Plant accessible phosphorus as a discriminator of native vegetation in the upper Blue Mountains.

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Abstract
Soil phosphorus is often considered a critical factor in the distribution of mesomorphic communities in south-eastern Australia. This is based largely on the measurement of total P concentrations in the surface soil rather than P accessibility, even though changes between vegetation patterns are often associated with a change in parent material. This study estimated plant accessible P with reference to mesomorphic forest (MF), dry sclerophyll forest (DSF), woodland (WO) and heath (H) on basalt and sandstone substrates in the upper Blue Mountains. Soil surface total P concentrations (P_t) were significantly greater in MF than in xeromorphic communities (DSF, WO & H) as reported by others. However, P_t for DSF was at levels typically associated with mesomorphic vegetation. Olsen P concentrations were not significantly greater in DSF than HE and Mehlich-3 P could not separate any of the xeromorphic communities. P_t may exaggerate the fertility status of DSF soils whereas available P is consistent with the occurrence of a xeromorphic community at this site. P accessibility was significantly lower in basalt-derived soils than on sandstone substrates, though available P still discriminated between MF on basalt and the xeromorphic communities.

Introduction
Soil phosphorus is often considered a critical factor in the ecology and biogeography of Australian vegetation (Beadle, 1966; Bowen, 1981). Soil P was revealed as a limiting factor in the growth and survivorship of mesomorphic species in greenhouse experiments (Beadle 1962, 66) and there is field evidence to suggest that soil P limits the distribution of mesomorphic communities in southeast Australia (Beadle, 1954, 62; Webb, 1969; Webb & Tracey 1981). However, soil P does not appear to discriminate between the distribution of xeromorphic vegetation types, such as dry sclerophyll forest, woodland and heath (Coaldrake & Haydock, 1958; Le Brocque & Buckney, 1994). These ecological studies relied on a measure of total P (P_t). Available P is theoretically superior as a comparative tool since it is sensitive to differences in soil P accessibility between diverse soil types and is widely used in agricultural contexts (Holford, 1997; Peverill et al., 1999). From an ecological viewpoint a significant relationship between vegetation patterns and soil P is most likely within an area containing heterogeneity of soil parent material (Beadle, 1962; Kelly & Turner, 1983b), but it is precisely these circumstances that the greatest disparity in P accessibility is expected. In addition, the separation of communities can be considered in two ways: (i) variation in P requirements of species, which is the basis of the distinction between mesomorphic and xeromorphic vegetation types used by Beadle (1954) and (ii) an inferred general relationship between plant community structure and soil P. The latter would predict significant differences between xeromorphic vegetation types coinciding with an overall increase in soil P from heath to woodland to dry sclerophyll forest to mesomorphic communities. The purpose of the following paper is to test whether or not accessible P provides a clearer distinction between species and communities than P_t and whether or not discrimination differs between the concentration of P in the near surface soil, as is usually undertaken, or the actual quantity P potentially accessed by roots within the profile.

Study Area
Site description
Two sites in the upper Blue Mountains, NSW at 950-1050 m elevation were investigated. The first is situated on the dissected Triassic sandstone of the Newnes Plateaux that occur throughout the region. A cap of residual Tertiary basalt occurs at the second site, Mt Wilson. The region experiences a warm temperate climate. Yearly average rainfall ranges from 1228mm at Mt. Wilson to 1097mm at Newnes plateau (Bureau of Meteorology, 1979).

Vegetation Patterns
Vegetation communities were defined using the structural system of Specht (1970) and further separated with indicator species. The Newnes plateau site supported sclerophyll woodland, dominated by

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Eucalyptus sieberi and dry heath with *Allocasuarina nana* and *Lepidsoperma viscidum*. The site consists of spurs on the western edge of a deeply dissected plateau with heath present on the exposed noses and woodland upslope. Boundaries between treed and treeless communities were relatively sharp, though many heath species persist as understorey components of the sclerophyll woodland. The Mt.Wilson site was sampled at approximately thirty metre intervals along a transect positioned to represent variation in vegetation structure across a hill (Figure 1). The crest of the hill supported wet sclerophyll forest, dominated by *Eucalyptus blaxlandii* and *E. viminalis* which extends downslope to the south through a broad wet sclerophyll forest/ rainforest ecotone into *Doryophora sassafras* warm temperate rainforest (Brough *et al.* 1924). These three associations were grouped as mesomorphic forest characterised by the presence of mesomorphic trees or shrubs and abundant ferns and lianes. The other three sites were situated on the west facing slope, each supporting open *Eucalyptus fastigata* forest with patchy bracken and xeromorphic shrub understorey referred to here as dry sclerophyll forest. This was subdivided into two associations depending upon the composition of the understorey: the *Pultenea daphnoides* association at sites Wa and Wf; and the *Pteridium esculentum* association downslope at Wd. Though an aspect influence occurs it is modified by other factors. McLuckie and Petrie (1927) stressed the importance of parent material especially via soil moisture holding capacity as well as fertility. The two sites together yielded four structurally based vegetation communities each with n=3: Heath (HE), woodland (WO), dry sclerophyll forest (DSF), and mesomorphic forest (MF).

Soil landscapes

Site selection incorporated variation in soil materials that typically forms the basis of ecological studies: infertile quartz sandstone soils supporting xeromorphic vegetation communities were contrasted with higher fertility, basalt derived soils supporting comparatively mesomorphic vegetation. In the upper part of the Newnes Plateau landscape under woodland the soil occurs as a continuous mantle characterised by a litter layer 3-5cm thick, overlying up to 50cm of yellow clayey sands and sandy loams (Earthy Sands - Uc5.21). Quartz gravel and ironstone floaters are common, comprising up to 50% of the bulk soil volume in some horizons. On heath covered sideslopes, soils occur in pockets between horizontal sandstone benches. A patchy litter layer <5cm thick overlies <10cm brownish black sandy loam topsoil and <30cm of dull yellowish brown sandy loam subsoil. This is underlain by bedrock or in places dull yellow, coarse gravelly clayey sand. Soil depth and gravel content varies between sandstone outcrops to form Lithosols (Uc1.22) and shallow (maximum depth of 39 cm) Earthy Sands (Uc 5.21). Quartz gravel and ironstone floaters are common comprising up to 50% of the bulk soil volume.

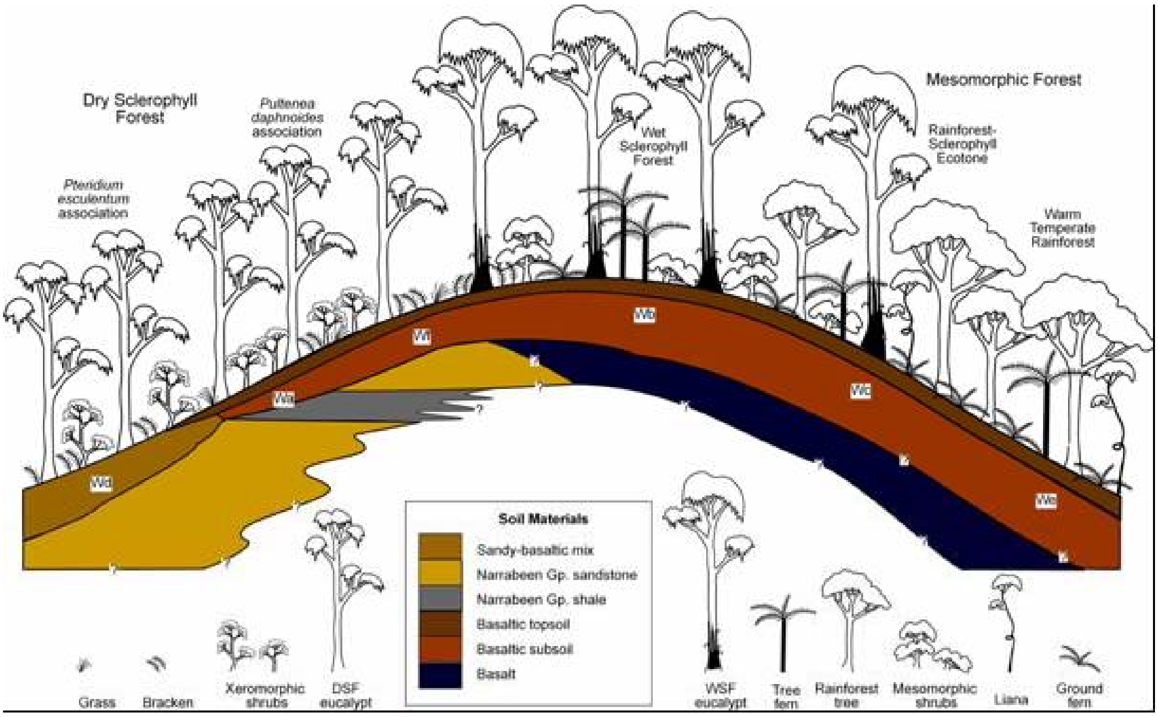

Figure 1. Vegetation-soil relationships at Mt. Wilson.

Deep basalt derived soils occur on the southern slope at Mt Wilson, though on the western slope basaltic material occurred as a mantle overlying Narrabeen Group derived soils (Figure 1). In the three southern profiles the topsoil consists of 10-30cm of friable, brownish black clay loam, strongly pedal worm casts (10-20mm). This overlies reddish brown light clay, over red light medium clay. Boundaries are gradual. Near the crest this was underlain by dull reddish brown medium clay with abundant strongly weathered basalt fragments (up to 60%). Down slope, subsoil continued to the depth of equipment failure (<140cm) though road cuttings suggest depths up to 300cm (red Kraznozems, Gn3.11). Basalt floaters occur throughout profiles and occasionally at the surface, becoming more abundant up slope. Charcoal fragments were present throughout profiles suggesting bioturbation to depths of at least 100cm. The upper two sites on the western slope (Wa and Wf) feature basalt-derived colluvium over sandstone and shale derived material respectively. Topsoil consists of 10-20cm of friable, brownish black clay loam, strongly pedal worm casts (10-20mm). This overlies yellowish brown clay loam thence light to light medium clay (brown Kraznozem, Gn 3.21). Boundaries are clear. The basaltic topsoil mantle was absent from the pit farthest down slope (Wd), replaced by 3-5cm of continuous eucalypt-leaf litter and <20cm of yellowish brown weakly pedal topsoil. This overlies >160cm of massive yellow sandy clay loam. Rare basalt pebbles occur to 60cm but sandstone gravel and sandstone floaters are common throughout the profile comprising up to 25% of bulk soil volume. Boundaries are diffuse to gradual (Yellow Earth, Gn 2.22). The character of the soil material varies with the composition of the underlying parent material and the degree of intermixing with basaltic material. The distinction between the *Pultenea daphnoides* association at sites Wa and Wf and the *Pteridium esculentum* association downslope at Wd roughly coincides with the downslope extent of basaltic topsoil. This pattern was also noted by McLuckie and Petrie (1927) and a more generalised account of soil distribution is provided in King (1993).

Methods

Soils were described using the system of DLWC in NSW which is very similar to Australian standard. Samples were obtained from pedogenic horizons and thus occurrs at irregular intervals between 7 and 25cm. Total P (P_t), Olsen P (P_o) and Mehlich-3 P (P_{m-3}) were obtained for each soil sample, permitting comparisons between the three tests. By virtue of the extraction technique used, each test estimates a different proportion of the soil P reserve (Peverill et al., 1999). P_t, recorded by x-ray fluorescence, provides an estimate of the total concentration of soil P. Olsen P utilises 0.5M $NaHCO_3$ with a relatively short extraction time and narrow soil: solution ratio. On slightly acid soils of south-eastern Australia P_o typically records the soil solution P concentration (Rayment & Higginson, 1992) though it may also extract comparatively soluble forms of solid phase P (Peverill et al., 1999). Mehlich – 3 P and the similar Bray available P tests are considered preferable on these soils by some workers since they extract a proportion of stored P that is more sensitive to soil P buffer capacity. Greenhouse correlation tests have shown that this characteristic is a useful predictor of plant uptake (Holford, 1997). P_{m-3} utilises an extractant composed of 0.2M CH_3COOH, 0.25M NH_4NO_3, 0.015M NH_4F, 0.013M HNO_3 and 0.001M EDTA. Phosphorus is extracted by reaction with acetic acid and the fluoride compounds (Sen Tran & Simard, 1993).

The quantity of P contained within soil profiles was determined through the combination of indices of soil P concentration (*c* in p.p.m.) with soil layer thickness (*t* in cm), fraction of soil as fine earth (*f*) and bulk density (d in g/m^3) factors: Quantity P (g/m^2) = $c \times t \times f \times d$. Layer thickness was defined by identified pedogenic horizons, quantity P calculated separately for each horizon then added to give the value for the whole profile. The base of profile was determined by the limit of hand held digging equipment, around 130cm in the deepest horizons. Profile thickness was also calculated to effective rooting depth (ERD), which is the depth at which the density of roots with diameter finer than 2 mm falls below 10 per 100mm^2 area on an exposed face since it is these roots that are thought to be responsible for the uptake of water and nutrients (Eissenstat, 1992). The percentage of soil as fine earth (particles <2mm) was calculated from the visual estimation of stone content in the field and the volumetric calculation of gravel (particles >2mm) content in the laboratory. Bulk density data was taken from comparable soils recorded in Stace *et al.,* (1968). Correlations between soil parameters were tested using simple linear regression analysis. One-Way ANOVAs were used to compare soil parameters between vegetation communities. Multiple comparisons were made using Fisher's Pairwise, performed with an individual error rate of 0.05. Data were log transformed ($\log_{10}$) to satisfy the Ryan-Joiner test for normality**.**

Results

Soil phosphorus and the distribution of vegetation communities

One-way ANOVA, comparing concentrations of P_t in surface soil samples, showed that soil P was a significant discriminator between vegetation communities (P=0.000) (Table 1). Patterns of separation match those previously reported in the literature, with soil P greater in mesomorphic forest (MF) than comparatively xeromorphic vegetation types (Beadle, 1954; Baur, 1957; Turner & Kelly, 1981). P_t was also significantly greater in dry sclerophyll forest (DSF) than either heath (HE) or woodland (WO). The range of results was generally consistent with that previously reported for southeast Australia. Notably P concentrations within MF were well over the suggested threshold concentration of 200 mg/L of Beadle (1962) for mesomorphic vegetation communities in the Sydney region.

Comparison of Available Phosphorus Tests

Simple linear regression of the two indices of available P showed that they were significantly correlated when all samples were compared (n=68, P=0.000). However the r^2 value of 60.34 suggests that they extracted different proportions of the soil P reserve. P_o recorded less variation in soil P than P_{m-3}, particularly at lower concentrations. Eight out of ten heath samples yielded P_o concentrations of 2mg/L whereas for the same sample set P_{m-3} yielded a range of concentrations from 1.1–4.4 mg/L in which no two values were identical.

Soil phosphorus accessibility of surface samples

Available P was compared with the P_t data to assess the importance of variation in P accessibility. Simple linear regressions conducted on soil surface samples (n=12) showed that P_t was correlated with both P_o (P=0.000, r^2 = 91.9%) and P_{m-3} (P=0.000, r^2= 90.6%). However one-way ANOVAs using available P data, yielded different relativities between communities than afforded by P_t (Table 1). Mean P_{m-3} was greater in WO than HE, whereas both P_t and P_o yielded greater mean concentrations in HE than WO though in each case these differences were not significant. P_o could not separate DSF from HE and P_{m-3} could not differentiate DSF from either HE or WO. This may be due to differences in the proportion of occluded P between soil types, specifically a higher proportion of P held in unavailable forms in DSF soils.

The ratio of available/total P was calculated for each community as an estimate of the proportion of occluded P (Table 1). The proportion of P as P_o was significantly less in MF than WO or HE (P=0.016). Despite the extremely low proportion of available P in MF soils the relative discrimination afforded by available P did not differ from P_t. Although the proportion of available P was lower in DSF than either WO or HE, the differences were not statistically significant. The Mehlich-3 P/total P data was not normally distributed and were not be compared statistically though the relative separation of communities was comparable to Olsen P/total P.

Table 1. Discrimination of vegetation communities by soil P.

	(P)	Heath	Woodland	Dry Sclerophyll Forest	Mesomorphic Forest
Surface concentration Total P	0.000	169.9(21.7)$_a$	93.7(18.7)$_a$	388(95.6)$_b$	1796 (396)$_c$
Surface concentration Olsen P	0.004	2.67(0.7)$_{ab}$	1.67(0.4)$_a$	3(0)$_b$	7.67(1.3$_c$
Surface concentration Mehlich-3 P	0.006	2.59(0.9)$_a$	3.6 (0.8)$_a$	3.67(0.5)$_a$	15.1(3.7)$_c$
Surface concentration Olsen P/Total P	0.016	0.015(0.01)$_a$	0.044(0.02)$_a$	0.012(0.01)$_{ab}$	0.008 (0.001)$_b$
Quantity Total P	0	42.62(3.0)$_a$	70.5(20.9)$_a$	276.3(22.5)$_b$	1010(309)$_c$
ERD-Quantity Total P	0	42.62(3.09)$_a$	63(17.6)$_a$	235.7(39.1)$_b$	961(279)$_c$
Quantity Mehlich-3 P	0.01	0.618(0.17)$_a$	1.023(0.17)$_{ab}$	1.853(0.7)$_{bc}$	4.34(1.3)$_c$
ERD-Quantity Mehlich-3 P	0.006	0.618(0.17)$_a$	0.93(0.13)$_{ab}$	1.521(0.47)$_b$	4.19(1.2)$_c$
Quantity Olsen P	0.005	0.647(0.11)$_a$	0.679(0.23)$_a$	1.911(0.12)$_b$	4.56(1.4)$_b$
ERD-Quantity Olsen P	0.004	0.647(0.11)$_a$	0.61(0.191)$_a$	1.652(0.12)$_b$	4.35(1.3)$_b$

Surface concentrations are mean values (mg/L). Olsen P/total is expressed as a percentage (%). Data in parentheses are standard errors of means. Quantities are mean values calculated through soil profiles (g/m^2). ERD denotes profile thickness calculated to effective rooting depth. P values are the result of One-way ANOVAs performed on log_{10} transformed data. Shared subscripts denote treatments that are not significantly different when compared with Fishers multiple comparisons performed at the 5% confidence interval level.

Soil phosphorus accessibility through soil profiles

There was a significantly higher proportion of available/total P at Newnes than at Mt. Wilson (P=0.000, Table 2) that is consistent with known P-fixation regimes. Figure 2 summarises the likely processes driving these regimes within the context of varying pH. This model is adapted from Scarseth (1962) though incorporates a general understanding of the relationship between P and other soil parameters (*cf* Holford, 1997; Vimpany et al., 1997). These have been confirmed by testing the correlation between P concentrations and pH, Al and Fe (Brennan et al., 1994; Bertrand et al., 2003).

A two sample-T test comparing pH at Newnes sites and Mt. Wilson showed that soil samples were significantly more acid at Newnes (P=0.000). Figure 2 predicts a zone of weak P fixation within the pH range at Newnes and a peak of high fixation at Mt Wilson. P fixation is inversely related to P accessibility and so this matches the reported trends in the ratio of available/total P. The standard errors of the means of available/total P show greater variability at Newnes than at Mt. Wilson. On Figure 2 this coincides with the curves representing P fixation by Fe and Al varying considerably through the range medium to low.

Table 2. Relative proportions of available/total P at Newnes and Mt. Wilson.

	P	Newnes soil samples	Mt Wilson Soil Samples
N		23	45
pH	0.000	4.73 (0.92)	5.85 (0.44)
Olsen P/Total P	0.000	0.015 (0.002)	0.00587 (0.005)
Mehlich-3 P/Total P	0.000	0.020 (0.004)	0.00631 (0.001)

Data are mean values with standard errors in parentheses. P values are the result of One-way ANOVAs performed on log_{10} transformed data

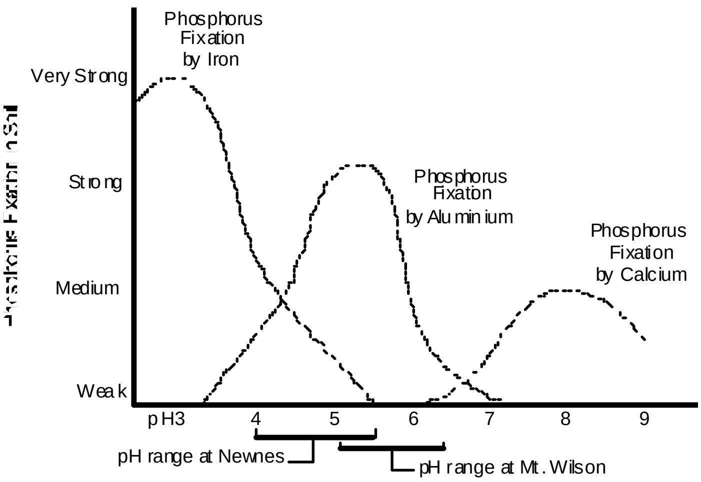

Figure 2. Patterns of Phosphorus Fixation in Soil.

Depth Distribution of Soil P

Simple linear regressions of soil P concentration with depth yielded no significant relationship between depth and either P_t or P_o (all samples, n=68). There was a significant negative relationship between Mehlich-3 P and depth (P=0.041) though depth explained very little of the variation (r^2= 6.2%). When Newnes samples were considered alone (n=23), P_t had a significant positive relationship with depth (P=0.003, r^2= 34.8%) whereas both indexes of available P were n/s. Mount Wilson samples (n=45) displayed a significant negative relationship with depth for P_{m-3} (P= 0.004) though depth explained little of the variation in P concentration (r^2= 17.3%). P_t and P_o were n/s. Thus soil P does not consistently decline with depth nor are there detectable trends in P accessibility with depth.

The Quantity of Phosphorus Contained in Soil Profiles

One-way ANOVAs performed on the quantity of P_t through soil profiles yielded highly significant differences between vegetation communities (Table 1). The relative separation of communities was the same as for analyses conducted on surface samples. Unlike soil P concentration, the quantity of soil P in WO was greater than in HE. This reflects significantly greater soil depths in WO than in HE (two-sample T test, P=0.021). Soil profiles at Mt. Wilson were considerably deeper than at Newnes and in four out of six cases were constrained by equipment rather than the base of profile. Available P quantities also differed between communities ($P<0.01$)(Table 1). However unlike concentration the mean quantity of P was greater in WO than HE, though the differences were still n/s. Calculating quantity P_{m-3} yielded significant differences between DSF and HE, though MF was no longer significantly greater than DSF. Similarly quantity P_o was significantly greater in DSF than both WO and HE though was n/s to MF. In summary calculating the quantity of P accentuated the differences between the shallow, infertile Newnes soils and the deep Mt Wilson soils though reduced the degree of separation between DSF and MF at Mt Wilson.

Calculation of quantity P_t to effective rooting depth (ERD) did not affect the relative separation of vegetation communities (Table 1). The quantity of Mehlich-3 P was significantly greater in MF than DSF when calculated to ERD ($P<0.05$), whereas when taken to the base of profile it could not separate the two communities. The relationship between profile thickness and ERD reflected differences in soil materials between sites. They did not differ in the HE communities though in WO two out of three sites had ERD less than profile thickness yielding a 10.64% reduction in mean quantity P_t. In MF calculation to ERD yielded a minor reduction in mean quantity P of 4.85%. The DSF yielded the greatest difference with a reduction in mean quantity P of 14.69%. Calculating the quantity of P to ERD reduced the degree of separation between HE and the other communities. However calculation to ERD increased the degree of separation between MF and both DSF and WO.

Discussion

Soil surface total P concentrations were significantly greater in the mesomorphic forest than in the three comparatively xeromorphic vegetation communities. The Mount Wilson results support other's findings that mesomorphic vegetation communities in near-coastal NSW are discriminated by soil P (Beadle, 1954, 62; Webb, 1969; Turner & Kelly, 1981). P_t concentrations for the dry sclerophyll forest at Mt. Wilson were relatively high (220 to 551 mg/L) such that Beadle's (1962) hypothesis would predict the presence of a mesomorphic community. Another factor may be limiting with respect to mesomorphic species. Topographic position and associated microclimate (*c.f.* Clements, 1983) or harsher fire regimes have been invoked to describe this pattern (*c.f.* Ashton, 1976a). Another explanation for these trends is that P_t provides a poor estimate of PAP and that an alternative index of P may better represent plant usage. P_t concentrations were not significantly greater in DSF than HE and P_{m-3} could not separate any of the xeromorphic communities. Thus total P may exaggerate the fertility status of DSF soils whereas available P is consistent with the occurrence of a xeromorphic community at this site. Of the available P tests P_{m-3} recorded the greatest variation in soil P at lower concentrations and so may be preferable on low fertility soils. Nevertheless the relative accuracy of the tests cannot be fully resolved without testing the correlation between soil test P values and measured plant uptake of P (Holford, 1997). This approach has been widely used to establish the efficacy of available P tests for agricultural crops though their value in native vegetation has not been confirmed (Handreck, 1997).

P accessibility was significantly lower in basaltic soils at Mt Wilson than sandstone soils at Newnes. This is usually expressed as variation in P-fixation regimes, which is a function of soil chemical properties such as pH, exchangeable Fe and Al (Vimpany et al., 1997). In particular low soil pH's activate the high concentrations of free ferric oxide in the soil, which readily adsorbs any P in solution and binds it to extremely insoluble complexes. A net loss of P from test plants to the soil has been reported in such soils (Krasnozems) with a pH<4.5 (Leeper & Uren, 1993).

The practice of relying on the surface concentrations of soil P in studies that use soil P as a measure of fertility appears to be based on the assumption that the bulk of plant accessible P is confined to soil surface layers and declines exponentially with depth. This type of depth function has been attributed to a biophillic distribution of nutrients (Adams et al., 1994) or to pedogenic processes associated with the mineral soil (McColl, 1956). However the results of the present study suggest there is no consistent relationship between depth and P_t or P_o in two contrasting materials. The significant negative relationship between P_{m-3} and depth is of doubtful importance since the correlation coefficient was extremely low ($P=0.041$, $r^2= 6.2\%$). Lamont (1982) proposed that the enrichment of surface horizons, due to association with organic matter, becomes increasingly more important as nutrient capital decreases. The available P results are restricted to P held in inorganic combination and so the importance of enrichment with organic matter cannot be ruled out. Nonetheless this proposal should predict a relatively greater proportion of total P in surface horizons at Newnes sites than at Mt. Wilson, since total P does incorporate P held in organic combination (Rayment &Higginson, 1992). However, the reverse is true at Newnes since there is a significant positive relationship between total P and depth but there is no relationship at Mt Wilson. The only other discernible trend was a significant but weak negative relationship between Mehlich-3 P and depth at Mt. Wilson. Both results explained little of the variation in P (r^2= 34.8% and 17.3% respectively) and so it is doubtful that they are ecologically significant. The lack of consistent trends between profiles suggests that spatial heterogeneity of soil-forming processes that influence P distribution such as weathering, erosion, redox reactions, illuviation and bioturbation (Uren & Leeper, 1993) is not easily predicted.

Recorded effective rooting depth (ERD) in most cases approached the maximum profile thickness. This reinforces the view that plants may exploit nutrients at considerable depth (Stone & Kalisz, 1991; Schenk & Jackson, 2002). Soil materials appeared to dictate the relationship between ERD and profile depth. The most notable variation occurred at Mt Wilson where ERD was close to maximum profile depth in MF soils though was considerably shallower in DSF soils. This reflects the distinction between deep basalt-derived soils of MF and a basalt-derived colluvial mantle overlaying Narrabeen Group soils in the DSF (Figure 1). The quantity of Mehlich-3 P was significantly greater in MF than DSF when calculated to ERD ($P<0.05$), whereas when taken to the base of the profile it could not separate the two communities (Table 1). The distribution of roots suggests that basalt derived material is a more favourable growth medium than Narrabeen group soils. This, as well as the demonstrated fertility differences, suggests that colluvial processes associated with basaltic material play an important role in the biogeography of vegetation in the region. Sampling only at the surface layer will not capture those changes in soil material at depth that impact on ERD.

The relative separation of communities by the various soil P tests provides another basis for their comparison. The magnitude of separation between vegetation communities is far greater for P_t than available P concentrations. It is likely that P_t exaggerates the fertility status of MF surface soils relative to the other communities. An inferred general relationship between structure and soil P predicts an increase in soil P from heath (HE) to woodland (WO) to dry sclerophyll forest (DSF) to mesomorphic forest (MF). Relative values of total P concentrations in surface samples depart from this trend in that HE had a greater mean concentration than WO. P_o displayed similar relativities though P_{m-3} yielded greater concentrations in WO than HE. Calculating the quantity of P_t through profiles yielded a greater degree of separation between communities than afforded by surface concentrations. The quantity of P produced patterns of separation that matched an inferred general trend in community structure ($MF>DSF>WO>HE$). Notably there were greater quantities of P_t in WO than in HE, the reverse of the trend for P concentrations. This result is due to significantly deeper soils in WO. The quantities of available P also matched the inferred structural relationships, though for P_o the difference between WO and HE was negligible. The quantity value of all P tests displayed similar general trends when calculated to effective rooting depth.

Despite attempts to improve the accuracy of plant accessible P estimation, the data could not discriminate between xeromorphic communities. This is consistent with the results of (Coaldrake & Haydock, 1958) and the interpretation of Beadle (1962), which suggest that soil P is only significant in limiting mesomorphic communities. This study did not estimate organic P, which is a significant component of the soil P reserve in many communities (Handreck, 1997). Nonetheless plant- response trials support these field observations: only exotic test plants and mesomorphic natives exhibit reduced growth and survivorship when grown on poor soils from xeromorphic communities (Beadle 1962, 66). Subsequent research, which found that soil P could separate various eucalyptus-dominated vegetation associations, compared taller, more productive and comparatively mesic forests with shorter, comparatively xeric forests and woodland (McColl, 1969; Turner & Kelly, 1981). Similarly the tall DSFs at Mt Wilson are discriminated from WO at Newnes by soil P, though WO and HE cannot be separated. Thus the biogeography of xeromorphic vegetation communities in the upper Blue Mountains is related to environmental parameters other than soil P.

Conclusion

This study is an attempt to refine the estimation of plant accessible soil P. There are clear differences in P accessibility associated with the various vegetation communities, which in turn can be related to substrate and associated soil parameters. An improved separation between communities occurs using the quantity of total P_t and P_{m-3} in the soil. Nevertheless, the differences are often minor and lack statistical backing especially between the xeromorphic communities. Hence in many circumstances P_t may provide an adequate discriminator between vegetation communities, even when restricted to concentrations in the surface soil. However, the utility of total P declines when soils with markedly different P fixation regimes are to be compared. Similarly surface soil concentrations may provide erroneous associations on skeletal soils or soils with high gravel content. There is a need for further research, comparing test values with measured plant uptake of P, to further resolve the influence of these soil factors upon the estimation of plant accessible P in native vegetation communities.

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