1993 we noted that possible nutrient limitations, especially phosphorus limitation, were important themes that had developed from studies of nutrient cycling (Attiwill and Adams 1993). In part, these themes developed as a result of concerns about nutrient removal from ecosystems caused by forest harvesting and/or fire, as well as nutrient requirements and balance for plant growth (e.g. as indicated by 'Redfield ratios', Redfield 1958), and the effects of time on soils (e.g. Walker and Syers 1976). These themes have become more central as concerns about global change have increased (e.g. Archer et al. 2001; Vitousek and Field 2001) and as scientists make many observations of increases in plant growth and carbon fixation in controlled, high CO_2 environments.

It is possible that nutrient limitations to growth could become more common across landscapes under a higher CO_2 environment, and there is thus even more reason to study nutrient cycling in forests and related ecosystems. For example, Lloyd et al. (2001) modelled the availability of soil phosphorus under a high CO_2 environment, albeit in an analysis limited to moist tropical forests. Somewhat surprisingly, their modelling suggested that phosphorus availability could increase to match the increase in rates of carbon fixation, due largely to an unexplained positive effect of increased soil carbon content resulting in the release of previously adsorbed phosphorus. This modelled outcome provides some support for an earlier, more general suggestion by Gifford et al. (1996) that, in a high CO_2 world, more of the less labile forms of phosphorus may be brought into circulation. These and other studies have emphasised, as did earlier concerns about logging and fire, the importance of improving our understanding of nutrient cycling in forests and heathlands.

Much of the 'northern' literature has a bias towards ecosystems where water and phosphorus are usually at least adequate for growth of many species and where, as a result of pollution, nitrogen availability may be in excess of plant demand. Even though that viewpoint is changing (e.g. Wassen et al. 2005), the view from the 'south' has always been different (e.g. Adams et al. 2004). For much of the Australian continent, for example, rates of evaporation are far in excess of rates of precipitation. Only on the continental fringe, and then only in small areas, does precipitation approach or exceed evaporation. Large areas of the African continent are dominated by similar, obviously water-limited, ecosystems. These continents also share an abundance of geologically and geomorphically old and thus highly weathered landscapes – landscapes that are more widespread in the southern hemisphere continents than they are in Europe or on the North American continent.

While it is obvious that fire goes hand-in-hand with either long-term or seasonal shortages of water in many of the world's natural ecosystems (or at least it did prior to European intervention), a far harder task is to unravel the role of fire in putative nutrient limitations or its interaction with global change (including nutrient enrichment, changes in CO_2 or in temperature and water regimes), via nutrient cycling and availability. The 're-discovery' of fire as an essential element of the global change research agenda for forests and heathlands is more than timely – it ought never to have been forgotten.

This chapter is not intended to duplicate the focus on more specific soil and plant processes found in other chapters in this volume [e.g. Chapters 1 (Baldock), 2 (McNeill and Unkovich), 3 (Bünemann and Condron) and 4 (Rengel)]. Rather, it attempts to bring together, at the ecosystem scale, some of the current knowledge of nutrient cycling in 'southern' forests and heathlands. Hopefully it enunciates strong reasons for developing a better understanding of the interaction of fire and global change with all aspects of nutrient cycling in water-limited forests and heathlands. Nutrient cycling in forests and heathlands is a huge topic that could not possibly be covered in a single chapter. Hence, in addition to providing an overview of the major pools and fluxes, this chapter focuses on N and P and several key questions:

- What are the key controls on nitrogen cycling in forests and heathlands?
- Phosphorus limitation – real or incidental to water limitations?
- Are southern forests and heathlands different to those in the north or in the tropics?

12.2 Internal Cycles of N and P

12.2.1 Ratios of Nutrients in Forest and Heathland Plants – are they Useful?

One of the most salient features of nutrient elements in plants is the relatively narrow ranges in the ratios of one element to another. These ratios, sometimes known as Redfield ratios after the pioneer of stoichiometric analysis in marine systems (Redfield 1958), remain widely discussed (e.g. Vitousek and Howarth 1991), with several recent regional and global treatments (Han et al. 2005; Kerkhoff and Enquist 2006; McGroddy et al. 2004; Reich and Oleksyn 2004). These syntheses have done much to provide strong guiding relationships for forests in particular, and, to a lesser extent, heathlands. Combined, these syntheses show that: (1) the N:P ratio of foliage increases with mean annual temperature (i.e. toward the equator, Reich and Oleksyn 2004, see Fig. 12.1, lines a–c); (2) the N:P ratio of total plant mass is invariant to changes in plant size (across three orders of magnitude in plant size; Kerkhoff and Enquist 2006); and (3) because productivity is allometrically related with biomass (or phytomass), productivity per unit N or P actually declines with increasing biomass (Kerkhoff and Enquist 2006). In other words, at a global scale, trees produce less biomass per unit N or P than the small shrubs that dominate heathlands.

Within these overarching relationships, there remains considerable room for variation – both within communities and between functional types. For exam-

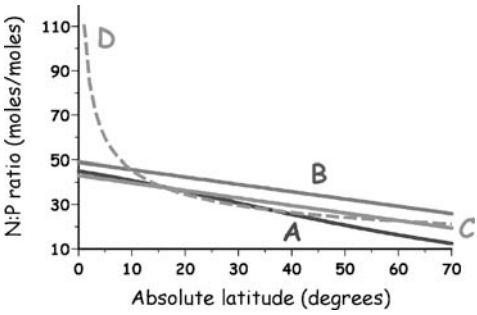

Fig. 12.1 Global patterns in N:P ratios in green foliage and leaf litter (from Hedin 2004)

ple, Kerkoff and Enquist (2006) point out that some of the reduction in productivity in forests (relative to other life forms) is due to small trees having almost zero carbon gain when growing under a canopy of larger individuals. Foresters often refer to these as 'suppressed' trees and they are widespread in Australian eucalypt forests. Kerkoff and Enquist (2006) also highlighted the more general case of dominant species or individuals in a community that can often access more resources than sub-dominant species/individuals, leading to considerable within-site variation in productivity per unit nutrient.

The slope of the N:P relationship in the global data set (e.g. Fig. 12.1) used by Reich and Oleksyn (2004) was less for conifers and angiosperm shrubs than for angiosperm trees or grasses and herbs. Similarly, at any concentration of P, concentrations of N were always least in conifers amongst the functional groups. Reich and Oleksyn discussed the previously made suggestions of 'break points' that act as indices of N or P limitation. This idea, which has been around for some time (e.g. Aerts and Chapin 2000; Koerselman and Meuleman 1996), arose from similar observations that within functional groups (e.g. heathland plants and trees), N:P ratios were clustered around a mean of roughly 15. Based on analysis of data from studies in wetlands, Koerselman and Meuleman (1996) concluded that plant growth was limited by P when N:P >16 and by N when N:P <14.

The work of Reich and Oleksyn (2004) refines this idea according to their observed patterns in N:P with changes in mean annual temperature (MAT), "… if it applied equally to all species types, would suggest a potential transition from P- to N-limitation at <25 °C, 20 °C, 15 °C and 12 °C for coniferous trees, herbs, grasses and angiosperm woody plants, respectively." These patterns seemingly owe much to the distribution of soils, especially soils of different age, on a global scale. The older soils common to the tropics are also highly weathered (as a result of greater rainfall and MAT) and seemingly lack P. Soils elsewhere are less weathered and are generally N-limited.

What do these global patterns look like at more local and possibly more practically useful scales? Using plantations of *Eucalyptus nitens* as an example where genotypic variation in physiology has been greatly reduced (Fig. 12.2), we see

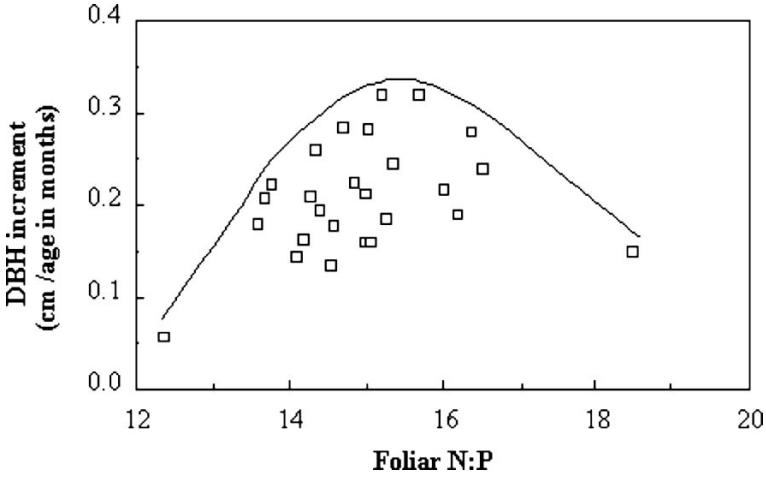

Fig. 12.2 N:P ratios in foliage of *Eucalyptus nitens* sampled from 35 plantations in southern Australia (after Judd et al. 1996)

evidence of the 'break-point' ideas. The N:P ratios in foliage from more than 25 plantations were clustered around a mean close to 15, and were clearly related to growth. Due to the strength and reliability of this relationship it has been proposed as a basis for decision-making about fertiliser needs by forestry companies (e.g. Schönau and Herbert 1982, 1983). Likewise, re-examination of data from a study of over 60 species from a range of arid heathlands and woodlands in Western Australia, Keay and Bettenay (1969) showed that of the 69 species investigated, 56 species had N:P ratios >16, often >>16, suggesting P limitation. Any wider analysis, including more Australian and overseas examples suggests the same – dominance of heathlands by plants with N:P >>16 and therefore P-limited. Unfortunately, some syntheses (e.g. Güsewell 2004) lack sufficient coverage of the Australian literature (e.g. the major data set collated by Judd et al. 1996) and as a result promote a somewhat different view.

12.2.2 Australian Case Study 1

A useful case study to illustrate several of the features of nutrient cycling combines heathlands with heathy woodlands and shrublands in a near-coast environment in south-east Australia (Taranto 2003). This study was conducted on a landscape dominated by duplex soils with sandy A horizons over heavy clay B horizons. Across the prevailing topography, which corresponds closely to water availability, there are clearly distinct communities. The tops of hills are communities of heathy woodlands, the mid-slopes are heathlands, and the valley

Table 12.1 Mean N:P ratios in foliage for selected dominant genera in three heathy communities at Anglesea, coastal southern Victoria. Also shown for each community are the mean proportional withdrawals of N and P during leaf senescence. See text for further details of the communities

	Bald hills heathland		Heathy woodland		Closed shrubland	
Genus	Mean (SE)	*n*	Mean (SE)	*n*	Mean(SE)	*n*
Eucalyptus	27 (0.7)	36	29 (0.9)	45	–	–
Gahnia	37 (1.3)	36	37 (1.8)	35	36 (1.4)	33
Leptospermum	28 (1.0)	40	28 (0.6)	35	33 (1.0)	43
Melaleuca	–	–	–	–	40 (1.0)	35
Resorption of N (%)	58		57		53	
Resorption of P (%)	92		87		80	

bottoms are closed shrublands. A range of parameters were compared among the three communities, using wherever possible the same species as the basis for comparison (Table 12.1). Hence, identical species of *Eucalyptus* (tree) and *Leptospermum* (heath) and *Gahnia* (sedge/herb) were common in the first two communities and *Eucalyptus* was replaced by *Melaleuca* in the closed shrubland. There are two clear points: first, all dominant species exhibited N:P ratios well in excess of 16, as has been shown for other heathland and heathy woodland ecosystems in Australia. Secondly, the lowest N:P ratios were observed for emergent trees; a clear expression of within-community variation in N:P caused by large individuals within a small-stature community – the big trees have better access to resources than the small shrubs and herbaceous species (Kerkhoff and Enquist 2006). Given the generally low nutrient status of soil supporting heathland plants in Australia and elsewhere, N:P ratios >>16 are consistent with the long-held hypothesis that low P status is a feature of heathlands.

12.2.3 Nutrient Remobilisation and Nutrient-Use Efficiency

In Fig. 12.1, we see another feature that provides a link to the topic of nutrient remobilisation and internal cycling. In addition to foliar N:P, McGroddy et al. (2004) also synthesised the N:P data for litterfall from forests. While much of the data (Fig. 12.1, Line d) show that the ratios of N:P are maintained as foliage senesces (i.e. the slope of the line is much the same as for Lines a–c) and that both N and P are withdrawn from green leaves in equal proportions, the situation changes as we move close to the tropics, with far more P than N being retained within the plant rather than shed in litterfall. Litterfall thus becomes poorer in P and has increasing N:P.

The general topic – nutrient resorption and re-use – is again contentious owing mainly to the methods of calculation of how much of any nutrient is withdrawn from foliage (or fine roots) prior to abscission. Errors in calculation, usually underestimates, arise principally from lack of consideration of all processes that contribute to losses of nutrients from foliage (e.g. leaching, herbivory and resorption; Aerts and Chapin 2000). Simple approaches (e.g. Chapin 1980) consider only the changes in concentration in nutrients between green foliage and leaf litter, ignoring the many other variables, including changes in mass. It has been shown that the underestimate that would have been produced using a simple approach can vary from as little as 3% to more than 25% depending on element (e.g. Luyssaert et al. 2005; Van Heerwaarden et al. 2003). The situation is worse for wet temperate deciduous forests than for ecosystems like many of those in Australia, where losses of leaf mass, C and nutrients via leaching and in situ decomposition in the canopy are greatly limited by the association of peak litterfall with the summer drought.

12.2.4 Australian Case Study 2

As an example, we might again consider the case study of coastal heathlands and heathy woodlands (Table 12.1; Taranto 2003). Using a simple method of calculation, withdrawal of N and P were similar for all communities. There was no obvious species dependency. Very clear is the far greater withdrawal of P – up to 90% of the P content of green foliage had been removed by the time leaves were shed as litter – than of N (removal averaged around 55%), in accordance with the patterns noted by Hedin (2004) for P-poor ecosystems.

12.2.5 N and P Uptake

Our understanding of N and P uptake by trees and heaths has undergone a revolution in recent years, with particular emphasis on the roles of mycorrhizal fungi and specific structures such as cluster roots. Much was summarised by Read and Perez-Moreno (2003), and more recently by Lambers and Colmer (2005). Amongst the many advances, there are a few worthy of special comment. First, the Proteaceae and other cluster-root forming species have long been noted as being highly sensitive to P supply (e.g. Handreck 1997) – so much so that many species are killed by even small additions of P fertiliser. Similar traits have been recorded for other species, genera and functional types endemic to low-nutrient soils in Australia and South Africa (e.g. Thomson and Leishman 2004; Witkowski 1991). Recently, considerable differences in capacity to regulate P

uptake have been demonstrated among paraphyletic, cluster-root-producing species that dominate heathlands in south-western Australia (Shane et al. 2004; Shane and Lambers 2006). This research has been linked with the ecology of species that differ only very slightly (a few grams per kilogram) in P status in a region noted for its diversity. Secondly, a wide range of fungi and plants, including cluster-root-producing species, have the ability to modify/solubilise/hydrolyse organic compounds in the rhizosphere (Adams et al. 2002; Chen et al. 2002; George et al. 2006; Marschner et al. 2005; Read and Perez-Moreno 2003). Thirdly, it is now confirmed that simple organic N is a potential source for trees and shrubs for a range of genera, including Australian native trees (e.g. Warren 2006), South African and Australian proteaceous shrubs (Hawkins et al. 2005; Schmidt and Stewart 1999; Schmidt et al. 2003) and most likely a considerable range of Australian heaths (e.g. Bell and Pate 1996).

These are important developments, yet must still be judged for significance in the context of the overall cycles of nutrients. Soil processes dominate the availability of N and P for native trees and shrubs, and plants influence soils via their inputs of organic matter both from above (leaf litterfall) and within (exudates, fine roots). For example, in relation to organic N uptake, Jones et al. (2005) noted that we still lack "evidence demonstrating this as a major plant N acquisition pathway". The same applies to organic P – the more likely scenario is that plant adaptations, including cluster roots (e.g. Adams et al. 2002), produce exudates that help solubilise and/or hydrolyse soil P (both organic and inorganic) at or close to the root surface. Most of the P taken up is in inorganic form. These points are dealt with further in the section on external cycles of nutrients.

12.2.6 Ammonium / Organic N Uptake – a Point of Difference to Herbaceous Species – and their Interaction with Water

Authors of even recent texts on plant and tree physiology (e.g. Buchanan et al. 2002; Heldt 1997; Kozlowski and Pallardy 1997) give little attention to the ammonium nutrition of woody plants in natural ecosystems. The lack of attention is all the more surprising given the decades-old and detailed knowledge of: (1) dominance of ammonium in plant-available nitrogen in forests and heathlands, (2) patterns of uptake and preference of ammonium over nitrate exhibited by woody plants (e.g. Kronzucker et al. 1997; see also Garnett et al. 2001, 2003 for studies on eucalypts), and (3) the significance of mycorrhizal symbioses, which allows woody plants to compete effectively with soil micro-organisms for immobile ions like ammonium. Instead, nitrate captures attention in forests and heathlands as a 'pollutant' of drainage waters and a sign of excessive N inputs (e.g. Aber et al. 2003; Goodale et al. 2003; see also special 2005 issue of Water, Air and Soil Pollution).

As noted above, the last 10 or so years has also seen the 'discovery' of simple forms of organic N, mainly amino acids, as sources of N for forests and especially for heathlands. Both the ability to degrade complex polymers (such as protein) and the ability to take up the products of that degradation (amino acids) provide significant advantages to mycorrhizal plants in competition with soil microorganisms. From a plant perspective, however, ammonium and amino N are equally suitable. Uptake of either is energetically cheaper than nitrate. Herein perhaps, lies one of the great differences between woody and herbaceous plants. The ability to take up and use ammonium and amino N saves woody plants a significant proportion (>30% by some estimates) of their reserves of carbon and energy-reserves that would otherwise be spent on nitrate reduction (e.g. Buchannan et al. 2002). In water-limited ecosystems, this saving could well be even more significant. Plants that must wait for and use water to transport nitrate to the root surface are clearly at a disadvantage to those that can decompose complex polymers in situ or that can compete strongly for adsorbed ammonium to obtain their N.

12.3 External Cycles of N and P in Forests and Heathlands

It is well documented that global patterns in forest litterfall (and thus in nutrient cycling) mirror those of productivity – greatest in the wet tropics (e.g. mean for evergreen tropical species > 7 t ha^{-1} $year^{-1}$; Scurlock and Olsen 2003) and least in arid and boreal zones (e.g. ~2 t ha^{-1} $year^{-1}$ for needle-leaved conifers; Scurlock and Olsen 2003) where either water availability or temperatures or both are extreme. Notwithstanding the difficulties in accessing litterfall data and cautionary notes about the quality of this data, especially from the tropics (e.g. Clark et al. 2001), the available data sets (e.g. from the Oak Ridge National Laboratory, see Scurlock and Olsen 2003; Scurlock et al. 1999; http://www.daac.ornl.gov/VEGETATION/vegetation_collections.html; or from Ecological Archives, http://esapubs.org/archive/archive.htm) have expanded rapidly in recent years owing to the now pressing need to better understand the relationships between net primary production and nutrient cycling.

Perhaps less well appreciated are the patterns of temporal and spatial variability that accompany large-scale productivity gradients. Figure 12.3 illustrates the changes in litterfall with productivity, as well as the spatial variability in litterfall, for a set of eucalypt forests in southern Australia. Apart from the expected positive relationship between litterfall and productivity, there is an inverse relationship between a measure of spatial variability (the co-efficient of variation) and productivity. This inverse relationship is readily observed in patterns of distribution of dominant trees and is due to an overriding water limitation – as

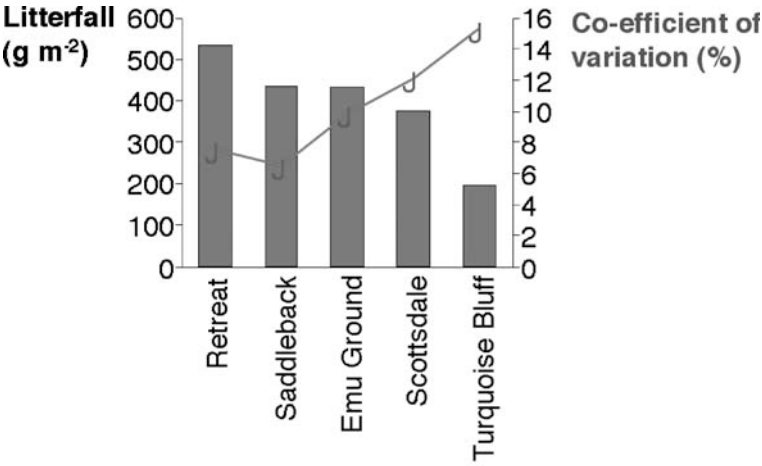

Fig. 12.3 Litterfall and the spatial variability in litterfall for eucalypt forests in northern Tasmania. Data were re-calculated from Adams and Attiwill (1991)

water becomes more and more scarce, both spatially and temporally, the trees in forests and woodlands become more widely spaced. The relationship between productivity and litterfall on the one hand, and spatial variability on the other, has yet to be fully explored, but offers considerable promise for use as a measure of impact because the variance is sometimes easier – and cheaper – to assess than the mean. Casual observation suggests that similar relationships exist for heathlands and grasslands – as water-limited productivity declines, spatial variability in productivity increases.

Below-ground, the inputs of carbon via root turnover are very difficult to quantify. Beyond making generalisations such as "proportionally, more carbon is allocated below-ground during dry periods" (e.g. Schenk and Jackson 2002), there is little we can say definitively about root turnover. Consequently, attempts to synthesise and model data for forests (e.g. Li et al. 2003) and heathlands generally fail to find the strong predictive relationships so readily generated for above-ground inputs. For example, Gill and Jackson (2000) summarised almost 200 studies of root turnover around the world and found only temperature to be a significant predictor of root turnover on a global scale. Even then it was only a moderately good predictor for grasslands ($r^2 = 0.48$) and shrublands ($r^2 = 0.55$); relations with root turnover in forests were weak ($r^2 = 0.17$). Gill and Jackson (2000) found other predictors (e.g. rainfall) were useful at smaller scales, but concluded that existing patterns of root turnover and climate were not particularly useful under future, possibly changed, climate conditions.

12.3.1 Soil Processes – N

Once on top of the soil or in it, plant organic matter contributes to the 'bottleneck' (sensu Chapman et al. 2006) or, alternatively, the key source of control in the N (and P) cycle. Although the focus of attention may shift from time to time, for example to rates of input and output as a result of concerns about excessive N inputs from the atmosphere (e.g. Aber et al. 2003; MacDonald et al. 2002), the central role of soil organic matter remains clear. This conceptual model has withstood the test of time.

While a model of the major soil N processes that contribute to making organic N once again available to plants can be drawn in any number of formats (see also Chapter 2 by McNeill and Uncovich, this volume), here I use a format (Fig. 12.4) from recent work by Cookson et al. (2006) that builds in turn on the knowledge gained during the 1980s and 1990s as synthesised by Schimel and Bennett (2004) and Chapman et al. (2006). The major evolution in thinking, from that of Jansson some 50 years earlier (see Attiwill and Leeper 1987), is the insertion of depolymerisation as a major and rate-regulating step between N in soil organic matter and plant-available N. Whereas we once thought conversion of simple organic N forms to ammonium (=mineralisation) controlled the overall flow of N from organic matter to forms available to plants, there is growing evidence that depolymerisation (e.g. of proteins to amino acids, of other more complex molecules to simpler constituents) regulates the overall process. This conceptual shift, after more than 50 years of little change, naturally throws up further questions. However, it is strongly supported by numerous lines of evidence, not the least being the aforementioned increase in our knowledge of the ability of plants to acquire simple forms of organic N.

One challenge is to understand the influence of root inputs of C, N and P. In contrast to the pronounced resorption of nutrients before leaf fall, resulting in

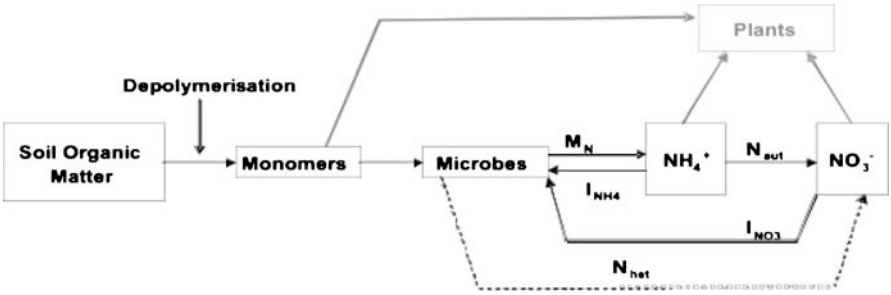

Fig. 12.4 Conceptual nitrogen cycling model. NH_4^+ Ammonium pool, NO_3^- nitrate pool, M_n organic N mineralization, N_{aut} autotrophic nitrification, N_{het} heterotrophic nitrification, I_{NH4} ammonium immobilization, I_{NO3} nitrate immobilization. After Cookson et al. (2006)

C-rich, nutrient-poor inputs from above-ground biomass to soil surfaces, available evidence suggests little nutrient resorption from the fine roots. Roots are also well-known for their exudation, both passive and active, of a wide range of carbon-based compounds, including sugars, sugar alcohols and amino acids (see also Chapter 5 by Neumann, this volume). Jones et al. (2005) recently suggested that at least part of observed amino acid uptake by roots was a means of retrieving amino compounds previously lost by exudation. The distinctions between additions of non-labile leaf litter of high C:N (or C:P) to the soil surface and highly labile root exudates, are particularly important and can lead to sometimes seemingly contradictory results. For example, Knops et al. (2002) highlighted below-ground inputs (carbon exudates, root turnover) as potential negative feedbacks to productivity (through slower mineralisation and/or enhanced immobilisation), at least for grasslands. Nevertheless, in some semi-arid grasslands, the processes that make N available to plants (including depolymerisation, mineralisation, nitrification) can be limited by lack of above-ground inputs of C as well as by N (Cookson et al. 2006). On the other hand, Monson et al. (2006) recently observed that in high altitude pine forests in Colorado, sugar alcohols accumulate in roots, where they serve to protect root cells against freezing. These same compounds are released into the soil early during the following thaw and help to kick-start soil respiration (Monson et al. 2006; Scott-Denton et al. 2006) and, presumably, other microbially dominated processes like nitrogen mineralisation. Hence, while input of litter to the soil surface usually favours immobilisation of N until sufficient carbon can be respired to allow mineralisation, below-ground inputs can produce rather more variable results, depending on the nature of the organic matter and whether it is an exudate or due to root sloughing.

It appears likely that woody plants distribute a much smaller proportion of their total annual carbon to either root exudation or root turnover than some grasslands, e.g. during drought. In addition, there is usually a substantial buffer to above-ground inputs of carbon to forest soils in the form of a litter layer that moderates plant-driven changes (e.g. temporal increases or reductions in leaf litterfall). Consequently, in heathlands and forests, feedbacks to productivity via soil processes are likely to be at least delayed if not obscured (e.g. Knops et al. 2002) by the buffer of leaf litterfall and litter layers.

12.3.2 Patterns in Nitrogen Availability and Processes

Notwithstanding our improved knowledge of organic N uptake and the role of depolymerisation, there are some remarkable patterns that underpin more traditional views of soil N processes and that provide predictive power. The most remarkable is the C:N ratio of soils. Figure 12.5 provides a summary of the influence of soil C:N for forests in Australia and Europe. Clearly, nitrification and attendant processes (denitrification and nitrate leaching) can be predicted on

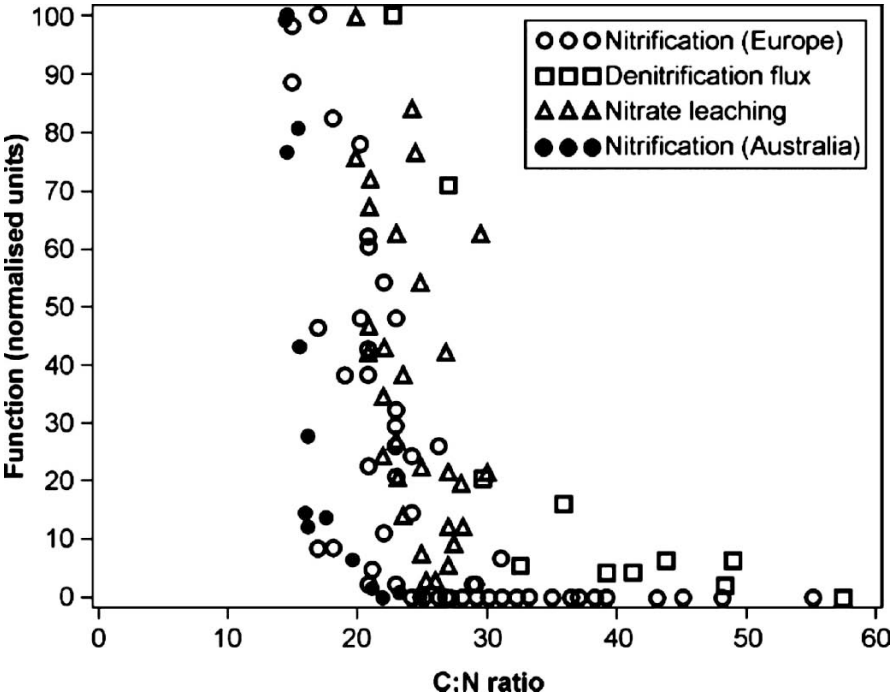

Fig. 12.5 Nitrogen cycling functions (normalised units) plotted against the C:N ratio of forest floor/litter layer. o Nitrate production in humus samples from northwestern German forest soils (100=68.1 mg kg^{-1}); □ nitrogen oxide fluxes (N_2O and NO) from humid wet and semi-deciduous dry tropical forests soils in Peurto Rico (100=14.5 ng N cm^{-2} h^{-1}); Δ nitrate leaching (100=40 kg N ha^{-1} $year^{-1}$) of forest floor at 33 temperate forest sites (two broadleaf and the rest coniferous) in Europe from the Element Cycling and Output-fluxes in Forest Ecosystems in Europe (ECOFEE) database; • nitrification (100=0.25 μg g^{-1} day^{-1}) in a range of Australian forest soils. After Adams et al. (2004)

the basis of soil C:N. When C:N ratios are low (<20), nitrification and attendant processes dominate rates of nitrogen transformation. When C:N ratios are high (>25), they rapidly decline in influence and other factors (e.g. moisture, temperature) exert more control. Many soils have C:N between these two values; hence, both the quality of the soil (e.g. its C:N) and edaphic factors exert some control.

The strength of the C:N influence is remarkable for its generality. As a further example, Lovett et al. (2002) found that watershed C:N strongly influences nitrate export from forested watersheds – the first such demonstration for North America. Owing to the observed strong influence of species composition on C:N (negative for sugar maple and white ash, positive for red oak and red maple), they suggested that changes in species composition by whatever means could have a significant influence on the capacity of watershed to retain N. These data

are also "a compelling example of how tree species can affect important ecosystem characteristics and processes at both the stand and watershed scales" (Lovett et al. 2002).

In Australian forests, species also have marked effects on soil and litter chemistry (Table 12.2). Using a series of experiments with the same tree species planted some 40 years ago, we can see conclusively that establishment of exotic eucalypts caused a reduction in C:N in total litter, leaf litter, fine litter fragments and surface soils. Soil C:N was strongly related to the C:N of fine fragments (r^2 =0.66). In many instances, there were highly significant differences among species, notwithstanding an obvious influence of site (which we could not test for). These results also counter the uninformed opinion that planting of trees

Table 12.2 C/N ratio of total litter, eucalypt leaves, fine fragments and surface soils for five exotic and one endemic eucalypt species grown for ~40 years in three common gardens (that spanned about 2° of latitude and mean annual temperature) in south-west Western Australia. Reference species were *Eucalyptus diversicolor* at Walpole and Pemberton and *Eucalyptus marginata* at Dwellingup. The effects of species was highly significant ($P < 0.01$) for most attributes across all sites. Mean values for soil C:N for each site are also given (Stillwell and Adams, unpublished data)

Site and species	Total	Leaf	Fragments <10 mm	Soil (0–5 cm depth)
Dwellingup				26.5
E. maculata	166.8	90.7	64.5	24.5
E. microcorys	150.1	87.9	56.5	20.9
E. pilularis	165.9	119.0	72.7	23.8
E. resinifera	148.6	109.5	60.6	29.3
E. viminalis	166.0	104.7	61.9	28.2
Reference	190.8	121.8	73.9	32.2
Pemberton				19.5
E. maculata	120.9	70.8	39.3	20.0
E. microcorys	117.7	70.6	49.9	17.9
E. pilularis	133.0	82.5	54.3	20.7
E. resinifera	120.6	77.9	40.9	15.0
E. viminalis	118.0	79.7	59.0	25.7
Reference	131.4	90.9	43.9	18.0
Walpole				14.6
E. maculata	128.5	73.3	47.8	13.6
E. microcorys	124.7	76.6	33.7	15.0
E. pilularis	120.4	100.1	49.7	13.9
E. resinifera	121.6	83.1	41.0	15.7
E. viminalis	89.2	49.6	41.0	12.7
Reference	141.8	94.3	54.0	17.0

may impoverish or make soils somehow less fertile. Curiously, the data also conform to the general pattern whereby exotic species typically increase N availability (Ehrenfeld 2003), even though in this case it is eucalypt replacing eucalypt.

12.3.3 Soil Processes – P

The most marked among soil P processes in southern hemisphere forests and heathlands is the commonly low concentrations of total P as a result of the age of parent materials. While the general patterns in soil P fractions have been known for decades (e.g. Attiwill and Leeper 1987; Walker and Syers 1976), recent studies have highlighted biotic aspects of the P cycle, and it is here that plants and micro-organisms play a role similar to that in the N cycle.

For example, P cycling via litterfall serves to enhance the pools of labile organic P in soils, at least over the periods between major fires or other disturbances. Polglase et al. (1992) provided a clear example from an age sequence of mountain ash forests (Fig. 12.6). In jarrah forests in Western Australia, the ac-

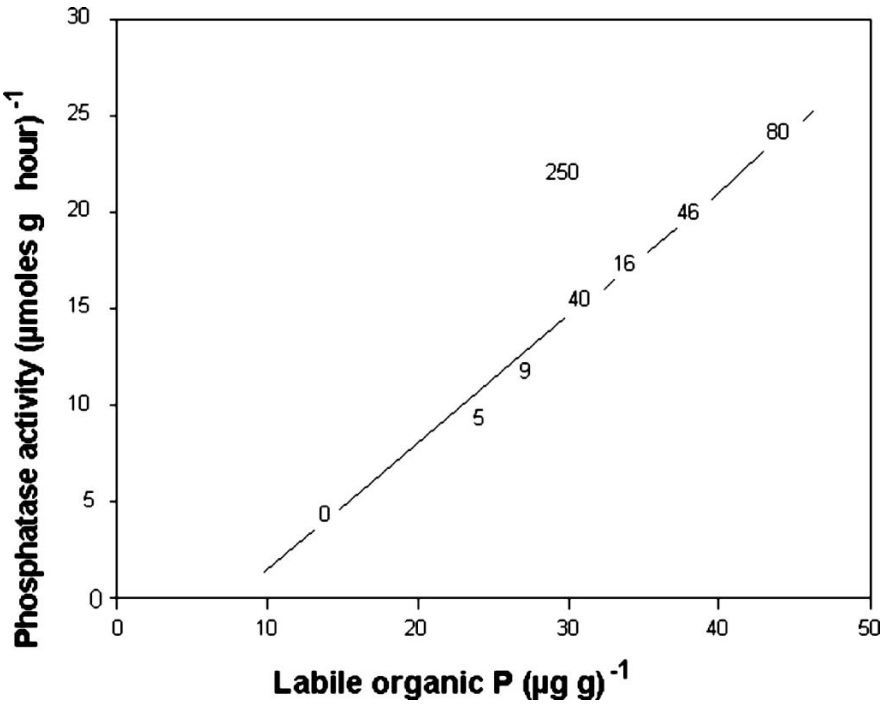

Fig. 12.6 The relationship between the activity of phosphomonoesterase and labile organic phosphorus (extracted in 0.5 *N* NaHCO3) in an age-sequence of *Eucalyptus regnans* forests in Victoria (after Polglase et al. 1992)

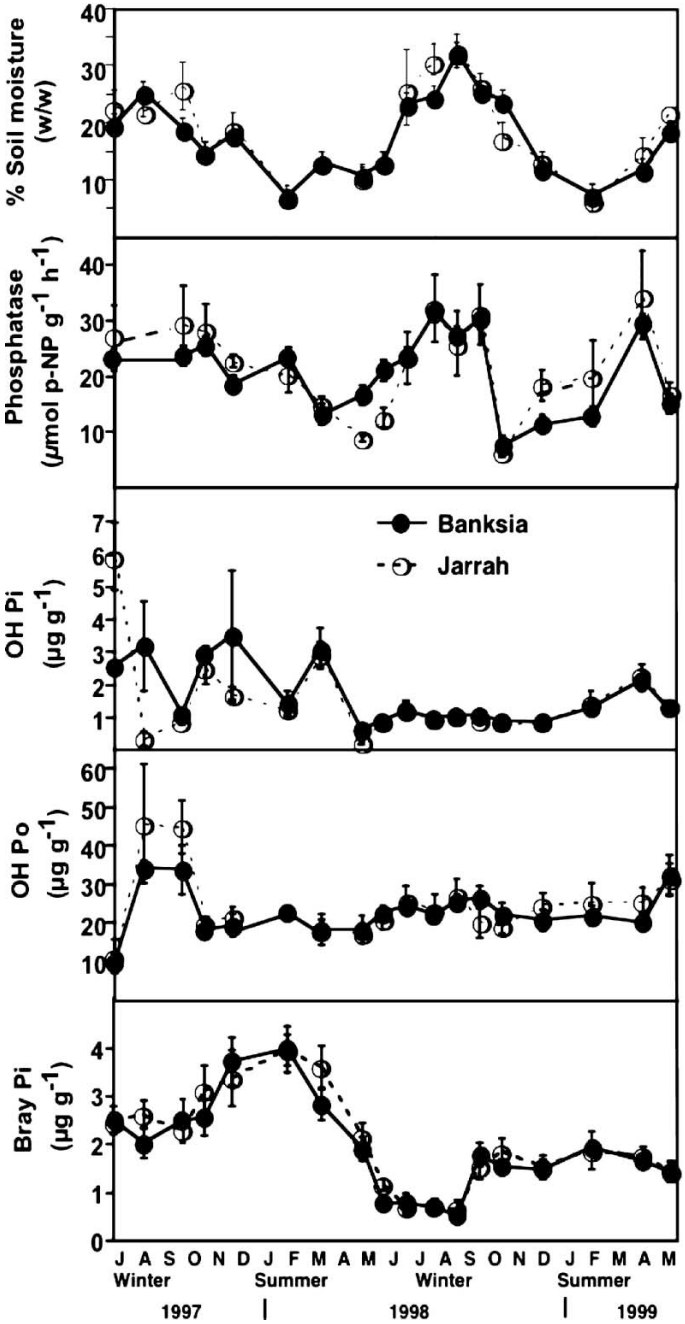

Fig. 12.7 Seasonal changes in soil moisture, acid phosphatase activity and P fractions in jarrah (*Eucalyptus marginata*) forest soil where *Banksia grandis* is present (jarrah + banksia) and absent (jarrah). Data for 0–5 cm depth only (after Grierson and Adams 2000)

tivity of phosphatase enzymes and labile organic P fractions were clearly related to climatic conditions and to the presence or absence of the major understorey species, *Banksia ornata* (Fig. 12.7), which was, in turn, related to fire regime (Grierson and Adams 2000).

Chronosequence studies (Wardle et al. 2004) highlighted the role of P limitation (e.g. Richardson et al. 2004, 2005) in collapse, or potential collapse, of forests without stand-replacing disturbances that serve to refresh and renew P supplies in the soil (and frequently stimulate N_2 fixation). These studies include Australian and New Zealand examples. The concerning aspect of this work is that we know so little of the ecologically relevant disturbance history of southern forests and heathlands (hundreds to thousands of years) and, despite some studies, so little of the detail of P cycling as influenced by parent materials, species and climate.

Instead, much attention has been focused on anthropogenic disturbance as a cause of potential losses of P and N (e.g. in fuel reduction fires) via deliberate burning. Despite some criticism (e.g. Kitayama 2005), Wardle et al. (2004) have proposed a hypothesis that rings true for many Australian ecosystems – vanishingly small pools of P in soils are locked away over time in occluded forms in soil or in plant biomass. This is discussed further in the next section.

12.4 Fire and Nutrient Cycling

Bond et al. (2005) recently drew attention to the role of fire in plant community distribution at the global scale. At around the same time, Mouillot and Field (2005) prepared a global fire map and fire history as a "first approximation for questions about the consequences of historical changes in fire for the global carbon budget". These latter authors noted the strong decline in area of temperate forest burnt annually during the twentieth century – a decline that was particularly pronounced for South American and Australian temperate forests. They also noted that there was some evidence of a reversal of this pattern in the closing years of the century. While Bond et al. (2005) and Mouillot and Field (2005) drew attention to the interaction of fire and future climates for biomass and carbon, the implications of these changes for nutrient cycling are too significant to be ignored.

Perhaps the most significant is the redistribution of nutrient elements and changes in their relative abundance (or stoichiometry) in ecosystems. As demonstrated by Hungate et al. (2003b), many biological processes in ecosystems have little effect on the stoichiometry (e.g. C:N, N:P, C:P, etc) of the major nutrient elements, whereas fires change those ratios substantially owing to the differing volatility of elements. In particular, fires greatly narrow the ratio of available N to available P owing to the far greater volatilisation temperature of P. Legumi-

nous species play a crucial role in promoting regrowth after fire by replacement of lost N.

The processes of nutrient loss, translocation and replacement are of great significance to diversity and productivity in Australia and other fire-prone, water-limited environments. For example, 10 years ago we noted for southern Australian heathlands that "over- or under-use of fire will significantly alter soil nutrient pools and availability and these changes may alter species composition and productivity" (Adams et al. 1994) – a conclusion supported by the work of Shane and colleagues (Shane and Lambers 2006; Shane et al. 2004). Likewise, Witkowski (1989) noted for Fynbos *Protea* spp.: "… the ratio of plant available nitrogen to phosphorus may be at least as important, in determining the range of species, as the absolute amounts of available N and P". Returning to the thesis advanced by Wardle et al. (2004), that reductions in P availability and cycling are inevitable without disturbance and are accompanied by losses of species diversity and productivity, we can recognise immediately that this situation gets worse with soil age, and that much of Australia and Africa is dominated by very old soils. Simply put, if the interval between fires increases, as a result of management and policy, we can expect to see losses of diversity and productivity. Indeed, there are many examples of changes in species composition and of losses of diversity in normally fire-prone heathlands as a result of changes in fire regime.

The debate about fire regime and the nutrient status of forests and heathlands has become of practical as well as of academic interest. For example, McIntosh et al. (2005) contrasted Australian and New Zealand forest soils and concluded that fires may play a significant role in the physical development of texture-contrast soils (which are common in lower rainfall areas) because "fire will encourage clay eluviation". These authors endorsed a previously advocated "feedback mechanism" [as proposed by Bowman et al. (1986) and Jackson (2000) for sedgelands] that "a fire-prone ecosystem proceeds irreversibly down a pathway of incremental nutrient loss and increasing susceptibility to further fires, because the decreasing nutrient status of the ecosystem encourages fire-tolerant forest communities" (see Fig. 12.8). On the other hand, Jurskis and colleagues (e.g. Jurskis 2000, 2005, Jurskis and Turner 2002) have been strident in their calls for restoration of more frequent low-intensity fire as a solution to many of the instances of tree and forest decline throughout southern Australia, which they attribute to a build-up of nutrients, especially N (see Fig. 12.8). Curiously, this could just as easily be an imbalance in N and P availability – too much N, too little P. These two hypotheses are drawn with that of Wardle et al. (2004) in Fig. 12.8. Whilst not ruling out any single hypothesis, there is little evidence to support suggestions that fire-tolerant forest communities are of low nutrient status. Here though, efforts to test such ideas are often stymied by confounding of water and nutrient status – many dry (and fire-prone) forests are also nutrient-poor. On the other hand, many if not all of the southern eucalypt forests – even the most productive and 'nutrient-rich' – require fire for regeneration. The

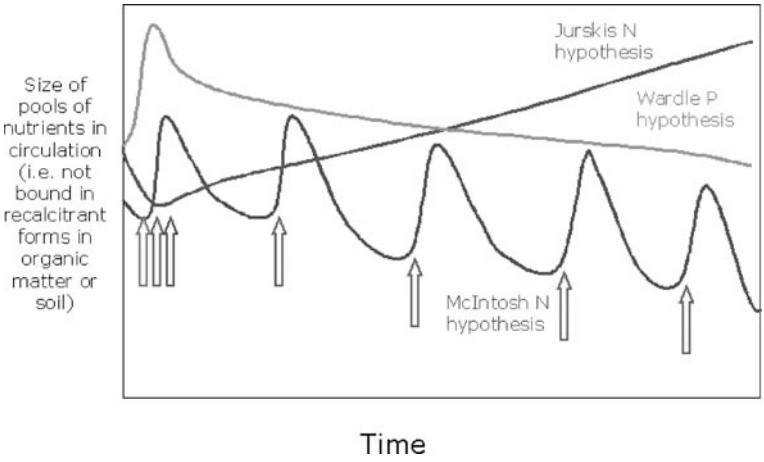

Fig. 12.8 Conceptual models of testable hypotheses regarding the influence of disturbance, mainly fire, on the availability of N and P. Models are the author's representations of suggestions by McIntosh et al. (2005), Jurskis (2000, 2005), and Wardle et al. (2004). *Arrows* Fires

weight of global evidence sits firmly on the side of widening N:P ratios without fire as the cause of large, even wholesale changes in diversity (e.g. change from grassland to heathland or forest) and productivity.

In all of the above, water and water availability play a major role. The dry heathlands common in the southern hemisphere are obviously more fire-prone than the extensively studied, wet heathlands of Europe and other parts of the northern hemisphere. It is frequently difficult to apply nutrient cycling knowledge generated from studies in the north to the south without including an assessment of the effects of fire. The same is true for drier forests – fires are integral to nutrient cycling. It is somewhat ironic that in Australia, as well as in Europe and North America, current interest, even controversy, about fire regimes stems in part from reduced rainfall in many areas over the past 10–15 years. In a study of Mediterranean oak stands, drought produced negative impacts for P cycling (e.g. Sardans and Peñuelas 2004; Fig. 12.9) that are likely to exacerbate losses of P from the active pools. Chief among these effects was a substantial increase in the increase of P in litter layers (as a result of leaf shedding), and a reduction in canopy P (from the same cause). Enhanced additions of organic P to litter layers can take many years to filter back to the active pools of P owing to extensive P immobilisation in organic matter in soils, and litter already poor in P.

Reductions in rainfall, irrespective of whether a short- or long-term change, increase both the risk of bushfire and the reluctance of authorities to use fire deliberately to control fuel loads and, possibly, maintain ecosystem characteristics such as nutrient cycling and species diversity and abundance.

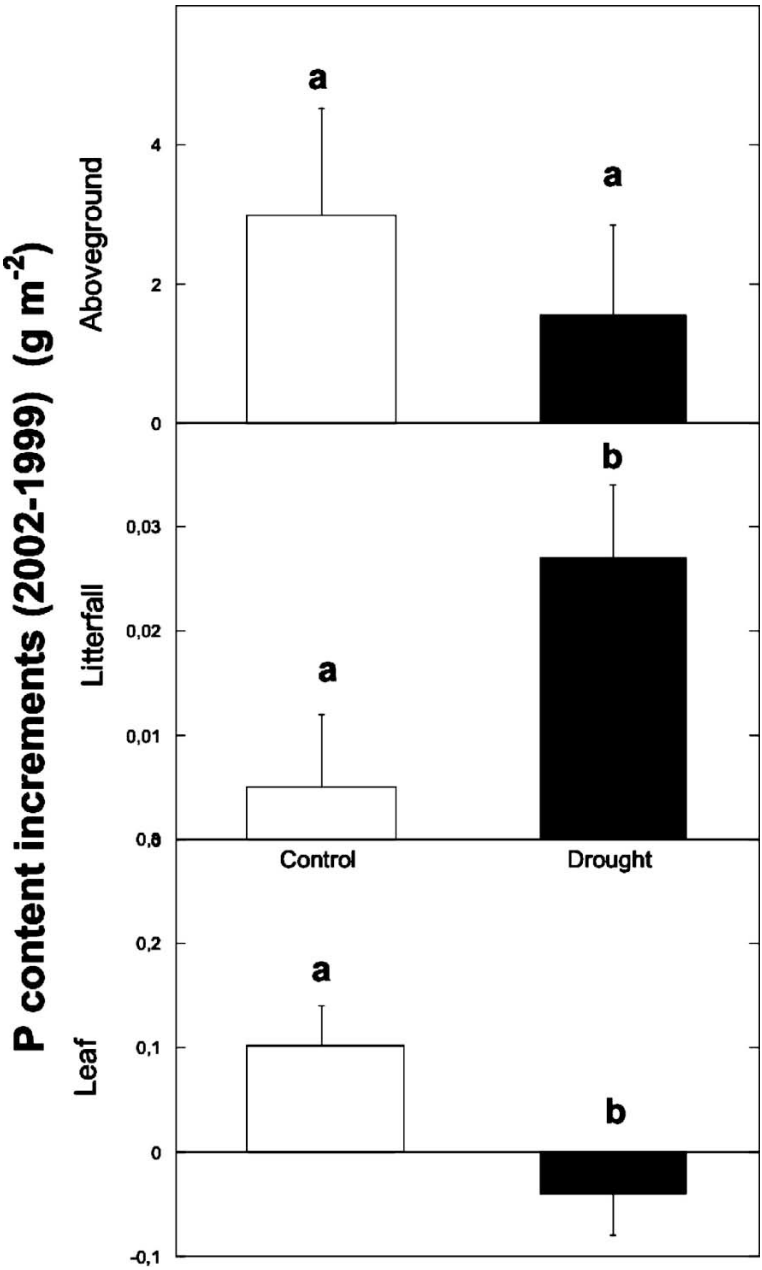

Fig. 12.9 Effects of drought on changes in P content in biomass, litterfall and canopy foliage in a stand of Mediterranean oaks. From Sardans and Peñuelas (2004)

12.5 Climate Change and Nutrient Cycling

The role of nutrients in modifying the capacity of forests and heathlands to adapt to a world of higher CO_2 concentrations and changes in temperature, rainfall and evaporation serves as an illustration of the utility of ratios. In their *Third Assessment Report*, the Intergovernmental Panel on Climate Change (IPCC) suggested that the then best-available process-based models of productivity indicated that terrestrial ecosystems, especially forests, could take up between 22% and 57% of expected CO_2 anthropogenic emissions. However, these models did not include N cycling. Hungate et al. (2003a) used the known C:N ratios in trees (~200), wood (~500), and soils (~15) to calculate, using the same models, the amounts of 'extra' N that would be required to synthesise biomass and soil C. They then calculated how much extra N might be available as a result of pollution or biological N_2 fixation. Finally, they calculated the shortfall between the amounts of N required and that likely to be available. Globally, those shortfalls ranged up to 37×10^{15} g N. Even allowing all the simulated increase in tree carbon to accumulate in the wood, reduced the amount of N required only slightly (owing to the small absolute change in amounts of N) and the shortfall. Changes to the soil C:N ratio were considered unlikely to result in additional N being made available due to the negative feedback between C:N ratio and rates of mineralisation (see also below and Fig. 12.5).

The point Hungate et al. (2003a) made was that failure to take nutrient cycling into account would likely result in an over-estimation of the capacity of terrestrial ecosystems to take up CO_2. This situation also depends on fire frequency (Hungate et al. 2003b). While Hungate et al. (2003a) made reasonable provision for biological N_2 fixation, Dan Binkley and colleagues (e.g. Binkley 2005; Binkley et al. 2000; Kaye et al. 2000; Resh et al. 2002) have shown that introduction or invasions, or even 'natural expansions', of N_2-fixing trees can produce "massive changes in soil N cycling" (Binkley 2005). There remains a possibility that increases in atmospheric concentrations of CO_2, particularly if accompanied by changes to climate and fire regimes, may result in changed abundance of N_2-fixing species that could significantly increase soil carbon storage and lower soil C:N ratios. Binkley (2005) also noted that rates of cycling of P always seem to be greater under N_2-fixing species – thereby solving another problem of the large requirement for P by biological N_2 fixation and possible future P-limitations. Incidentally, it is only for those ecosystems with an abundance of biological N_2 fixation that we have significant evidence of changes in species or changing edaphic conditions bringing less labile forms of phosphorus into active circulation, in support of suggestions by Gifford et al. (1996).

12.6 Conclusions

Vitousek (2005) posed the rhetorical question as to how N limitation could ever develop in a world where biological N_2 fixation is abundant. Perhaps the view from the south provides an answer – fire. Without fire it is hard to imagine that most sclerophyllous Australian forests and heathlands would ever be truly N limited – but with fire it seems axiomatic that they can be, or at least could be. However, the evidence collated here argues strongly, even strenuously, that shortages of plant-available P dictate much of the nature of nutrient cycling in Australian forests and heathlands, which often exhibit extremes of observed global ranges in key measures of nutrient efficiency and productivity. Fortunately, it seems that, in some cases, if the supplies of P are too low for one species, there is another species better able to make use of what there is. Eventually, though, there are very few species that can cope with vanishingly small supplies of P, and ecosystems both stagnate and become rather species-poor. There are already many such examples in Australia. Fire is essential to refresh P-cycling, species diversity and productivity. This suggestion supports the arguments put forward by Körner (2003) in the sense that rather than focus on limitation, we should focus on changes in resource availability as producing new sets of conditions that favour one species or community over another.

In keeping with previous arguments (Adams 1996), I propose that it is and will remain fire – including frequency and severity – that plays the major role in delineating boundaries between eucalypt communities as well as many of the different features of their nutrient cycles, including N and P availability and the ability to cope with other aspects of global change (high CO_2, changes in water availability). Fire plays a similar defining role for the distribution and species composition of heathlands (and related vegetation types, e.g. Adams et al. 1994; Manders 1990) and their nutrient cycles. How fire frequency is affected by global change in much of the south will probably be through soil moisture, a function of site water balances and a direct influence on nutrient availability, especially P availability. The recent and important contributions from Bond et al. (2005) and Mouillot and Field (2005), highlighting the neglecting of fire from global change scenarios and from the mindsets of land managers, serves to reinforce the tentativeness of predictions of climate-driven changes in distribution of community types and species as well as productivity and carbon sequestration. This is a truly southern view.

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