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Native vegetation in Western Australia is actively involved in soil formation

Native vegetation in Western Australia is actively involved in soil formation

By Doug Sawkins[1], William H Verboom[1,2], and John S Pate[2]

[1.] Western Australian Department of Agriculture and Food, Western Australia (Narrogin Office)

[2.] University of Western Australia, Perth

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Introduction

Many adverse situations in Western Australian agriculture have arisen because in the past we cleared native perennial vegetation below safe ecological limits in order to grow annual crops and pasture. In retrospect, we did not fully understand the functioning of the native ecosystems concerned and thus did not foresee the long-term consequences.

Research into the survival techniques of native species provides important lessons for future farming. By understanding the behaviour of plants and soils we can maximise their use in a sustainable way.

Knowledge of the water acquisition and storage strategies of native plants in seasonally dry areas may be critically important to reducing the impact of farming practices on land degradation and associated threats to biodiversity.

Longer term applications of the research described in this bulletin may be the development of agricultural systems more in tune with native soils, leading to improvements in water-use efficiency, reduced recharge and salinity, and more economic and sustainable agriculture.

Research has demonstrated that soil and landscape formation in Western Australia has been largely driven by the recently advanced ‘phytotarium concept’ (Verboom & Pate 2006a). We define this concept as the system whereby major plant species and their microbial associates bioengineer the soil profiles in which they occur to their own advantage so that they can monopolise water and nutrients. This not only supports their own survival but also determines the direction of ecosystem evolution in their particular geographical and climatic region.

The concept of a biological (or organic) basis of soil formation is not new (Buol et al. 1980; Jenny 1941) but it has languished in the wake of theories of inorganic soil formation put forward in the latter half of the 20th century. We outline the major differences in Table 1.

Table 1 **Comparison between inorganic theories of soil formation and the phytotarium concept**

Inorganic theories	Phytotarium (organic) concept
Laterites are either the end product of humid tropical weathering of rocks and/or the consequence of alternating oxidation and reduction processes.	Certain plants and associated microbes mine iron and other elements and precipitate them in the B horizon where they continue to be reworked during phosphorus cycling.
Erosion of laterites has exposed underlying layers, thereby creating regular down-slope sequences (or catenas) of soils, any one of which would eventually become colonised by a specific group of plant communities best adapted to that particular soil setting.	While this may be true in general, many complex patterns appear to be insensitive to topography and may have been driven by purely biotic forces.
The build-up of salts has caused physical movement of clay downward through the soil, forming duplex soils.	Evidence of microbial involvement in clay formation is clear. See the origins of the B horizon clay in Table 2.

Table 2 summarises major features of soil formation that have not been adequately explained by inorganic theories but that are consistent with the phytotarium concept.

Table 2 **Major soil formation features with corresponding phytotarium concept explanation**

Soil formation feature	Explanation	Page
Sudden emergence of new clay minerals and soil types in the evolutionary record	The emergence and increasing production of clays such as kaolinites and montmorillonites mirrors the emergence and evolution of plant life on land, their increasingly complex forms and interactive associations with other biota and the earth's mantle. See Verboom & Pate 2011 (in preparation).	3
Close relationship between plant and soil geography—often restricted to particular regions of the world	Plants construct particular soil types to support their survival strategy.	4,11
Gradation from one soil type to another across the same land surface and over the same parent material	Competing vegetation communities deliberately construct contrasting phytotaria (soil types) to support their survival strategy.	14, 16
Examples from WA include gradations between any of the following soil types: sodic duplexes, calcareous soils, laterites and podzols (soils with iron and aluminium concentration but without hard gravels or ironstone)		
Soils transgress each other by 'overprinting' (newer soil creates differing characteristics over older soils)	Invading communities overprint phytotaria of previous communities.	16
Chemical reactions (particularly in the A and B soil horizons) don't conform to simple inorganic reactions	Biotically mediated chemical reactions can be exceedingly complex.	6
Concentration of chelatable elements such as thorium in newly formed clays and ferricretes	Concentration can be explained by biologically sponsored organic acid secretions and transport.	8
Origin of clays in many texture contrast soils including podzols	Plants can mine, transport and precipitate metallic elements such as iron and alumnium in chelated form. Microbial life feeds on secreted metal-chelate complexes and control how metals precipitate out (as a specific type of clay, oxide coating or crete).	8, 14,20
Remarkably uniform A and B horizons in soils across entire landscapes despite millennia of erosion and deposition	Plants and microbes continually repair the phytotaria.	6
Relationship between vegetation, A and B horizons and pH of underlying groundwater	Element pumping by plants causes vertical segregation of (for example) basic cations from lower acid groundwater.	22
Presence of podzols and texture contrast soils around the boles of individual trees	Podzols and texture contrast soil types form in the rooting catchment of these woody species.	20

This bulletin shows how new insights into biological functions of woody plants and their associated microorganisms provide a viable alternative to entrenched inorganic theories.

We explain how plants have actively shaped our soil and landscapes, and discuss the implications for modern agriculture and resource management.

A fuller description of the concepts and evidence advanced in this bulletin can be found in the papers cited in the references.

Soil formation over geological time

There is ample evidence that increasingly complex forms and interactive associations of life have affected atmospheric, oceanic and terrestrial conditions throughout geological time and have in turn shaped soil-forming processes (Verboom and Pate in press).

The biological manipulation of geological elements such as iron (Fe) in soil was already on stage two billion years ago when the earth was in an intermediate stage between an anoxic atmosphere (without oxygen) and an oxic atmosphere (with oxygen).

Apparent increases in atmospheric oxygen, weathering and clay production accelerated alongside the proliferation of life on land from about 800 million years ago.

Fuelling of such processes would have been implemented by photosynthate—the energy-rich organic molecules produced during photosynthesis—from the ever-burgeoning plant biomass.

At the same time major shifts took place in clay mineralogy from mildly weathered micas and broken down feldspars to active 2:1 and 1:1 kaolinitic clays formed in soils. These increases in clay production, particularly those relating to the active 2:1 types, may have contributed to massive sequestration of organic carbon in marine sediments leading to declining levels of atmospheric carbon dioxide (CO2).

A close, supposedly causative, association occurred in the Cretaceous era (150 million years ago) between lateritic bauxite production and the radiation of certain cluster root-bearing plants.

This was followed 100 million years later by the widespread establishment of grassland ecosystems and their associated Mollisols—soils characterised by a thick dark fertile surface A horizon.

If we examine long-term changes in global climate, rates of laterite formation and plant evolution we find an exceptionally strong relationship between rates of formation of the so-called tropical laterites and the evolution of specific groups of flowering plants (angiosperms), particularly Proteaceae. Conversely, the relationship between hot humid weathering and rates of laterite production is weak, particularly in Western Australia.

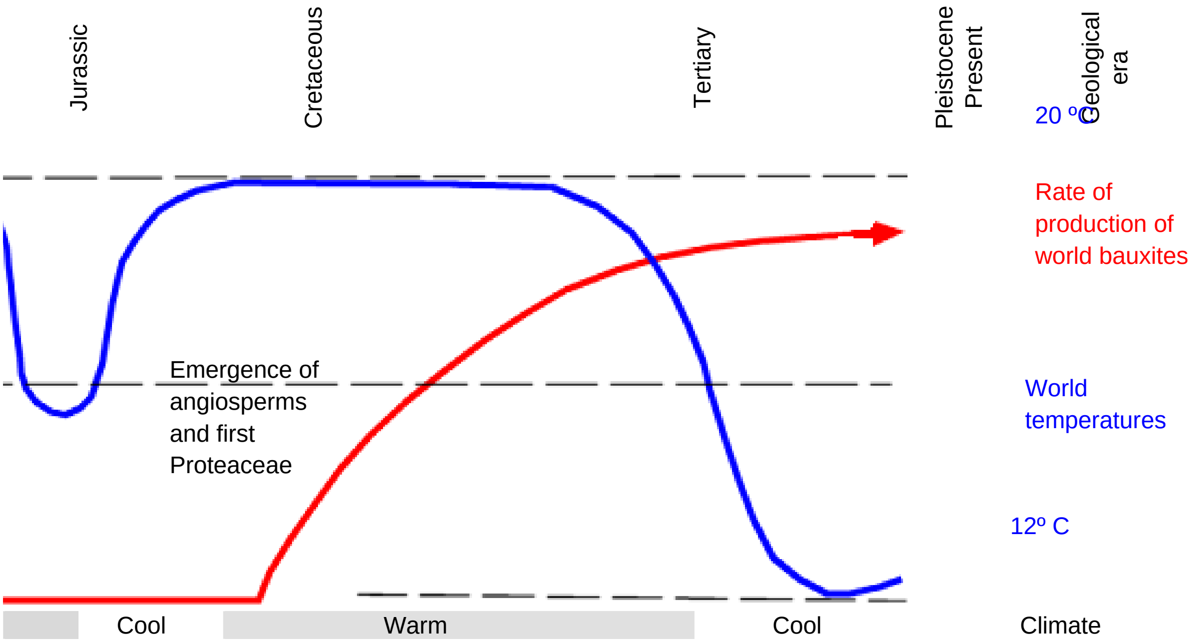


Figure 1 **Global climate and laterite formation**

Despite world temperatures being higher in the Early Tertiary period, the climate in the south-west of the continent at that time was considered to be warm temperate. Since then Australia has drifted northwards as global temperatures cooled and so the south-west has remained more or less within the same climatic belt for eons. Incidentally, laterites are also encountered in Tasmania, which, over the same time span, enjoyed cool temperate conditions.

Competition for nutrients

There are remarkable coincidences between the global distribution of laterites (Figure 2) and that of cluster-root bearing Proteaceae (Figure 3), with proliferation of this family and formation of laterite achieving greatest prominence in south-west Western Australia.

The morphology of tropical laterites varies across the world, and at regional scales. Examples of tropical laterites in south-west Western Australia include the jarrah pea gravels, the tamma gravels of the yellow sand plain and the pale sandy gravels of what used to be called lateritic podzols.

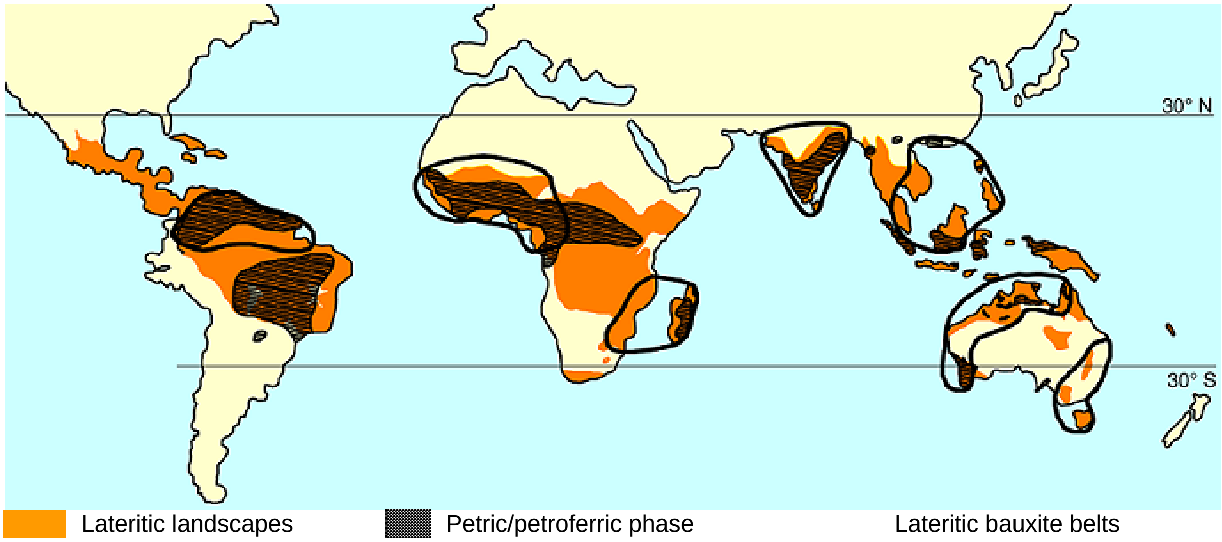


Figure 2 **Worldwide distribution of laterite landscapes (Bardossey 1983)**

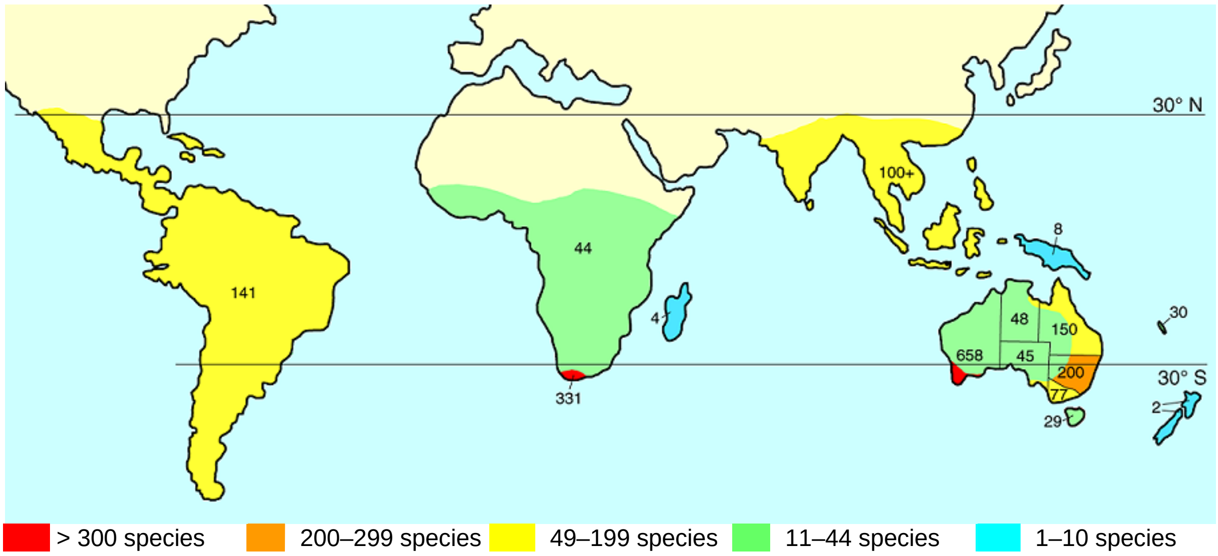
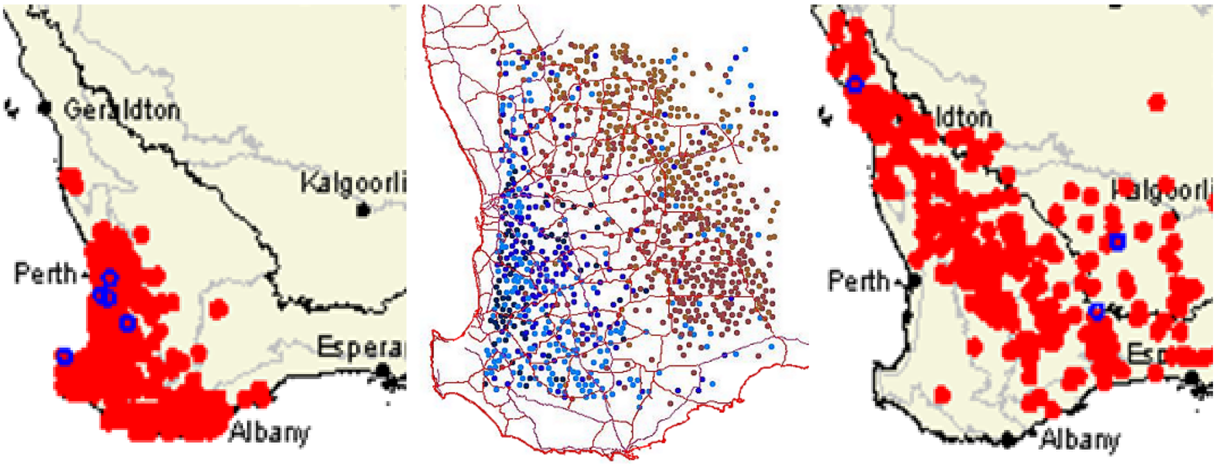


Figure 3 **Worldwide distribution of Proteaceae (Gidagasu 1976)**

Figure 4 provides an example of the relationship between plant communities and chemical composition of lateritic gravels.

The coloured dots in the central image indicate the location of populations of lateritic pisoliths (gravels) with differing chemical composition (Griffin & Verboom unpublished). The blue dots, which denote gravels high in both Fe and aluminium (Al), are coincident with jarrah forest. The brown dots, which denote gravels low in Fe and Al but high in silicon (Si), correspond with areas vegetated by wodjil/tamma plant communities. One might argue that such effects are simply a consequence of physico-chemical processes influenced by existing rainfall gradients, but this would not fit with tropical weathering theories and certainly ignores the spatial clustering of the data.

The alternative biologically based explanation is that dissimilar gravel types arise from differences in biomineralisation under the very different species of plants responsible for their formation—the phytotarium concept.



Jarrah Laterite types Tamma

Figure 4 **Florabase maps of jarrah (*Eucalyptus marginata),* left, and tamma (*Allocasuarina campestri),* right. The distribution of chemical types of laterite is designated brown or blue (centre).**

Scientists are puzzled by how certain communities of plants unusually rich in species can grow and survive in Australian soils which are so inordinately deficient in phosphorus (P) and other nutrients, especially in situations where lateritised layers sit atop deep depleted pallid zones (Figure 5).

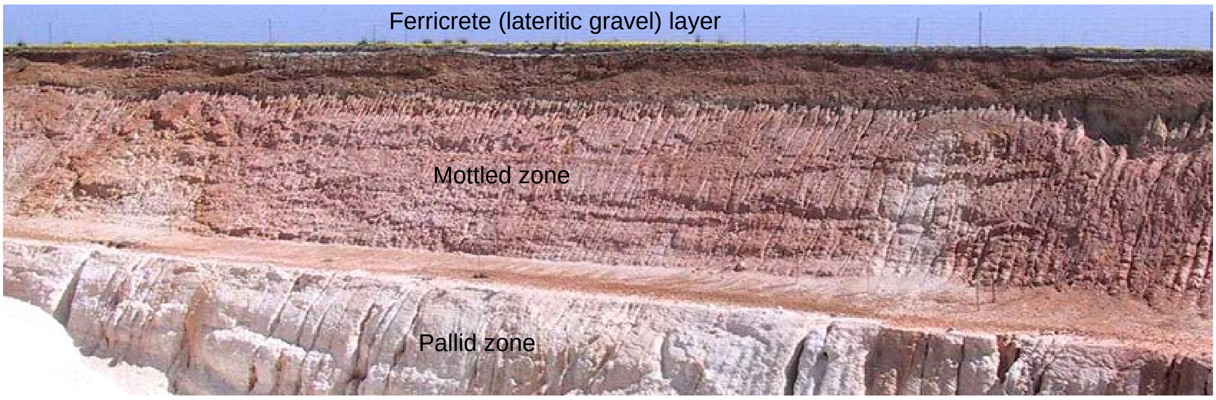


Figure 5 **Open pit exposure of a laterite on gently undulating uplands in the north-east of Lake Toolibin, Western Australia. Much of the profile has residual features of the granitic basement in which it has developed.**

Such laterites have always been regarded as being very old and weathered, yet in Western Australia they often have intact A, E (eluviated or leached) and Bs (Fe and Al sesquioxide enriched) horizons which accurately demarcate the rooting zones of existing native species.

Given the relatively rapid rates of surface stripping, the A, E and Bs horizons should not have remained intact. It is hard to interpret such phenomena without invoking the formative activity of plants and microorganisms.

Even more puzzling is the fact that in a profile uniformly deficient in P, where total mean element content ranges from 5 ppm to 30 ppm, the P element can be many fold higher (Pate et al. 2001) on the coats of gravel stones (Beadle 1962). As far as we can gather, this reserve of P seems to remain inviolate in situations where the parent profile is being depleted of P by surface wash and various forms of leaching. Figure 6 shows the chemistry of a laterific profile.

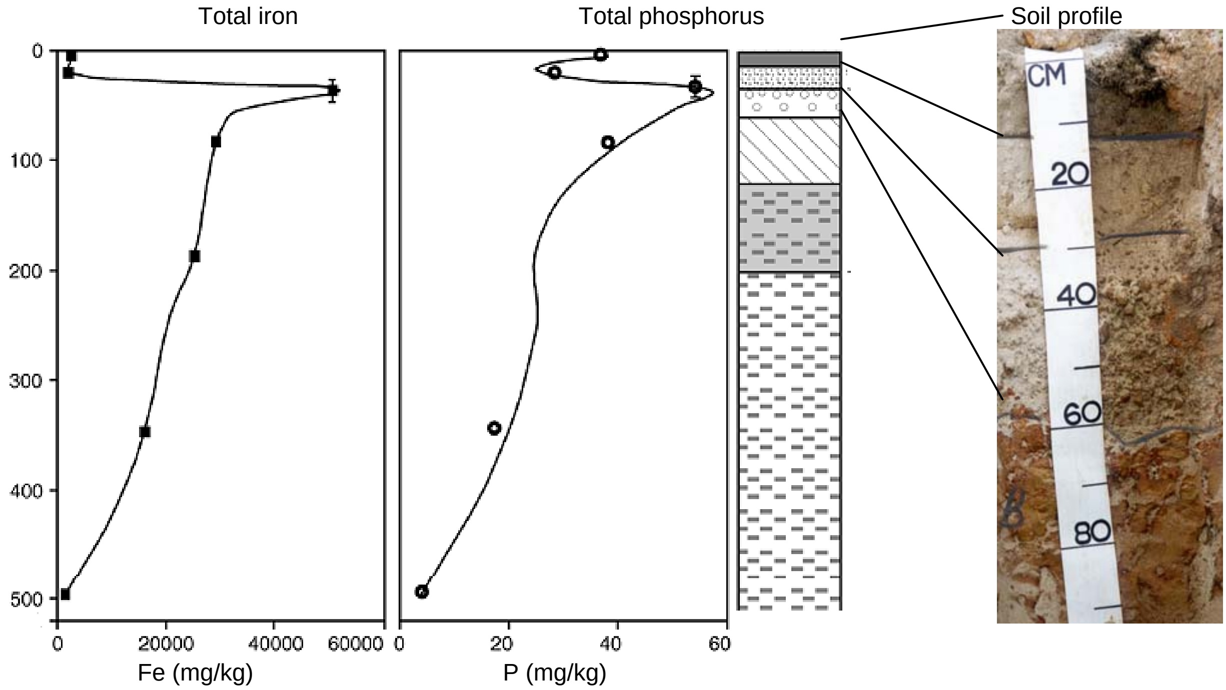


Figure 6. **Profile distribution of iron and phosphorus together with a close-up view of the upper 80 cm of the same lateritic profile (Verboom & Galloway 2001)**

The remarkable similarities between the laterites of south-west Western Australia and other infertile systems in Australia and elsewhere suggest that such resemblances may reflect common formation processes.

Examples include laterites under proteaceous heath and the large (sometimes giant) podzols under tree banksias in Australia, kauri trees in New Zealand and podzolic counterparts under conifers in North America.

Consistent with the above, early pedologists in south-west Western Australia marvelled at the profusion of laterites and classified them as a form of podzol. Pedologists have seen many cases where laterites and podzols co-occur on the same land surface in tropical and temperate regions and some mineralogists have suggested that closely similar forces may be shaping formation of laterites and podzols across the globe.

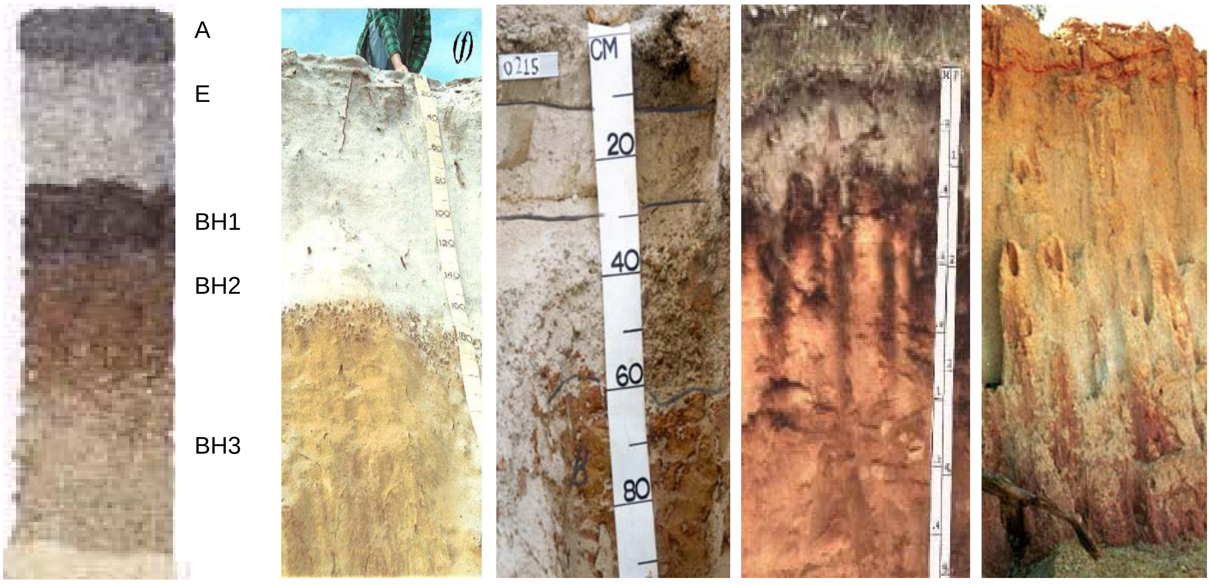
As seen in the profiles of Figure 7 both podzol and laterite commonly exhibit depleted sandy A and E horizons overlying a lower horizon where chemically reactive precipitates of Fe and Al accumulate, in what is termed a Bs (sesquioxide enriched) horizon.

Like laterites there is also co-concentration of P in Bs horizons of podzols with P strongly bound to the hydroxylated surfaces of Fe and A.

Pate et al. 2001 have described how laterites might be developed by proteaceous plants through the agency of their cluster roots and suggested that communities of such plants would show a competitive advantage in the acquisition of soil P in infertile soils.

These P resources are essentially unavailable to plants not adapted to such grossly impoverished conditions, thus generally giving cluster-root bearing species a competitive advantage in accessing and sequestering their own resource of P.

Casuarinaceae (tammas and sheoaks) also have cluster roots.



Podzol under conifer

Podzol under Proteaceae

Laterite under Proteaceae

Pipey podzol under conifer

Pipey laterite under Proteaceae

Figure 7 **Examples of podzols and laterites under Proteaceae in south-west Western Australia and their North American podzol counterparts under conifers**

Australian chemist Hingston (1963) was among the first to implicate plants in soil-forming processes when investigating a possible role of litter leachates in segregating Fe in soil and concluded that LMCs (low molecular weight carboxylates) were likely to have only limited involvement in the process.

Unfortunately, he was not aware, at the time, that liberal quantities of such compounds (for example citrate and malate) were exuded by the cluster roots of some of the species he was examining.

Thorium (Th) and uranium (U) are particularly interesting markers of soil formation for three reasons.

- Both elements have very different red-ox chemistries but very similar chelation chemistries
- Both co-concentrate with neo-formed clays and ferricretes in subsoil horizons under conditions of near neutral pH.
- The penetrating nature of the gamma rays produced by their respective daughter elements allows us to map the spatial extent of these precipitated layers even when buried. This provides vital clues about the forces governing the lateral growth of soil types. See ‘Competition for space’, page 14.

The primacy of LMCs in laterite and podzol formation is also indicated by the fact that when in primary mineral form both Th and U are normally highly resistant to inorganic weathering, yet both are seen to decline markedly and specifically in podzolic and lateritic topsoils derived from granite, and specifically wherever organic acids such as citrate are being exuded by roots.

The fact that distributions of Th and U in podsols developed on granites under pines in North America and Asia closely resemble those encountered in lateritic and podsolic profiles on granites of south-west Western Australia also suggests a common mechanism of formation centred on plant production of LMCs.

There is now solid evidence from study of the transport systems in plants and composition of plant root secretions that LMCs are indeed vital for the solubilisation and transport of metals in both plant and soil environments.The consumption of these organic acid:metal complexes by specifically zoned bacteria and fungi in the soil is pictured as being responsible for precipitation and crystallisation of the ferric and aluminosilicate compounds mentioned above.

Although much still has to be learned about this aspect of soil mineralogy, it is worth noting that:

- Cluster roots proliferate in the Bs and ferricrete layers of laterites particularly in the P-rich gravel layers. Chelated mineral elements are apparently transported and secreted into upper soil layers via hydraulic redistribution phenomena (Verboom & Pate 2009, 2010).
- Laboratory studies by Lambers et al. have shown that *Banksia* trees produce cluster roots only where P is present in intractable form in their rooting zones, for example, when located in the Bs. This may well be a widespread phenomenon.
- Microbial communities appear to be closely confined to specific soil horizons.
- Some LMC-secreting crop plants produce protons and specific anti-bacterial and anti-fungal agents that optimise function while reducing bacteria and fungi degradation of their metal- and P-solubilising agents.

A logical conclusion is that natural selection in south-west Western Australia facilitated the evolution of nutrient-limited ecosystems capable of effectively sustaining themselves while forbidding non-specialised plants.

Each ecosystem perpetuates a tightly controlled P equilibrium through the agency of certain large deep-rooted woody plants that mine, uplift and conserve P via their microbial components. A plethora of understorey species coexist by drawing on, utilising and conserving the primary input of P.

With operation of such a process, the pallid zone becomes deepened across a relatively sharp front, enclaves of pallid weathering develop below ferricrete, and apatite mining by microbes may possibly contribute further inputs of P from underlying rock.

Considerable work has been done on the strategies used by tree banksias to access and control the key limiting nutrient P in deep sands. This provides a good example of a functioning nutrient limiting system. Figure 8 shows the cluster root development of *Banskia prionotes.*

Banksias such as *B. grandis* and B. *attenuata* survive fires while others such as *B. prionotes* succumb. All possess large seeds loaded with nutrients including phytate, a molecule packed with P and other reserves. Robust cones protect the seeds from predation and cones of certain species release their seeds only following fire. The seeds fall on a nutrient-impoverished A horizon already liable to be densely populated with cluster roots.

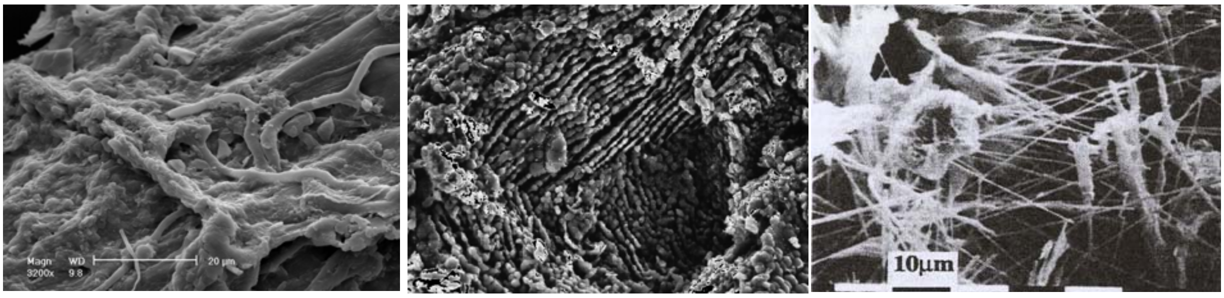
Night-time transfer of water by roots of the already present adult trees, from deep soil layers to upper A1 horizon and out to cluster roots, result in LMCs being secreted into the soil ensuring that organic P is mopped up even following leaf fall in a dry summer season. Such intensive scavenging of nutrients results in little rotted organic matter in the A horizon, so much so that the total carbon sequestered in the soil may actually increase following decomposition of crop residues after clearing for agriculture.

Figure 8 **Targeted cluster root development of *Banksia prionotes***

While intense competition for P at the soil surface may disadvantage seedlings and, small species, *Banksia* seedlings and juveniles possess a sufficiently large reserve of nutrients to extend their roots downwards thereby gaining access to nutrient and groundwater reserves lower down during that critically important summer of growth. The next season they can develop a system of fully functioning cluster roots.

Below the cluster root zone and bleached E horizon, one commonly finds sand coated by a bright yellow form of goethite (an iron mineral) which some researchers have suggested to be formed via a biological route. Below this, one encounters a Bs, in which substantial quantities of P are strongly bound to Fe and Al, particularly near the top of thin ferric-coated surfaces. The uppermost portion of this Bs may have irregular, rough-faced gravels surrounded by cluster roots. While root proliferation and competition for P in this horizon is nowhere as great as that encountered in the A horizon, it may still provide a critically important input to a juvenile *Banksia* tree as it approaches adulthood.

Although we know less about the nutrient-acquiring strategies of eucalypt woodland than those of banksia woodland, it is well known that acquisition of P by many Myrtaceae is mediated by ectomycorrhizal and other kinds of fungi (Figure 9).



Fungal involvement in the synthesis of kaolin in a duplex soil

Bacterial involvement in goethite precipitation in a gravel. Each string of spheres in the latter represents a coat of goethite. Some kinds of fungi (not shown) are also implicated in Fe and other precipitations.

Calcified micro-filaments, needle calcite and micro rods presumably derived from hyphae of ectomycorrhizal fungi associating with mallee eucalypts

Figure 9 **Scanning electron micrographs**

Since P is strongly bound to calcium (Ca) carbonate and citrate metal complexes are destabilised by Ca ions, cluster root-bearing species tend to be absent from alkaline environments yet profuse in those low in Ca and of acidic character.

Competition for water

The ability of a particular plant community to sequester P is not the only means by which it might out-compete other less well-adapted plant communities of the same geographical region. Competition for water may play an equally, if not more, important role and this may be especially the case for survival of vegetation of semi-arid ecosystems.

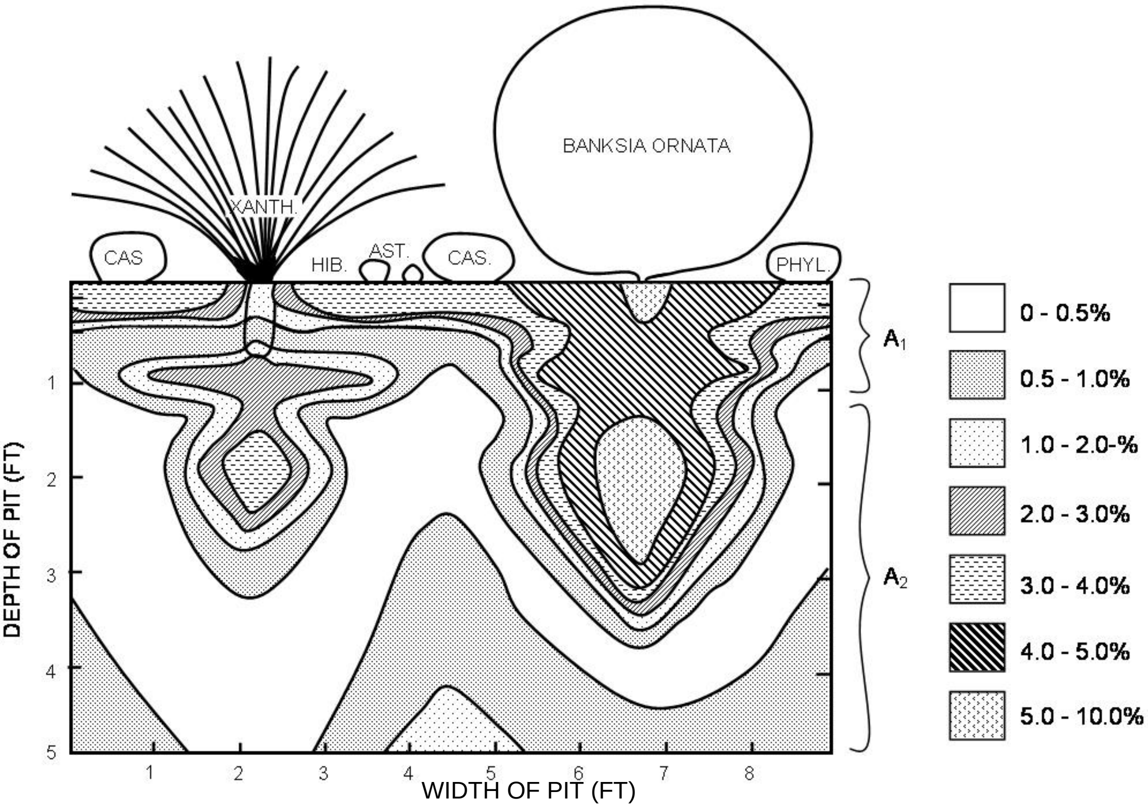


Figure 10 **Wetting profile in south Australian heath**

One well-known strategy of large woody species of semi-arid ecosystems is to capture water with their foliage and direct it down into the soil by channelling it down the stem (stem flow). This phenomenon is known to occur widely in both myrtaceous and proteaceous species and is reflected in the steeply ascending branches and increasing funnel-like canopies of tree species as one moves towards drier ecosystems. These attributes undoubtedly increase the proportion of incident rain available to the plant.

We do not understand fully why heaths are so species diverse in ferricrete (ironstone gravel) situations, what their hydraulic redistributions look like, why the cluster-root habit is so competitive nor what the cause-and-effect relationships involved in such a framework might be.

However, we do know that ferricretes hold substantial amounts of tightly-bound water and that the spectra of organic acids secreted by cluster roots differ between taxa and that the functioning of each species component is strongly influenced by pH and stability constants. With effects of cationic charge also likely to be involved, one can appreciate more fully why Proteaceae flourish in some ecosystems while being virtually excluded from others.

Let us now turn to a number of highly specialised Western Australian plant communities where woody species have been shown to engineer a number of characteristic effects on soil profiles and plant–water relations.

Banksia prionotes **woodland on deep sands overlying a Bs horizon**

This ecosystem has already been discussed in relation to P but there is now evidence that banksia roots also substantially modify the surface properties of soil particles—particularly water repellence—in upper sandy horizons. This leads to infiltration hotspots following rain and associated fingering and funnelling of this water down to the Bs horizon (Verboom & Pate 2006a).

While some of the water directed downwards in this manner is adsorbed some may perch transiently on the deep Bs horizon and thereby act as a source of water well into the dry season.

Brown mallet ***Eucalyptus astringens***

The brown mallet pictured in Figure 11 (left) is typical of loamy soils on the flanks of lateritic scarps. Upslope contribution to surface water is negligible in such situations and the soil surface is invariably water repellent. There is a lack of other tree species and an absence of understorey.

Casual observations during heavy rain show that the umbrella canopies and steeply ascending branches of the mallet are highly effective in collecting rain and channelling it down stems. Furthermore, observations during a rain storm showed that rain channelling down trunks was rapidly absorbed by the bark which became sodden and sticky with frothing tannins, to the extent that very little water actually reached the base of the tree. The bark of the species dries rapidly once dry weather intervenes. Interestingly, tannins are known to act as thinners and dispersants and might therefore aid transfer of water to deep soil layers via vessels within the body of the tree.

Again, from a competitive standpoint, it is reasonable to suppose that traits such as these are most effective in combination with soil conditions that deny water to other plants. In this case the water-repellent soil surfaces typical of mallet are known to be generated by the breakdown products of its own leaves.

Figure 11 **Brown mallet (left) and wodjil heath (right)**

Wodjil acacias

The term wodjil covers a number of stiff-leaved *Acacia* species (Figure 11 right) that are found in the eastern and north-eastern wheatbelt. Wodjil soils are surprisingly acid with high levels of exchangeable hydrogen and exchangeable Al^3 in the subsoil.

These qualities limit subsoil rooting and water uptake by crops following clearing of land. Agriculturalists have found this situation difficult to ameliorate but acacias and other species of their alliance are clearly equipped to thrive in these conditions, again raising speculation that generation of these restrictive soil conditions may specifically benefit the acacias but not potential competitors. The patchy nature of these soils at tree- and ecosystem-scale supports this contention.

Mallee eucalypt woodland

Mallee-melaleuca scrub associations are generally associated with shallow duplex soils, where mallee species with associated fungi have created specific layers to deny access to soil water from potential competitors. Figure 12 shows the extensive mallee root system.

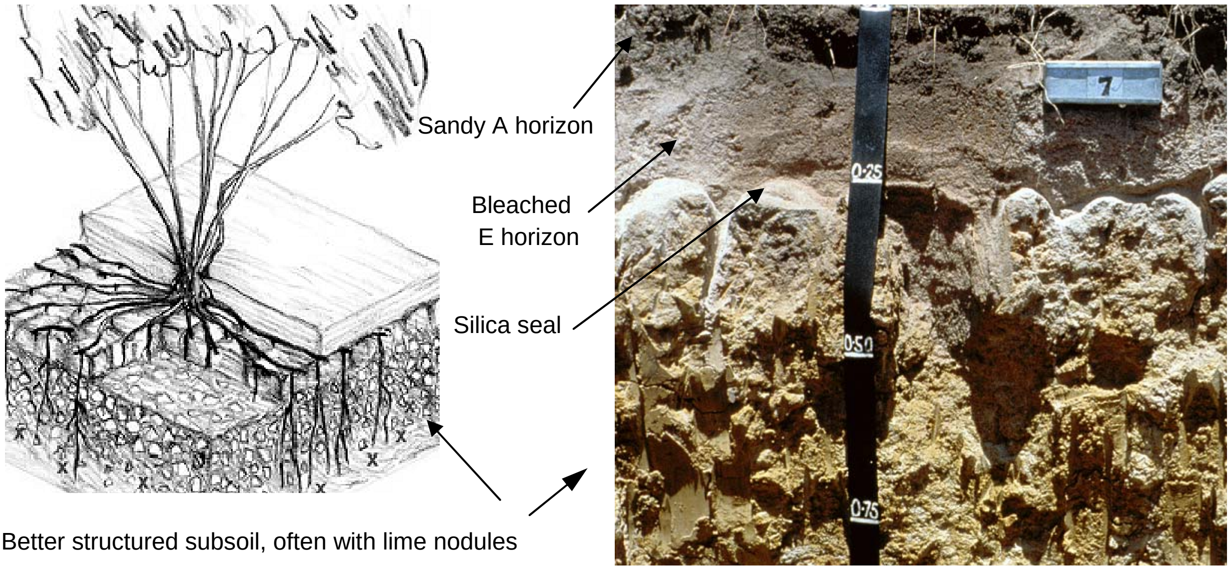


Figure 12 **Diagram of mallee sandy duplex soil (left) and sandy duplex with a silica seal over domed clay (right)**

The clayey B horizon, which is sealed at its surface by amorphous silica and clays, sits on top of often calcareous loamy subsoil with a high capacity to store water. Here one finds a harmony between the morphology of the profile, the survival strategy of the mallee and repressive influences on competing species.

Competition for space

General changes in the soil profile across an ecotone (transitional area between differing plant communities) and even between species within the same community are illustrated in Figures 13 and 14, 15 and 16.

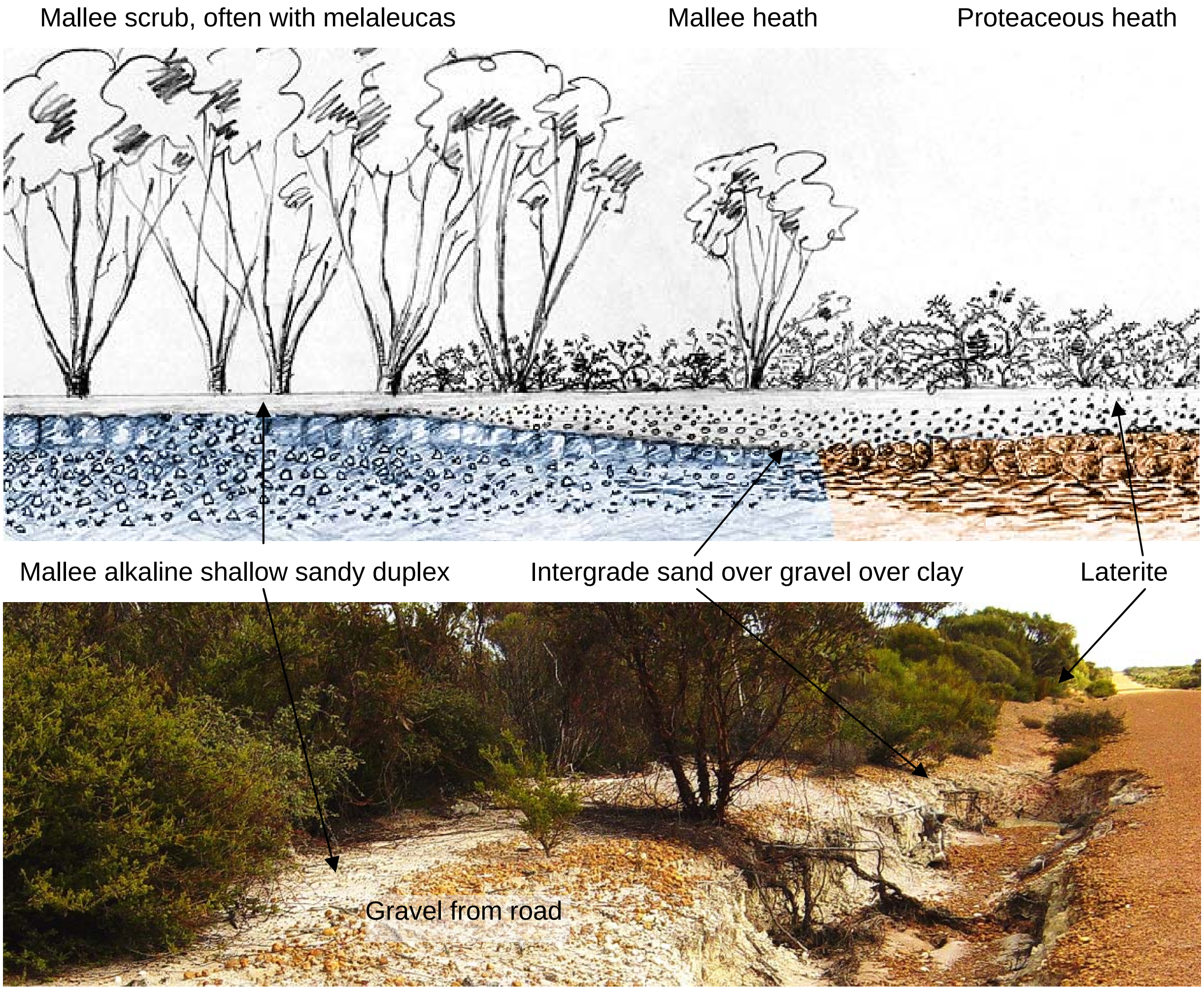


Figure 13 **Schematic cross-section of soil type change from laterite to alkaline duplex (Verboom & Pate 2006b) (top) and laterite grading to duplex near Lake King (above).**

Soil overprinting is common in the mallee zone and is very likely related to the niche construction activities of the invaders.

In Figure 14 the roots of an invading mallee have been exposed by removal of the sandy topsoil using an air spade. Removal reveals the root system with sinker roots penetrating the seal at regular intervals up to 3 m from the bole. Note that the thin layer of gravel that is often found above the clay in intergrade soil areas has a ‘cap’ of amorphous silica that is being deposited by the mallee community to form the seal.

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Figure 14 **Air-spade exposure of B horizon under mallee broombush (*Melaleuca* spp) vegetation where it is invading a lateritic heath (top) and close-up of a sinker root penetrating the silica seal, and overprinted gravel stones (above)**

Figure 15 shows a soil exposure in a railway cutting where a laterite has been invaded by an alkaline duplex soil. The fact that contrasting horizons formed more or less contemporaneously within the same geological, climatic and topographic setting is difficult to explain by non-biological theories of soil formation.

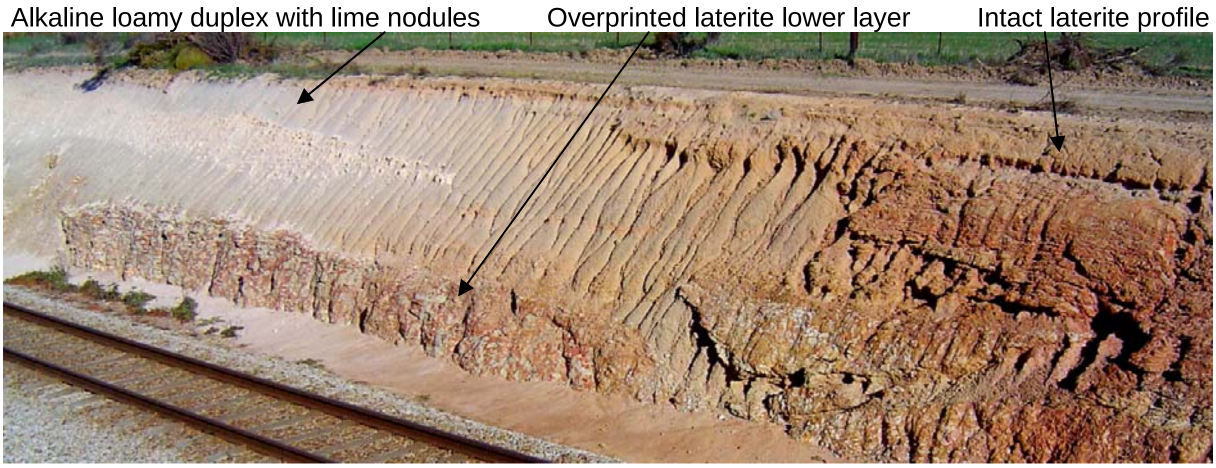
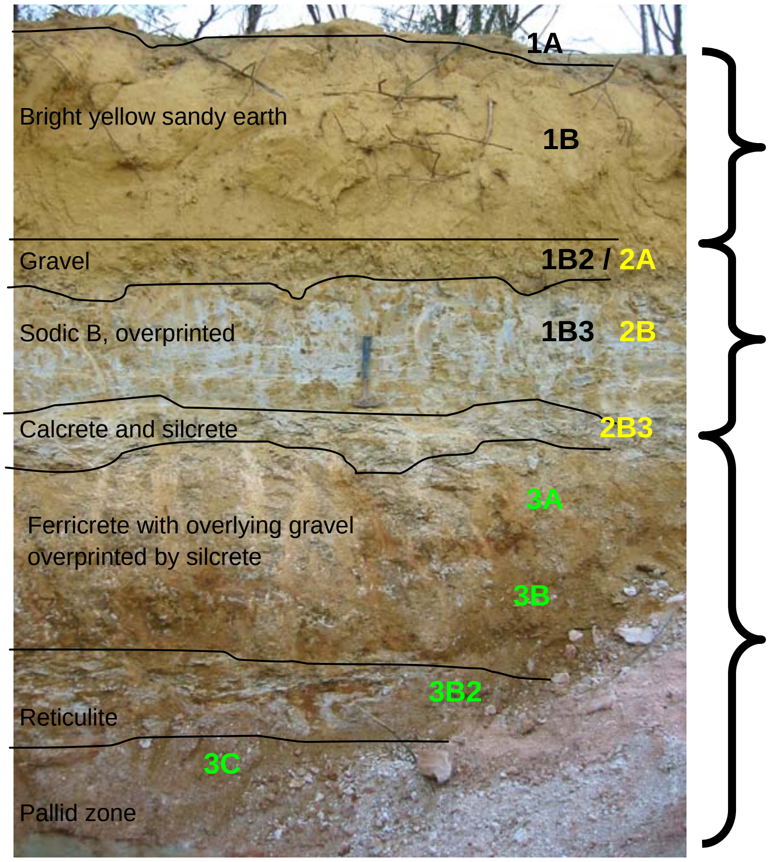


Figure 15 **Changes encountered along a 500 m stretch of profile exposed by a rail cutting show a horizon of calcrete under myrtaceous vegetation transgressing lateritic reticulate fabric and wedging out to ferricrete under proteaceous heath.**

Figure 16 shows changes across the surface of a duplex B horizon after the topsoil has been removed using an air spade. On the left a pale silica seal was associated with the red-brown fibrous roots of *Eucalyptus scyphocalyx*, while calcium carbonate and clayey precipitates were associated with the smooth darker *E. flocktoniae* roots.

Figure 16 **Air-spade exposure of patterns in B horizon formation in relation to rooting of two species of mallee**

Vertical overprinting is also evident in situations where aeolian deposition has alternated with soil formation. The photograph in Figure 17 shows stacked fossil soils situated on a lower slope at Kalannie, a location 210 km north-east of Perth near Dalwallinu. The simplest interpretation of these formations involves the three major soil-forming events depicted on the image.



Present day soil: under grevillea or wodjil scrub

Old duplex, originally under eucalypts?

Tertiary laterite overprinted with silica. The original ferricretes fine towards the surface. This arrangement is common under present-day heath soils.

Figure 17 **Fossil soil sequence in a cutting at Kalannie**

According to the phytotarium concept, the intricate lateral patterning of soil types encountered across much of the south-west will have arisen from the history of occupation and the contrasting effects that each plant community has engineered when acting on its own. Indeed the ecological forces underlying ecosystem successions may well be reflected in the horizontal patterning of soil types on water-shedding uplands.

Consider the high-resolution Ternary radiometric images of the Elashgin catchment in the wheatbelt of Western Australia (Verboom & Pate 2003) draped onto a digital elevation model (Figure 18). The images reveal many patterns that are easily understood with current knowledge. For instance, fans (labelled F) from granitic terrain (labelled G), and sandy (dark red) dendritic flow structures in valleys can be seen to contrast with areas of stagnation and clay and salt accumulation (pale colours in the valley).

However, the swirling black and bluey-green structures detected in the radiometric images of the uplands appear to be largely independent of topography and exhibit sharp transitioning from black (sandy) to bluey-green (gravelly) signals.

These structures can be seen in air photographs and were used to map lateritic sandplain during the Corrigin Area Land Resource survey. The inset enlargement of these structures shows spiral wave-like patterns that can arise from intercommunity competition. Another type of moving ecological pattern is seen as a standing wave in species density (Verboom 2007).

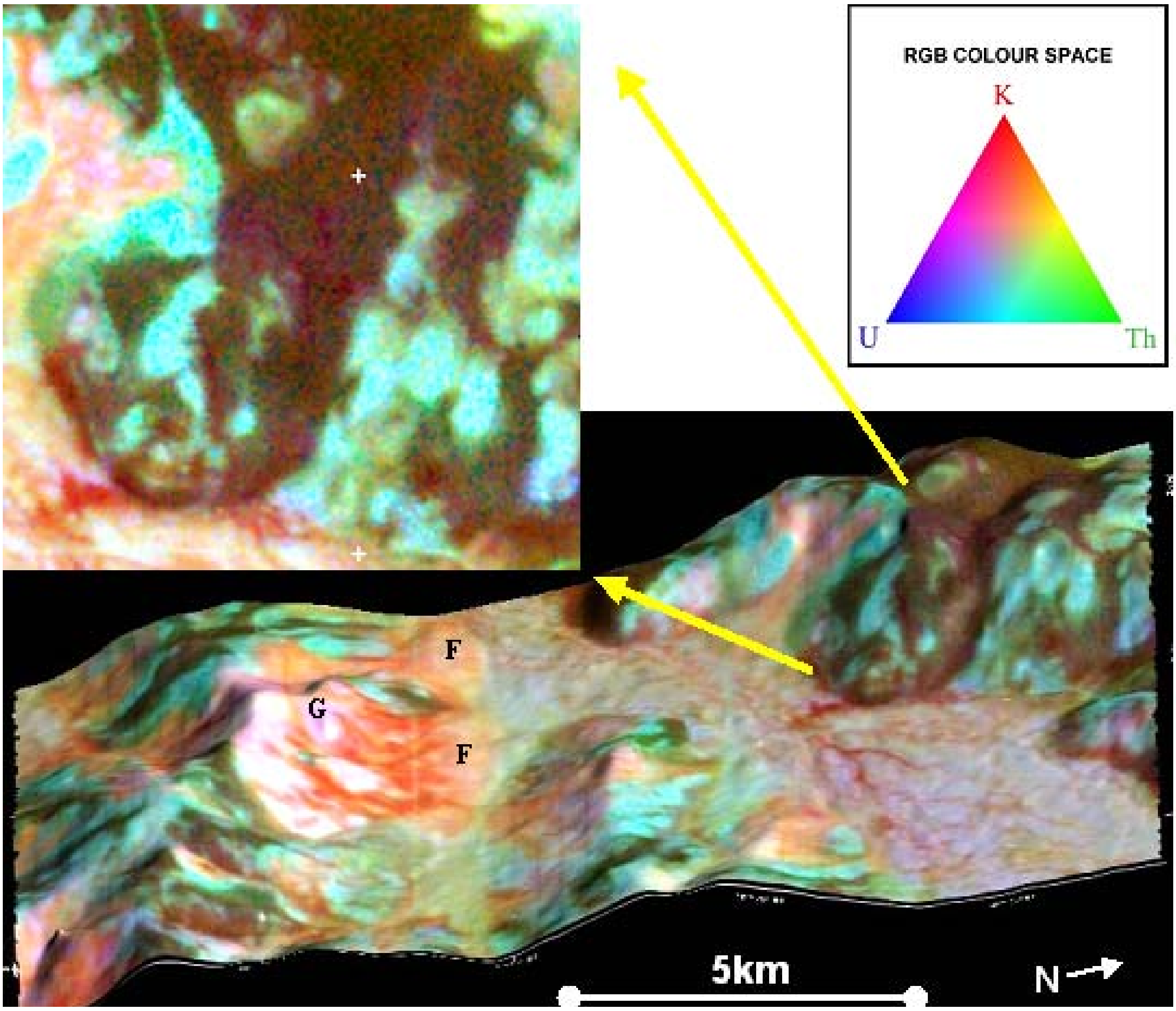


Figure 18 **Ternary radiometric images of the Elashgin catchment draped onto a digital elevation model**

Bioengineering in action

Our investigation of mallee eucalypts colonising a recently formed quartzitic sand dune at Lake Chillinup in the South Stirlings (Pate & Verboom 2009) provides unique insights into clay pavement construction. Such pavements are akin to those seen widely in duplex soils across large tracts of southern Australia.

The sand dune to the south-east of Lake Chillinup is considered to have formed in the past 10 000 to 19 000 years. Figure 19 shows the dune is currently vegetated by a mosaic of myrtaceous and proteaceous woodland. A cutting made by the local shire in 2006 bisected the dune exposing a clay layer (pavement) formed by the overlying eucalypt vegetation.

On the far side of the dune, heath vegetation overlies a normal aeolian sand profile that changes to a developing clay pavement with clay columns associated with *E. decipiens, E. incrassata, and E. pleurocarpa* roots 60–100 cm below the dune surface. The pavement becomes a continuous layer until a vegetation change to *E. occidentalis* that has formed another pavement above the original one, within 30 cm of the surface.

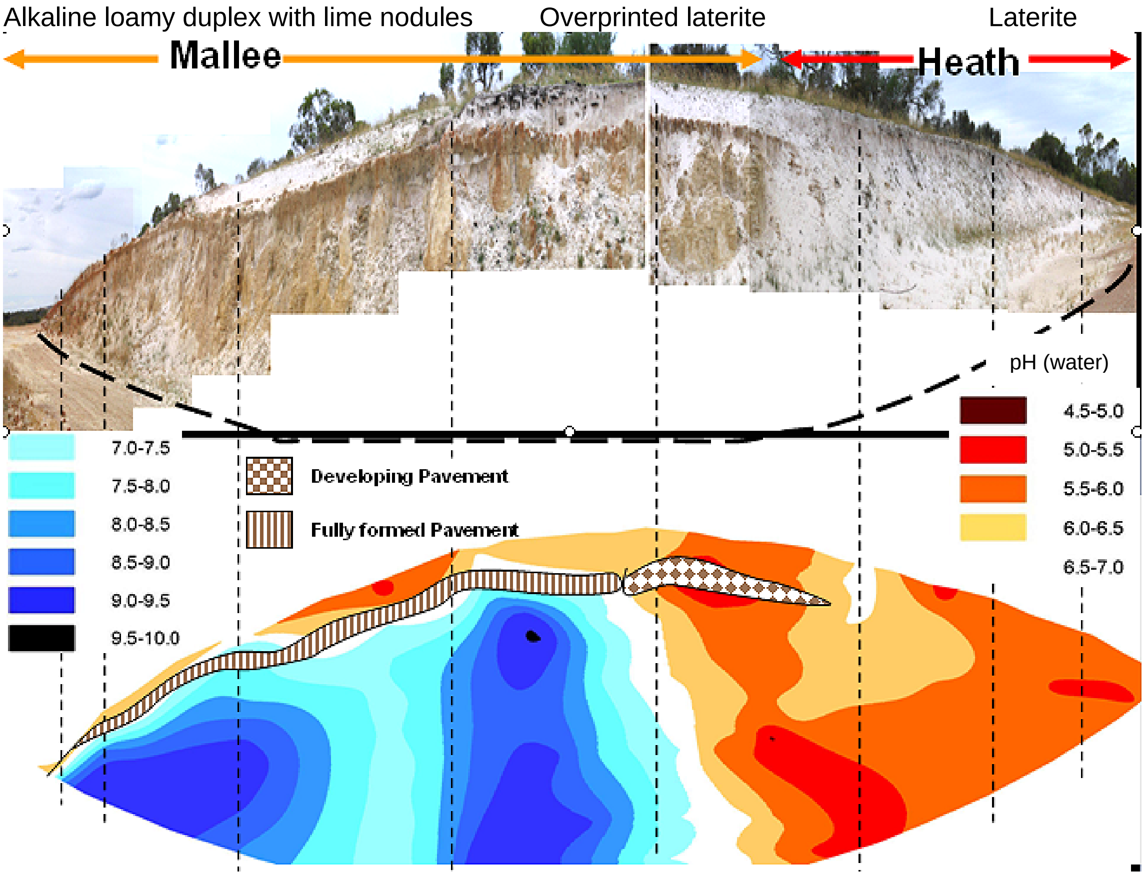


Figure 19 **Composite image of a cross-section of a sand dune at lake Chillinup in which a clay pavement has formed under eucalypt vegetation (top); diagram of the pH profile of the dune (above).**

Figure 20 shows the clay pavement construction under *E. occidentalis* on the dune and the root systems of *E. decipiens*.

Figure 20 **Clay pavement formation under *E. occidentalis* (top left); air-spade exposure of the columnar pavement surface generated by the same tree (top right); developing clay columns under *E. decipiens* (above left) and close-up view of a developing *E. decipiens* column still attached to umbilical root (above right). *Occidentalis* and *decipiens* columns are respectively approximately 15 cm and 10 cm in diameter.**

In the specific case of *E. incrassata*, clayey pavements are synthesised in situ at a depth of 80–100 cm from locally sourced Si and taproot mediated uplift of Fe and Al from water perched on the mineral-rich lake bed underlying the dune (Figure 21). These mineral elements are delivered at night during summer via an ascending xylem stream (Figure 22) to sites of pavement construction in lower regions of the lateral root system.

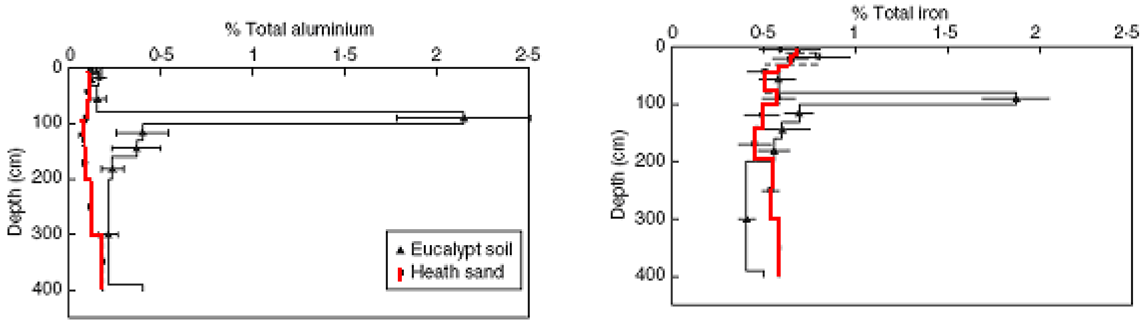


Figure 21 **Iron and aluminium composition of soil under *E. incrassata* and heath**

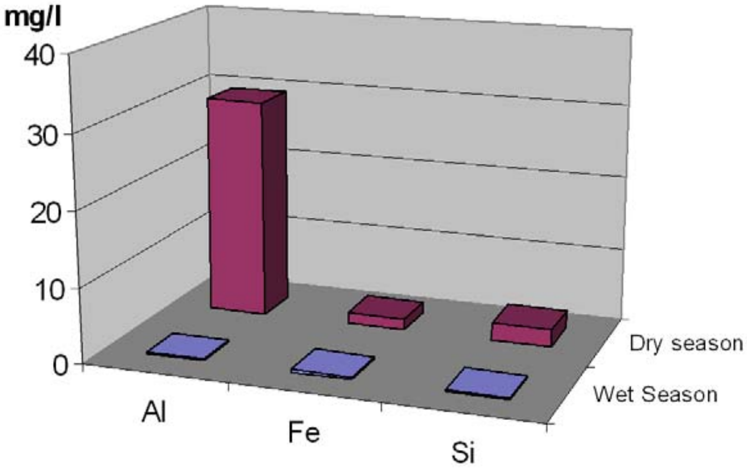


Figure 22 **Seasonal change in concentration of aluminium, iron and silicon in xylem sap extracted from lateral roots of *E. incrassata***

As seen in Figure 19 there was marked progressive enrichment in Ca and Mg carbonates beneath pavements under mallee with pH values accordingly elevated. This contrasts with the situation under heath where, despite mild podzolisation, mineral statuses remain more or less as expected of the original quartzitic sand dune deposit.

An interesting parallel to the contrasting situation found in mallee woodland versus heath at Lake Chillinup has been recorded by Berger et al. (2006) in their studies of deep mining of Ca and alkalinisation of soil profiles by European beech (*Fagus sylvatica*) versus the strongly acidifying effects of competing spruce (*Picea abies*). Regardless of whether mallee or beech is the responsible agency, long-term deep-mining, and subsequent deposition, of divalent cations as carbonates in upper soil profiles would inevitably result in acidification of basement profiles and associated groundwaters.

Wider ramifications of the phytotarium concept

Impacts on salinity

A number of well-defined soil problems peculiar to Australian agriculture arise as after-effects of such niche construction activities of perennial native plants once land is cleared for pastures and crops.

For example, prior to clearing, mallee eucalypts continuously gathered salts beneath their sodosol clay seals over multiple cycles of water storage and usage. When trees are cleared, water is no longer redistributed from the A to the B horizon during winter while uplift of water from deeper layers during spring is also halted. The A horizon thus waterlogs more frequently.

Highly impermeable B horizons can also cause salinity to wick up to the surface (Rengasamy 2006) while in more permeable situations, and particularly where topsoils remain saturated for some time, pulses of water may enter the subsoil. In the latter situation water is less likely to be intercepted by annual roots, leading to salts gradually leaching out of lower horizons. Accompanying changes in electrical conductivity profiles after clearing (Figure 23) can contribute to the degradation of soil structure and increased onsite and offsite recharge. Offsite recharge in particular is considered to be the main factor in raising saline groundwaters in low-lying land.

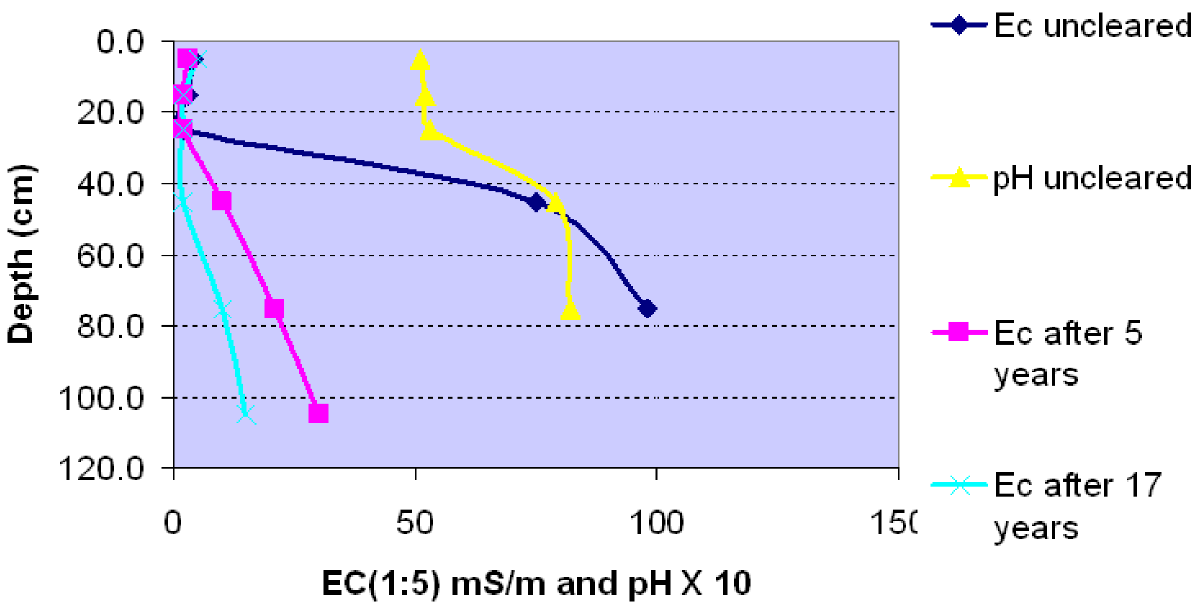


Figure 23 **Changes in electrical conductivity in a Newdegate sandy duplex before and after clearing**

Impact on pH and groundwater geochemistry

By actively raising and concentrating metal cations into upper profiles, plants profoundly affect the geochemistry of the groundwaters above. For example, many eucalypts raise and concentrate Ca and Al into their B horizons in the form of carbonates and clay and in the process leave behind Fe and hydrogen ions. This results in groundwaters becoming progressively iron rich and acidic. Conversely, proteaceous heaths and acacia scrublands tend to lift and concentrate Fe as ferricrete while excluding basic cations such as Ca^{++}. As a result, their groundwaters are neutral to alkaline but show relatively low levels of iron (Lillicrap & George 2010).

Impact on plant evolution

The landscapes of the south-western botanical province appear to reflect varying degrees of dynamism in patterns of phytotarium building, ranging from the spiralling structures described earlier under ‘Competition for space’, page 14 with some transience to phytotaria settlements that appear to have been maintained over long periods.

Each of these situations is likely to have implications for the development of speciation of the plant families concerned. For example, the ability of phytotarium builders to expand into a competitor’s territory, as in the spiral wave situation, is due either to some sort of succession spearheaded by supporting invaders, or to the ability of niche-constructing species to persist, for short periods, in initially hostile environments.

In the case of more settled phytotaria communities—those species on crestal laterites for example—it is reasonable to suppose that progeny fitness in these situations is much more dependent on the conditions found within the parent phytotaria. The operation of such phytotaria over extended periods probably requires phytotarium maintenance in the face of erosion and may well lead to species flocking and high levels of species turnover along geographic and other environmental gradients.

Conclusion

As indicated above, many adverse situations in agriculture have arisen because we cleared native perennial vegetation in favour of annual pasture and crops. In retrospect, we did not understand the functioning of native vegetation communities and thus could not foresee the consequences of our actions.

Our present knowledge is still largely limited to the simplistic view that perennials use more water than annuals. More importantly, little is known about the water acquisition and storage strategies of native plants in seasonally dry areas of Australia. However, this knowledge may be critically important to reducing the impact of farming practices on land degradation and associated species extinctions.

Biological processes appear to be involved in the generation of many soil landscape patterns and these can be mapped using radiometric and other data sets currently being commissioned by the state. The knowledge gained during these investigations helps us to generate farm-scale maps of the original native vegetation. These detailed maps could be used to help restore soil landscapes to the previous native condition.

Benefits of such restoration for farmer-driven land conservation might be the endemic revegetation of underperforming land and site selection for high water-use options. State-driven land conservation measures might include the recovery of catchments of high conservation value such as Toolibin and Lake Bryde. Longer term applications of this research may be the development of agricultural systems more in tune with native soils, leading to improvements in water-use efficiency, reduced recharge and salinity, and more economic and sustainable agriculture.

Further research may well lead to revegetation programs in which selected plant species are employed to improve the structure of duplex soils and the water- and nutrient-holding properties of the sandplains. In the former case there is also an opportunity for sequestrating carbon in the soil in inorganic forms.

Finally, this bulletin has dwelt mainly on the most important tenet of the phytotarium concept—namely, that dominant woody taxa of ecosystems have the capacity to engineer functionally strategic changes in composition and physical characteristics of soil profiles.

However, it is clear that these concepts have further ramifications and that the full extent of the reciprocal relations between plant speciation, microbes, phytotarium building and land-form development has yet to be established.

We would argue that further evidence of deep-seated biotic effects on the pedological and geomorphological development of Western Australian landscapes will only emerge when their study is interdisciplinary and focused on the kinds of holistic effects touched on in this bulletin.

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Glossary

Cation	Positively charged ion
Catena	Sequence of different soil profiles that occur down a slope
A horizon	Surface mineral horizon with organic matter accumulation. Usually darker than the lower horizons
Apatite	Group of phosphate minerals
B horizon	Subsoil horizon consisting of one or more mineral layers differing to the A Horizon by: • clay, iron, aluminium or organic matter concentrations • structure and/or consistence • colour
Bs horizon	Subsoil horizon whereby the 'B' refers to the B horizon and the 's' to the sesquic horizon. Iron compounds are strongly dominant or codominant (with aluminium) and there is little evidence of organic matter
E horizon	Conspicuously bleached horizon
Ecotone	Transitional area between differing plant communities
Electrical conductivity (EC)	Measure of the conduction of electricity through water, or a soil water extract. The value can reflect the amount of soluble salts in a soil extract, therefore providing an indication of soil salinity.
Ferricrete	Hard insoluble deposits of ferric and aluminium oxides in the form of ironstone blocks, gravel and caprock
Laterite	An infertile soil containing ferricrete
Leaching	Removal in solution of soluble minerals and salts as water moves through the profile

LMC	Low molecular weight carboxylate
Mollisol	Soils characterised by a thick dark fertile surface A horizon
Overprinting	Newer soil creating differing characteristics over older soils
Pedologist	Soil scientist studying soil formation and distribution
pH (soil)	Measure of soil acidity and soil alkalinity on a scale of 0 (extremely acidic) to 14 (extremely alkaline).
Photosynthate	chemical product of photosynthesis, especially a sugar
Photosynthesis	Process that a plant goes through when turning sunlight and carbon dioxide into sugar that it uses for food. Most forms of photosynthesis release oxygen as a byproduct
Phytotaria	Soil type constructed by plants
Phytotarium concept	System whereby major plant species bioengineer the soil profile to their own advantage
Podzol (or podsol)	Soils with iron and aluminium concentration but without hard gravels or ironstone
Sesquic	Sesquic B Horizon (or Bs Horizon) is where iron compounds are strongly dominant or codominant with aluminium and there is little evidence of organic matter
Soil horizon	Soil layers within the profile which are reasonably homogeneous in terms of morphological characteristics and properties (e.g. colour, texture, and structure) to the layers above and below
Taxa	In biology, a taxonomic category or group, such as a phylum, order, family, genus, or species