Can Darwinian principles explain the species of regolith under some of Australia’s native flora?

A viewpoint based on critical field observation during the Corrigin Survey.

Verboom, W.H.

Discussion on notes pages


It is increasingly apparent that plants and microbes, as well as animals, engage in niche building activities that not only support their own and each other’s survival, but also determine the trajectory of their evolution (see Day et. al. 2003). The proposition that different types of vegetation generate different types of soil is one of the oldest in soil science (see Field, J.B., 2003. In: Roach I.C. ed. Advances in Regolith, pp. 115-118. CRC LEME, Canberra, Australia). But the idea has languished, with little known concerning the roles of plants and microbes in niche building, particularly in relation to the functioning of ecosystems and development of soil landscapes.

During the Corrigin Survey we found evidence linking cluster-root bearing taxa and microbes to formation of ferric layers (Pate et. al., 2001 A.J. Bot. 49: 529-560). We suggest that this partly relates to phosphorous acquisition strategies. Further work on climax communities indicates that different niche building activities occur in different groupings of plants. These activities result in different soil-landscape patterns indicative of inter-community competition (Verboom and Pate, 2003, Plant and Soil 248: 321-333).

In pursuing this topic, we have been fortunate to engage the talents of John Pate. We have also received valuable information, advice and criticism from Ravi Anand, Mehrooz Aspandiar, John Beard, Rob Fitzpatrick, Philip Hinsinger, Marty McFarlane, and Neil McKenzie.

This presentation is divided into six parts:

1. Interesting relationships between plants and habitat soil.
2. Banksia strategies in relation to the limiting nutrient P- the generation of a nutrient-limited system.
3. Questions arising from the collapse of a Banksia ecosystem, persistence of ‘old’ intact lateritic podzol, and apatite mining by microbes.
5. Are there other examples of niche construction by plants and microbes?
6. How the niche construction hypothesis aids interpretation of Western Australian paleosols
Part 1. Interesting relationships between certain plants and their habitat soil.

This slide shows a selection of conifer, cycad and banksia cones.

Conifers and Cycads are progenitors of the Banksias, which themselves provide some of the earliest fossil examples of flowering plants. Banksias are a genus in the Proteaceae family. This slide highlights the superficial similarities in these plant’s cone-like fruiting bodies, despite very distant relationships between the groups concerned.

We return to the Banksia cone later when we consider aspects of a Banksias survival strategy.
Similarities between the three groups extend underground. Here examples of podzols and laterites from south-west Western Australia are compared with their North American podzol counterparts under conifers. Displayed from left to right:

- a North American podzol under pine with the lowest horizon, (labelled ‘E’), looking suspiciously like a pallid zone
- a W.A. giant podzol under Banksia trees (Note nodulation in upper sesquioxide (Bs) horizon (coloured))
- a W.A. laterite under proteaceous heath
- a pipey N. American podzol, and;
- a pipey W.A. laterite.

If we look closely at structures in the podzols and laterites we see that both have thin iron rinds (placic horizons) and yellow-brown regions cemented by imogolite-type compounds (basi horizons) and both may also have pipey horizons (definitions in Isbell, 1996. Australian Soil Classification. CSIRO Publishing, p 118-119, Collingwood, Australia)

Indeed, early soil scientists in south west Western Australia marvelled at the profusion of laterites, regarded intact laterites as a kind of podzol and classified them that way (See Stace et.al.,1968 ‘A Handbook of Australian Soils’, Rellim Technical Publications: Glenside, South Australia). Hingston even investigated the role of litter leachate in segregating iron in soil, suggesting that low molecular weight carboxylates might be involved to limited extent (Hingston, 1963, A.J.Soil Res. 1:63-73. At the time he was not aware that liberal quantities of such compounds were exuded by the roots of some of the species he examined.

Botanists in WA also marvelled at the diversity of Proteaceae. There is nothing like it anywhere else, with some 700 species present.
Podzols and laterites also have remarkably similar chemistries.

Both have ‘Bs’ horizons that generally (but not always) pass the reactive Al test. (See Fieldes M and Perrott K W 1966 Rapid field and laboratory test for allophane. New Zealand Journal of Science 9, 623-629 and Isbell R F 1996 The Australian Soil Classification. CSIRO Publishing, p, Collingwood, Australia.

Both have other chelatable metals like U, Th, V, Mo and Ga co-concentrating with Fe and or Al (See: The chemistry and mineralogy of lateritic soils in the south west of Western Australia by Turton et al.,1962, CSIRO Australian Division of Soils, Soil Publication No. 20,CSIRO: Australia). We also get co-concentration of Phosphorous, which is strongly bound and intractable to plants not adapted to these soil conditions (see Pate et al., Australian Journal of Botany. 49: 529-560). The extra peak of total P at the surface relates to the litter layer.

Resistate minerals drop off markedly in top soil where low molecular weight carboxylates [LMC’s] concentrate. Th and U released during the dissolution of these minerals turn up in association with P and ferricretes. Interestingly, concentrations and distributions of U and Th in podzols developed on granites in North America ( see Morton et al. J. Environ. Qual. 31: 155-162) are almost identical to those encountered down lateritic profiles on the granites of the south west of WA. Literature from Europe (see Melkerud (2000) Geoderma 94: 125-148) shows that the same is true for P distribution in Podzols over there. For new insights into podzolisation chemistry and aspects of laterite chemistry see Farmer et al. (1984) Journal of Soil Science 35, 333-340; Farmer V C and Lumsden D G 2001 Euro. J. Soil Sci. 52, 177-188 and Verboom and Pate (2003) Plant and Soil 248: 321-333. Gamma-ray emissions from U and Th in ferricretes can be used to map intractable P. We return to this later in slide 10.
Interesting relationships between plants and soil on pleistocene deposits in Western Australia

Part 2. Banksia strategies in relation to the limiting nutrient P- the generation of a nutrient-limiting system

Let's examine habitat soil under certain tree banksias and focus on the key limiting nutrient, P. We start with banksia cone and work downwards. I do this to put you in a biological frame of mind.

*Banksia* species such as *grandis*, *prionotes* and *attenuata* are direct seeders. Their large seeds are loaded with nutrients including phytate, a molecule packed with P. Robust cones protect the seeds from seed eaters and fire, and the cones only release the seeds following fire.

The seeds fall on a hostile A horizon crammed with cluster roots. A combination of hydraulic lift (transfer of water by roots from deep soil layers to A1 horizon) and targeted cluster root development directs the secretion of Low Molecular weight Carboxylates (LMCs) to where they are most needed, ensuring that P is mopped up even during leaf fall in the dry summer. Indeed if one looks closely one finds little rotted organic matter in the A horizon.

These cut throat conditions at the surface disadvantage many plants, but the banksia seedling has the reserves to push roots downwards. Below the bleached cluster root zone one commonly finds a high chroma yellow sand (which Schwertmann attributes to precipitation of goethite via an organic route). Below that, one encounters the Bs, where substantial quantities of P are strongly bound to Fe and Al, particularly near the top of this layer on thin ferric (placic) surfaces. This uppermost portion of the Bs has irregular, rough faced, ‘ferric’ nodules infested with cluster roots. In this horizon, root proliferation and competition for P is nothing like that encountered in the A horizon. It is likely that a banksia seedling gaining access to this layer now has the nutrient resources to push on towards adulthood.

Although banksias like *grandis*, *prionotes* and *attenuata* function very similarly, their survival strategies in respect of fire, growth rate, root placement and seed production vary appreciably.

At this stage it's interesting to step back and look at some related observations and studies across a range of disciplines.

- Cluster roots also proliferate in the ‘Bs’ (ferricrete layers) of laterites particularly in the P ‘rich’ pisolith layers (See Pate *et al.*, *Australian Journal of Botany*. 49: 529-560).

- Lab studies by Lambers *et al.* (*Plant and Soil* 238: 111–122) show that B. Grandis only produces cluster roots when P is in intractable form as in the Bs.

- LMC’s are metabolisable by many microbes but there is little knowledge of what goes on although there are some hints (See Jones *et al.* (2003) *Plant and Soil*, 248: 31-41 and slide 9 in Part 4).
Part 3. Questions arising from the collapse of a Banksia ecosystem, survival of ‘old’ intact lateritic podzols, and apatite mining by microbes.

Studies by Thompson and others in Queensland (see Walker et al. (1982), *Forest Succession: Concepts and application* pp 105-131, Springer-Verlag: New York) suggest that a collapse of Banksia ecosystems on giant podzols, similar to the Western Australian example pictured above, occurs when access to P and other nutrients in the Bs is lost as the Bs migrates downwards over time.
Laterite profile under Kwongan heath on crest overlying crystalline basement of the WA wheatbelt

This phenomena of a lowering Bs and run down of P is fine in dynamic coastal environments where ecosystems can move on to new dune systems with fresh sources of P.

However, WA wheatbelt ecosystems on ‘old’ laterites appear to be stable over very long periods of time as:

• They have intact A, E and Bs (ferricrete) horizons which accurately follow the rhizosphere of the native proteaceous heaths.
• These layers sit atop deep depleted pallid zones (see above photograph).
• The fossil record, continental drift in relation to shifting climatic belts, the degree of speciation amongst the Proteaceae, and depth of pallid weathering suggests prolonged ‘stability’ in climate and ecosystem development.

How do they sustain themselves with regard to nutrients given that:

• There is no evidence for P ever having been blown into South-western WA yet P can be as high as 1300ppm on the coats of pisolith (Beadle NCW (1962). Aust. J. Agric. Res. 13, 434-442).
• Surface wash and other kinds of leakage are likely to run down near-surface P reserves.

It is reasonable to suppose that natural selection has produced nutrient-limited ecosystems that sustain themselves. P equilibrium may result from the mining and uplift of P involving deep rooting or microbial components of the ecosystem. Evidence for such a dynamic includes the gradual deepening of the pallid zone across a relatively sharp front, enclaves of pallid weathering below ferricrete (see Anand and Smith (1993) Kalgoorlie Conference. AGSO Record, 1993/54, pp. 187-193) and evidence of apatite mining, from underlying rock, by microbes (see Banfield, J.F. and Eggleton, R.A (1989) Clays and Clay Minerals, 37, 113-127.)
We also suggest that activity directed at sustenance of the ecosystem includes construction of protective ‘earth works’ to counter rejuvenation (the enemy of communities generating nutrient-limiting conditions). We believe that such activity results in the above kinds of mesa and is carried out by microbes, fuelled by their associated vegetation. (see Pate et al, Australian Journal of Botany. 49: 529-560 and Verboom and Galloway (2000) In: Proceedings of the Australian Society of Soil Science Inc. (WA Branch). Soils 2000 Conference. Pp 24-35, Muresk Institute of Agriculture, Western Australia).

So far, we have drawn together pieces of evidence that others might consider highly speculative, but if we are talking about development and evolution of ecosystems we must find signs of this wherever we look. At the scale of individual microbes and plants, at plant community/ ecosystem scales, in the distribution of plants and soil across Australia and the world, and in the geological record.

Let's first look at microbial scales, bearing in mind that many Proteaceae secrete extraordinary amounts of readily metabolisable LMCs. It is reasonable to suppose that these food sources are likely to support microbial communities, some of which will be symbiotic.

Tantalizing evidence for this comes from studies of a bacterium (isolated in northern UK, podzol area?) which consumes citrate-metal complexes, precipitating the metals and releasing inorganic P to its surface. The enzyme system involved is stimulated by citrate (see Yong P, Macaskie LE (1995) Bulletin of Environmental Contamination and Toxicology, 54, 892-899. Yong P, Macaskie LE (1997) Biotechnology Letters 19, 251-255. and related papers).

It is also interesting to note that types of microbial community in European Podzols appear to be most faithful to soil horizons, with bacteria dominating in the Bs layer (Fritze, et. al. European Journal of Soil Science, 51, 565-573).

Each string of spheres in the above electron-micrograph represents one coat of goethite on a Western Australian pisolith. It reveals structures resembling communities of bacteria. Are these pseudomorphs betraying microbial accumulation of Fe?
What about lateral patterns of soil at the scale of plant communities? In the ‘chemistry profile of a Laterite’ slide we saw circumstances in which Th and U could be used to map intractable P. High resolution radiometric images of the Elashgin catchment, in the wheatbelt of Western Australia, reveal many patterns that are easily understood with current knowledge. For instance, fans (labelled F on slide) from granitic terrain (labelled G) show well known axial and radial structures. Sandy (dark red) dendritic flow structures in valleys contrast with areas of stagnation and clay and salt accumulation (pale colours in valley).

But what about the strange black and bluey greens structures on the uplands that appear to be largely independent of topography and why the sharp transition from black to bluey green signalling. This result is contrary to our concept of the catena. In fact these structures can be seen in air photographs and were used to map lateritic sandplain during this survey.
Aligning air photographs with radiometric imagery allows us to inspect the broader spatial patterns of soil and vegetation and we find that these structures commonly align with native vegetation communities. This particular slide shows the distribution of tall Grevillea shrubs versus mixed communities of tammar scrub, Eucalypts and proteaceous heath. The distribution of their habitat soil is revealed by the radiometric image. One can see rapid change in soil properties at ecotones, the transitional area between the two adjacent ecological communities.
Windowing out from the previous radiometric view we see spiral wave (circular) patterns. As seen in slide 10, these structures seem to resist perturbation by the physical environment, in this case topography. Some ecologists believe that this behaviour betrays intercommunity competition. (See Rohani P, Lewis T J, Grunbaum D and Ruxton G D (1997) Trends in Ecology and Evolution 12, 70-74).

Compare these vegetation/soil patterns, each with different rhizobial associations, with patterns generated by competing microbial populations in the following slide.
How competing species organise themselves in space

Simulation (a) absence of perturbations
(b) presence of perturbations

Microbes in a Petrie dish exhibiting self organisation in spiral wave forms

The left image on this slide shows simulations of spatial distribution of competing populations without (a) and with (b) stochastic influences. The right image shows actual aggregation of cellular slime moulds exhibiting self organisation of spiral waves. (See Rohani P, Lewis T J, Grunbaum D and Ruxton G D (1997) Trends in Ecology and Evolution 12, 70-74).
He showed that ‘low’ soil P across the continent corresponded with increasing scleromorphy in native vegetation, a characteristic now considered indicative of adaptation to low nutrient environments (see Hill 1998 *Australian Systematic Botany*. 11, 391-400.

Beadle and others suggested that sclerophyll vegetation evolved and radiated from the rainforest populations in the east. He also saw that the ability to cope with intractable P gave the plants concerned a great advantage, a fact that early agriculturalists found to their cost.

Proteaceae are largely sclerophyllous and have probably radiated from the rainforests of Eastern Australia where we find many genera but few species. Conversely in the south west of Western Australia there is an abundance of species (700+) but few genera.

But do these trends really reflect radiation away from a rainforest situation and necessary adaptation to an existing P gradient (supposedly generated by humid tropical weathering during the Cretaceous and Tertiary) or an underlying causal relationship?
There is a remarkable coincidence between the global distribution of laterites and the cluster root bearing Proteaceae- for a full discussion see Pate et al, A.J. of Bot. 49: 529-560. We also point out that proliferation of Proteaceae and laterite both peak in the south-west of WA.

**In summary**, this section points to lines of evidence, from soil and biological studies conducted over a range of spatial and temporal scales, that is generally supportive of a causative association between certain plants and microbes and their habitat soil.
Belka Drains WA exposing Pedogenetic ferricretes wedging into pedogenetic carbonates.
A wakeup call?

5. Are there other examples of niche construction by plants and microbes?

This photograph shows sharp soil changes across an ecotone in the wheatbelt. The left of picture shows laterite with an acidic ferricrete layer, wedging out laterally over less than a metre to an alkaline duplex with a nodular carbonate/silcrete layer - right of picture. Both soils are formed in young alluvium on the same geomorphic surface. Iron is more differentiated in the laterite than in the duplex (compare pale colouration above ferricrete to redder colours above carbonate). The vegetation, which is now cleared, would have been proteaceous heath on the left and salmon gums on right (see next slide). It is difficult to explain the proximity of such radical chemical and physical differences using theories based on inorganic chemistry.

If one instead considers both of these segregations from a biological viewpoint, one recognises that P is strongly bound to both ferricrete and silcrete/calcrete, both are of a concretionary nature - indicative of episodic formation of new coats. Both profiles also have very different water flow regimes (for more on why this should be so interesting see slide 21).

Many chemical factors influence the solubility of metal complexes involved in P mobilisation, including stability of the complex and the charge of the organic anion verses the charge of the positively charged species being chelated. Where both charges are of the same magnitude, we may well get precipitation. In other words, many LMO’s might not function effectively in high Ca environments, particularly at pH’s above 8.5. There is obviously much to be learned, but the point is that the chemical and physical properties of profiles may be purposefully built by plants, particularly in climax situations with the make up of the profile betraying some of the plants competitive strategies.
This slide shows similarly close association between Salmon gum roots and carbonate concretions. Note that the concretions concentrate as a halo under the bole of the Salmon gum. We also know that the salmon gums generally occur on duplex soils and also channel rain down their stems. Are all these phenomena connected with the plants strategy to command nutrients and water? (see slide 21 for more on segregation of water).
Calcified micro-filaments, needle calcite and micro rods possibly developed from hyphae of ectomycorrhizal fungi


This scanning electron micrograph of calcrete, taken from Anand et al, 1997. Australian Journal of Earth Sciences, 44, pp.87-103, shows calcified micro-filaments, needle calcite and micro rods possibly developed from hyphae of ectomycorrhizal fungi. Such fungi help plants access P and indeed associate with many Eucalypt sp. It is curious that these kinds of carbonates sport pseudomorphs of ecto-mychorrhizal fungi, which are known to associate with many Eucalypt species. The significance of these features should be considered along-side the bacterial pseudomorphs on pisoliths under proteaceae (See slide 9 and discussion of slide 12).
Protecting ones niche by sequestrating P is not the only way to out-compete other plant communities. Other strategies likely to deliver benefits include active water capture and the generation of soil conditions that enhance storage and restrict root access of potential competitors. The examples on this slide serve to illustrate such concepts.

Photo a shows mallet eucalypts on sodic duplex soil, on the flank of a lateritic scarp, its typical habitat. Up-slope contribution to surface water is negligible and the soil surface is invariably hydrophobic. Note the lack of tree diversity and absence of understorey. The suspicion is that habit of umbrella canopies with ascending branches collect rain and channel it down stems. Observations made during a rain storm showed that rain channelling down the stem of a silver mallet was rapidly adsorbed by the bark with little water reaching the base of the tree. The bark itself was sodden and sticky and rapidly dried. Interestingly, tannins act as thinners and dispersants increasing a fluids “pumpability”. From a competitive stand point, its reasonable to suppose that traits such as these are most effective in combination with soil conditions that deny water to other plants ie. hydrophobic surfaces and sodic B horizons.

Soil under wodjil acacia’s, shown in photo b, are surprisingly acid. Acidity and exchangeable Aluminium in the subsoil limits subsoil rooting and water uptake by many plants, including crops, and is difficult to ameliorate. But the wodjils thrive in these conditions. Again, are these soil conditions engineered for competitive purposes?

Photograph c shows a stand of morrel near Lake Toolibin. Similar stands with a salt bush understorey can be found on salt-affected dolerite soil on high country. It is difficult to explain the level of accumulation of carbonate and sodium chloride in water-shedding landscape positions. Some salt bush species do concentrate salts, so one might speculate that morrel has water-capturing mechanisms akin to mallet and mallee. If this is so, it may be that salts are actively concentrated at the surface for competitive reasons.
6. How the niche construction hypothesis aids interpretation of WA Paleosols

Let’s start with some general principals.

Paleosols are recognised by horizons, root channels and other structures only found in soil. The nature and arrangement of root traces and soil horizons and soil features betrays original vegetation and its habitat soil. High up in the landscape, soil profiles tend to represent the integrated effect of past and present soil forming conditions. Overprinting of older horizons remaining close to the surface is common in these localities.

The slide above, shows a feature encountered in the face of a gravel pit south of Wickepin. It is interpreted as a termitaria that ferruginised after burial because a ‘living’ termite mound, with an aerial component and identical chambers, was found upslope of this site. Like the living mound, the buried structure has no gravel in the mound material, despite it being buried in colluvial gravel. Ferric rinds coat the structures exterior surface as well as the root channels that invaded its interior. Since no such coating occurs on and in the living mound, its reasonable to suppose that such overprinting happened after burial and colonization by proteaceous communities. Indeed, remnants of these communities are still present at this locality.
Lower down in the landscape episodic burial results in soil sequences reflecting soil forming conditions operative over a narrower window in time.

This profile records at least two cycles of soil differentiation involving movement of iron and clay with the most recent (uppermost) episode apparently contemporaneous. The sandy A horizons appear intact and remain so 50m down slope in two other exposures. All these profiles have similar sequences:- Red crystalline ferric oxides, principally haematite, can be seen along the margins of vertical root channels in horizon 1B, with their older counterparts, which are yellow, hydrated and possibly depleted in P and Fe, in the buried 2B. So, contemporary root channel precipitation appears limited to uppermost B-horizon, and indeed, we have observed ferric precipitates surrounding living Banksia spherocarpa roots.
The next two slides show multiple soil formations in the northern wheatbelt.

This view of the face of an upland gravel pit reveals two formations.

The top formation consists of weakly cemented ferricretes developed in a high chroma yellow loamy sand matrix. This site was under *A. campestris* and the features described are typical for this kind of vegetation (includes *A. acutivalvis* communities). The second lower formation sports pale ferricretes over reticulite and pallid zone. Ferricretes in this layer appear to be depleted and Fe and possibly P may have been uplifted by the extant *A. campestris* communities.
VERMIFORM LATERITE

1m

High chroma yellow sandy earth

Pisolith layer

Sodic B Over printed

CaCO₃ and silcrete

Ferricrete with overlying pisoliths over printed by Silcrete

Reticulite

Pallid Zone

1A₁

1B

1B₁, 2A₂

2B₁

2B₁, 2A₂

3A₂

3B₁

3B₁, 3B₃

C

Present day soil: originally under ‘grevillea’ or wodjil scrub

Old duplex, originally under eucalypts?

Oldest lateritic profile with ferricrete fining towards surface. This morphology is common under present day heath soils. Subsequently overprinted with Si coming either from above or rising with ground water.

This soil sequence is sited on a lower slope in the Northern wheatbelt. Our simplest interpretation of these formations involves 3 major pedogenetic events, designated on the slide. It is possible that the precise climatic/vegetation changes responsible for this particular succession may be resolved with a closer inspection of the chemistry and morphology of the cretes and morphology of root traces.
Most of our work has focused on laterite landscapes and the nutrient P, but as indicated earlier, pioneering farmers also experienced major problems with micro nutrients (which are also found in ferricretes out of reach of most crops) and modern day farmers continue to be affected by salinity, poor subsoil structure and high acidity and Al. If these and other ‘adverse’ soil conditions have been purposefully generated by native plants and microbes, it is important that environmental engineers understand the underlying mechanisms. We don’t claim to have all the answers but we do believe that we are asking the right questions. We also believe that Australian landscapes have been misunderstood by many and that the science of pedology will mature when Darwinian principals are applied to its understanding.

As a final remark, it is interesting to relate what is said above to the perennial problem of soil classification. There are an astonishing number of soil classification systems ranging from global to national to provincial, which may have arisen because people haven't understood the nature of the beast. Bill Purvis (Bill V’s mentor in Africa) encouraged the division of soils into natural units without regard to these systems. We believe that there truly are ‘species’ of regolith that grade with their biotic components from place to place across the world. No wonder then that Australia has adopted its own system of soil classification, WA has constructed its own and we, here in the WA wheatbelt, have been disregarding the lot.