

C:N:P stoichiometry in Australian soils with respect to vegetation and environmental factors

Elisabeth N. Bui · Brent L. Henderson

Received: 26 February 2013 / Accepted: 19 June 2013 / Published online: 5 July 2013
© Springer Science+Business Media Dordrecht 2013

Abstract

Aims We estimate organic carbon (C): total nitrogen (N): total phosphorus (P) ratios in soils under Australia's major native vegetation groups.

Methods We use digital datasets for climate, soils, and vegetation created for the National Land and Water Resources Audit in 2001. Analysis-of-variance is used to investigate differences in nutrient ratios between ecosystems. Linear discriminant analysis and logistic regression are used to investigate the relative importance of climatic variables and soil nutrients in vegetation patterns.

Results We find that the N:P and C:P ratios have a greater range of values than the C:N ratio, although major vegetation groups tend to show similar trends across all three ratios. Some apparently homeostatic groupings emerge: those with very low, low, medium, or high N:P and C:P. Tussock grasslands have very low soil N, N:P, and C:P, probably due to frequent burning. Eucalypt woodlands have low soil N:P and C:P ratios, although their total P level varies. Rainforests and *Melaleuca* forests have medium soil N:P and C:P ratios, although their total P level is different. Heathlands, tall open eucalypt forests, and

shrublands occur on soils with low levels of total P, and high N:P and C:P ratios that reflect foliar nutrient ratios and recalcitrant litter.

Conclusions Certain plant communities have typical soil nutrient stoichiometries but there is no single Redfield-like ratio. Vegetation patterns largely reflect soil moisture but for several plant communities, eucalypt communities in particular, soil N and P (or N:P) also play a significant role. Soil N:P and the presence of Proteaceae appear indicative of nutrient constraints in ecosystems.

Keywords Soil organic carbon · Soil nutrient · Stoichiometry · C:N ratio · N:P ratio · Edaphic factors · Eucalypt communities · Heathlands · Rainforests · Proteaceae · Understorey · Australia

Introduction

Now a fundamental quantity in biogeochemistry, the Redfield ratio refers to the atomic ratio of C:N:P found in plankton and well-mixed seawater. Both are well constrained and equal to molar 106:16:1 due to “the biological control of chemical factors in the environment” (Redfield 1958). The Redfield ratio is instrumental in estimating C and nutrient fluxes in global oceanic circulation models; it is also used to ascertain whether and which nutrients are limiting in aquatic ecosystems (e.g., Elser et al. 2007).

Prompted by an unprecedented rate of change in biogeochemical cycles, recent work has attempted to elucidate global patterns in plant-nutrient interactions, mainly through syntheses of existing data (e.g., McGroddy et al. 2004; Reich and Oleksyn 2004; Elser et al. 2007; Lambers

Responsible Editor: Hans Lambers.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-013-1823-9) contains supplementary material, which is available to authorized users.

E. N. Bui (✉)
CSIRO Land and Water, GPO Box 1666, Canberra,
ACT 2601, Australia
e-mail: elisabeth.bui@csiro.au

B. L. Henderson
CSIRO Mathematics, Informatics and Statistics,
GPO Box 664, Canberra, ACT 2601, Australia

et al. 2010; Cleveland et al. 2011; Peñuelas et al. 2012). Recent analyses of global data suggest that, like in aquatic environments, there are parallels in C:N:P ratios in plant communities and terrestrial ecosystems (McGroddy et al. 2004; Reich and Oleksyn 2004; Elser et al. 2007; Yuan and Chen 2009; Lambers et al. 2010; Reed et al. 2012) and soil microorganisms (Cleveland and Liptzin 2007) and that these follow biogeographical gradients. Fertilization changes the natural ecological stoichiometry and creates imbalances that will have consequences for biogeochemical cycles including C-sequestration and long-term structure and function of ecosystems (Lambers et al. 2010; Vitousek et al. 2010; Peñuelas et al. 2012).

The C:N ratio in soil and litter has long been recognized as a useful indicator of the source of organic matter, its state of decomposition and its potential contribution to soil fertility (e.g., Alexander 1977; Swift et al. 1979; Paul 2007). Very high C:N ratios (>25 on a mass basis) indicate that organic matter accumulation is occurring faster than decomposition. Such high ratios are observed typically in peats and cold temperate forest litters. C:N ratios between 12 and 16 suggest that organic matter is well broken down. Cultivated soils in temperate regions usually have a C:N ratio between 10 and 12; C:N ratios below 10 usually occur only in the subsoil (Rayment and Higginson 1992).

Although infrequently used, the C:P ratio in soil and litter is also a useful indicator of the source/nature of organic matter, its state of decomposition and its potential contribution to soil fertility (Swift et al. 1979; Paul 2007). Generally, a C:P<200 implies net mineralization, a C:P>300 implies net immobilization, and a C:P between 200 and 300 means little change in soluble P concentrations (Paul 2007).

The foliar N:P ratio is thought by some to be indicative of nutrient limitation at the plant community level (Koerselman and Meuleman 1996; Aerts and Chapin 1999; Güsewell 2004). High foliar N:P is linked to sclerophylly in Australia and southern Africa (Specht and Rundel 1990; Lambers et al. 2010), sclerophylly itself being a response to low soil fertility (Hill 2004). The N:P ratio in litter is an important determinant of its decomposability (Güsewell and Verhoeven 2006; Güsewell and Gessner 2009) and molar N:P>16 (7.2 on mass basis) in fresh litter may be indicative of P limitation, as in retrogressive ecosystems (Wardle et al. 2004). Thus by analogy, the soil N:P ratio is also potentially of diagnostic value and it is this ratio in particular that is changed by fertilization (Peñuelas et al. 2012).

Taking an ecological stoichiometry approach, here we examine all three elements and their ratios in soil with respect to the overlying vegetation. This paper is an offshoot of our earlier work on modelling and mapping soil organic C (SOC) and our motivation is to understand why there is a link between vegetation types as reflected in the bioregionalization of Australia and SOC (Bui et al. 2009). We discuss the hypothesis that there is a 'Redfield ratio' (e.g., Cleveland and Liptzin 2007; Redfield 1958) in Australian soils associated with native vegetation. Furthermore we investigate the relative importance of climatic and edaphic variables as predictors of vegetation distribution, in particular in the distribution of eucalypt communities.

Materials and methods

Data

Digital datasets for soils (the Australian Soil Resources Information System, ASRIS) and vegetation (the National Vegetation Information System, NVIS) that initially were created as part of the National Land and Water Resources Audit of Australia in 2001 are used to investigate the macro-scale vegetation and soil nutrient patterns in Australian ecosystems. This underscores the multiple utility of these datasets that were produced mainly as baselines for environmental monitoring.

The data are a collation of soil and vegetation survey data collected from the 1950s to 1990s. While these data have been collected for differing purposes and by different agencies, they represent a valuable resource for investigating relationships between soil nutrients and plants at the national scale. The 2001 ASRIS database included 12 072 geo-referenced measurements of % SOC, 4 746 measurements for % total N, and 8 403 measurements % for total P from topsoil, representing sampling from the A-horizon or, rarely, depth 0–30 cm if no horizon was specified (Johnston et al. 2003; Henderson et al. 2001). Where recorded, O-horizons were not included; they are uncommon in the database. Their median thickness is 2 cm, therefore major distortion of any 0–30 cm soil organic matter estimates in this dataset from poorly decomposed plant litter in O-horizons is unlikely.

Analytical methods used for assessing total SOC were the Walkley and Black (6A1, 6A1 UC), Heanes wet oxidation (6B1) and the combustion methods (6B2, 6B3 and 6.DC) (Rayment and Higginson 1992). All methods were

assumed to estimate total organic C although the Walkley-Black method is generally known to give incomplete recovery, historically quoted in the vicinity of 75–80 % (Rayment and Higginson 1992). Although a correction factor from the incomplete Walkley and Black methods to total organic C of 1.3 (i.e. 1/0.8) is sometimes used, Skjemstad et al. (2000) found that, Australia-wide, the appropriate correction factor was less than 1.3 and for a large part of the data not needed at all. Moreover not actually knowing whether the correction factor had already been applied or not to the ASRIS data, no correction factor was used. That this dataset was adequate to represent the spatial pattern of SOC across Australia was demonstrated against independently collected data (Bui et al. 2009).

For total N, results from methods 7A1, 7A2 (semi-micro Kjeldahl) (Rayment and Higginson 1992) and 7A5 (high frequency induction furnace, thermal conductivity cell) were pooled (Henderson et al. 2001). For total P, results from a number of analytical methods (X-ray fluorescence, HCl, HF/HCl digests) were pooled (Henderson et al. 2001). A total of 3 060 points had analyses for % organic C, total N and P in the topsoil. Because this paper is focused on ratios, not stocks, the possible variability in thickness of A-horizons is not a major issue. New South Wales and Victorian agencies analysed for available, not total P, and thus are largely not represented. Much of these states is under agriculture so even if there had been better data coverage, many points would have been excluded from the analysis as explained below.

To investigate the relationship between soil nutrients and plants, C:N and N:P by mass have been calculated for the ASRIS data points and intersected with the map of estimated pre-1750 major vegetation groups (MVG) in the National Vegetation Information System (NVIS 3.0; a map of NVIS 3.0 major vegetation groups can be viewed at: <http://www.environment.gov.au/erin/nvis/publications/major-veg-brochure.html#map>). MVGs are defined on the basis of structural (strata height and cover), physiognomic, and floristic systems (DEWR 2007), and are used here as surrogates for ecosystems (refer to Table 1 for a list and description of MVGs). In NVIS 3.0, where native vegetation has been cleared, no estimated pre-European vegetation is mapped. More than half the available ASRIS points occur on such cleared sites, thus only 1 183 points are useful to investigate plant-soil nutrient relationships (Fig. 1). The ASRIS data exhibit sampling bias towards sites with potential for

agriculture. Some extensive NVIS 3.0 major vegetation groups, e.g., hummock grasslands (MVG 20), are not represented but generally, the extensive MVGs have been sampled more than the small ones; most have >7 observations spread across different regions (Table 1). The NVIS3.0 map is an equal area (Albers projection) raster product with 100-m resolution and the positional accuracy of the soil data points is around ± 100 m, so any points falling on the edge of MVG map units could be misclassified. Given sampling bias, potential errors in measurement of soil nutrients, positional accuracy of data points, and assignment of vegetation group, the results of this study are indicative only and would need to be confirmed by further research. Nevertheless this is a large dataset compared to other synthesis studies that pool data from the literature to make global generalizations.

Statistical analyses

Analysis-of-variance followed by Tukey HSD (Honestly Significant Difference) tests are used to examine potential differences in the means of $\log(\text{C:N})$, $\log(\text{N:P})$, and $\log(\text{C:P})$ ratios for different MVGs. The role of climatic and edaphic variables in describing the differences in the Australian plant communities is investigated by a series of linear discriminant analyses (LDA), to look for those linear combinations of the climate and soil nutrient variables that give the maximum separation in the vegetation groups. As the LDA focuses on the separation or discrimination between the MVGs the statistical analyses will not be affected by the differing sampling frequencies of the MVGs. In the first LDA, all NVIS3.0 MVGs are studied; then we focus on eucalypt MVGs where the dominant genera are *Eucalyptus*, *Corymbia*, and *Angophora* and where soil total N and P reportedly play a role in the distribution of different communities (Specht 1996).

All environmental variables were standardized for LDA. The climatic variables included as predictors of MVGs were mean annual precipitation (MAP), mean annual temperature (MAT), and annual mean moisture index (AMMI). AMMI reflects interaction between precipitation, water-energy balance, and soil texture.¹ Soil organic C is not considered a limiting nutrient for plants

¹ The AMMI is an indexed estimate of the average weekly soil moisture content that mimics the effect of soil texture on the water balance (Houlder et al. 2000). It requires input data for rainfall, evaporation, and soil water storage/availability, all in mm.

Table 1 Soil nutrient data points for NVIS 3.0 Major Vegetation Groups by region. ‘NQld’ refers to northern Queensland sites, defined as longitude >140° and latitude >18°S; ‘SQld’ refers to southern Queensland sites, at longitude >150° and latitude >33°S;

‘SWA’ refers to southern Western Australia sites, at longitude <121° and latitude <28°S; ‘Tas’ refers to sites in Tasmania, at latitude <39.7°S; ‘other’ indicates all remaining sites

MVG	Description	NQld	SQld	SWA	Tas	Other
1	Rainforests and vine thickets	39	0	0	0	5
2	Eucalypt tall open forests (trees>30 m)	0	0	1	11	3
3	Eucalypt open forests (trees 10 to 30 m tall)	15	55	29	65	198
5	Eucalypt woodlands	67	46	27	3	254
6	<i>Acacia</i> forests and woodlands	0	2	0	4	13
8	<i>Casuarina</i> forests and woodlands	6	1	0	4	5
9	<i>Melaleuca</i> forests and woodlands	13	4	0	1	19
10	Other forests and woodlands	0	2	6	1	3
11	Eucalypt open woodlands	1	0	0	2	80
14	Mallee woodlands and shrublands	0	0	18	0	3
15	Low closed forests and tall closed shrublands	0	1	2	11	0
16	<i>Acacia</i> shrublands	0	0	7	0	0
17	Other shrublands	0	0	13	8	1
18	Heathlands	0	2	0	8	0
19	Tussock grasslands (C4)	0	0	0	4	86
21	Other grasslands (wet)	11	0	1	6	1

and as it is highly correlated to total N ($r=0.81$), only N is used as a predictor in the LDAs. The linear discriminant analyses considered are summarized in Table 2.

For individual plant communities, to investigate whether N and P play a role over and above the climate variables, we have compared simple logistic regression models with MAP, AMMI, and MAT and with either log (N), log (P), or both, and tested for a difference in predictive power. All analyses were performed using R (R Development Core Team 2005).

Results

Soil organic C, total N, and total P ranges for NVIS3.0 MVGs are summarized as boxplots in Fig. 2. Compared to geographic regions, MVGs show more variation in soil nutrient chemistry. The distribution of data points for MVGs by region is shown in Table 1. To summarize the relationship between nutrients for

MVGs, Fig. 3 shows the median SOC, N, and P levels for MVGs as a scatterplot matrix.

Nutrient ratios

Nutrient ratios for each MVG were strongly positively skewed thus the medians of C:N, N:P, and C:P are reported as measures of central tendency in Table 3. Because of the positively skewed distributions for soil nutrients, Spain et al. (1983), who last reviewed SOC and nutrients Australia-wide, also presented their synthesis of data as medians and interquartile ranges. The ASRIS dataset includes some of the points (~300) they used for their synthesis.

Soil nutrient ratios for the estimated pre-European major vegetation groups for Australia (DEWR 2007) shows that the median C:N ratio ranges from 12:1 to 31:1 (Table 3), although the 10th and 90th percentiles of the data indicate that there is a lot of scatter within

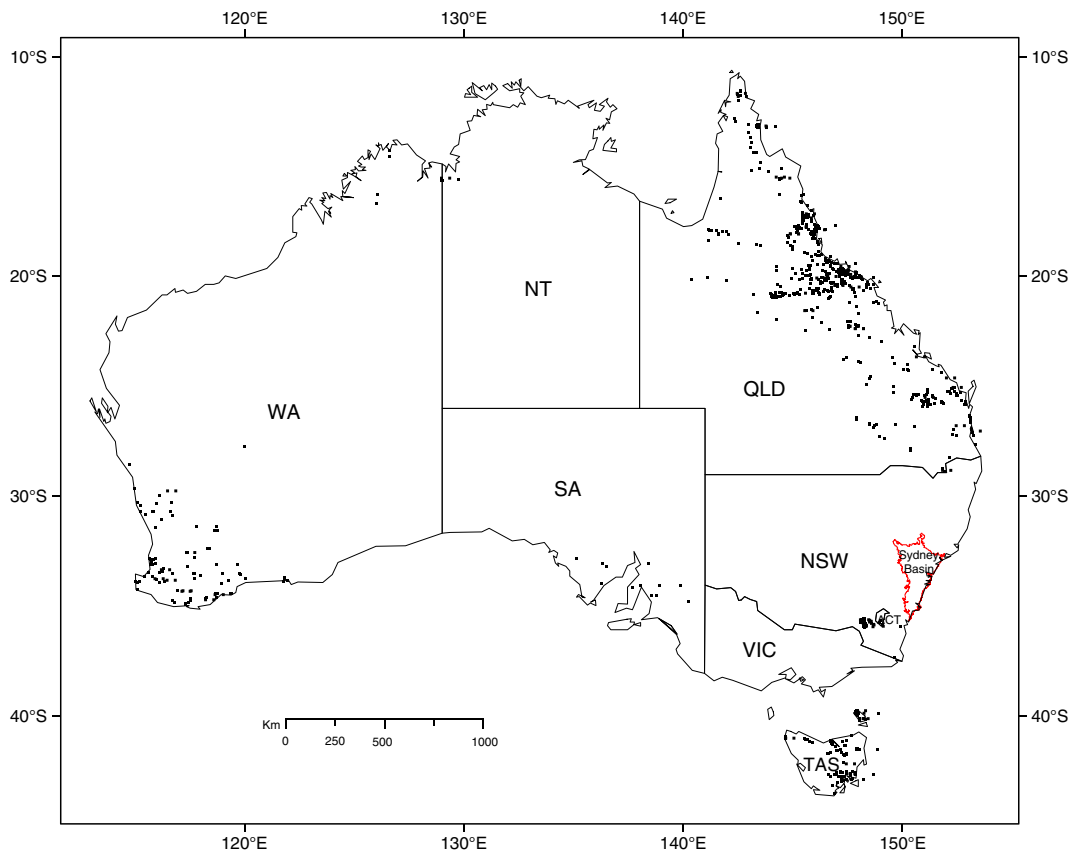


Fig. 1 Locations of 1 183 sites with analyses for topsoil % organic C, total N, and total P used to estimate C:N:P ratios in NVIS 3.0 major vegetation groups. For reference, the state

boundaries are shown. The Sydney Basin, location of the study by Beadle (1954, 1962), is outlined

MVGs (e.g., for MVG 3 and 5). The trends in C:N ratios between MVGs are consistent with those reported by Snowdon et al. (2005). The median N:P ratio by mass observed in Australian soils ranges between 2:1 and 43:1 (Table 3). The median C:P observed exhibits the widest range, from 25:1 to 983:1 (Table 3).

Analysis-of-variance on log-transformed soil nutrient ratios shows that there are significant difference between MVGs (Table 3 and [Supplementary material](#)) but eucalypt woodlands (MVG 3 and 5) do not show significant differences across the three nutrient ratios; neither do rainforest, wet grasslands, and *Melaleuca* forests (MVG 1, 21, and 9); nor do eucalypt tall open forest, tall closed shrublands, and heathlands (MVG 2, 15, and 18) ([Supplementary material](#)).

Environmental factors

LDA were used to examine whether differences in the Australian plant communities could be described by temperature (MAT), rainfall (MAP), soil moisture as captured by the AMMI, total N and P in soil (Table 2). Results show that soil moisture plays an important role in explaining the spatial pattern of MVGs across Australia (Fig. 4).

Soil P and N:P only play a noticeable role in the distribution of eucalypt communities (LDA2 and LDA3 in Table 4). In both these LDAs, the first linear discriminant function (LD1), in which climate variables again have the largest coefficients, explains 87 % or more of the variation. When log (N:P) is used as a predictor (LDA3 in Table 4), its role is similar in scale to that of log (P) in LDA2.

Table 2 Summary of linear discriminant analyses

	Predictors considered	MVGs
LDA1	MAP, AMMI, MAT, log(P) and log(N)	All
LDA2	MAP, AMMI, MAT, log(P) and log(N)	Eucalypt only
LDA3	MAP, AMMI, MAT, and log(N:P)	Eucalypt only

Soil N and P played a highly significant role beyond that of climatic variables for rainforests (MVG 1), tall eucalypt forests (MVG 2), open eucalypt forests (MVG 3), low closed forests/tall closed shrublands (MVG 15), and heathlands (MVG 18). Soil P appears more important than N alone (Table 5).

Discussion

What explains vegetation pattern: climate or soil fertility?

Vegetation pattern in bioregions reflects the SOC content (Bui et al. 2009) and soil nutrient stoichiometry, with feedback between the two. Areas with high SOC correspond to rainforests and eucalypt forests and AMMI is a key predictor in the spatial pattern of SOC across Australia (Bui et al. 2009). Vegetation pattern is itself driven by climate and, to a lesser degree, by soil fertility (Table 4). AMMI plays an important role in explaining the distribution of all plant communities. Those, along the wetter coastal zones, with high primary productivity (rainforests and eucalypt forests, MVG 1, 2, and 3) are associated with high levels of SOC and N (Fig. 2). Eucalypt open woodlands (MVG 11) and tall open eucalypt forests (MVG 2) are found at opposite ends of a soil moisture gradient and there is a height progression from eucalypt open woodland (MVG 11) to woodland (MVG 5) to open forest (MVG 3) to tall open forest (MVG 2) along that gradient (Fig. 4b). The soil N:P of eucalypt MVGs (Table 2) also follows this soil moisture gradient. Specht and Specht (2010) have shown that foliar N:P is a determinant of tree height, thus it seems that soil nutrient ratios are reflected in plant nutrient ratios and plant size at the community level for eucalypts (i.e. there is allometric scaling). In the drier inland, eucalypt and *Acacia* forests and woodlands grade into grasslands. Proteaceae-rich MVGs (15, 18) are restricted to sandy soils with low levels of total P (Figs. 2c and 5); this association was noted also by Pate et al. (2001) and Lambers et al. (2010).

Beyond climate, all MVGs are relating more distinctively to P than N. Adding log(P) as a predictor to climatic variables in logistic regression models has more impact than adding log(N); it explains more of the deviance for five out of 15 MVGs at the 0.001 significance level and for seven out of 15 at the 0.05 significance level (Table 5). Six MVGs respond to both N and P in addition to climate at the 0.05 significance level. In addition to climate, rainforests (MVG1) respond to each nutrient alone but eucalypt forests (MVG 2 and 3) respond to P alone or in combination with N. The results of the LDA and logistic regressions reinforce each other.

C:N:P stoichiometry and the role of mid-stratum vegetation

Our results contrast sharply with those of Cleveland and Liptzin (2007) who found that soil (total pools) nutrient ratios did not vary significantly between forests and grasslands. While relatively consistent stoichiometry appears to characterize the savanna and grassland biomes (N:P<10 and C:P<100 across MVGs 5, 6, 11, 16, and 19), the stoichiometry of rainforests (MVG 1) and tall open eucalypt forests (MVG 2) is very different (Table 2). Some MVGs, notably heathlands (MVG 18), eucalypt tall open forests (MVG 2) and low closed forests (MVG 15) have higher relative soil C:P (>300) and N:P (>20) ratios than other plant communities (bottom of Table 2). Their high C:P ratios suggest net immobilization of nutrients. By analogy with foliar N:P (e.g., Koerselman and Meuleman 1996; Aerts and Chapin 1999; Güsewell 2004; Güsewell and Verhoeven 2006), their large (>20) N:P ratios suggest P-limitation whereas soil N:P ratios<10 suggest that many other MVGs tend toward N-limitation.

The different stoichiometry between MVGs appears to be a function of the composition of the mid-stratum vegetation. Heathland and shrubland groups (MVG 15, 17, and 18) have a much higher N:P level than the other groups. These plant communities are rich with leguminous families and other N₂-fixing plants (DEWR 2007).

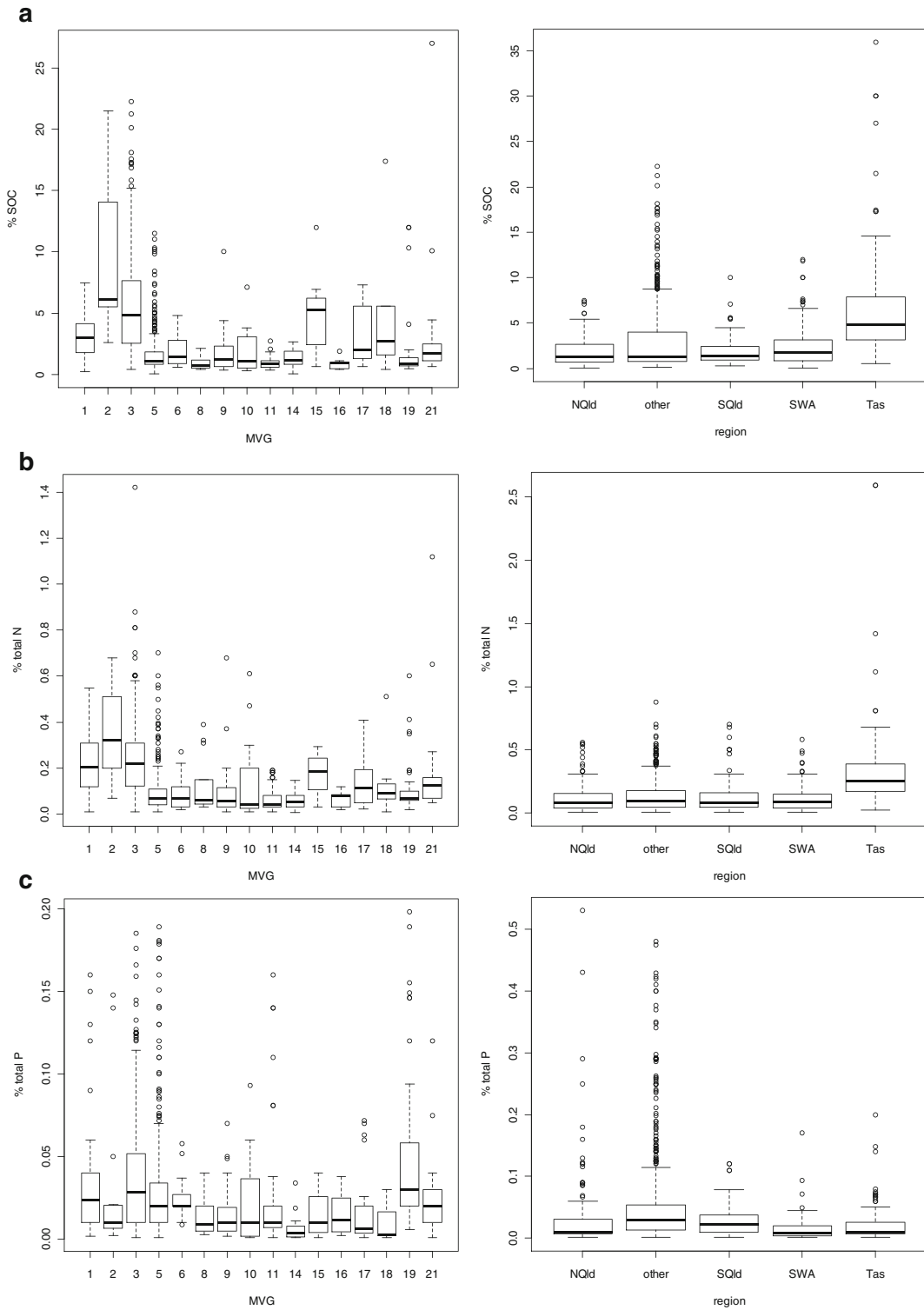


Fig. 2 Boxplots of (a) soil organic C; (b) total N; and (c) total P levels for NVIS3.0 MVGs (see Table 1 for description of MVGs) and by geographic regions. ‘SWA’ corresponds to data sites at

longitude <121° and latitude <−28°; ‘NQld’ ≡ longitude >140° and latitude >−18°; ‘SQld’ ≡ longitude >150° and latitude >−33°; ‘Tas’ ≡ latitude <−39.7°; ‘other’ indicates all remaining sites

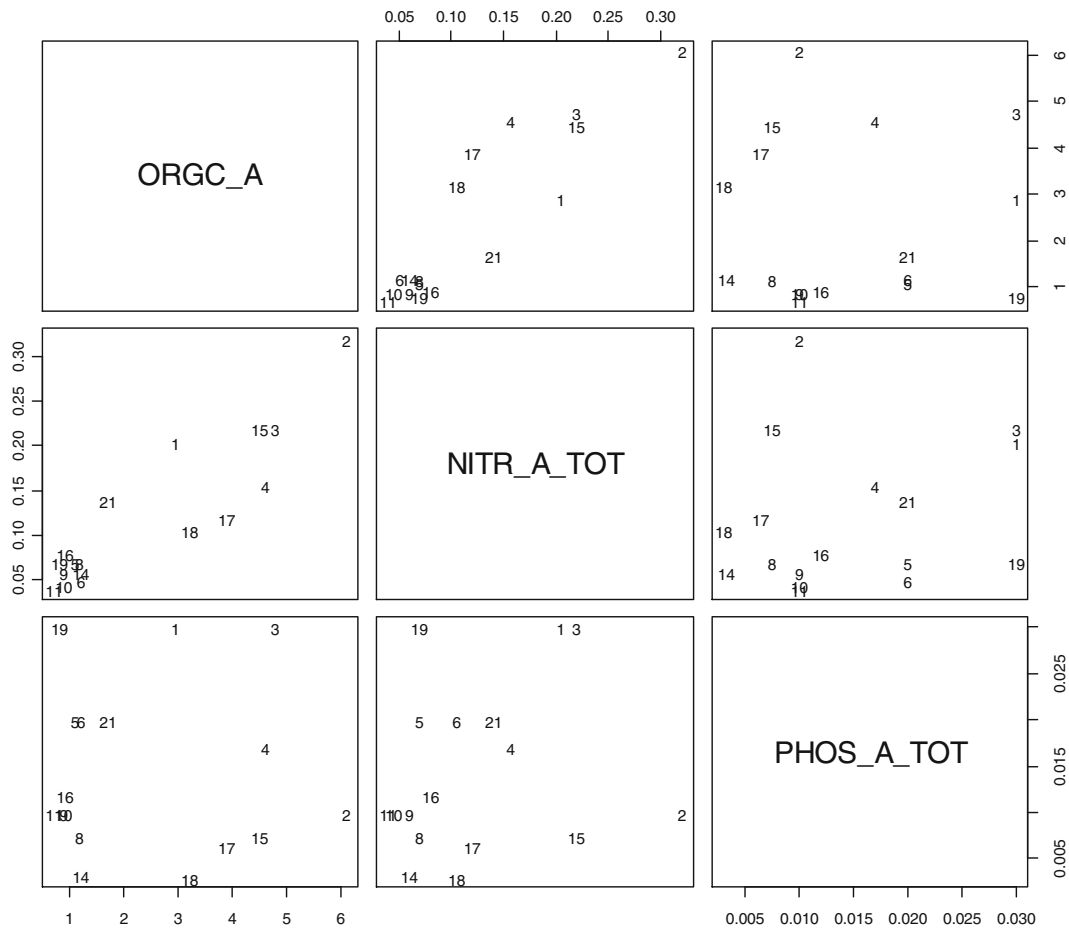


Fig. 3 Pairwise scatterplots showing median SOC, N, and P levels for MVGs. Tall open eucalypt forests (MVG 2) occur on soils low in P but high in N

N_2 -fixing shrubs may be a source of the difference in C:N:P between eucalypt tall open (MVG 2) and open forests and woodlands (MVG 3, 5, and 11). In Victorian tall open eucalypt forests, the role of understorey *Acacia* is critical in forest regeneration, especially after fire (e.g., Polglase and Attiwill 1992; Attiwill et al. 1996; Attiwill and May 2001). In WA, O'Connell and Grove (1996) have underscored the role of N_2 -fixing understorey species in nutrient cycling in karri (*Eucalyptus diversicolor*) forests. The presence of proteaceous species in eucalypt open forests is noted in NSW (e.g., Knox and Clarke 2006; Keith and Bedward 1999; Beadle 1954) and WA (Hopper et al. 1992). Heathlands and shrublands are also rich in Proteaceae (refer to descriptions of NVIS MVGs in DEWR (2007)). Proteaceae are a unique southern hemisphere plant family that have multiple adaptations for dealing with very low soil P: cluster

roots for P uptake and extremely efficient resorption of P from senescing organs (Lambers et al. 2010) but *Acacia* species growing on low-P soils also exhibit efficient P-resorption during leaf senescence (He et al. 2011).

Soil and foliar N:P in southwest Australia are well correlated (Lambers et al. 2010) and there is a direct relationship between soil, litter, and foliar C:N ratios in Australian ecosystems (Tables 16–18 in Snowdon et al. (2005)). Foliar C:N:P that can be re-calculated from the data in Specht and Rundel (1990) show that many plant species found in eucalypt open forests and heathlands have a very high foliar C:N:P ratio (Supplementary Table S2), of magnitude similar to the soil C:N:P ratios under these vegetation groups. Frequently they are Proteaceae, with high cellulose and lignin in their foliar tissues, that produce recalcitrant litter. Lambers et al.

Table 3 Estimated soil C:N:P ratios for NVIS 3.0 major vegetation groups using ASRIS point data. MVGs are ranked by median N:P to aid in the discussion of soil nutrient relationships with plant communities. q10 and q90 are the 10th and 90th percentiles respectively. One-way ANOVAs for testing of difference between MVGs were conducted on the log of the ratio

scale for C:N, N:P, and C:P. All were significant at P -value <0.001 . The shading shows MVGs that were not significantly different in pairwise tests of differences in mean log C:N, N:P, and C:P across all three ratios. See Supplementary material for all pairwise tests of MVG differences in mean of the log of ratios by Tukey Honest Significant Difference

MVG code	No. of sites w soil C:N:P	NVIS 3.0 major vegetation groups	C:N			N:P			C:P		
			median	q10	q90	median	q10	q90	median	q10	q90
19	90	Tussock grasslands (C4)	12	8	17	2	1	6	25	9	86
6	19	<i>Acacia</i> forests and woodlands	17	10	33	2	1	10	70	16	169
5	399	Eucalypt woodlands	16	11	29	3	1	11	56	20	172
11	84	Eucalypt open woodlands	17	10	32	4	1	9	60	22	131
21	19	Other grasslands (wet)	16	10	28	5	3	33	84	38	588
9	37	<i>Melaleuca</i> forests and woodlands	16	10	30	6	3	22	105	35	428
1	44	Rainforests and vine thickets	14	10	27	7	2	16	102	23	245
16	7	<i>Acacia</i> shrublands	14	11	18	7	2	10	92	25	175
3	365	Eucalypt open forests (trees 10 to 30 m tall)	23	14	34	7	2	28	146	35	617
10	12	Other forests and woodlands	16	11	28	11	1	32	117	26	455
8	16	<i>Casuarina</i> forests and woodlands	14	12	19	13	3	18	174	52	277
14	21	Mallee woodlands and shrublands	24	12	32	13	5	29	253	64	786
17	22	Other shrublands	22	11	41	17	6	43	332	76	984
4	7	Eucalypt low open forests (trees <10 m)	16	11	36	18	13	78	230	157	2762
15	14	Low closed forests and tall closed shrublands	22	16	29	20	9	93	479	158	1690
2	15	Eucalypt tall open forests (trees >30 m)	31	14	45	22	6	50	675	78	1670
18	10	Heathlands	31	21	43	43	4	115	983	181	3588

(2010) argue that low leaf P in Proteaceae is indicative of low ribosomal RNA and thus low protein and slow growth, which also would account for their recalcitrant litter.

That the soil C:N:P results are consistent with foliar nutrient ratios in plants present in MVGs suggests that they are credible. The relationship between the soil nutrients and plant communities shows that there is positive feedback between the two and thus support statements by Hobbie (1992): “most likely, distribution of plant species are both a cause and an effect of patterns of nutrient cycling in natural ecosystems... those that grow on nutrient-poor soils produce recalcitrant litter that decomposes slowly, whereas those that grow on fertile soils produce easily degraded litter.” Plants in communities with high soil N:P ratios, such as heathlands and tall open eucalypt forests, are those adapted to low soil fertility that produce

recalcitrant litter, whereas plants in tussock grasslands represent the opposite end of the relationship (Table 2 and Fig. 3).

Fire and soil N

Smoke from burning native vegetation is required by some Australian plants that are normally hard to germinate (Dixon et al. 1995; Flematti et al. 2004). Many proteaceous species also require fire to propagate (Handreck 1997; Knox and Clarke 2006). The growth of understorey shrubs that often belong to leguminous families is promoted by regular fires in eucalypt open forests (Florence 1996; Raison et al. 2009). In *Eucalyptus regnans* forests (MVG 2), which rely on fire for their regeneration, growth of understorey *Acacia* ensures the forest stands never become N-deficient (Polglase and Attiwill 1992).

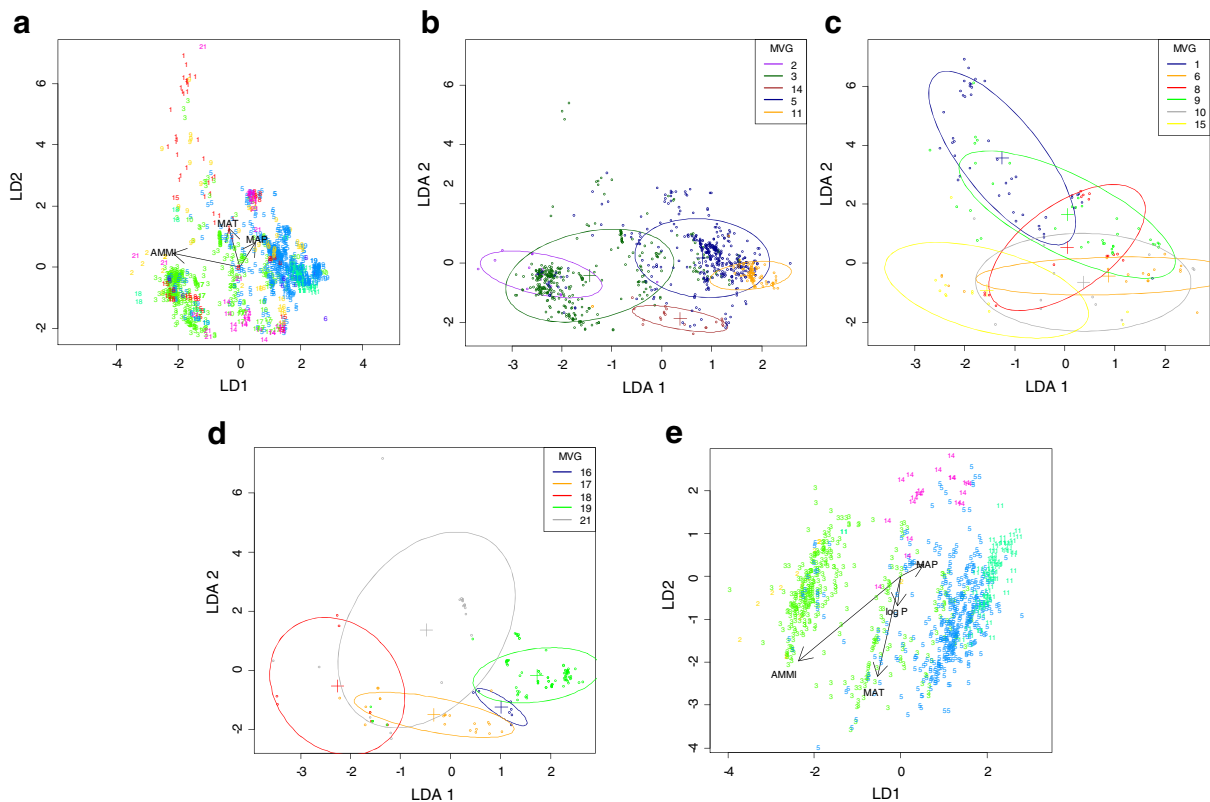


Fig. 4 **a** Results for LDA1, LD2 versus LD1. See Table 4 for LDA results. **b** Eucalypt plant communities follow a soil moisture gradient, i.e. they lie along LD1 which has a large contribution from the mean annual soil moisture index (AMMI), with the tall open forests at the wet end and the open woodlands at the dry end of the gradient. Their soil N:P ratios (Table 2) also follows this gradient. **c** Shrublands, heathlands, and grasslands. **d** *Acacia* and

other forests. Rainforests (MVG 1) and *Melaleuca* forests (MVG 9) respond strongly to mean annual temperature, i.e. they lie along LD2 which has a large contribution from MAT. *Ellipses* show one s.d. from the centroid of each MVG in multivariate space. **e** Results for LDA2 (on eucalypt communities only), LD2 versus LD1. See Table 4 for LDA2 results

However fire, which results in the production of stable, recalcitrant char (Krull et al. 2003), does not appear to contribute to the relatively high SOC and C:N:P ratio for eucalypt open forests given that fires are more frequent in tussock grasslands and woodlands than open forests (Craig et al. 2002; Bradstock 2010). In fact SOC (Fig. 2a) and C:N:P ratios for these plant communities (Table 2) are inversely related to expected fire frequency.

Fires burn extensively across Australia's northern savannas every year (<http://www.savanna.org.au/all/fire.html>). C_4 (tropical) grasslands have a high N use efficiency and rapid growth rate that leads to accumulation of plant biomass relatively high in lignin and low in N which serves as fuel for fire (Dubeux et al. 2007). Frequent fire burns off up to 90 % of N in biomass therefore tussock grasslands (MVG 19) have

a very low soil N (Figs. 2 and 3). Fire does not impact soil P level as much; P remains in the ash (Raison et al. 2009). Thus the soils under tussock grasslands are not particularly low in P relative to other MVGs and their low N:P ratio is typical of other tropical grasslands (Dubeux et al. 2007). We infer then that low soil N:P appears indicative of N-limitation in tussock grasslands due to frequent fire.

Variations in fire frequency and intensity are primarily related to fluctuations in available moisture and dominance by either woody or herbaceous plant cover. Fire in forests (wet climates) is limited by fuel moisture (availability to burn) and propitious fire weather whereas in woodland communities (dry climates) limitation is by growth of herbaceous fuels (biomass) (Bradstock 2010). Fires in forests occur less frequently (on the order of decades to centuries) but are more

Table 4 Results of linear discriminant analyses

LDA1 Model: lda(mvg ~ scale(MAT) + scale(MAP) + scale(AMMI) + scale(log(P)) + scale(log(N)), data = CNP.data)					
Coefficients	LD1	LD2	LD3	LD4	LD5
scale(MAP)	0.505611545	0.8061069	0.7323053	-2.5380425	-0.6240087
scale(MAT)	-0.334888612	1.2655398	-0.9544775	2.8010914	1.0410742
scale(AMMI)	-2.165069562	0.4585925	-1.5209702	4.0348431	0.2668957
scale(log(P))	-0.013380319	0.1434405	0.7600407	0.8773076	-0.6895815
scale(log(N))	-0.009196788	0.1578588	0.3503408	-0.5980363	1.5451655
Proportion of trace	0.5884	0.3082	0.0559	0.0338	0.0137
LDA2 Model: lda(euc.mvg ~ scale(MAP) + scale(MAT) + scale(AMMI) + scale(log(P)) + scale(log(N)), data = euc)					
Coefficients	LD1	LD2	LD3	LD4	
scale(MAP)	0.5405168	0.2785599	-0.1560405	-1.6195785	
scale(MAT)	-0.5337040	-2.3382103	-0.8911436	2.0164615	
scale(AMMI)	-2.3632914	-1.9662701	-0.4115390	3.6153836	
scale(log(P))	-0.0748867	-0.6939235	1.0518869	0.4097198	
scale(log(N))	-0.1221630	-0.1787954	-0.7454646	-1.2672805	
Proportion of trace	0.8769	0.1104	0.0086	0.0041	
LDA 3 Model: lda(euc.mvg ~ scale(MAP) + scale(MAT) + scale(AMMI) + scale(log(N.P)), data = euc)					
Coefficients	LD1	LD2	LD3	LD4	
scale(MAP)	0.54281420	0.3967722	-0.2491491	-2.1940581	
scale(MAT)	-0.43653404	-2.3821438	-0.7618019	2.4047628	
scale(AMMI)	-2.39330773	-2.6526440	-0.1544719	3.5233281	
scale(log(N.P))	0.04482425	0.6549941	-0.9595398	-0.1648754	
Proportion of trace	0.9049	0.0845	0.0088	0.0018	

Table 5 Analysis of deviance comparing the impact of soil nutrients beyond that of climate on the MVGs

MVG	Model 1 Dev		Model 2: clim + log N		Model 2: clim + log P		Model 2: clim + log N + log P	
	Model 1 Dev	Diff in Dev	P(> Chil)	Diff Dev	P(> Chil)	Diff Dev	P(> Chil)	
1	197.78	12.494	0.0004084 ***	13.55	0.0002323 ***	16.047	0.0003277 ***	
2	115.24	0.56334	0.4529	8.6688	0.003237 **	17.015	0.0002019 ***	
3	911.81	0.62159	0.4305	12.447	0.0004185 ***	14.939	0.0005702 ***	
5	6.7066e-09	0	1	0	1	0	1	
6	1277.9	0.3074	0.5793	2.7096	0.09975.	6.63	0.03633 *	
8	171.98	0.86508	0.3523	0.0036781	0.9516	1.3415	0.5113	
9	6.7066e-09	0	1	0	1	0	1	
10	151.00	0.00017617	0.9894	3.0003	0.08325.	4.7555	0.09276 .	
11	222.08	3.2022	0.07354.	4.2877	0.03839 *	4.6719	0.09672.	
14	124.95	1.9395	0.1637	3.7008	0.05439.	3.7181	0.1558	
15	412.94	18.601	1.611e-05 ***	41.038	1.493e-10 ***	41.059	1.214e-09 ***	
16	6.7066e-09	0	1	0	1	0	1	
17	6.7066e-09	0	1	0	1	0	1	
18	127.35	20.937	4.746e-06 ***	24.241	8.502e-07 ***	26.001	2.259e-06 ***	
19	115.77	1.2156	0.2702	5.3937	0.02021 *	5.5898	0.06112.	
21	69.308	1.1259	0.2887	0.68832	0.4067	1.1359	0.5667	

Model 1: (data\$NVIS3 == i) ~ AMMI + MAP + MAT

Model 2: (data\$NVIS3 == i) ~ log N or log P or (log N + log P) + AMMI + MAP + MAT

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

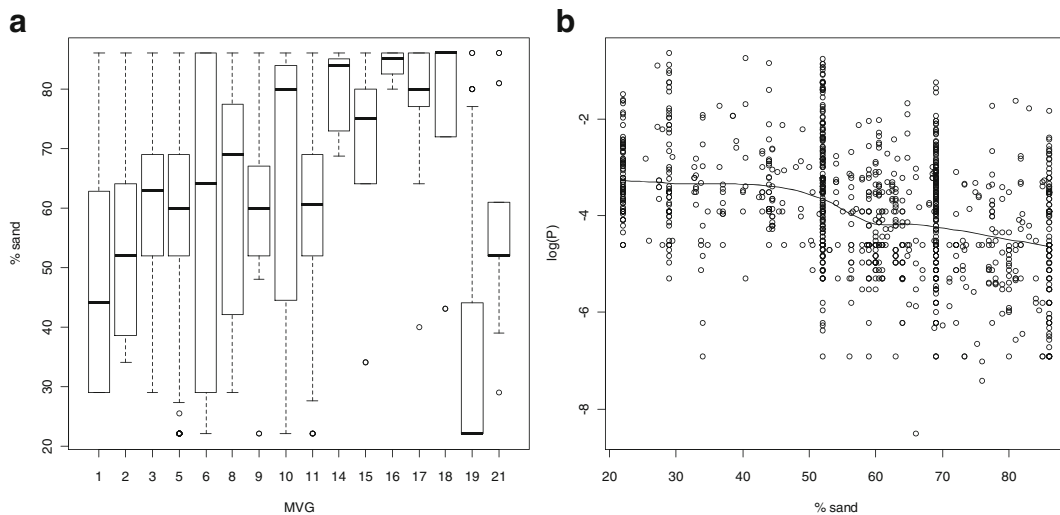


Fig. 5 **a** Boxplot of % sand for NVIS3.0 MVGs. Note mallee and shrubland MVGs occur on very sandy soils. **b** relationship between soil P and % sand (as a surrogate for quartz)

intense than fires in savanna (Bradstock 2010). Fire is thus an important control on the annual to decadal flux of N from soil and biomass to the atmosphere.

Vigorous regrowth of leguminous and proteaceous understorey shrubs after fires in eucalypt forests (Keith et al. 2009; Raison et al. 2009) is an indication of ecosystem return to stoichiometric homeostasis. Immediately after a fire the soil C:N:P ratio will be low but after a few years of regrowth it will increase. With fires of decadal frequency as recorded in eucalypt open forests, the C:N:P ratio should tend back toward a median value around 146:7:1. Whereas with regrowth after partial stand-replacing fires of centennial frequency as in old-growth tall eucalypt open forests (e.g., Polglase and Attiwill 1992; Keith et al. 2009), the C:N:P ratio should rise toward a median value of 675:22:1. We surmise that this is why SOC and C:N:P ratios for plant communities are inversely related to expected fire frequency.

Is P limiting?

The role of soil P in the distribution of native vegetation in Australia is a question that has long been controversial (Beadle 1954; 1962; Adams 1996; Handreck 1997). According to many (e.g., Florence 1996), Beadle was the first to propose that the level of soil nutrients, particularly P, was the critical factor delimiting plant communities in eastern Australia. By using the word ‘delimitation’, Beadle was saying that soil P controls the spatial

distribution of plant communities but in the subsequent controversy an implicit equivalence between P delimitation and P ‘limitation’ arises. The notion that N and P limit plant growth has widespread acceptance throughout the world; however the idea of nutrient limitations to plant growth in native ecosystems, especially P-limitation, is questioned, in Australia in particular (Adams 1996; Adams et al. 2004). Using sclerophylly, nutrient resorption, cluster roots, mycorrhizal symbioses and associations with various N₂-fixing and P-scavenging organisms, Australian native plants are well adapted to their soils’ nutrient status (Handreck 1997; Adams et al. 2004; Lambers et al. 2006; Lambers et al. 2008). Sclerophylly is now shown to have arisen as an adaptation to low soil fertility through the fossil record of Proteaceae (Hill 2004), an adaptation that also confers resistance to drought. Sclerophylly, as characterized by high lignin and cellulose content, responds more strongly to soil fertility than to low rainfall (Specht and Rundel 1990).

The ASRIS results (which as evident from Fig. 1 are mostly from Queensland and Tasmania in the east and thus are independent of Beadle’s who was working in the Sydney Basin) support the conclusion that soil P is an important variable associated with the delimitation between rainforest, tall open and open eucalypt forests (Figs. 2c and 3). But in fact, it is the level of P relative to N or the N:P ratio that is the key. Eucalypts are found on soils with a wide range of P but open forest formations occur on soils with relatively higher N content than

woodlands; tall open forests (MVG 2) are restricted to soils with high N relative to P (Fig. 3). The soil N:P ratio for tall open eucalypt forests is much larger than that of other eucalypt vegetation classes (Table 2). By analogy with foliar N:P ratios, large soil N:P ratios, >20 as in MVG 2, suggest P-limitation.

That *Acacia* communities (MVG 6 and 16) occur on soil with moderate levels of P (Fig. 2) is consistent with the theory that a P threshold exists before rhizobial N₂-fixation can occur (Beadle 1962).

The data for Australia belie some widely held views, namely, that soil P and N:P decrease with latitude, reaching a low at the Equator (e.g., Hedin 2004). North Queensland tropical rainforest soils are not particularly low in total P or N:P; in Tasmania and in southwest WA, both at higher latitudes, soil P is very low (Fig. 2c). The widely held view that old soils are those depleted in P also needs to be tempered. Soil age is not the sole cause of low P (Vitousek et al. 2010). Mineralogy of the soil is key here (Fig. 5b): Over the extensive Tertiary or older landscapes in Australia, soils are not all low in total P but all of the low-P soils have a quartz-dominated mineralogy (e.g., southwest WA (McArthur 1991); Hawkesbury sandstone in Sydney Basin, NSW, studied by Beadle (1962); and coastal dunes in southern Queensland (Skjemstad et al. 1992)).

Conclusions and implications

Although there is no single Redfield-like ratio in soils across all plant communities in Australia, the notion of “the biological control of chemical factors in the environment” seems to hold within terrestrial ecosystems as Redfield (1958) posited for the ocean; moreover “P is the master element” that regulates the cycling of the others. Total soil P ultimately controls the amount of P available in various forms for plant growth, and thus total P is linked to total N and C in soil.

The stoichiometric relationships follow biogeographical gradients insofar as vegetation patterns are a function of climatic and edaphic factors. Soil moisture is the single largest predictor of native vegetation patterns but for eucalypt plant communities soil N and P (or N:P) also play a role (Table 4). Interestingly the stoichiometry of rainforests (MVG 1) and tall open eucalypt forests (MVG 2) is very different (Table 2) but is consistent with Beadle’s thesis on the role of P in delimiting these two plant communities. Low soil P

and consequently P-limited plant communities (MVG 2, 15, and 18) have high soil N:P ratios and are characteristic of quartzitic, sandy parent material.

Fire and mid-stratum vegetation play critical roles in nutrient cycling in Australian ecosystems. Fire resets an ecosystem’s N level to ‘very low’ and it promotes the growth of understorey shrubs that often belong to leguminous and proteaceous families. Plant communities on infertile soils, that rely on the nutrient cycling adaptations (nutrient resorption, symbiosis with N₂-fixing rhizobia, mycorrhizas, or cluster root structures) of their mid-stratum vegetation, are characterized by more recalcitrant litter and soil organic matter with high C:N:P ratios. This then implies that plant litter decomposability is correlated with plant nutritional strategies and underscores the link between above-ground and below-ground ecology.

The findings broaden our understanding of the biogeochemical cycling of C, N, and P between plants and soils across Australia and of the fundamental constraints on across a wide range of environmental factors. They also provide a data synthesis that should enable better parameterization of multi-element biogeochemical models such as that of Wang et al. (2010). Given the data presented here and in Lambers et al. (2010), it is clear that the range of values used to estimate N:P (by mass) of new organic matter in Wang et al. (2010) is too narrow. Work in progress will report further on ecosystem stoichiometry and biogeochemical cycling of C, N, and P between vegetation and soils across Australia.

Acknowledgments I want to thank John Raison and Alister Spain for useful comments on the draft of this paper.

References

- Adams MA (1996) Distribution of eucalypts in Australian landscapes: landforms, soils, fire and nutrition. In: Attiwill PM, Adams MA (eds) Nutrition of eucalypts. CSIRO Publishing, Melbourne, pp 61–76
- Adams M, Ineson P, Binkley D, Cadisch G, Scholes M, Hicks K, Tokuchi N (2004) Soil functional responses to excess nitrogen inputs at global scale. *Ambio* 33:530–536
- Aerts R, Chapin FS (1999) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67
- Alexander M (1977) Introduction to soil microbiology, 2nd edn. Wiley, New York

- Attwill PM, May BM (2001) Does nitrogen limit the growth of native eucalypt forests: some observations for mountain ash (*Eucalyptus regnans*). *Mar Freshw Res* 52:111–117
- Attwill PM, Polglase PJ, Weston CJ, Adams MA (1996) Nutrient cycling in forests of south-eastern Australia. In: Attwill PM, Adams MA (eds) *Nutrition of eucalypts*. CSIRO Publishing, Melbourne, pp 191–227
- Beadle NCW (1954) Soil phosphate and the delimitation of plant communities in eastern Australia. *Ecology* 35:370–375
- Beadle NCW (1962) Soil phosphate and the delimitation of plant communities in eastern Australia II. *Ecology* 43:281–288
- Bradstock RA (2010) A biogeographic model of fire regimes in Australia: current and future implications. *Glob Ecol Biogeogr* 19:145–158
- Bui EN, Henderson BL, Viergever K (2009) Using knowledge discovery with data mining from the ASRIS database to inform soil carbon mapping in Australia. *Glob Biogeochem Cycles* 23:GB4033. doi:10.1029/2009GB003506
- Cleveland CC, Liptzin D (2007) C:N:P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass? *Biogeochemistry* 85:235–252
- Cleveland CC, Townsend AR, Taylor P, Alvarez-Clare S, Bustamante M, Chuyong G, et al. (2011) Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecol Lett* 14: 939–947
- Craig R, Heath B, Raisbeck-Brown N, Steber M, Marsden J, Smith R (2002) The distribution, extent and seasonality of large fires in Australia, April 1998–March 2000, as mapped from NOAA-AVHRR imagery. In: Russell-Smith J, Craig R, Gill AM, Smith R, Williams J (eds) *Australian Fire Regimes: Contemporary Patterns (April 1998–March 2000) and Changes Since European Settlement*. Australia: State of the Environment Second Technical Paper Series (Biodiversity), Series 2, Department of the Environment and Heritage, Canberra. <http://www.environment.gov.au/soe/2001/publications/technical/fire/pubs/part1.pdf>. Accessed 20 April 2011
- DEWR, Department of the Environment and Water Resources (2007) *Australia's Native Vegetation: A summary of Australia's Major Vegetation Groups*. Australian Government, Canberra, ACT. <http://www.environment.gov.au/erin/nvis/>. Accessed 20 April 2011
- Dixon KW, Roche S, Pate JS (1995) The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* 101:185–192
- Dubeux JCB, Sollenberger LE, Mathews BW, Scholberg JM, Santos HQ (2007) Nutrient cycling in warm-climate grasslands. *Crop Sci* 47:915–928. doi:10.2135/cropsci2006.09.0581
- Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* 10:1–8
- Flematti GR, Ghisalberti RL, Dixon KW, Trengrove RD (2004) A compound from smoke that promotes seed germination. *Science* 305:977. doi:10.1126/science.1099944
- Florence RG (1996) Ecology and silviculture of eucalypt forests. CSIRO Publishing, Melbourne
- Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytol* 164:243–266
- Güsewell S, Gessner MO (2009) N:P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. *Funct Ecol* 23:211–219. doi:10.1111/j.1365-2435.2008.01478.x
- Güsewell S, Verhoeven J (2006) Litter N:P ratios indicate whether N or P limits the decomposability of graminoid leaf litter. *Plant Soil* 287:131–143. doi:10.1007/s11104-006-9050-2
- Handreck KA (1997) Phosphorus requirements of Australian native plants. *Aust J Soil Res* 35:214–289
- He H, Bleby TM, Veneklaas EJ, Lambers H (2011) Dinitrogen-fixing *Acacia* species from phosphorus-impooverished soils resorb leaf phosphorus efficiently. *Plant Cell Environ* 34:2060–2070
- Hedin LO (2004) Global organization of terrestrial plant-nutrient interactions. *Proc Natl Acad Sci U S A* 101:10849–10850
- Henderson BL, Bui EN, Moran CJ, Simon DAP, Carlile P (2001) ASRIS: Continental-scale soil property predictions from point data. Technical Report 28/01. CSIRO Land and Water, Canberra
- Hill RS (2004) Origins of the southeastern Australian vegetation. *Phil Trans R Soc B* 359:1537–1549
- Hobbie SE (1992) Effects of plant species on nutrient cycling. *Trends Ecol Evol* 7:336–339
- Hopper SD, Keighery GJ, Wardell-Johnson G (1992) Flora of the karri forest and other communities in the Warren Subdistrict of Western Australia. Occasional Paper 2/92, Research on the Impact of Forest Management in South-west Western Australia. WA Department of Conservation and Land Management, Perth
- Houlder D, Hutchinson M, Nix H, McMahon J (2000) ANUCLIM, Version 5.1, User Guide. Centre for Resource and Environmental Studies. The Australian National University, Canberra
- Johnston RM, Barry SJ, Bleys E, Bui EN, Moran CJ, Simon DAP, Carlile P, McKenzie NJ, Henderson B, Chapman G, Imhoff M, Maschmedt D, Howe D, Grose C, Schokneck N, Powell B, Grundy M (2003) ASRIS: The database. *Aust J Soil Res* 41:1021–1036
- Keith DA, Bedward M (1999) Native vegetation of the southeast forests region, Eden, New South Wales. *Cunninghamia* 6:1–60
- Keith H, Mackey BG, Lindenmayer DB (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *PNAS* 106:11635–11640
- Knox KJE, Clarke PJ (2006) Response of resprouting shrubs to repeated fires in the dry sclerophyll forest of Gibraltar Range National Park. *Proc Linnean Soc NSW* 127:49–56
- Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J Appl Ecol* 33:1441–1450
- Krull ES, Baldock JA, Skjemstad JO (2003) Importance of mechanisms and processes of the stabilisation of soil organic matter for modelling carbon turnover. *Funct Plant Biol* 30:207–222
- Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Ann Bot* 98:693–713
- Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant-nutrient acquisition strategies change with soil age. *Trends Ecol Evol* 23:95–103
- Lambers H, Brundrett MC, Raven JA, Hopper SD (2010) Plant mineral nutrition in ancient landscapes: high plant species

- diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant Soil* 334:11–31. doi:10.1007/s11110
- McArthur WM (1991) Reference soils of south-western Australia. Department of Agriculture Western Australia, Perth
- McGroddy ME, Daufresne T, Hedin LO (2004) Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. *Ecology* 85:2390–2401
- O'Connell AM, Grove TS (1996) Biomass production, nutrient uptake and nutrient cycling in the jarrah (*Eucalyptus marginata*) and karri (*Eucalyptus diversicolor*) forests of south-western Australia. In: Attiwill PM, Adams MA (eds) Nutrition of eucalypts. CSIRO Publishing, Melbourne, pp 155–189
- Pate JS, Verboom WH, Galloway PD (2001) Co-occurrence of Proteaceae, laterite and related oligotrophic soils: coincidental associations or causative inter-relationships? *Aust J Bot* 49:529–560
- Paul EA (ed) (2007) Soil microbiology, ecology, and biochemistry, 3rd edn. Academic, Amsterdam/Boston
- Peñuelas J, Sardans J, Rivas-ubach A, Janssens IA (2012) The human-induced imbalance between C, N and P in Earth's life system. *Glob Change Biol* 18:3–6
- Polglase P, Attiwill P (1992) Nitrogen and phosphorus cycling in relation to stand age of *Eucalyptus regnans* F. Muell. *Plant Soil* 142:157–166
- R Development Core Team (2005) R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna. <http://www.r-project.org/>. Accessed 13 Jan 2010
- Raison RJ, Khanna PK, Jacobsen KLS, Romanya J, Serrasolses I (2009) Effects of fire on forest nutrient cycles. In: Cerda A, Robichaud PR (eds) Fire effects on soils and restoration strategies. Science Publishers Incorporated, Enfield, pp 225–256
- Rayment GE, Higginson FR (1992) Australian Laboratory Handbook of Soil and Water Chemical Methods. Inkata Press, Melbourne
- Redfield A (1958) The biological control of chemical factors in the environment. *Am Sci* 46:205–221
- Reed SC, Townsend AR, Davidson EA, Cleveland CC (2012) Stoichiometric patterns in foliar nutrient resorption across multiple scales. *New Phytol* 196:173–180. doi:10.1111/j.1469-8137.2012.04249.x
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *PNAS* 101:11001–11006
- Skjemstad JO, Fitzpatrick RW, Zarcinas BA, Thompson CH (1992) Genesis of podzols on coastal dunes in southern Queensland. II. Geochemistry and forms of elements as deduced from various soil extraction procedures. *Aust J Soil Res* 30:615–644
- Skjemstad JO, Spouncer LR, Beech A (2000) Carbon conversion factors for historical soil carbon data. National Carbon Accounting System, Technical Report 15. Australian Greenhouse Office, Canberra
- Snowdon P, Ryan P, Raison J (2005) Review of C:N ratios in vegetation, litter and soil under Australian native forests and plantations. National Carbon Accounting System Technical Report No. 45, Australian Government, Canberra. <http://www.climatechange.gov.au/ncas/reports/tr45final.html>. Accessed 20 Dec 2008
- Spain AV, Isbell RF, Probert ME (1983) Soil organic matter. In: Soils: an Australian viewpoint. CSIRO Publishing, Melbourne, pp 551–587
- Specht RL (1996) The influence of soils on the evolution of the eucalypts. In: Attiwill PM, Adams MA (eds) Nutrition of eucalypts. CSIRO Publishing, Melbourne, pp 31–60
- Specht RL, Rundel PW (1990) Sclerophylly and foliar nutrient status of Mediterranean-climate plant communities in southern Australia. *Aust J Bot* 38:459–474
- Specht RL, Specht A (2010) The ratio of foliar nitrogen to foliar phosphorus: a determinant of leaf attributes and height in life-forms of subtropical and tropical communities. *Aust J Bot* 58:527–538
- Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Blackwell Scientific Publications, Oxford
- Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecol Appl* 20:5–15. doi:10.1890/08-0127.1
- Wang YP, Law RM, Pak B (2010) A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences* 7:2261–2282. doi:10.5194/bg-7-2261-2010
- Wardle DA, Walker LR, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305:509–513
- Yuan ZY, Chen HYH (2009) Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Glob Ecol Biogeogr* 18:11–18. doi:10.1111/j.1466-8238.2008.00425.x