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REVIEW PAPER

Bioengineering of soil profiles in semiarid ecosystems: the 'phytotarium' concept. A review

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Abstract This review draws attention to information from the literature and our own observations supporting the view that higher plants and micro-organisms display an intrinsic capacity to be proactively involved in pedogenetic processes. 'Bioengineering' of this kind is deemed to be spearheaded by principal deep-rooted tree and shrub species and to result in optimisation of command and conservation of water and nutrients within an ecosystem. Specific examples discussed in the paper include, the formation of silicon- or iron-based linings of vertical channels and pores, binding of sand on roots, generation of organically derived hydrophobicity, development of clay-based hardpans and texture-contrast seals, precipitation of silcrete, calcrete and ferricrete pavements, effective accessing and conservation of P resources, including mining by microbes and the biological cycling of Si and Al via plants and micro-organisms. In each case, definitive roles and mechanisms are suggested for the organisms involved, particularly in relation to formative effects relating to secretion of organic acids, dispersing agents and other classes of exudate. We introduce the term 'phytotarium' to connote the collective outcomes of the above biotic influences in construction and maintenance of niches peculiar to specific vegetation types and then review the evidence of imprinting of soil profiles due to operation of phytotaria. Examples given relate to the lateral and vertical facies encountered in certain contemporary soil profiles and paleosols with which we are familiar and are described in a companion paper.

Keywords Minerals · Niche-building · Soil · Water · Woody plants

Introduction—towards a biogenic interpretation of soil-formative processes

It is well known that the distributions and productivities of many of Australia's vegetational communities are governed more closely by the forms, amounts and spatial distributions of nutrients in circulation than by the total chemical contents of their respective habitat soils (Adams 1996; Charley and Richards 1977, 1983). The original biologically based explanation for such relationships was that different types of vegetation alter the forms and locations of elements in soils in various ways, thereby causing development

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of characteristic associations between plant successions and soil-formative processes (see Jenny 1941). Within this framework, certain well-authenticated examples of formative associations between plant players and soil-forming processes come to mind, particularly the podzolisation or calcification processes occurring, respectively, under coniferous and beech ecosystems of the North hemisphere (Berger et al. 2004; Buurman and Jongmans 2002; Jenny 1941; Lundstrom et al. 2000). Yet even here uncertainties are encountered concerning the exact nature and drivers of the process.

During the 1950s through to 1970s interest within Australia became focussed on understanding the relationships between its highly specialised native vegetation and soils deficient in available phosphorous (P). Wild (1958) linked such characteristics to a history of extensive leaching and weathering during the mid- to late-Tertiary, while Beadle (1954) drew attention to the prevalence within many such associations of worked and transported materials associated with progressive erosive losses of P-rich fines and coarser plant material. However, it has yet to be properly explained why such degradative processes are so pronounced on the Australian continent, nor indeed why they are so dramatically evident in the open woodland and heathland ecosystems of south-west Western Australia.

In his later work Beadle (1962) suggested that the distribution of the 'scleromorphic' habit across specialised native vegetation of Australia might have derived from pre-existing gradients in soil P, while also noting that remaining resources of P of certain soils tend to become immobilised in the Fe-rich bands on ferricrete surfaces. Using this standpoint, he advanced the somewhat novel hypothesis that it might be this low availability status in respect of P which protected native plant communities against invasion by unspecialised plant species.

At the same time soil scientists were becoming increasingly aware of the close association between certain sclerophylous species and the podzolic and lateritic soils so widely encountered across landscapes of south-west Western Australia. For example, contemporary knowledge of podzolisation processes in the Northern Hemisphere led Hingston (1963) to search for a formative role for polyphenolic constituents of leaves of eucalypt and other species in segregation of iron in laterites. While no simple correlation was shown to exist between total quantities of polyphenols and amounts of iron oxide solubilised under aerobic conditions, he did suggest that simple carboxylic and hydroxy acids recovered from leaves of certain species of Casuarinaceae and Proteaceae might be involved in release of limited amounts of P.

It is now generally agreed that the scleromorphic characteristics of native vegetation are closely associated with growth and survival of specialised taxa across a wide range of oligotrophic environments (e.g. see Hill 1998). Nevertheless, the concept that scleromorphy and longevity of foliage are invariably associated with effective conservation of nutrients is difficult to accept, since the same xeromorphic features might prove equally valuable in situations where growth is constrained more by available water than by nutrients.

It is now also well apparent that secretion of large amounts of various low-molecular-weight organic acids comprises a principal agent involved in the phosphate-desorbing processes effected by certain cluster-root bearing members of Proteaceae, Casuarinaceae, Leguminales and a few other taxa (see Hinsinger 1998; Jones 1998; Lambers et al. 2002; Pate et al. 2001; Pate and Watt 2002; Shane and Lambers 2005). Alternatively, in the majority of other sclerophylous woody taxa, limitation of growth by P availability is deemed to be overcome through various mycorrhizal agencies (Brundrett 1991; Brundrett and Abbott 2002; Brundrett and Cairney 2002; Hinsinger 1998) as well as by a range of other nutrient conservation strategies (Pate 1994). In this connection, our earlier review (Pate et al. 2001) presented evidence that nutrient storage and accessing strategies of cluster-root bearing taxa were prime agents in formation of laterite and podzol-like soils in semiarid regions of south-west Western Australia.

In this paper, we explore and extend the above-mentioned scenarios to develop the hypothesis that a range of broadly similar biogenic activities might underpin various pedogenetic processes across semiarid ecosystems. We will deal particularly with those which we are familiar in southwest Western Australia.

In deference to the joint role played by microbes and plants, we will employ the general term 'bioengineering' to denote any one or more of a range of biologically driven influences modifying soil profile characteristics. We also coin the word 'phytotarium' to denote the players and end-products of such habitat modification, and in so doing wish to convey an analogy with the term 'termitarium'. The latter thus involves symbiotic relationships between termites, gut flagellates and cellulose-decomposing bacteria and nitrogen-fixing bacteria, whereas the 'phytotarium' concept embraces the broadly similar mutualistic cooperation of higher plants and associated mycorrhizae or rhizosphere bacteria.

In this review and in our companion paper (Verboom and Pate, 2006), we combine information from a number of disciplines with our own local observations to support a hypothesis in which elements of bioengineering piloted by woody plants are depicted as being oriented collectively towards effective command of resources of nutrients and water by principal participants within various classes of phytotaria. Our prime examples come from proteaceous shrub-heaths and open woodlands and eucalypt-dominated open woodlands for which we highlight certain features exhibited by contemporary ecotones and paleosols to further substantiate our hypothesis.

Pedogenetic structures likely to control resources of nutrients and water

In soil profiles of many semiarid and seasonally dry regions of the world, one encounters a variety of nodular cretes, water conduits, hydrophobic surfaces and various silicified structures which clearly render the profile concerned variably penetrable to water or roots. It is our contention that many such features result in part from plant-directed reworking and mobilisation of soil and plant-derived materials and thereby confer important implications for uptake, partitioning and conservation of the resources of water and nutrients within an ecosystem. At the same time we would of course concede that thermo-chemical processes, particularly the effects of temperature, ionic force and pH on components such as Si, Al, Fe, Ca and soil colloids, are likely to be operating as important complementary influences of an essentially non-biotic nature.

Pedogenetic cretes

Occurrence

Pedogenetic cretes, defined as those originating within the vadose zone of the rhizosphere of a profile, are characterised externally by nodules, duricrusts and other structures sheathed and cemented by amorphous or microcrystalline secondary compounds such as calcium carbonate (calcretes), oxides of silicon (silcretes), iron (ferricretes) or aluminium (alcretes) (Fookes 1997; Goudie 1983; McFarlane 1983a; Milnes and Hutton 1983; Milnes and Twidale 1983; Summerfield 1983). They typically show a concretionary internal structure, presumably resulting from an intermittent pattern of growth. However, they may grade chemically from one to another and do so even within the same structural entity. It accordingly becomes difficult to classify the various types involved purely on the basis of their bulk elemental composition (Summerfield 1983).

Relationships at larger scales may be equally diverse and complex, although alcretes and ferricretes tend to occur in regionally wet situations, whereas calcretes and silcretes are typical of areas receiving an annual precipitation from 400 to 600 mm (Goudie 1983), or even less in regions of predominantly winter rainfall (Anand et al. 1997). In certain cases, alcretes may grade into ferricretes, calcretes into silcretes, and ferricretes may change abruptly to calcretes. Furthermore, it is common to observe that such changes may be encountered within the one contiguous land surface, with or without attendant changes in parent rock (McFarlane 1983a; Sadlier and Gilkes 1973; Twidale 1983).

In certain cases, a crete horizon may be absent altogether under certain vegetation types (McFarlane 1983a), while in others relative accumulation of Fe in a ferricrete, or of carbonate in a calcrete, may change appreciably according to atmospheric or ground sources of Fe and carbonate (Anand et al. 1997; Glassford and Semeniuk 1995; Hunt et al. 1977). In yet other situations, ferricrete fabrics and surfaces may be overprinted by alcrete (gibbsitisation) or calcrete (Goudie 1983; McFarlane 1987), or ferricretes may form synchronously alongside secondary gibbsite and kaolinite (see Farmer and Lumsden 2001; Verboom and Pate 2003).

Any of the above pedogenetic cretes exhibit fine porosity, possess microbial pseudomorphs and show generally higher levels of carbon and nitrogen than found in surrounding loose soil. At the same time, the hydroxylated surfaces of poorly ordered Al- and Fe-oxide coatings of many cretes are likely to be highly reactive to P, thereby imparting great long-term stability and poor availability status to resident resources of this key nutrient (see Gilkes and Hughes 1994; Samadi and Gilkes 1998, 1999).

Evidence for biological influences in crete formation

Acid, low calcium ferricrete–alcrete series: A biological origin based on the activity of temperate micro-organisms was first proposed for this class of crete over a century ago by the geochemist Holland (1903). This view was subsequently endorsed by McFarlane (McFarlane 1983b, 1987) and McFarlane and Bowden (1992) who went on to propose that accumulations of iron- and aluminium-rich residua in ferricrete and alcrete formations might depend on dissolution of kaolinite and concomitant precipitation of iron, silicon and aluminium. McFarlane (loc. cit) favoured some microbial form of complexation, as indicated by the geological record, the complexity of occurrences in the field in leaky environments and the high concentrations of presumably respired CO_2 encountered deep within a profile.

The above concepts are particularly consistent with our recent hypothesis (Pate et al. 2001) that podzol and laterite (ferricrete) formation under proteaceous vegetation are cluster-root driven, carboxylate-based systems in which targeted secretions by proteoid roots of copious amounts of citrate and various other low-molecular-weight organic acids are pivotal to release of P from insoluble complexes and associated mobilisation and subsequent reprecipitation of Fe within a soil profile.

As alternatives to a biological role in ferricrete formation proposed above, one might ascribe the process either to iron impregnation of sediments in ancient depressions, or to humid tropical weathering during the Tertiary. The first of these views (see Ollier et al. 1988) is now largely discarded since low relief would be expected to militate strongly against the formation of many kinds of laterite (McFarlane 1987).

The second widely held opinion dates back to Woolnough (1927), who argued that a combination of stable peneplains and seasonally moist tropical climates would limit rejuvenation, thereby prolonging processes concentrating insoluble forms of iron, aluminium and silicon and lead eventually to formation ferricretes. At the same time, prolonged loss of iron, aluminium, combined silica and basic cations from an underlying permanently saturated horizon might cause development of a thick white kaolinitic horizon.

Subsequent refinement of these ideas, in terms of kinetics of reactions and localised thermodynamic equilibria between minerals and percolating solutions would then enable one to predict the bulk mineralogical composition of soils within a climatic zone. However, as Lucas (2001) points out, the expected vertical arrangement of minerals within a well-drained profile is rarely observed, even in highly leached tropical situations.

Leaching models based on non-biological mechanisms have been particularly difficult to test since the various phases involving Fe, Si and Al occur as intimate mixtures at very fine scale. Even so, such models clearly give an indication of the chemical environment in which precipitations of these elements might occur and the likely durability of such precipitates. However, they fail to properly identify the mechanisms of element transport involved, nor explain the structural intricacies of such precipitates observed by Bocquier et al. (1983) in their micromorphological examination of African laterites.

Alkaline calcrete series: As already seen, the field occurrences of this class of crete are just as complex as that of laterites and cannot be explained simply in terms of ground and air-borne-sources of calcite (Anand et al. 1997). Nevertheless, a biological origin is to be suggested from the finding that pedogenetic and ground water silcretes resemble phytoliths in their relatively high levels of titanium (Drees et al. 1989) and depletion in 30Si (Basile-Doelsch et al. 2005). The latter stable isotope-based criterion, is now regarded as indicative of biologically mediated processing of Si. In parallel fashion, Derry et al. (2005) regard the germanium/silicon ratios found in soil water from chronosequences of basaltic soils of Hawaiian islands as pointing to biologically mediated cycling of Si as a significant contributor to the formation of amorphous and crystalline fractions of relevant clays and phytoliths. Particularly strong evidence supporting a biological origin comes from the finding within crete matrices of living or fossilised remains of various types of organisms. Relevant examples are given below:

1. Krumbein (1968) showed that Israeli calcretes contain microflora which after isolation are able to produce large amounts of calcite, in vitro.
2. Klappa (1978, 1979) demonstrated occurrences of calcified organic filaments of soil fungi actinomycetes and root hairs in calcites from the Western Mediteranean Basin and suggested that the finding of microdium grains might signify calcification of mycorrhizal fungi.
3. Possible roles of mycorrhizal fungi and associated bacteria have been suggested for calcrete formation in Spain (Esteban 1974), South Australia (Phillips et al. 1987; Phillips and Self 1987) and south-west Western Australia (Anand et al. 1997).

Silcretes: Silcretes with little P-absorbing activity, yet potentially active in water control, occur widely as layers and linings to root channels across semiarid landscapes of south-west Western Australia. As indicated above for alkaline calcretes, their genesis is likely to be biological and to involve distinct Si-depositing mechanisms mediated by plants and microbes.

Hydrophobic surface layers

Many semiarid native ecosystems of southern Australia are renowned for the non-wettable character of their surface layers. In some cases, evidence points strongly to comminuted litter of plants being involved, for example in ecosystems almost totally dominated by mallet type vegetation [open woodland dominated by tall single stemmed eucalytpts such as *Eucalyptus astringens* (Maiden) Maiden] (see McGhie and Posner 1980, 1981). Furthermore, where distribution of hydrophobic material is heterogeneous, patterns of runoff and percolation of recent rain are likely to be highly uneven (Garkaklis et al. 1998; Nulsen et al. 1986). In such cases, wetting is reportedly least impeded around the bases of tree trunks, which are also likely to be in receipt of 'extra' water channelled preferentially by stemflow. In areas of open woodland beyond tree canopies, little hydrophobic material originating from litter is to be expected, yet patches of crustaceous lichens and Cyanophyceae may still confer poor wetting qualities at a localised level. Similarly in proteaceous woodland, mats of dead cluster-root material accumulating close to the surface can show remarkable resistance to re-wetting in winter, to the extent that soil immediately below such mats may remain dry for most of the year (Fig. 1). In this last instance, a contrasting situation, involving uniform seasonal wetting and drying of a profile, will be evident in the 'control' situation afforded by an annual field crop growing in adjacent cleared land. Effects such as shown in Fig. 1 find a counterpart in the preferential channelling of water below large shrubs on deep sands reported almost 50 years ago by Specht (1957) for sclerophyllous heathland of Dark Island Heath on the Ninety Mile Plain, South Australia (see Fig. 2).

In certain cases, such as topsoils heavily populated by fungal hyphae (McGhie and Posner 1980), or subjected to diggings of marsupials such as woylies (*Bettonia penicillata*) (Garkaklis et al. 1998), the regions concerned may become locally permeable to water within an otherwise impermeable surface. It must also be remembered that wherever water percolates through a partly hydrophobic A horizon of a sandy profile, further

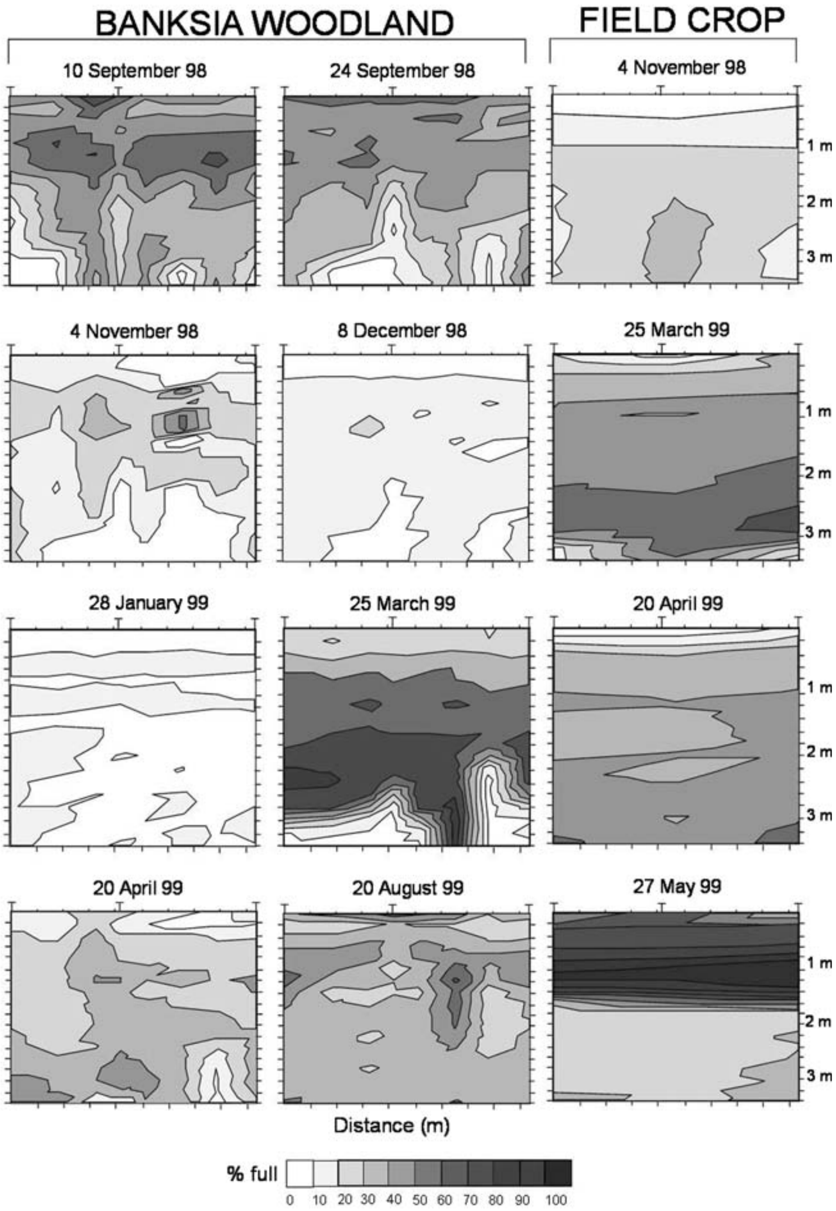


Fig. 1 Chronosequences of neutron moisture meter-based profiles showing uneven distribution of soil water in the rooting zone of pristine *Banksia* woodland at Moora, south-west Western Australia. A comparable (control) profile for an adjacent cereal crop shows more regular pattern of wetting and drying of the soil profile (adapted from J.S. Pate and D.J. Arthur, unpublished data)

downward flow is likely to become fingered. Then on meeting some sort of physical barrier, water may accumulate and become transiently 'perched' unless exploiting bio-pores or cracks elsewhere in the same pavement. Such effects may then result in highly uneven wetting further down the profile.

Barriers to water in B and C horizons

Soils exhibiting abrupt decreases in hydraulic conductivities in their lower horizons are widespread in parts of the world experiencing alternating wet and dry seasons. As suggested by Chittleborough (1992), they are especially

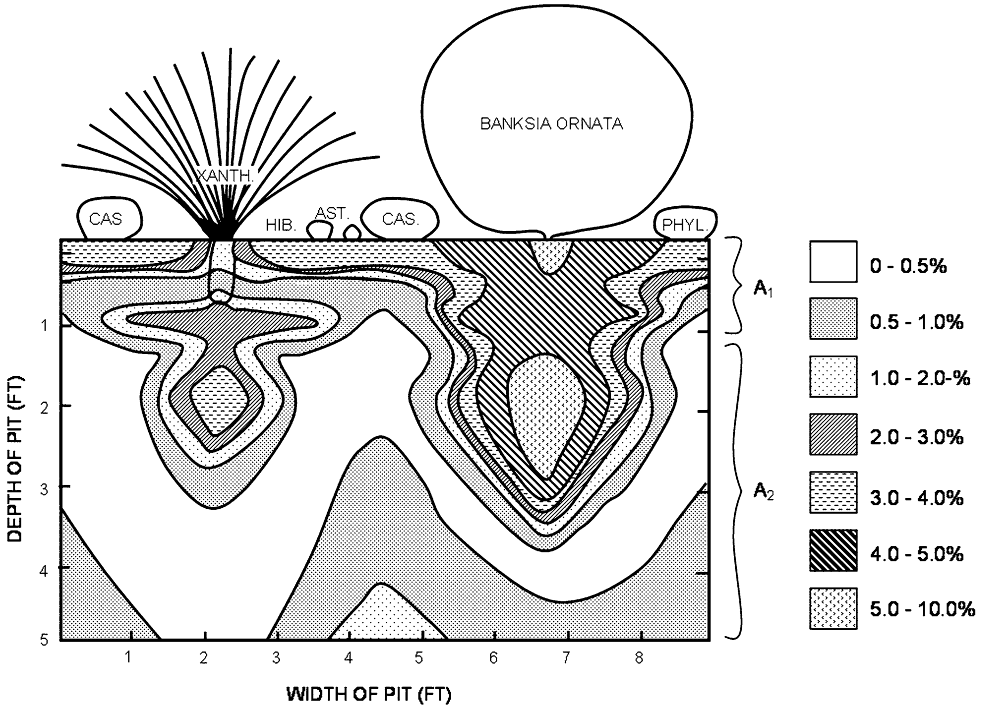


Fig. 2 Schematic representation of typical pattern of soil water (mass percentage scale) under *Banksia ornata* and *Xanthorrhoea australis* (Xanth), in Eastern Australia after heavy rain has wetted an initially dry profile. Other understorey species coded as CAS, HIB, PHYL and AST (adapted from Specht 1957). Note spearheading of penetration of water immediately below root boles of large taxa

prevalent across a range of texture-contrast soils of South Australia. Comparable occurrences in south-west Western Australia relate mostly to:

a) sodic texture-contrast soils vegetated by woodland dominated by small multi-stemmed, lignotuberous, eucalypts (mallee);
b) mildly acidic sandy loams with hardpans under york gum (*Eucalyptus loxophleba* Benth.) and certain mallees (e.g. *Eucalyptus kochii* Maiden and Blakely);
c) highly acidic, deep sandy earths underlain by silcrete and vegetated by wodjil-type acacias such as *Acacia coolgardiensis* Maiden, *Acacia neurophylla* W. Fitzg. and *Acacia assimilis* S. Moore (Frith 1985);
d) podzolic and lateritic soils of mixed heath woodland where a previously porous lateritic fabric has become occluded by siliceous or other precipitates in superficial or deeper silcrete horizons of a profile (see Hubble et al. 1983; Lee and Gilkes 2005; Stace et al. 1968).

In some of the above cases, continuous or sporadic bleaching, accompanied by depletion of clay, may be clearly visible above a poorly permeable layer. Temporary accumulation of free water will then occur following protracted winter rain or cyclonic or convective events during summer. As far as one can ascertain, such perched water is more likely to be found in cleared land of a region than in neighbouring areas still carrying original vegetation (Peck 1978).

Studies of soil chronosequences generally suggest that a degree of texture-contrast layering will result where clays at a junction between an A and B horizon 'break down', leading to a previously permeable subsurface matrix becoming blocked with clay. This infill may then consist of distinctly crystalline material or poorly ordered precipitates such as amorphous and crypto-crystalline quartz, namely Opal-A and Opal-CT, respectively. According to several authors (see Chittleborough 1992; Hubble et al. 1983; Stace et al. 1968), such materials may either be dispersed and translocated from above or synthesised in situ from reworked resident minerals or imported constituents.

What one would generally refer to as siliceous hardpans or silcrete horizons collectively embody a whole continuum of classes of materials. However, all resemble the above-mentioned texture-contrast horizons in that Fe, Si and Al released from soil above will comprise the most likely sources of Opal-A, Opal-CT, siliceous allophane, neo-formed kaolinite and iron infillings (Basile-Doelsch et al. 2005; Butt 1983; Chartres 1985; Monger and Kelly 2002). In any of such cases, voids in hardpans may also become occluded through depositions of carbonate.

Biological mediation of translocation of clay

Break-down of soil matrices at texture-contrast interfaces has been generally ascribed to purely chemically based processes such as hydrolysis and ferrolysis, the latter involving alternate oxidation and reduction of iron, production of protons and displacement of basic cations, and thereby the creation of an acidic environment (see Brinkman 1970, 1977). Such processes would fit well with various observations denoting temporary water perching, acidic reaction, moderate levels of exchangeable protons and precipitation of microcrystalline silica and comminuted clay.

There is strong evidence that release of silicic acid may be linked to redox processes in which prolonged saturation occurs in the presence of free iron oxides. However, van Ranst and De Coninck (2002) point to difficulties in explaining the whole ‘ferrolytic cycle’ in many such situations. While not excluding the possibility of clay dissolution following other proton-producing phenomena, they do concede that development of many strongly defined texture-contrast soils may derive more from dispersion and translocation of clay than from ferrolysis.

According to what one might regard as the standard view (Frenkel et al. 1978; Quirk and Schofield 1955; Shainberg and Caiserman 1971), dispersion in the absence of clay-stabilising agents results mostly from interaction of ions in the soil solution with the soil matrix via the electrical double layer. These processes are normally associated with low electrolyte concentrations within the soil solution coupled to a presence of significant proportions of sodium on cation exchange sites.

According to literature referred to by Isbell et al. (1983) and Chittleborough (1992), the traditional view is that sodic texture-contrast soils form as part of a genetic sequence involving salt accumulation from rain, dust and indigenous ground sources, thereby leading to formation of a so-called Solonchak. Leaching of salt, deflocculation and transport of negatively charged clay minerals then result in laying down of a texture-contrast soil (Solonetz; FAO 1998), possibly with eventual hydrolysis of clay to form an acidic Soloth. While exchangeable-sodium percentages are typically high in lower regions of such texture-contrast soils, upper dispersed horizons typically show well below critical levels. Indeed, Isbell et al. (1983) doubt whether many of the diverse and widespread varieties of sodic soil represented in Australia ever went through the above-mentioned sequences.

The most plausible biological agents likely to be involved in dispersion and transport of clay are various classes of exudates from roots. Thus, low-molecular-weight carboxylates would be capable of chelating and solublising the ferric coatings on certain clay minerals and, as mentioned earlier, are well known to be exuded in quantity by the roots of many taxa. Intermediate weight carboxylates and polyphenols, particularly at low concentration, are also known to form organo-mineral complexes with kaolinitic clays, thereby causing dispersion by offsetting positive charges on their edges. Highly effective dispersive agents of the latter type have been identified in the roots of Douglas fir by Durgin and Chaney (1984) and in the upper soil horizon of a Canadian soil by Visser and Caillier (1988). Indeed, they have long been considered as agents responsible for formation of clay pans (Jenny and Smith 1935) or clay-depleted A horizons typical of podzols (Bloomfield 1954). Chittleborough (1992) raises the possibility of similar processes operating in certain texture-contrast soils of Australia.

Biological mechanisms of transport and precipitation of silicon

Podzolic soils have received considerable recent attention in respect of possible displacement of Fe, Al and Si ions from minerals and clays through the agency of biologically formed low-molecular-weight carboxylates. Resulting complexes are then pictured as being decomposed microbially to yield ferrihydrite- and imogolite-type materials, such as encountered in Bs horizons of podzols of the Northern Hemisphere (Farmer and Lumsden 2001; Lundstrom et al. 2000) or laterites of the Southern Hemisphere (Farmer et al. 1984; Verboom and Pate 2003). The concept of microbial involvement in formation of associated clay minerals has been recently bolstered by the discovery of bio-halloysite in laboratory cultures derived from natural sediments (Tazaki 2005).

One of the principal chemical differences between laterites and podzols is that only the latter possess a humic (Bh) horizon overlying their sesquioxide-rich (Bs) horizon (Farmer and Lumsden 2001). Processes described in the previous paragraph would then explain the close associations observed between poorly ordered alumino-silicates (imogolite-type materials), cluster-root bearing taxa and associated soil chemical and mineralogical properties. The latter would include (a) P-sorption (Gilkes and Hughes 1994); (b) intimate associations between secondary gibbsite and Al-rich imogolite-type material and between neo-formed kaolinite and imogolites equally rich in Si and Al and (c) co-concentration of uranium, thorium and Fe in both podzolic (see Morton et al. 2002) and lateritic profiles (see radiometric surveys of Verboom and Pate 2003).

It is now well known that Si may be solubilised directly by low-molecular-weight organic acids exuded by roots and micro-organisms or may be released indirectly to solution following similar dissolution of poorly ordered Fe- and Al-containing compounds (see Barker et al. 1997; Hinsinger et al. 2003; Jones 1998; Jones et al. 2003; Little, et al. 2004). However, the underlying biochemical processes have yet to be evaluated.

Biologically engineered accumulations of large amounts of Si are also well known to occur in the Si-based leaf armouries developed by grazing-resistant grasses and sedges, while the widespread occurrence of phytoliths (plant opals) across many taxa also speak of selective biotic uptake of the element. As shown by Clarke (2003), the existence in soils of readily identifiable skeletal phytoliths following decomposition of leaf litter is also well authenticated, while silicification of micro-organisms including bacteria and diatoms may often lead to deposition of massive Si horizons in a regolith or, for example, as ‘diatomaceous earth’ deposits at the exits to large reservoirs or lakes (Clarke 2003; Ferris 1997).

Bacteria are known to dissolve silicates through secretions of enzymes and organic acids (Silverman 1979) and to store and secrete monomeric Si in their slime layers (see Clarke 2003). Yet, despite all this information, there is still no evidence to indicate how important these pools of biologically accumulated Si might be to the broader biogeochemical cycling of the element.

Water conduits in B and C horizons

It is well known that highly preferential infiltration of water can take place within soil profiles of many ecosystems and does so mostly through the agency of any one or more of a range of pore- or pipe-like entities of more or less vertical alignment. Some of these structures are clearly fabricated by higher plants and may thus be classified as genuine ‘bio-pores’. In certain of such cases formation is unequivocally a contemporary phenomenon, since the formative plant structures concerned are still either in living state or have recently died and their outer remains are currently occupied by roots of the same or other species.

In other cases one might dispute whether descending channels or pipe-like structures through indurated profiles have really been engineered by plant roots or merely reflect secondary exploitation by roots of already-existing fractures or structural weaknesses in otherwise isotropic substrates. Furthermore, in some cases, current occupancy of a particular conduit might well reflect the last of a series of causal occupancies by many successive generations of roots. Nevertheless, there is still good evidence to indicate that pores or channels, whether of biological origin or not, may become modified through deposition of materials sourced from the rest of the rhizosphere by roots and associated microbes. This then results in formation of permanent pipe-like structures in profiles under living vegetation, or clearly discernible in ancient paleosol formations or transgressions between successive autochthonous formations. We present below some local examples of the various classes of conduit we have observed in south-west Western Australia's semiarid ecosystems.

Sand-binding roots

The inventory of Pate and Dixon (1996) pictures these highly specialised structures as occurring widely across genera of certain families of monocotyledons and dicotyledons inhabiting deep sands of heathlands and open woodlands of south-west Western Australia. The strategy involves entrapment of sand particles within variously structured mantles of persistent lignified root hairs to form long-lived, desiccation-resisting rhizosheaths. Each sand-encrusted layer may be from 1 to 15 mm in thickness and extend vertically downwards for 0.5 to as much as 5 m (J.S. Pate, personal observations).

Whilst still alive, the central vascular core of a sand-binding root typically occupies less than 40% of the diameter of the whole structure and, in the case of monocotyledons, is typically bounded by a highly impermeable sclerified endodermis. Upon death of the root, these central regions decay, while the surrounding epidermal sheath and adhering sand grains persist for many years as a potential tube-like conduit for fine roots of the same or other species to exploit when sourcing deeply located reserves of water and nutrients.

The usefulness of such bio-pores in ecosystem functioning is particularly well demonstrated upon finding that seedling recruits exploiting old root tubes exhibit much greater chances of surviving their first dry summer than do sibling seedlings forced to extend their tap roots through bio-pore-free sand (see Bowen and Pate 1991 for recruitment of sandplain species of Proteaceae after fire).

Root channels lined by ferricrete and silcrete

These structures are generally of greater diameter and tend to persist much longer than the rhizosheaths alluded to above. We have commonly observed that where roots have passed through highly indurated materials, they have clearly taken a circuitous route to circumnavigate large obstacles. However, if present in a less consolidated profile (Fig. 3a) a straight downward path will be engineered (e.g. see Fig. 3c).

We find that the iron-based linings of root channels in lateritic profiles of south-west Western Australia are generally pale brown on the outside and red on the inside, indicative of goethite and haematite, respectively (e.g. see upper horizon in Fig. 3a). A similar but less distinct and faded colour contrast may be evident in paleosol formations (e.g. see Fig. 3a, lower horizon and Verboom and Pate, 2006), as well as in quite recently formed channels currently occupied by roots. By contrast, in non-lateritic profiles, channel coatings can be cream to white (Fig. 3b) and appear to consist of predominantly silicified matrices. As shown by Lee and Gilkes (2005), channels of this nature may even contain silicified cells of plant roots.

Lined root channels in laterite may occasionally transgress other fabrics, as seen for example in Fig. 3d for a fossil termitarium buried in lateritic colluvium. Here one finds compelling evidence of a recent root having constructed a channel through a biotically formed entity formed in a much earlier epoch.

The origin of supposedly biogenic Si in silicon-impregnated layers and silcrete tubes is still poorly understood. However, since such structures are generally in close proximity to roots, a link is to be suspected between uptake, processing and cycling by plant roots and precipitation of Si in the soil. Possible mechanisms would then include a direct exudation of silicic acid by roots, or precipitation phenomena engineered by microbes supported metabolically by root exudates. Lucas (2001) and Clarke (2003) suggest that since phytoliths are of relatively high solubility they may

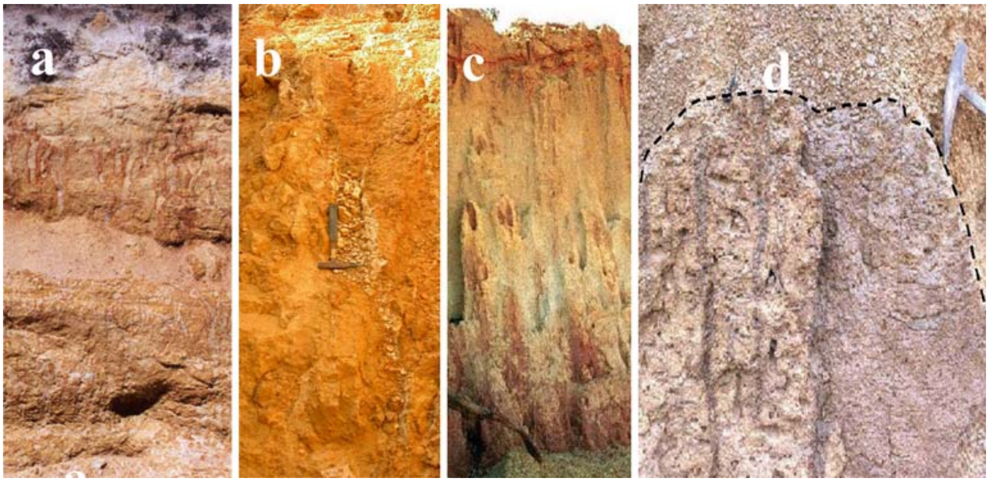


Fig. 3 **a** Ferric-lined channels through a series of vertically stacked lateritic pavements in cleared land near Narrogin. *Red linings* to root channels in the upper pavement are thought to have been engineered by the proteaceous scrub-heath present prior clearing for agriculture. Similar channels were observed enveloping living roots of *Banksia sphaerocarpa* R.Br. shrubs growing close to the profile. Faded channels in the lower bench of the profile are thought to have formed by similar processes during an earlier epoch; **b** silcrete-lined root tube in a silicified sandplain profile near Kalannie; **c** silcrete-lined root tubes in lateritic colluvium in a profile north-east of Narrogin. The tubes were probably occupied, and their linings engineered, by earlier myrtaceous trees at the site; **d** ferric-lined root channels passing through the centre of a fossilised termitarium mound buried in lateritic colluvium. The outer boundary of the mound is marked by a *broken line*. Contemporary aerial mounds currently occupied by termites occurred close by. These showed a similar basic structure but lacked root channels

comprise principal sources of biogenic Si, following decomposition of plant material. It is perhaps significant that abundance of phytolith remains in Australian soils is particularly high above water-impeding layers (Clarke 2003).

Lucas (2001) concluded that high rates of Si cycling in the Amazon appear to be linked to the formation and stability of clayey horizons, especially in relation to the formation of secondary alumino-silicates. The latter author's conclusions were based partly on comparisons between pedogenetic conditions in ferralsol under diverse rainforest and adjacent podzolic sand underlying different less diverse vegetation. Particularly relevant was the finding of lower levels of organometallic complexes and higher levels of soluble Si in the ferralsols concerned.

Structural and functional features of woody taxa relevant to uptake and flow of water and nutrients in heaths and woodlands of south-western Australia

As background to this final section of the review and to our companion paper (Verboom and Pate, 2006), we will now assemble the somewhat sparse information currently existing on structural and functional features relevant to uptake and flow of water and nutrients in dominant woody taxa of myrtaceous and proteaceous heaths and woodlands.

Water relationships of vegetation of open woodlands, shrub-heath and mallee

Capture and fate of water falling on canopies

Branching patterns of trees and shrubs indigenous to semiarid areas tend to be mostly of a steeply ascending character and accordingly prone to accentuate stemflow. The resulting water may then be channelled preferentially down into deep soil via annular pathways at the interfaces of soil with lower trunks, sides of lignotubers, and tap roots.

Dealing specifically with rain falling on canopies of trees of semiarid vegetation, information is available on proportional interception versus through-fall in the publications of Specht (1957) (70% interception for *Banksia: Xanthorrhoea* communities), Slatyer (1965) (40% interception for mulga communities) and Nulsen et al. (1986) (40% interception for a mallee system). The last mentioned authors showed that over one third of the incident rain on canopies can be lost, presumably as evaporation, the remainder running down the stem.

As recently shown experimentally by Wildy et al. (2004) for alley plantings of the oil mallee *E. kochii* in the northern wheatbelt of Western Australia, experimentally based relationships between interception, through-fall and stemflow vary predictably with amount of precipitation (see Fig. 4a). As one might expect, proportions of through-fall are shown to increase progressively with size of rainfall event, while evaporation losses relative to stemflow tend to be greatest with small events. The lower parts of the figure (Fig. 4b, c) show how such empirically based relationships can be used to predict cumulative values for stemflow, through-fall and interception for consecutive intervals of a study period. Thus, in the wet period A, 74% of the incident rain was accounted for as through-fall plus stemflow compared to only 51 and 58%, respectively, for the much drier subsequent periods B and C.

Another feature of importance is the proportion of incident rain which falls outside as opposed to within leafy canopies of an open woodland. Relevant in this connection are the densities and patterns of canopy coverage by trees and understorey species. For example, there is noticeable sparsity of shrubs and herbs relative to trees in most mallee ecosystems, while an almost closed canopy of similar growth-forms proliferates at high density after each fire event under the well-spaced dominant trees of proteaceous woodland.

As shown by Nulsen et al. (1986), for a mallee system similar to the one mentioned above, stemflow may account for only 5% of incident rain, yet both he and Pressland (1976) have suggested that selective channelling of such water into deeper soil horizons may well be a vital element in long-term survival of trees in semiarid environments. Following the fate of tritiated water generated during atomic tests, Allison and Hughes (1983) provided evidence that labelled rain did not mix freely with that of bulk soil but passed selectively into deeper horizons. They also suggested that such penetration occurred particularly down spaces between trunk, sinker roots and closely surrounding soil. The studies of Nulsen et al. (1986) comparing mallee with adjacent proteaceous shrub-heath indicated similar targeted percolation and redistribution of recently deposited water within both types of vegetation. Furthermore, depending on the intensity of rain, from 2 to 27 times more runoff was evident from isolated 4 m^2 plots within shrub-heath than from corresponding plots in mallee. However, their observations on the fate of rhodamine-B dye applied to the soil surface of a study area of mallee suggested that distances of overland flow after heavy rain were generally less than 25 m, indicative of effective infiltration, despite localised restriction of permeability by cryptogamic crusts and other hydrophobic areas. As for most arid ecosystems, long distance runoff from the catchments studied by Nulsen et al. (1986) proved to be negligible.

Exploitation of water resources by roots

As a number of studies have already shown (Pate et al. 1984; Pate and Dixon 1996), the rooting architecture displayed by trees and shrubs of semiarid ecosystems is what we have referred to as dimorphic (e.g. see Pate et al. 1995 and Fig. 5). This is where a clear demarcation exists between sinker (tap) roots capable of accessing water many metres down a profile, and superficial, horizontally extending lateral roots capable of using water only from the uppermost parts of the soil profile. In certain cases, e.g. the proteaceous species described by Bowen and Pate (1991), upper lateral parts of a root system may comprise from 70 to 90% of below ground dry weight and are strictly confined to the upper 30 cm of the soil profile. As already mentioned, fine roots may be ectomycorrhizal as in Myrtaceae (Fig. 6a), or may carry specialised cluster roots, as occur widely in Proteaceae and certain other taxa [see Pate and Watt 2002 and example from *Allocasuarina acutivalvis* (F. Muell.) L. Johnson (Fig. 6b)].

Studies of the anatomy and hydraulic conductivity of the xylem conducting tissue of roots and trunks of a range of proteaceous shrubs and trees

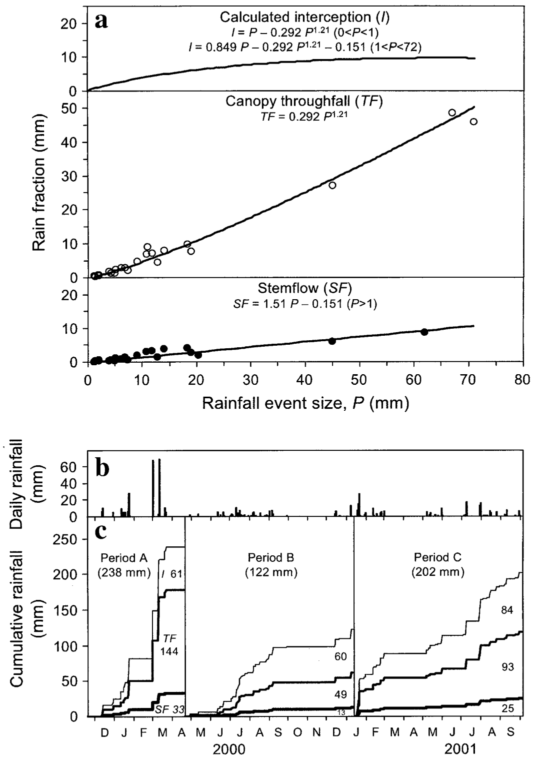


Fig. 4 Fate of rain falling on canopies of uncut trees of the oil mallee *Eucalyptus kochii* subsp. *plenissima* at Kalannie, Western Australia. **a** Measured losses of canopy throughfall (*TF*) and stemflow (*SF*) covering 24 consecutive rainfall events, with interception losses (*I*) calculated from relationships between TF and SF; **b** rainfall events over the study period; **c** cumulative totals for stem flow through-fall and interception for three successive periods based on relationships given in (**a**) (data from Wildy et al. 2004)

Fig. 5 Excavated root system of *Banksia* sp. showing dimorphic habit with deeply penetrating sinker root and radiating lateral roots. The distal parts of laterals have been cut away to facilitate photography. The removed parts bear many fine roots on which dense proliferations of cluster roots have developed. A few cluster roots remain on a short second-order lateral pictured at the front of the photograph

by Pate et al. (1995) showed surprisingly large differences in transmissive qualities between these contrasting parts of the system. Thus, tap (sinker) roots of all study species carried extremely wide and long vessels (1–1.5 m in length), thereby giving the root in question an unusually low resistance to flow of water. Also, with the widths of its vessels increasing downwards, despite progressive attenuation in its diameter, tap roots were found to exhibit highly uniform conductive qualities along their length. A tap root was thus pictured as ideally equipped to draw water up from considerable depths. By contrast, lateral roots possessed much shorter vessels of lesser width while those of trunks, while vessels of branches and vessels of twigs were even shorter and narrower. Uppermost, above-ground parts of the plant will accordingly comprise the major impedance to water flow and it is against such resistances that stomata of foliage will be able to fine tune their closing and opening responses seasonally and diurnally in relation to the extent of water stress currently experienced in the remaining body of the plant.

Using *Banksia prionotes* Lindley as a test subject, Burgess et al. (2000) investigated flow of water between different parts of root system and shoots using dye feeding experiments and heat-pulse transfer probe technology. Dye feeding involved stabbing of lateral or partly exposed sinker roots with a syringe filled with basic fuchsin (Fig. 7a). The dye was then shown to flow short distances to become progressively adsorbed on xylem elements lining the specific pathways in

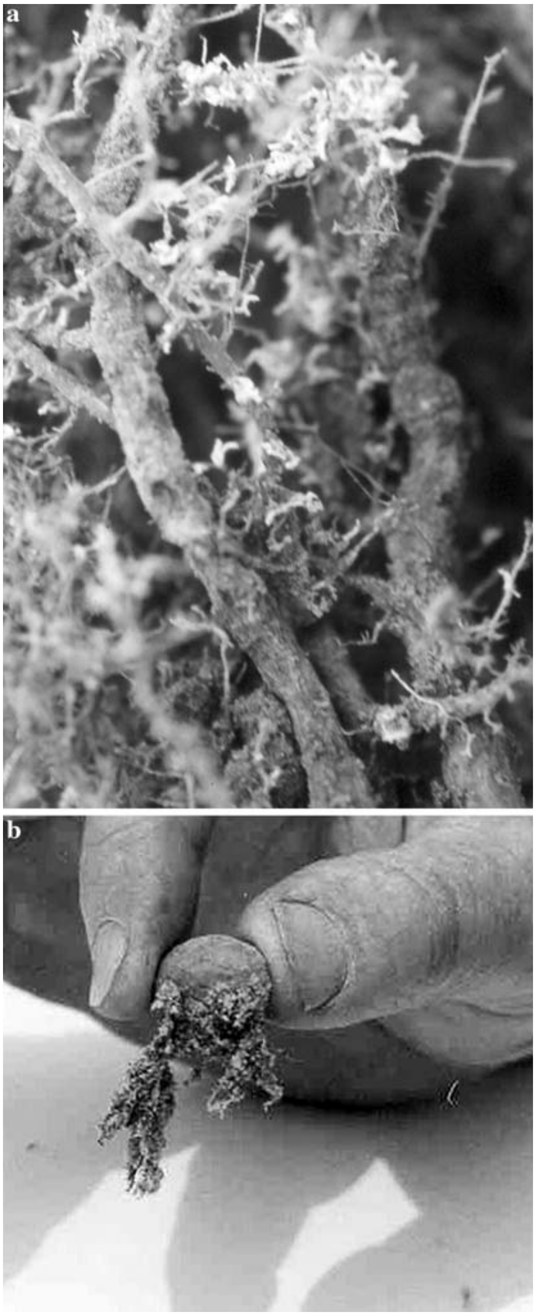


Fig. 6 **a** Ectomycorrhizal coatings to seasonally produced fine feeding roots of the mallee *Eucalyptus kochii*. **b** Cluster-type roots of *Allocasuarina acutivalvis* collected deep down in a soil profile in close proximity to pisolithic ferricrete

which bulk flow of water was currently occurring (see Fig. 7b). Distal movement in laterals, i.e. away from the main trunk, was then shown to occur only at night and principally during summer when laterals were being recharged with water from sinker roots. On the other hand, proximal adsorption of dye from the point of injection occurred predominantly when upper soil was wet and presumably when recently absorbed minerals were being exported from lateral roots up into the shoot (see Fig. 7c, d).

More definitive examination of water flow in the same woodland was obtained using heat transfer probes inserted in lateral and sinker roots and lower trunks of *B. prionotes* (see Burgess et al. 2000). Results confirmed and quantified the above-mentioned reversible flow in laterals shown by dye feeding experiments, while also validating the flexible diurnal shift which may take place in the sharing of sinker-derived water root between transpiring shoot and laterals. Cases were even recorded where one lateral was supplying the shoot with water while another was being recharged with water from the sinker. Furthermore, it was estimated that during phases of distal flow in certain laterals, some of the entering water was secreted to the surrounding soil.

We view the recharge of laterals sited in upper dried-out A horizons as paramount to survival of the lateral root system of a tree during high summer, while also possibly facilitating a prompt start to the initiation of a new clothing of fine feeding roots on the same laterals at the onset of a wet season.

We also find analogies between functioning of the above *Banksia* system and the hydraulic lift phenomena recorded widely for mostly temperate ecosystems of other parts of the world by authors such as Caldwell and Richards (1989), Dawson (1993), Horton and Hart (1998) and Pate and Dawson (1999). However, as far as we can gather, heat-pulse transfer studies so far conducted on Australian species tend to show less net losses of water to the A horizon through the agency of hydraulic lift than recorded, for example, during summer for forest ecosystems of the Northern Hemisphere (see literature cited above).

Studies by a number of workers across the world have used heat-pulse transfer technology to indicate that flexible and fully reversible flow of water can take place between virtually all parts of

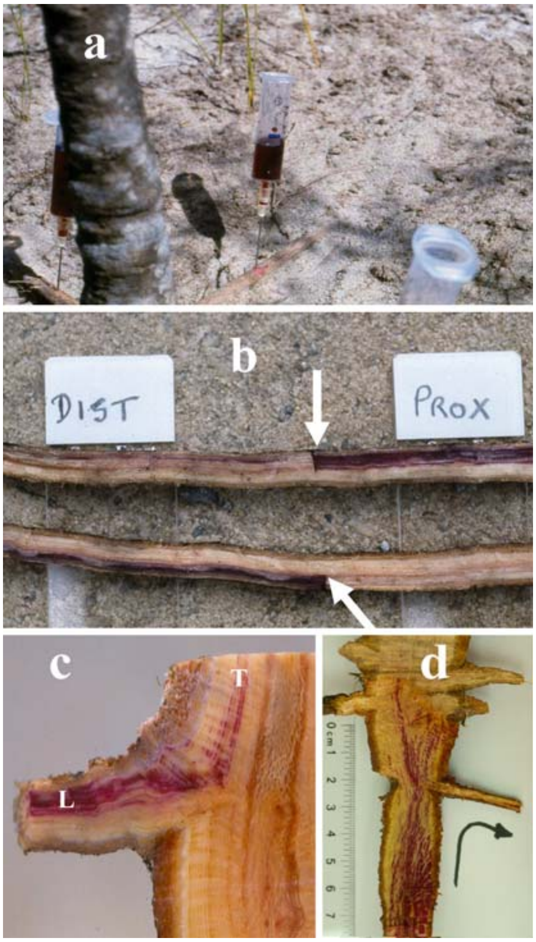


Fig. 7 **a** Syringes containing basic fuchsin dye inserted into lateral roots of an intact tree of *Banksia prionotes* to trace directions of water flow in the roots. **b** Results of dye feeding studies showing proximal finger of flow progressively adsorbing dye (*top example*) and opposite pattern of distal flow away from trunk in the *lower example*. *Arrows* show points at which syringes were originally inserted; **c** results of long-term (48 h) dye injection into the lateral (*L*) of an intact tree of *B. prionotes* showing that proximal flow of dye has stained xylem of the lower trunk (*T*). **d** Section through junction of sinker root, lateral roots and trunk, following injection of dye at depth into sinker of intact tree. Note, flow mostly towards shoot but also into lateral on right (see *arrow*). The wood of the species is *orange* coloured and should not be confused with the *purple* overlay caused by absorbed dye

the root system of a woody plant. With such capacities, a tree might therefore be able to take up or release water within and between essentially all soil compartments of its rooting catchment. As an example of this, cases are on record of 'reverse' hydraulic lift, namely where laterals in upper parts of a wet soil are clearly donating water downwards into tap roots, and thence even to a replenishment of water resources in dry lower soil horizons (Brooks et al. 2002; Burgess et al. 1998, 2001; Schulze et al. 1998; Smith et al. 1999). A further important element in flexibility of water flow in trees or shrubs is what is referred to as 'transverse hydraulic redistribution', namely where lateral roots occupying well wetted zones of soil are able to transfer water to recharge other laterals in dry zones (e.g. see definitive study on grape vines by Smart et al. 2005, and the situation in nature, say, where riparian vegetation has free access to water in a flowing creek on one side of its rooting catchment while the other side roots extend into dry soil).

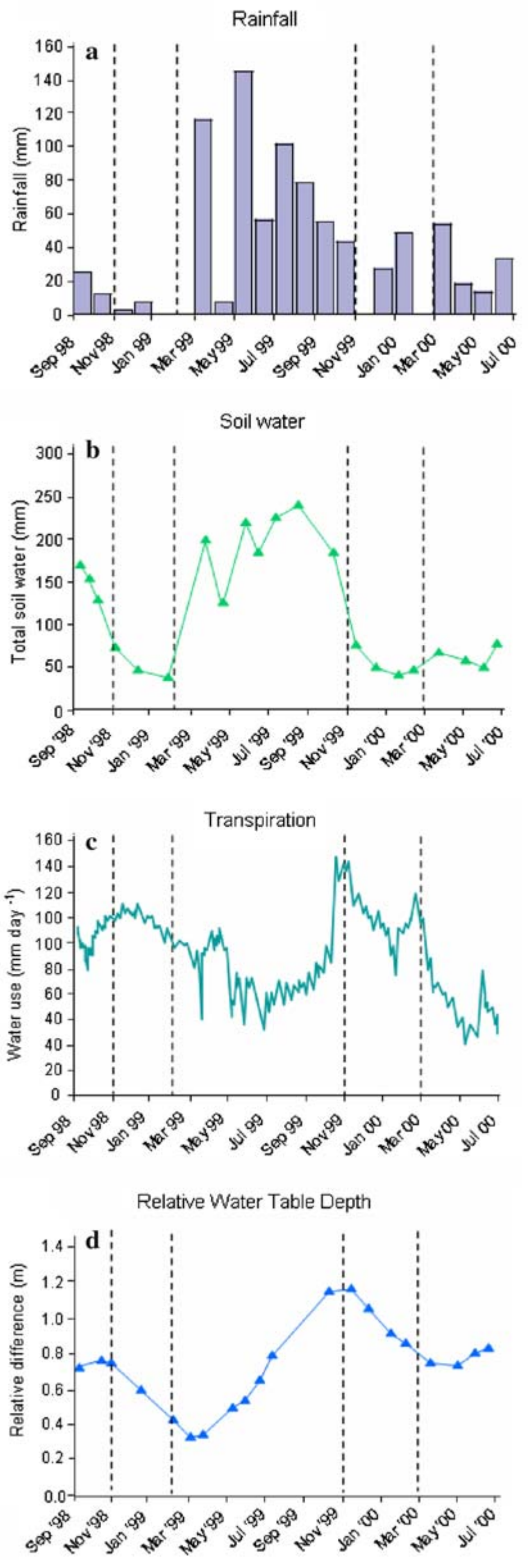
As a result of all the phenomena mentioned in the preceding paragraphs, one would conclude that woody trees with dimorphic root systems carry structural and physiological qualities fostering flexible manipulation of water resources of a rooting profile transversely and vertically in time and space. This might take place, for example, against the background of an uneven wetting of the soil profile early in a wet season and then progress gradually towards an essentially complete exploitation of all water reserves by the end of the following dry season. However, despite this flexibility in sharing and redistributing underground resources of water, daytime transpiration by the shoot system will always exert a dominant influence on water flow through its overriding capacity to command available water from virtually all parts of a root system.

Seasonal water budgets for open woodland ecosystems

We will first refer to a study of *B. prionotes* woodland at Moora, Western Australia. Vegetation at the site has been detailed by Pate and Bell (1999) and Grigg et al. (2000). Water relations of the system were assessed by monthly measurements of (a) rainfall received; (b) soil water reserves in the 4-m deep profile of uniform sand above the water table; (c) relative depth to water table and (d) transpiration of trees assessed by heat-pulse transfer.

All relevant data are assembled in Fig. 8. Note that while the first summer was drier than the second, soil water reserves were still reduced to the same extent by the end of each dry season. As to be expected, water tables rose during the wet season and then became progressively reduced through the following summer until commencement of appreciable rain at the ‘break’ of the next wet season. Transpiration losses (Fig. 8c) varied two- to threefold from a minimum in mid winter to peak values in November, the latter month marking the midway point in the seasonal extension growth of new shoots and foliage by the study species. Soil water reserves were still relatively high at that time. Declining transpiration losses were then recorded for the rest of the summer, as to be expected from stomatal responses of trees to declining soil water and progressive lowering of the water table. Integrating the values from Fig. 8 one arrives at the summer water balances of water usage exhibited by the species shown in Fig. 9.

The situation regarding utilisation of water resources by mallee root systems is less well documented than for Proteaceae. In particular, there is no evidence to date comparing the hydraulic conductivities of tap and lateral roots of mallees with those of *Banksia*. However, unpublished information kindly provided by K. Brooksbank (personal communication) indicates that hydraulic lift can take place readily from tap root to laterals of *Eucalyptus* sp. and that transverse flows between one lateral and another can occur under certain circumstances. This, combined with exceptional rooting depths for mallees (for example, down to 26 m as cited by Nulsen et al. 1986), compared to only 2–8 m for Proteaceae, would indicate that the mallee growth-form is particularly well adapted to low rainfall environments and highly uncertain patterns of



◀ **Fig. 8** **a** Patterns of rainfall; **b** changes in soil water content; **c** transpiration rate and **d** changes in depth to water table in pristine banksia woodland on deep sand at Moora, Western Australia (adapted from T. Dawson, M. Unkovich, D. Arthur and J. Pate, unpublished data). The water balances for two successive summer periods of the 22-month study are given in Fig. 9

replenishment of both deep and superficial resources of water.

Major differences in seasonal responses to dry conditions have been recorded between different woody species of a number of semiarid ecosystems. The experimental strategies employed have typically involved measurement of daily gas exchange characteristics of foliage (rates of photosynthetic uptake of CO_2, stomatal conductances and transpiration losses), carbon isotope discrimination ($\delta^{13}C$) of dry matter laid down in new shoot growth, and pre-dawn water potentials of shoots assessed by Scholander pressure bomb. For example, a recent study conducted by Mappin et al. (2003) on semiarid shrublands on deep sands at Kalannie in the Northern Wheatbelt of Western Australia, showed that all shallow-rooted species relied solely on water resources from within an upper 6-m layer of uniform sand above a silcrete horizon and accordingly gave every indication of being severely stressed by mid summer. Not surprisingly this group of study species put on new growth and reproduced only in the wet winter–spring period. By contrast two large myrtaceous species (*Eucalyptus leptopoda* Benth. and *Melaleuca uncinata*), possessed deep roots extending well below the calcrete. The species remained only mildly stressed and continued growing vegetatively and reproducing right through the summer.

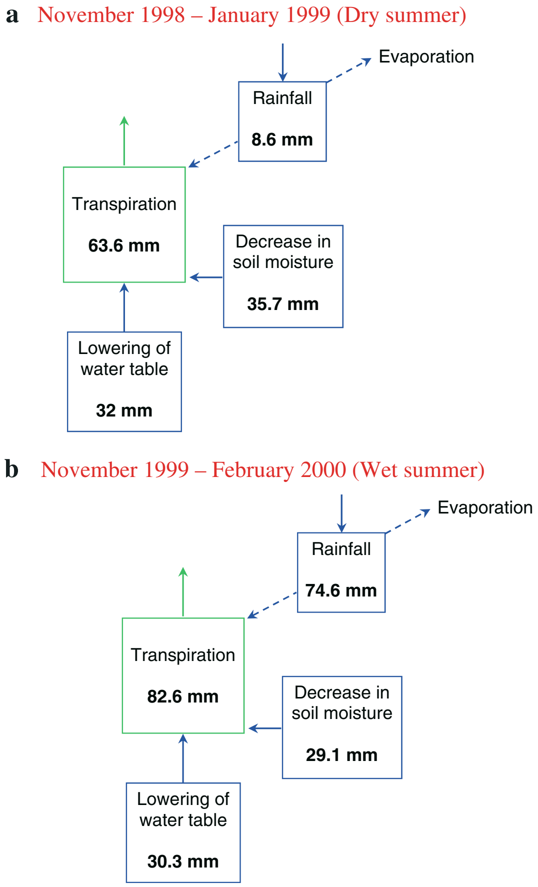


Fig. 9 Water balances for pristine banksia woodland at Moora over **a** a dry first and **b** a wetter second summer. Information presented utilises the primary data of Fig. 8 (adapted from T. Dawson, M. Unkovich, D. Arthur and J. Pate, unpublished data)

Similar principles were found to apply to *Banksia* woodlands at Moora (Grigg et al. 2000) and to southern coastal heath near Denmark (Pate et al. 1990). Studies in both ecosystems indicated that measurements of pre-dawn water potentials during high summer offered the easiest and most reliable means of distinguishing stress-prone, shallow-rooted species from deep-rooted counterparts which typically remained only moderately stressed even during intense summer drought. Incidentally, Bell and Pate (2001) recorded substantial differences in wood anatomy between species of different rooting depth, growth and life form and fire response characteristics. Of particular interest was their finding of greatest vessel diameters in deep-rooted, drought-resistant species and least diameters in shallow-rooted fire-prone species which shut down almost completely on their transpiration losses throughout a dry summer period.

The study of Nulsen et al. (1986) provided an instructive commentary comparing seasonal soil moisture profiles under mallee and adjacent proteaceous shrub-heath. Their data indicated consistently drier surface soil horizons in mallee than shrub-heath, a finding presumably indicative of faster drying out of the surface horizon of mallee after rainfall events of some magnitude. A second major difference comprised the pronounced mid soil profile bulge in soil moisture under mallee during January and February. This was not evident under adjacent proteaceous shrub-heath.

Detailed seasonal water budgets for pristine south-western Australian mallee vegetation have yet to be undertaken, but considerable work is in

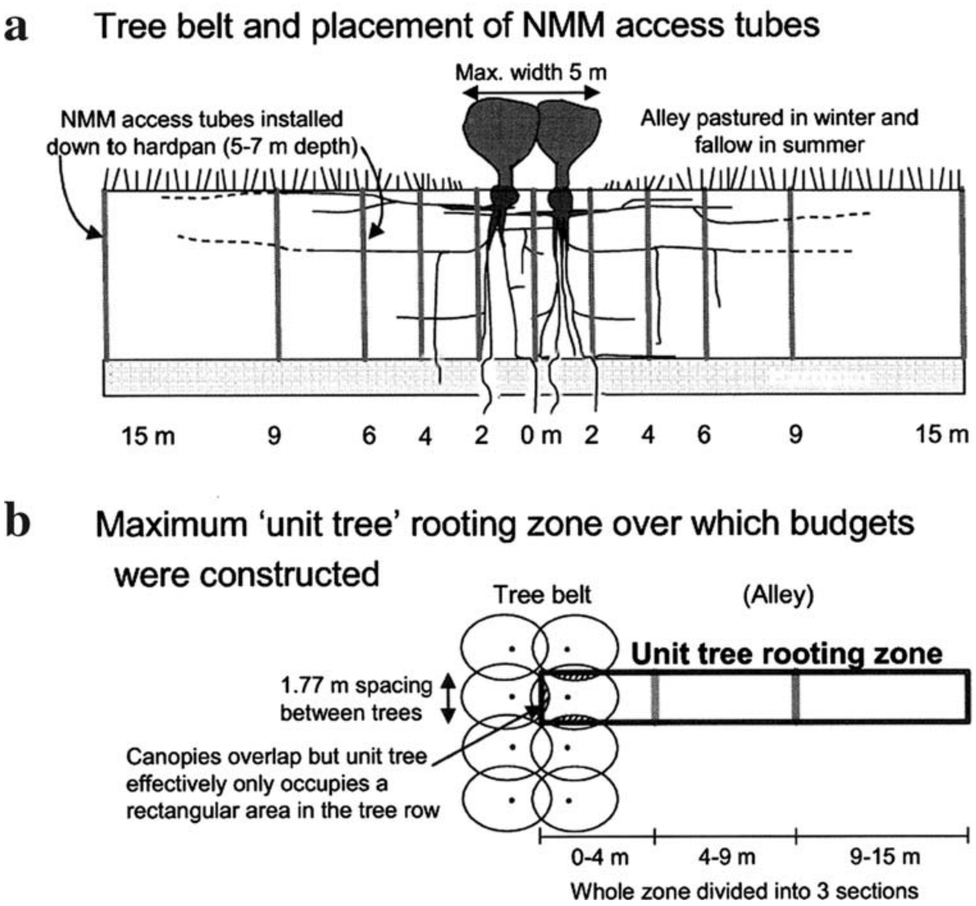


Fig. 10 Detailed seasonal water budgets for alley planted 4-year-old uncut trees of the oil mallee *E. kochii* subsp. *plenissima* at Kalannie, Western Australia showing **a** cross section of tree belt with double rows of trees, rooting morphologies and placement of transects of neutron moisture meters and **b** the single tree row, 15-m-wide rooting zone around which water budgets were constructed (data from Wildy et al. 2004)

progress on native oil mallees subjected to row:alley culture in certain semiarid parts of the wheatbelt. The study of Wildy et al. (2004) at Kalannie provided a particularly instructive example, with focus in this case on determining what area of landscape would be required under tree cover to halt rising ground water levels across a region previously devoted solely to annual herbaceous crops.

The behaviour of the plantation-grown mallee (*E. kochii*) studied by the authors mentioned above is highly relevant since the species employed is indigenous to the deep sands on which the project was undertaken and is now extensively planted in the same region. Figure 10 shows the lay out of the tree belts, placements of neutron moisture tubes and the 'unit-tree rooting zone' used for construction of water budgets. Figure 11 presents the resulting budgets for water usage of trees over three consecutive intervals of a 22-month study period. Neutron moisture meter (NMM) profiles for each period are shown with a white/black colour grading to denote increasing water content. Comparable NMM profiles are given for pastured-alley areas beyond the rooting influence of the mallees. The silcrete hardpan horizon at 5 m depth is indicated in Fig. 10 and note that several of the multiple tap roots of each 4-year-old sapling had typically penetrated well below this horizon (Wildy and Pate 2002). Evidence from NMM profiles assessed after heavy rain (Fig. 11, period 1) suggested that this silcrete horizon was acting as a

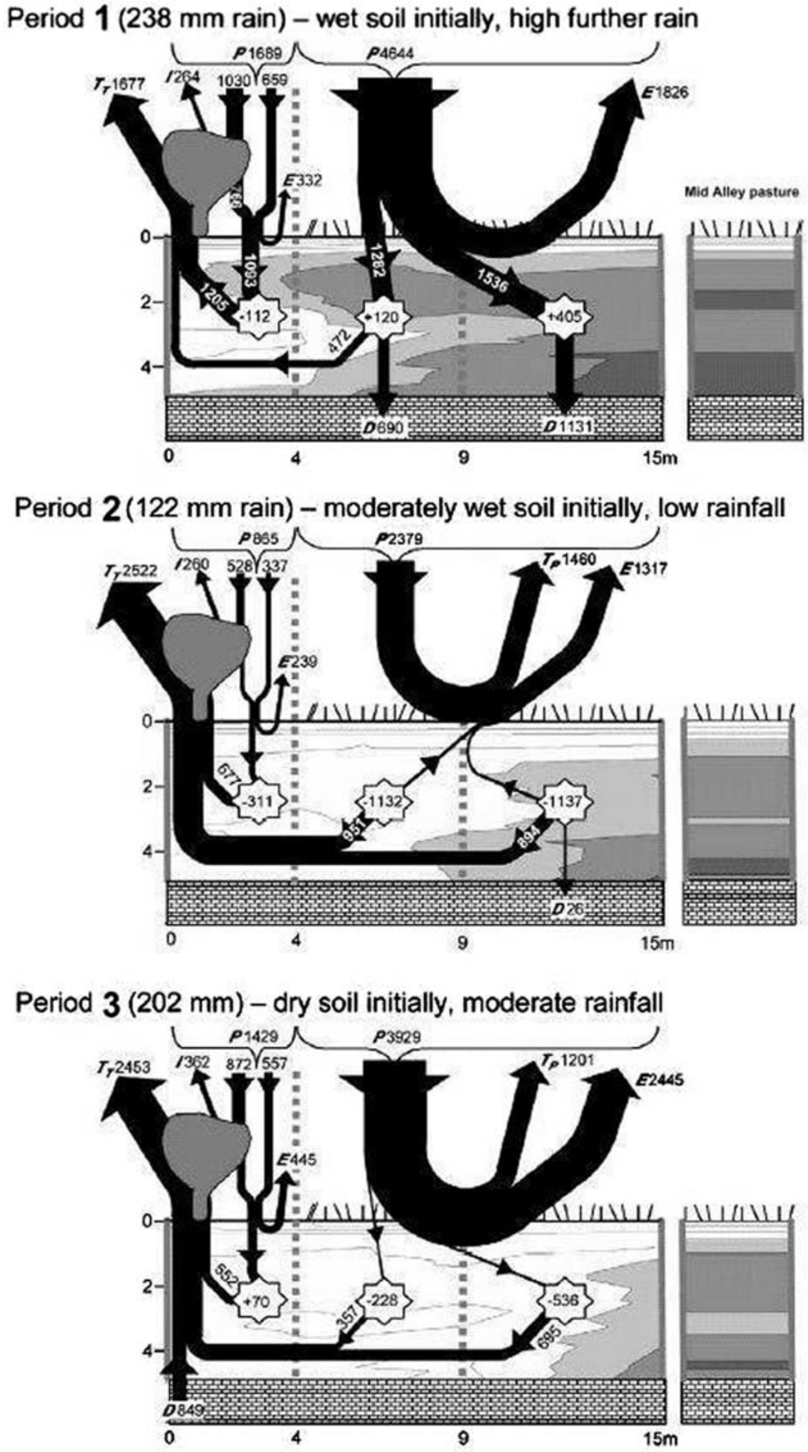


Fig. 11 Water budgets for the same oil mallee alley system shown in Fig. 10. Three successive periods of a 22-month study interval are depicted. A grey scale (*white* least, *darkest* most) underlay depicts relative amounts of soil water for each period within the unit-tree zone and for a tree-free area in adjacent pastured alleys devoid of tree roots. See text for information on coding of budget items and significance of patterns of water use under the contrasting conditions experienced by trees in each interval of the study (data from Wildy et al. 2004)

temporary barrier to recharge of the water table below.

The empirically based budgets shown in Fig. 11 utilised the already mentioned values for canopy interception detailed earlier in Fig. 4. Fluxes for the tree zone (shown in Fig. 11) are indicated as precipitation (P) and transpiration (T_t) by tree canopy; transpiration from pasture (T_p) occupying areas beyond canopy cover, but still within rooting catchments of trees; evaporation from soil surfaces (E); interception losses (I) and deep drainage (D, downward directed arrows). Uptake of water from ground water below the hardpan is shown by upward pointing arrows. The white star designations in each budget denote changes in soil moisture for each region of the 'unit-tree rooting zone' from start to end of the study period in question, with negative values denoting decreases, positive values increases in soil reserves. Values for each budget item are given in litres for the study interval and arrows indicating directions of flux are drawn proportional to relative amounts of water moving between the various compartments of the system.

The budget constructed for period 1 (Fig. 11) illustrates the effect of further rain on an already-wet upper profile. Trees are then pictured as meeting their water budget mostly from stemflow, through-fall of rain and additional uptake of water from soil above the hardpan. Rain falling outside the canopy is seen to add further to soil reserves but is mostly depicted as being lost through deep drainage. Period 2 was one of low rainfall with most of the water transpired by trees obtained by depletion of soil water reserves. Period 3 involved moderate fall of rain on a soil which was initially dry. It witnessed further drying of the profile almost to the full extent of lateral root development, with trees therefore forced to draw substantially from water below the hardpan.

The examples given in Fig. 11 and comparable budgets provided by Wildy et al. (2004) for uncut saplings and saplings recently coppiced within the same mallee plantings, collectively demonstrate the amazing flexibility shown by rooting systems of the species in optimising utilisation of all currently available resources within a catchment. The study as a whole demonstrated how important it is to conduct long-term detailed studies on progressive utilisation by trees of rain and water in a profile, in order to obtain a comprehensive assessment of the ability of a species such as *E. kochii* to survive against uncertainty in rainfall within a semiarid landscape.

Mineral relationships of vegetation and soil of open woodlands, shrub-heath and mallee

Much less is known of this aspect of the behaviour of woody species of arid ecosystems than demonstrated above for utilisation of resources of water. Furthermore, we know of no studies in which nutrients and water have been investigated together, with the objective of appreciating how uptake and possible release of nutrients back to soil might relate to source–sink relationships between plant organs and directionalities of water flow in relevant transport systems of xylem and phloem. Similarly, deficiencies in knowledge extend to responses of species to rooting substrates of different composition and especially as to how they utilise specific nutrient elements of limited availability. As an even more glaring gap in our knowledge, virtually nothing is known about possible mobilisation, uptake and transport of elements not directly involved in plant functioning (e.g. Al, Ge, Ti, U, Th and Ga), despite their importance in terms of our understanding, interpretation and mapping of pedogenetic processes. Finally, deficiency of knowledge extends to the processing of Si by woody species, notwithstanding evidence provided earlier on the importance of this element in biogeochemical cycles and structural entities within various plant taxa (see earlier discussion and Clarke 2003).

A limited amount of information is available on transport of nutrients in xylem and phloem of *B. prionotes* in its native woodland (Jeschke and Pate 1995) and for *Eucalyptus globulus* Labill. in plantation culture (Pate et al. 1998). As shown in Table 1, these two species show unusually low levels of K, but high ratios of Na:K and higher levels of Ca in their phloem than one would typically find for published data on other mostly cultivated herbaceous taxa. These characteristics suggest that the above tree species might use Na to replace K for meeting their requirement for

Table 1 Comparisons of the mean concentrations of major organic and inorganic solutes in phloem and xylem sap *of Eucalyptus globulus* and *Banksia prionotes*. Ranges in concentration are given for monthly samples taken across a year. Data from Pate et al. (1998) for *E. globulus* and from Jeschke and Pate (1995) for *B. prionotes*

Solute	*E. globulus*				*B. prionotes*			
	Phloem sap (mM)		Xylem sap (mM)		Phloem sap (mM)		Xylem sap (mM)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Amino acids	11	0.7–20.2			5.8	±1.2	0.42	±0.07
Total sugars	674	539–824	0		537	± 68	0	
K	29.1	±0.38	3.28	±0.59	17.1	±2.3	1.65	±0.19
Ca	0.245	±0.01	1.08	±0.22	6.1	±1	0.46	±0.1
Mg	2.09	±0.26	0.68	±0.15	12.2	±2.4	0.43	±0.07
Na	10.48	±1.30	1.18	±0.24	30.9	±3.5	1.5	±0.15
Total S	1.85	±0.13	0.92	±0.58				
Total P	1.88	±0.27	0.18	±0.06	0.83	±0.16	0.054	±0.01
Cl	2.16	±0.30	1.64	±0.38	60.1	±9.6	2.4	±0.9
NO_3	Trace		0.03	±0.00	0.29	±0.09	0.003	±0.004
Malate	NA		NA		9.8	±1.8	0.61	±0.28

NA not measured

monovalent cations in phloem transport, while also showing a greater than normal ability to translocate Ca away from sites of initial deposition in foliage. One would also suggest that the relatively high levels of organic acids in transport channels of xylem and phloem of the two species might carry implications for chelate-based transport of Fe and certain trace elements from roots via xylem, as well as for secretion of organic acids from roots to facilitate uptake of P.

The studies by Jeschke and Pate (1995) on seasonal changes in composition of xylem bleeding sap of cluster roots, lateral roots, sinker roots and trunk bases of 6-year-old trees of *B. prionotes* have pinpointed cluster roots as principal sites of uptake of P, K, Na, Cl and demonstrated that the same roots have an ability to reduce nitrate and synthesise and export amino acids following such reduction. Sinker-root xylem sap also contains generally lower levels of nutrients than corresponding xylem sap of lateral roots, e.g. situation for PO_4^{3-} in roots of *B. prionotes* reported by Jeschke and Pate (1995). However, bearing in mind the dependence of trees throughout the dry season on sinker-derived ground water, appreciable amounts of Mg^{2+}, Ca^{2+}, Na^{+}, Cl^{-} and SO_4^{2-} would still be arriving in the shoot at such times. This might well indicate capacities by the species to mine and retrieve nutrient resources of this nature from great depth. The possibility also exists that cluster roots borne deeply down in a profile might provide shoots with P via sinker roots.

Unfortunately, no comparable information is available for mineral relationships of mallee-dominated ecosystems despite a limited set of determinations of composition of above-ground biomass of woody taxa of semiarid ecosystems (e.g. see Pate and Dell 1984 and Foulds 1993). These data would indicate that wide variations may exist in mineral balances of dry matter between taxa, with a general trend towards lower levels of the limiting nutrients N, P and K than in corresponding taxa from soils of higher nutrient status. There are also cases of taxa carrying outstandingly high loads of Ca and Fe and occasionally also of certain trace elements. Nevertheless, our unpublished data (P.D. Galloway, J.S. Pate and W.H. Verboom) from a recent comparison of myrtaceous and proteaceous woodlands has failed to uncover consistent differences between the two ecosystems in such respects.

A further general aspect of the mineral nutrition of Australian ecosystems is the unusually great efficiency with which N, P and K are withdrawn prior to senescence of older foliage (e.g. see review of Pate and Dell 1984). By contrast, other elements such as Na, Ca, Mg and Fe are mobilised with much lesser efficiency. As a result, naturally falling dead leaves and senescing shoot material should normally provide a substantial return to the soil of the latter group of elements but not of N, P and K.

Another common feature concerns the remarkable ability of taxa to concentrate nutrients such as N and P and certain trace elements in their seeds and to do so mostly by coupling fruit filling to very effective mobilisation from old foliage. A spectacular example of this is found in large-seeded Proteaceae (Pate et al. 1986) where the well stocked and balanced mineral reserves of cotyledons of seeds turn out to be more than sufficient to permit a first-year seedling to develop its juvenile foliage and extend its deeply penetrating root system without having to recourse to mineral reserves from its immediate rooting environment.

Before one is able to understand fully the role of a particular species in uptake, utilisation and cycling of a specific mineral within an ecosystem, a number of items of information need to be available. Firstly, one requires information on the compositional changes across an annual cycle in xylem and phloem streams of the system, i.e. essentially along the lines summarised above for *B. prionotes* and *E. globulus*. Secondly, one should measure the net increments of each element occurring in specific dry matter of new parts of the tree produced during a growing season. This would comprise analysis of amounts of biomass produced in and mineral composition of new foliage and shoot extensions, production and filling of any reproductive structures formed in the same period, and seasonal investments of dry matter in fine feeding roots and in secondary thickening of trunk and perennial parts of the root system. Such balance sheets for increments of nutrient capital of parts and whole body of the tree would then have to be balanced against any nutrient losses from a tree, through-fall of dead leaves, twigs and branches and death of ephemeral parts of its root system.

There is of course the possibility that uptake of an element by one part of a root system might be followed by excretion elsewhere in the rooting profile. Unfortunately such processes cannot be evaluated on the basis of the budgeting procedures outlined in the previous paragraph. As far as we are aware there is no concrete evidence of such absorption:secretory processes operating in woody species of arid ecosystems, despite their attractiveness in explaining phenomena such as the progressive accumulations of Ca, Na, Mg, Si and Al occurring in certain mid-profile regions of texture-contrast soils under mallee. Nevertheless, there are tantalising instances elsewhere in the literature where biological processes have been invoked to explain anomalous accumulations of such elements and clay minerals (see Lucas 2001).

To provide an indication of the likely complexities of nutrient cycling processes occurring within a phytotarium due to a single woody species, we refer to an earlier published example depicting the annual cycling of P, Fe and C in rhizosphere and soil of a woodland ecosystem dominated by stands of 30-year-old proteaceous trees (*B. prionotes*) at Moora, Western Australia (see Fig. 12). Note that the schemes illustrated place heavy involvement of micro-organisms in cycling processes and the extensive involvement of photosynthetically fixed C in energisation of the biological activities concerned. Associated with this there would of course be a considerable expenditure of water in mediation of nutrient uptake and transfer processes, and, more importantly, in fuelling the transpiration losses of the tree which accompany photosynthetic uptake of CO_2 by its foliage.

As documented in our recent paper (Pate et al. 2001), the situation in relation to P in laterites and podzols under cluster-root bearing taxa typically shows concentration of the element in nodular parts of ferric horizons (see Fig. 12) which are also unusually rich in amorphous Fe, Si and Al. Involvement of micro-organisms in such processes is suspected. Similarly, comparisons of compositional features of ferricrete and calcrete 'nodules' versus closely associated soil from across the wheatbelt (Table 2), show a much higher content of oxalate-extractable P, Cu, Zn and Ti on crete coatings and associated amorphous constituents. Furthermore, it would seem that the degree of such micro-element segregation between components may vary widely between sites and structural entities.

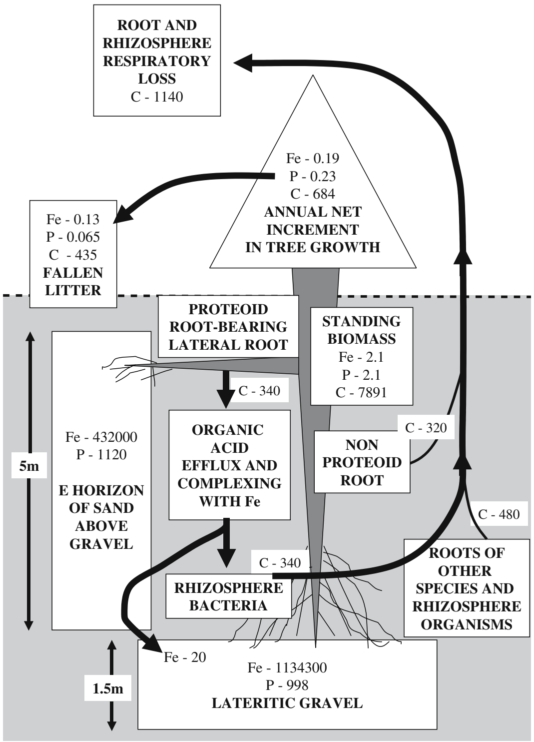


Fig. 12 Pictorial representation of annual cycling of phosphorus, iron and carbon in plant and rhizosphere components of a *Banksia prionotes* woodland at Moora, Western Australia, in relation to pools of iron and phosphorus in the overlying sand and lower lateritic gravel. Iron deposition in ferric rinds of the laterite is depicted as resulting from leaching of ferric-citrate complex from the upper proteoid root zone and subsequent breakdown of the complex by citrate-utilising bacteria associated with the lateritic gravel (reproduced from Pate et al. 2001)

The concentration of P in pisolithic ferricrete horizons contrasts noticeably to the situation in depleted pallid horizons lying between it and nutrient sources in the underlying crystalline rock. Despite this disconnection and a modicum of losses of the element via erosion, vegetation continues to thrive, possibly assisted by retrieval of P following microbial deep mining of apatite (see Banfield and Eggleton 1989). The situation in texture-contrast profiles has yet to be evaluated but, in view of the exceptional deep-rooting capacities of mallees and other Myrtaceae, the possibility exists that such plants might mediate retrieval of P from deep crystalline basements. Again, microbial effects may be involved.

Table 2 Concentration of acidic ammonium oxalate-extractable elements in ferricrete and calcrete coatings and in samples of closely associated soil. Data relate to individual cretes collected at stations scattered across the Western Australian wheatbelt. Extraction methods used are described in Blakemore et al. (1981) and Rayment and Higginson (1992)

Dominant woody community	Crete type	Element (mg kg^{-1})													
		Al		Fe		Si		Cu		Zn		Ti		P	
		Soil	Coat	Soil	Coat	Soil	Coat	Soil	Coat	Soil	Coat	Soil	Coat	Soil	Coat
A. Proteaceous shrub-heaths/woodlands	Pisolitic ferricrete	130	3,100	82	16,800	21	780	<1	38	<1	20	1	25	2	15
	Pisolitic ferricrete	290	4,500	130	12,100	27	1,000	2	5	2	4	1	16	6	12
	Pisolitic ferricrete	310	5,400	110	123,000	25	1,100	4	27	2	20	1	26	4	13
	Pisolitic ferricrete	280	2,200	120	6,900	19	150	<1	4	<1	4	<1	10	1	7
	Soft nodular ferricrete	34	700	12	950	9	110	<1	17	1	29	<1	2	<1	3
B. Myrtaceous woodlands	Calcrete overprinting ferricrete	700	2,900	420	1,600	430	1,900	<1	18	3	12	5	5	20	30
	Calcrete	1,000	3,400	300	68,000	370	2,400	3	14	1	10	3	6	10	27
	Calcrete	690	780	300	680	310	670	4	8	1	5	4	1	2	11
	Calcrete	140	1,800	120	14,700	33	620	4	45	1	40	1	25	5	42
	Calcrete	690	770	400	380	280	640	6	3	1	3	2	<1	3	10
	Calcrete	640	680	230	1,100	240	470	4	2	1	4	2	1	3	14
	Calcrete	78	830	26	950	9	1,000	<1	10	<1	9	<1	1	2	20

Especially crucial to our current hypothesis is whether any or all of the above differences in soil mineral status are simply endemic to the parent soil in which a specific vegetation type is growing, or, as we would contend, have been partly engineered and sustained through mineral relations peculiar to the woody macro elements of the communities concerned.

Bioengineering of soil profiles and the 'phytotarium' concept: evidence to date and some unanswered questions

The hypothesis defended in this review is that large woody plants of semiarid ecosystems, and the micro-organisms with which they are associated, have the capacity over time to alter radically the soils which they inhabit and thereby create niches optimising capture and utilisation of limited resources of water and nutrients. Construction and maintenance of this so-called 'phytotarium' is fuelled in time and space by photosynthate, which in turn requires continued access to water and nutrients for growth and survival of constituent plant biomass and the interdependent micro-organisms which feature constructively in the system.

Our hypothesis further states that progressive major changes in compositional and structural features of a soil profile over long periods of time may be brought about by organisms of the phytotarium working alongside undirected reworking of materials by physical and chemical influences associated with weathering, erosion and deposition across a landscape. The latter processes are of course already well known and documented by soil chemists and geologists, and may well comprise dominant formative influences in many situations.

Table 3 summarises a range of biotic influences on soil profiles which we consider to comprise minor and major elements in construction and functioning of phytotaria. The sixteen items listed have already been documented and discussed at various places in this literature review and in an accompanying paper (Verboom and Pate, 2006), the latter dealing exclusively with our own observations in a south-west Australian setting. Each item in Table 3 is annotated in terms of classes of biota involved, the underlying mechanisms that are likely to be operating, and what we would regard as significant end results to functioning of the ecosystem in question.

It should be emphasised that Table 3 is by no means exhaustive. There are, for example, local cases of presumed niche-building to be found in the generation of exceptionally acidic rhizospheres under certain acacias and the high accumulations of salt under typical eucalypt woodlands carrying understoreys of halophytic Chenopodiaceae. These further examples are not mentioned and discussed simply because little or no study has been conducted on their edaphic qualities and the roles which indigenous flora and micro-organisms might play in their functioning

Application of the phytotarium concept to water relations of ecosystems embodies the principle that dominant trees and shrubs have a capacity to manipulate the outcomes of rainfall through features such as (a) stemflow following interception by canopies, (b) preferential flow of water into deep subsoil horizons via spaces, pipes and channels (Items 1 and 2, Table 3) and (c) monopolisation of recent rainfall events through the agency of dense proliferations of seasonally produced feeding roots. These features, combined with incomplete wetting of a sandy A horizon through various forms of hydrophobicity (Items 3 and 4), are likely to result in effective harvesting and storage of recently fallen rain in lower as opposed to upper parts of a rooting profile. We would suppose that these features will collectively favour deep-rooted trees and shrubs over small understorey components. Indeed, in certain cases they might well be responsible for an almost total suppression of ground cover in an ecosystem [e.g. woodlands of mallet (*E. astringens*)].

The mallee system we describe in our companion paper carries the additional feature of a texture-contrast seal (Item 5, Table 3) composed of clay and various Si-based components. Such seals effectively decouple hydrologically a sandy A from B and C horizons, thereby again creating a phytotarium which should strongly favour woody macro elements over smaller plant species. The review of Rengasamy (2002) and our

Table 3 Bioengineering attributes and outcomes suggested as plausible elements of a phytotarium concept. See text for further details and relevant literature references

Item no.	Soil feature	Formative agents	Mechanisms involved	Function
1	Silicon-lined root channels	Precipitation of Si	Root-secretion of biogenic Si by certain eucalypts	Downward channelling of water
2	Ferric-lined root channels	Precipitation of Fe	Processing of Fe by proteoid root exudates and bacteria	Downward channelling of water
3	Water repelling soil surfaces	Mallet leaf litter, cryptogammic crusts	Chemically based hydrophobic effects	Uneven wetting of upper profile
4	Localised water repellency in subsurface soil	Fungal mycelia and old cluster root mats	Chemically based hydrophobic effects	Uneven wetting of lower profile
5	Texture-contrast seal	Dispersed clay and precipitated Si in certain mallees	Root-secretion of biogenic Si and dispersing agents?	Hydrologic decoupling of A from B horizon
6	Finely divided carbonate	Precipitation of carbonate	Processing of Ca by bacteria	Enhancement of water storage in B horizon
7	Nodular calcretes	Precipitation of carbonate and Al and Si	Processing of Ca by ectomycorrhizal fungi and bacteria	Sequestration of P and refugia for microbes
8	Hardpan horizons	Precipitation of Si and some Fe	Root-secretion of biogenic Si by certain eucalypts	Restricts deep drainage
9	Silcrete horizons	Precipitation of Si	Root-secretion of biogenic Si by certain acacias	Restricts deep drainage
10	Pisolithic ferricretes	Precipitation of ferric rinds	Processing of Fe by proteoid root exudates and bacteria	Sequestration of P and refugia for microbes
11	Overprinting of ferricrete by amorphous Si, carbonate or clay	Incursion of proteaceous vegetation by certain Myrtaceae	Root-secretion of biogenic Si, Ca and dispersing agents	Commandeering of existing niche by other vegetation type?
12	Sand-binding roots	Monocotyledon understorey species	Permanent entrapment of sand on lignified root hairs	Bio-pore for water or occupancy by seedling roots
13	Nutrient enrichment of upper profile	Biota operating in the lower regolith	Phosphorous mining by microbes and absorption by roots	Maintenance of P capital in ecosystem
14	Soil phytoliths	Si accumulation as plant opal	Release of Si from decomposing plant biomass	Contribution of biogenic Si to layers and root pipes
15	Abrupt lateral facies changes from one crete to an other	Transition between vegetation types	Vegetation specific effects on soil profiles	Protection of the adjoining niches
16	Multiple vertical facies changes	Sequential long-term formation and burial of several distinct phytotaria	Phases of aggradation and plant growth under climatic change	Probably none

unpublished measurements provide tentative evidence that salts in the lower horizons of pristine mallee profiles are deposited and maintained in situ over time through the agency of tree roots and micro-organisms. Furthermore, levels of finely divided carbonates and clays (Item 6, Table 3) are especially concentrated below the seal, thereby enhancing retention of available water in lower parts of the profile. Mechanisms by which fine carbonates and nodular calcretes (Item 7, Table 3) accumulate in specific regions of a profile under myrtaceous vegetation are obscure, yet our tentative conclusion is that calcium leached or channelled from above, or even actively secreted by sinker roots, may well be reworked by micro-organisms and thence transformed to carbonate. The latter process might possibly occur via oxalate, as recently suggested by Braissant et al. (Braissant 2002, 2004).

Given that the benefits of the texture-contrast seals and calcareous subsoils are manifestly in favour of dominant woody species, it would seem reasonable to assume that selection pressure in dry environments will direct large woody plants and associated biota towards achieving such outcomes. This being so, many parallels are then likely to be found on a world-wide basis to that recorded here for mallee vegetation. More specifically we would suggest that mechanisms that effect dispersion of clay and depletion of Fe in the A horizon of texture-contrast soils might well be generally fuelled by secretion of low and intermediate weight carboxylates emanating from fine roots and associated micro-organisms in upper parts of soil profiles.

As mentioned earlier in this review, the origin of Si in texture-contrast, hardpan and silcrete horizons (Items 8 and 9, Table 3) and in various types of tubes and bio-pores is still poorly understood, despite growing evidence of biogenic Si being primarily or secondarily involved.

Pure and mixed proteaceous ecosystems on deep sands provide what one might regard as the least equivocal examples of bioengineering so far encountered. This relates generally to the formation of ferricrete pavements (Item 10, Table 3) at the base of rooting profiles of Proteaceae, with attendant deposition of Fe, Si and Al and associated sequestration of P at depth. As mentioned earlier, these effects flow secondarily from the secretion of low-molecular-weight organic acids by P-absorbing mats of proteoid roots. With poorly ordered clays and humic residues accumulating in and below this ferruginous horizon, a relatively effective hydrologic barrier forms, possibly leading to temporary perching of water during a wet season. As also shown in our earlier review (Pate et al. 2001), ferricrete horizons appear to provide not only a secure long-term reserve of P but may also act as a refugium for micro-organisms exploiting its tightly bound water during the dry season. Incidentally, the same deep sand systems dominated by Proteaceae may carry features conferring both incomplete wetting and preferential channelling of water, as mentioned above for texture-contrast soils vegetated by mallee.

The transect described in our companion paper (Verboom and Pate, 2006) provides an instructive example of lateral transitions between a complex intermixing of Sodic Calcisols and Calcic Solonetzes (FAO 1998) under mallee and contrasting layering of ferricrete under proteaceous shrub-heath. The overprinting of pisolithic ferricrete by fine siliceous deposits and clay (Item 11, Table 3) in mid regions of this ecotone bear what we regard as the hallmarks of an advancing myrtaceous ecosystem. Elsewhere in the transect, under pure proteaceous shrub-heath, an upper sandy horizon containing lateritic pisoliths occurs above a lateritic pavement, with essentially no evidence of overprinting. Principal evidence of bioengineering then comes from the prominent ferric linings to current or previously occupied root channels. Similar Fe and Si coatings to root channels are alluded to elsewhere in this review, essentially as biotically induced modifications relevant to channelling of water. In the same vein, sand-binding roots (Item 12, Table 3), commonly encountered amongst herbaceous and semi-woody understorey components of woodlands and shrub-heath on deep sands, provide unequivocal evidence of plant involvement in certain channel-building exercises.

We highlight the dimorphic root system, with its extensive lateral roots, tap roots and seasonally formed trappings of fine feeding roots as playing a key role in accessing, transferring and recharging current resources of water and nutrients between roots and shoots of large woody species. Using detailed season-by-season water budgets for plant and rooting catchment and heat-pulse probe analysis of flow pathways, we conclude that certain tree species of semiarid systems are eminently equipped to utilise preferentially the water resources most readily available at a specific point in time. This they do through capacities to transfer water both transversely or vertically from regions of current availability to ones of deficiency. Indeed there is increasing evidence that certain aspects of their transport activities might even be targeted specifically towards storage of water for use later in a season.

It is likely that rooting behaviour of dimorphic type, and the functional attributes which accompany it, may turn out to be a commonly displayed feature of woody macroflora on a world-wide basis, just as has already been well documented for podzolic forest ecosystems across the Northern Hemisphere.

Turning to exploitation of nutrient resources within phytotaria of semiarid ecosystems, a much less clear picture emerges. Nevertheless, we hypothesise that bioengineering principles may well predominate, particularly in relation to formative effects of major plant taxa and relevant microorganisms on uptake, transfer and depletion or concentration of specific nutrient elements between and within soil compartments. Such processes are likely to result mostly from secretions by various biota of low and intermediate molecular weight organic anions. Under this same banner would come the microbially mediated processes associated with cycling of P, Ca, Si, Al and Fe and alleged instances of root exudate-induced dissolution and dispersion of clay and related accumulations of major elemental components within crete pavements.

When viewing the above general framework one cannot fail to pose questions concerning the starkly contrasting behaviour of vegetation dominated by Proteaceae versus that by Myrtaceae. The former class of community is driven nutritionally by cluster roots through the agency of secretion of low-molecular-weight organic acids and is consistently associated with rooting environments of low pH and Ca content but high in reactive Fe and Al. We cannot understand fully how the cluster-root habit is so competitive in such situations and what cause and effect relationships exist within such a framework. However, according to recent studies of Shane and Lambers 2005, the spectra of organic acids secreted by cluster roots differ between taxa, with functioning of each species component strongly influenced by pH and stability constants. With effects of cationic charge also likely to be involved, the flourishing of Proteaceae in some ecosystems compared to their virtual exclusion from others may become much more understandable.

In sharp contrast to the above, soil profiles carrying myrtaceous systems, including those dealt with in our companion paper (Verboom and Pate, 2006), typically exhibit a shallow, acid, leached, sandy upper horizon effectively separated from lower horizons by a sparingly permeable texture-contrast seal-like barrier. The lower horizon is typically of high pH and contains segregations and concretions involving Ca and Si. It is difficult to understand to what extent large woody plants might be involved in construction, operation and maintenance of such structures, nor why there is such dominant involvement of ectomycorrhizal agencies in this class of phytotarium. Even more puzzling is why understorey vegetation of such systems tends to be so sparse and species depauperate.

Equally important to mineral relationships is the well-authenticated ability of deep-rooted woody species to abstract elements such as P, Ca, Al and possibly Si from uppermost parts of a regolith and below (Item 13, Table 3) and eventually to deposit a proportion of such elements in their shoots. This inevitably leads to a return of the same elements to the A horizon as litter, possibly accompanied by bio-cycling of Si via phytoliths (Item 14, Table 3). If one then adds different capacities by different taxa to absorb and cycle particular elements, a useful platform emerges for assessing experimentally how the mineral balance of the soil profile under one ecosystem might become biotically modified in such a different direction from that shown by other ecosystems on the same regions of a landscape.

Perhaps the most compelling evidence attesting to biological as opposed to abiotic mechanisms operating within regoliths comes from the examples of lateral and vertical facies changes (Items 15 and 16, Table 3) described in our companion paper (Verboom and Pate, 2006). These comprise vertically aligned or horizontally opposed horizons of lateritic and Solonetzic soils, presumed to have been bioengineered in near contemporary or earlier periods when proteaceous or myrtaceous taxa dominated. In the case of lateral facies changes, a horizon of calcrete under myrtaceous vegetation abuts on ferricrete under proteaceous heath. In such cases we would conclude that the contrasting horizons formed contemporaneously within the same deposit. Conversely, in the vertically stacked facies described by Verboom and Pate (2006), imprints of a sequence of different layerings are interpreted as denoting epochs of different vegetation type. In another situation alluded to by the same authors for the Gnangarra mound near Perth, Western Australia, vertical facies changes are encountered comprising successive layerings of ferricrete/humicrete alternating with broad bands of bleached sand. The interpretation in this case is that each ferricrete/humicrete horizon denotes an imprint of bioengineering activity left behind by a distinct phase of proteaceous woodland, with each of such formations becoming successively buried by incursions of sand during intervening periods of aeolian activity.

By way of general comment we note that Paton et al. (1995) trace the apparently intractable position of modern pedology to an adoption of the ‘five-state factors’ of soil formation, climatic determinism and the associated concept of soil zonalism. Our present hypotheses stand in contrast in building on a large body of very early Russian work which is well summarised in the recent thesis of Ackert (2004). Kostychev cited by Ackert visualised soil formation as a process broadly linked to the geography and physiology of higher plants and their microbial associates while Rizpolozhenskii went further by suggesting that soil formation involved the interaction of two primary factors—organisms and rock. In other words, he relegated state factors such as climate and topography to a mere status of external conditions. He thus concluded that the differentiation of parent materials in soil formation centred upon the ‘the circulation of elements between organisms and nature’, or ‘the seizure (zakhvat) of food by organisms from the unorganised environment and its reciprocal return (obratnyi vozvrat)’.

We admit to being a long way off from properly fledging our ‘phytotarium’ hypothesis in relation to semiarid ecosystems and more specifically for accounting for the puzzling differences in composition between soil types under different classes of vegetation. However, we do contend that the evidence presented of deep-seated biotic effects is adequately substantiated and appropriately focussed as a basis for future study. Indeed, it may well be that our Australian examples will provide a series of interesting counterparts to a plethora of biogenic influences at work in other ecosystems on a world-wide basis.

Acknowledgements In our earlier review (Pate et al. 2001), we gathered information showing that laterite and podzol generation in south-west Western Australia may have arisen from niche-building activity of cluster-root bearing taxa. Since then many colleagues have pointed out interesting work that we should have referred to or which has been undertaken since the review was written. In this regard we are particularly grateful to Neil McKenzie, Hans Lambers, Mehrooz Aspandar, Jim Charley, Paul Galloway and Peter DeBroekert. Alicia Gardner helped with preparation of the references and some of the figures. The Chemistry Centre performed and contributed to the costs of the analyses presented in Table 2 and we thank David Allen for facilitating this service.

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