

Contemporary biogenic formation of clay pavements by eucalypts: further support for the phytotarium concept

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- **Background and Aims** Clayey (sodosolic) pavements were studied in lateral root catchments of eucalypts where mixed myrtaceous:proteaceous vegetation was colonizing a dune of quartzitic sand blown out from a playa lake during late Pleistocene times. The site at Chillinup in south-west Western Australia provided an opportunity to examine these signature pavements in an unequivocally recent setting, and to assess their effects on competing non-eucalypt vegetation.
- **Methods** Pavements were located, and their extents and depths assessed by probing with steel rods, followed by corings and pit excavations using an air spade. Listings of plant species, growth forms and root morphologies were assembled for different vegetation zones in a representative transect across the dune. A deep cutting through the dune provided details on pavement morphology and modifications to the sand deposit bioengineered by eucalypt and heath vegetation.
- **Key Results** Clay pavements comprised closely spaced, round-topped columns whose mean diameters and depths varied between eucalypt species. Incipient pavement formation was characterized by clumps of clay deposited around fine root material. Pavements appeared to have been synthesized *in situ* from locally accessed and imported constituents. Understoreys on superficial pavements of a tree eucalypt were considerably less dense and biodiverse than on the deeper pavements of two mallee species, whilst most profuse vegetation cover was encountered in heath on unmodified (non-pavemented) sand. Certain species were restricted to superficially located pavements, whilst other 'generalist' species occurred widely across the dune. Relict pavements formed by earlier generations of eucalypts were present in certain areas of the transect and in soil profiles of the cutting. Some relict pavements colonized by proteaceous shrubs were overprinted with ferricrete.
- **Conclusions** Clay pavements formed by eucalypts have pronounced effects on understorey vegetation and may have been instrumental in establishment of the complex mosaics of mallee-woodland and proteaceous heathland observed across semi-arid landscapes of south-west Western Australia. Findings are related to earlier observations on the range of plant-mediated changes in soil profiles discussed in the recently advanced 'Phytotarium' concept.

Key words: Biomineralization, eucalypt roots, niche construction, soil profiles, woody plants, semi-arid ecosystems, vegetation mosaics, competing phytotaria.

INTRODUCTION

It remains a daunting challenge for soil scientists to disentangle the respective biotic and abiotic influences through which resident and advected materials have been transformed into the complex soil profiles encountered across ecosystems of the world today (Lucas, 2001; Gregory, 2006; Amundson *et al.*, 2007).

The authors' contributions in this connection have been limited so far to semi-arid heathlands and woodlands of south-west Western Australia, where a number of examples have been identified in which bioengineering by major woody taxa and their microbial associates have apparently led to the formation of uniquely structured soil profiles. Principal situations studied are the iron-rich ferricretes precipitated under Proteaceae-dominated heaths and woodlands (Pate *et al.*, 2001), and the platform-like clay (sodosolic) layers intimately associated with the lateral root systems of mallee-type eucalypts (Verboom and Pate, 2006a, b). In the former, phosphorus-acquiring cluster roots have been identified as principal agents of iron (Fe) mobilization

(Hinsinger, 1998; Jones, 1998; Lambers *et al.*, 2002; Shane and Lambers, 2005) prior to, and possibly during, ferricrete formation (Pate *et al.*, 2001). In the latter, intimate associations between microbial symbionts and fine roots of the eucalypts are suspected candidates for biogenesis of the clay material from which pavements are constructed (see discussion in the review of Verboom and Pate, 2006a).

The term 'Phytotarium' was recently introduced (see Verboom and Pate, 2006a) to embrace a range of activities, such as described above, and these are collectively viewed as instances where targeted changes in soil profile characteristics appear to optimize control of resources of water and nutrients by the principal plant players involved.

During a recent survey of the Kalgan catchment, the authors came across a series of crescent-shaped sand dunes (lunettes) considered by geomorphologists to have been formed by blow out from playa lakes during episodes of aridity in the final phases of the Pleistocene (12–19 thousand years ago) (see Bowler, 1976; Wasson, 1986; Harper and Gilkes, 2004). One of the few lunettes still covered with pristine native vegetation was selected and found to consist of uniform quartzitic

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aeolian sand deposited at up to 9 m depth on old lacustrine deposits. Currently vegetated by a mosaic of myrtaceous:proteaceous shrubland intermixed with open woodland dominated by eucalypts, the lunette was immediately recognized for its potential in unravelling interactions of competing phytotaria colonizing the same rooting substrate in an indisputably recent setting.

MATERIALS AND METHODS

Study site

The lunette selected for study is located at Lake Chillinup (LC; grid ref S34°32'54" E118°04'12") in the South Stirlings region of the South West Botanical Province. The latter, as defined originally by Diels (1906) and dealt with in detail by Beard (1984), comprises approx. 300 000 km² of Mediterranean-type vegetation occupying the south-western coastal region

of Western Australia. Moving inwards from the south-west tip, the zone traverses moderate, dry and extra-dry Mediterranean climates, with the study site located in the second of these, some 35 km east of Mount Barker. A digital elevation model of the area (Fig. 1A) showed LC to be a large seasonally wet salt lake in receipt of water from the Stirling Ranges 15 km to the North. Other minor salt lakes (L) are also seen in Fig. 1A. The study dune (SD) represents the last major blow out from the lake. Other, earlier formed dunes deposited from the same ancestral lake system are indicated by 1, 2, 3 and 4. The contours of these have been subdued with time. A corresponding aerial photograph (Fig. 1B) demonstrates the extent of the native vegetation currently vested in the Chillinup Nature Reserve (R). The governing body (Department of Environment and Conservation) responsible for the reserve (No. 25386) gave the authors permission to proceed with the investigation. The transect chosen for study (ST, Fig. 1B), is approx. 200 m wide and

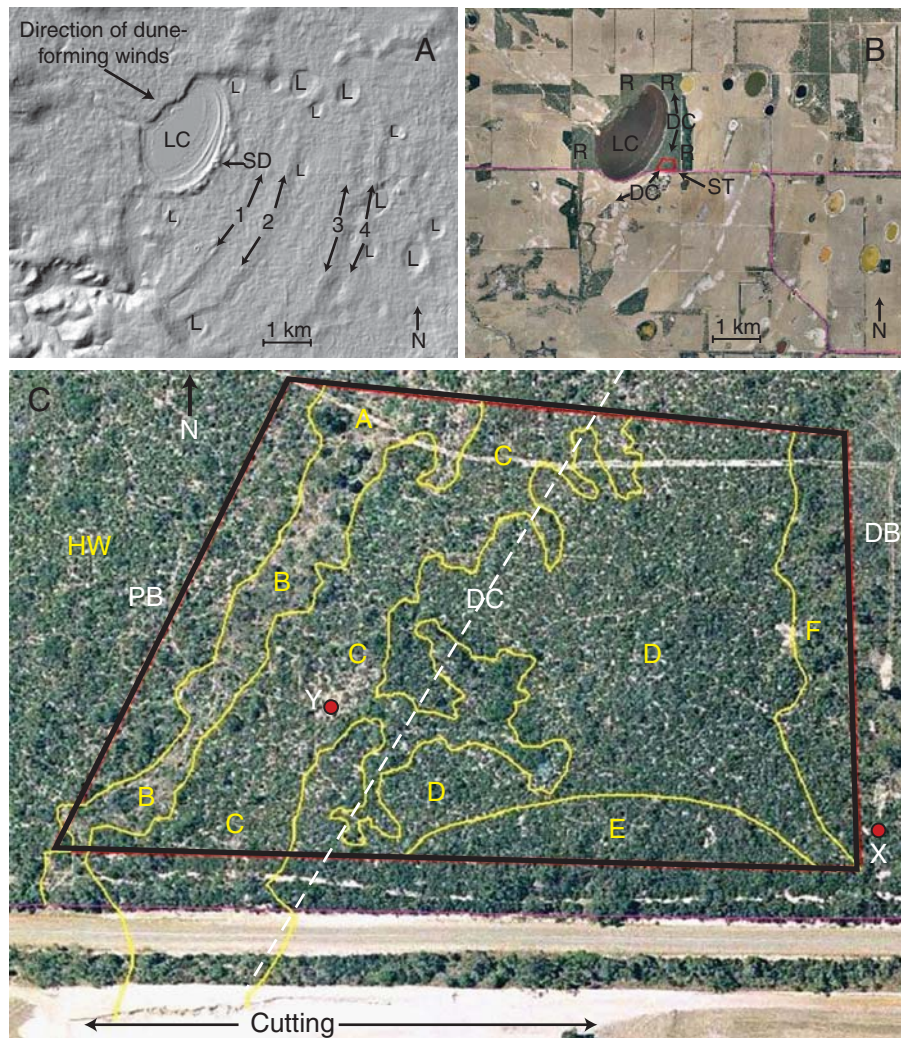


FIG. 1. (A) Digital elevation model of Lake Chillinup (LC) and surrounding area showing the location of the study dune (SD), earlier formed dunes numbered 1, 2, 3 and 4, and minor salt lakes (L). (B) Aerial photograph corresponding to (A) showing the extent of the reserve of relict vegetation (R) in relation to the orientation of the crest (DC) of the study dune and study transect (ST). (C) Large-scale aerial photograph of the study transect (outlined by a black line) showing principal zones of vegetation (A–F) and sites of lateritization X and Y. A band of low-lying heath woodland (HW) lies between the proximal boundary (PB) of the transect and the lake. Eucalypt woodland (not shown) lies eastwards of the distal boundary (DB) of the transect. The position of the cutting through the dune in cleared land outside the reserve is indicated.

400 m long, and orientated essentially at right angles to the crest of the lunette (DC, Fig. 1B).

A large-scale aerial photograph of the study transect (enclosed area, Fig. 1C) and its surroundings shows a band of low-lying heath woodland (HW) between the proximal (lake side) boundary of the dune (PB) and the shore of the lake. The dune rises sharply in height to its crest (dotted white line, DC), and then more gently down to its distal boundary (DB). The transect includes six representative zones of the vegetation typically seen throughout the dune (see zones labelled A–F in Fig. 1C).

Cutting through lunette

The southern flank of the lunette was cleared in the mid 1960s, and a cutting (Fig. 1C) driven through this area by the local Shire, in late 2006, to obtain material for road construction. The 200 m cutting essentially bisected the dune and removed sand to a depth close to that of the original lacustrine basement on which the sand had accumulated. The cutting exposed two opposing, well-preserved soil profiles stretching from proximal to distal ends of the lunette. The northern face closest to the reserve was selected for study, and changes in clay and bulk density with depth were assessed for selected regions of the profile. A modified pipette procedure (Indorante *et al.*, 1990) was used for clay determinations, and bulk densities were assessed by a core technique where soil was loose, or by a wax technique where soil was brittle and hard (Blake and Hartge, 1986). The former technique involved driving a bevelled steel core (70 mm long and 73 mm in diameter) into a clean face of the cutting. The cored material was dried and weighed, and its bulk density determined by relating weight to core volume. The latter technique involved coating a clod of known dry weight with paraffin wax and applying Archimedes' principle to assess volume. All samples were taken in triplicate.

Determinations of depths of sand deposited at different regions of the dune transect and cutting

Hand augerings measured depths to lacustrine deposits in lower regions of proximal and distal faces of the dune. Depths of intervening areas of deeper sand up to and beyond the dune crest were assessed from digital elevation models. Parallel assessments of depth of sand cover were made by direct measurements of heights from the soil surface down to the dune basement for different parts of the profile exposed in the cutting.

Vegetation of study site

Records were made of the presence or absence of all common species encountered in each vegetation zone, and growth and life forms of each species were assessed. Libby Sandiford of the Department of Environment and Conservation of Western Australia kindly confirmed identities of all common species collected.

General examination of soil profiles

Spot excavations by spade were conducted to 1.6 m depth to examine the upper rooting morphologies of all major herbaceous and woody species, while also characterizing the soil profiles which each was inhabiting. Extensive probings were conducted across all vegetation types using hand-driven, high-tensile stainless steel rods (5 mm in diameter and 120 cm long). The presence of a clay pavement was suspected wherever the probe encountered a zone of resistance. This was then confirmed or otherwise by spade, auger and further probing in the vicinity. No instance was recorded where the depth to the top of a pavement exceeded 100 cm, i.e. within the 120 cm length limit of the probe.

Pit excavations and air-spadings for examining surface topographies of clayey pavements

Pits of approx. 5×2 m area were excavated in the lateral root catchments of the tree eucalypt, yate (*Eucalyptus occidentalis*) and two common mallee eucalypts (*E. pleurocarpa* and *E. decipiens*). Mature specimens were selected where earlier probings had demonstrated well-defined paved layers to be present. After removing a superficial layer of sand by hand, an air spade (model 150 scfm/90 psig, Air-Spade Technology, Verona, PA, USA), activated by an Ingersoll-Rand compressor supplying air at $0.8 \text{ m}^3 \text{ s}^{-1}$ at a pressure of 0.6 Mpa (see Nadezhdina and Cermak, 2003), was deployed to blow sand gradually out of each pit and thereby expose the major and minor roots ramifying through the pit area, while also uncovering the upper regions of the columns of which the pavement was constructed. Further sand was then removed down to the bases of the columns, after which air-spading became impossible on reaching an intractable layer. Pit excavations of *E. decipiens* extended out to the advancing front of a sector of the lateral root system where clay pavement was still under construction.

RESULTS

Distributions and surface morphologies of clay pavements under the study eucalypts in the reserve

Pavements were encountered in root catchments of the study eucalypts throughout the proximal face of the dune and extending slightly over its crest. The scattered small sized and presumably young trees of *E. decipiens* in the main body of heathland on the distal face of the dune (Zone D, Fig. 1C) lacked or showed only poorly developed pavements. Almost all individuals of *E. pleurocarpa*, and *E. decipiens* in Zone F, exhibited substantial pavements.

Pit excavations of study species showed upper regions of pavements to consist of regularly arranged, round-topped columns of uniformly dense clay material (CP, Fig. 2A). The exposed columns (Fig. 2B) proved to be of near constant diameter and height, and their surfaces generally smooth. However, shallow indentations (C) and well-defined polyp-like outgrowths (P) were present on some column surfaces. Columns in some pits were red (ferrihydritic/haematitic); in other excavations columns were yellowish brown (goethitic) or greyish, the latter suggesting low iron content.



FIG. 2. (A) Air-spaded exposure of a sector of the columnar pavement (CP) formed in the lateral root catchment of a yate (*Eucalyptus occidentalis*). The parent tree (PT) is at the far end of the excavation. (B) Close-up of columns showing occasional polyp (P), clefts (C) in and spaces between (arrows) round-topped columns (mean diameter 300 mm). Larger roots of eucalypts and other species traverse the pit, some roots occluded for part of their length by column material. (C) A fractured column (FC) showing a bright red (ferrihydritic or haematitic) interior with residues of fungal mycelium (M) exposed on the interior surface. Lateral roots (R) of a co-habiting species (*Conothamnus aureus*) lie above, penetrate into or descend between columns. (D) Site of nascent column formation in the outlying region of the lateral root catchment of a *Eucalyptus decipiens* tree showing reddish clay deposits surrounding a major root and associated fine roots of the eucalypt.

Most of the major lateral roots traversing a pit area belonged to the eucalypt species whose rooting catchment was being examined. Regions of some of the larger roots were encased within columns and emerged on diametrically opposed sides to extend horizontally further across a pit (Fig. 2B). Small roots were evident as bristle-like coatings projecting randomly from column surfaces. Some of these roots were of eucalypts, others of understory species. Breaking of columns with a hammer revealed that red colouring extended to their interior (Fig. 2C). Remains of fungal mycelia (M) were visible on some fractured faces (FC).

Roots of large co-habiting shrubs (e.g. species of *Calothamnus*, *Acacia*, *Banksia*, *Conothamnus* and *Melaleuca*) descended between columns into the sand profile below, while lateral roots of the same shrubs radiated outwards over long distances between and occasionally through the columns (see R, Fig. 2C). Herbaceous perennial species

(e.g. *Mesomelaena stygia*, *Harperia lateriflora* and *Gahnia ancistrophylla*) and ephemerals had relatively shallow root systems, mostly confined to the sandy A horizon and down into spaces between columns.

Mean depths to tops of columns were assessed by probing mid-catchment regions of ten individuals of each study eucalypt. Those of yate terminated significantly ($P < 0.001$) closer to the surface (mean 23.5 ± 3.8) than did those of *E. pleurocarpa* or *E. decipiens* (mean for both species 62.2 ± 5.9). The advancing front of the lateral root system at the far end of the pit under *E. decipiens* exhibited patches of fine root material around which small domains of clay had been deposited (Fig. 2D). Such areas were presumed to be sites of incipient pavement construction.

Evidence was obtained that columns of yate were of greater mean diameter (26.4 ± 0.5) than those found under the mallees (10.2 ± 0.4 , $P < 0.001$).

Distribution of clay pavements in transect areas outside rooting zones of eucalypts

Pavements were generally absent throughout non-eucalypt areas on proximal and distal faces of the dune (zones marked D and E in Fig. 1C). However, an interrupted zone of sparse understorey traversed the lower proximal face of the dune (delimited as Zone B in Fig. 1C) and this overlay a double-layered, superficially located pavement. It had presumably been constructed during two successive earlier phases of colonization by eucalypts. The boundaries between Zone B and surrounding unpaved heath were assessed by probing (see delineation in Fig. 1C).

Probing and pit excavations close to the south-eastern corner of Zone F (marked X, Fig. 1C) and at two sites close to the crest of the lunette (marked Y, Fig. 1C) uncovered further relict pavements, again probably derived from earlier eucalypt phases. Both of these were currently vegetated by large specimens of *Banksia plumosa* (Proteaceae) which appeared to be in the process of reworking the surface of an earlier formed clay pavement (RC, Fig. 3A) into ferricrete gravel (Fig. 3B, C). Cluster roots of this species (Fig. 3C) were closely associated with fully formed gravel (Fig. 3B) and nascent ferricrete (NFC, Fig. 3A). Similar, more advanced, instances of such overprinting have been encountered in cursory examinations of older dunes of the lunette series (unpubl. res.).

Vegetation and plant taxa found in the reserve and various zones of the transect

Table 1 lists major taxa, their families and presence or absence of each species in the six zones of the transect

(Zones A–F, Fig. 1C). There were 74 common species in the transect, 50 of these dicotyledons and 24 monocotyledons. Typical of sandplain floras generally in south-west Western Australia (see Beard, 1984; Hopkins and Griffin, 1984), vegetation of the reserve was dominated by proteaceous and myrtaceous shrubs and trees, alongside lesser representations of woody Papilionaceae, Mimosaceae and Epacridaceae, and a number of other families. Herbaceous species were mostly of the Restionaceae and Cyperaceae, accompanied by a range of dicotyledonous and monocotyledonous representatives from many families.

The spread of growth and life forms encompassed nine species of trees, 33 shrubs of varying stature, 23 herbaceous perennials, five geophytes, two ephemerals and one climber.

Rooting morphologies of woody taxa conformed to any one of the categories W1–W7 and those of herbaceous species to categories H1–H7 (see Table 2). As shown earlier for rooting systems of a range of open woodland and heath ecosystems of south-west Western Australia (e.g. see Dodd *et al.*, 1984; Pate *et al.*, 1984; Pate, 1994; Pate and Bell, 1999), rooting morphologies at Chillinup were species specific and related predictably to life and growth form. Trees typically showed a dimorphic root morphology with deeply penetrating tap-(sinker) roots and superficially extending laterals (W2). Most shrubs had a strong tap-root with laterals borne most of the way down (W3) or with only a few laterals (W1). A number of small shrubs showed a weakly developed, relatively shallow tap-root, with few (W4 and W6) or many (W5) laterals borne down almost to the base of the tap-root.

Root morphologies of herbaceous perennials (H1–H7) showed mostly fibrous feeding roots borne adventitiously on geophytic, rhizomatous, stoloniferous or tufted (caespitose) shoot stocks.

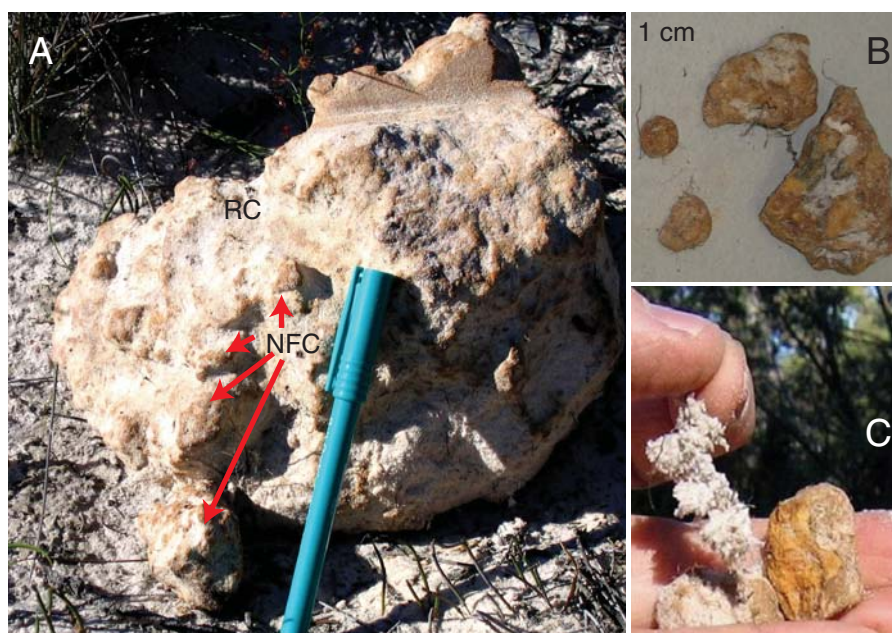


FIG. 3. (A) Surface view of a column excavated from pavement formed by an earlier phase of mallee vegetation now colonized by *Banksia plumosa*. It shows reworked surfaces with nascent ferricrete (NFC). (B) Fully formed ferricrete gravels recovered from pockets just above the relict pavement. Bleached indentations on the gravel denote where cluster roots were operating. (C) A cluster root and closely adjacent ferricrete pebble recovered from the same pavement as in (A) and (B).

TABLE 1. Common taxa encountered in different zones of the transect with information on life and growth forms and rooting morphologies

Species	Life/growth form	A	B	C	D	E	F	Rooting morph.
Proteaceae								
<i>Adenanthos cuneatus</i>	TS			✓	✓	✓	✓	W5
<i>Banksia arctotides</i>	LS	✓	✓	✓	✓			W4
<i>Banksia attenuata</i>	T					✓		W2
<i>Banksia baxteri</i>	T					✓		W2
<i>Banksia brunnea</i>	TS	✓	✓	✓	✓			W4
<i>Banksia coccinea</i>	T				✓	✓		W5
<i>Banksia nutans</i>	TS				✓	✓		W5
<i>Banksia plumose</i>	TS			✓	✓	✓	✓	W4
<i>Banksia repens</i>	LS	✓	✓	✓	✓	✓	✓	W2
<i>Franklandia fucifolia</i>	MS			✓	✓	✓	✓	W4
<i>Hakea corymbosa</i>	TS			✓	✓	✓	✓	W2
<i>Hakea nitida</i>	LS	✓	✓					W5
<i>Isopogon trilobus</i>	MS			✓	✓	✓	✓	W1
<i>Lambertia inermis</i>	T			✓	✓	✓	✓	W3
<i>Petrophile media</i>	MS			✓	✓	✓	✓	W3
<i>Petrophile phyllicoides</i>	MS			✓			✓	W3
<i>Petrophile rigida</i>	MS						✓	W5
<i>Stirlingia latifolia</i>	MS			✓	✓	✓	✓	W3
Myrtaceae								
<i>Beaufortia empetrifolia</i>	TS			✓	✓	✓		W3
<i>Calothamnus gracilipes</i>	MS	✓	✓	✓	✓	✓	✓	W1
<i>Calytrix flavescens</i>	MS			✓	✓	✓	✓	W5
<i>Conothamnus aureus</i>	MS	✓	✓					W1
<i>Eremaea pauciflora</i>	TS			✓	✓	✓		W4
<i>Eucalyptus decipiens</i>	T(M)			✓	✓	✓	✓	W2
<i>Eucalyptus pleurocarpa</i>	T(M)			✓	✓	✓	✓	W2
<i>Eucalyptus occidentalis</i>	T	✓					✓	W2
<i>Melaleuca rigidifolia</i>	LS	✓	✓					W3
<i>Melaleuca striata</i>	TS			✓	✓	✓	✓	W3
<i>Melaleuca suberosa</i>	LS	✓	✓					W4
<i>Melaleuca subtrigona</i>	TS	✓	✓	✓				W4
<i>Melaleuca thymoides</i>	TS			✓	✓	✓		W3
<i>Verticordia hybrantha</i>	LS	✓	✓	✓				W6
Cyperaceae								
<i>Cyathochaeta avenacea</i>	HP			✓	✓	✓	✓	H7
<i>Gahnia ancistrophylla</i>	HP	✓	✓					H4
<i>Lepidosperma</i> sp.1	HP	✓	✓					H4
<i>Lepidosperma</i> sp.2	HP			✓	✓	✓	✓	H4
<i>Mesomelaena stygia</i>	HP	✓	✓	✓		✓	✓	H7
<i>Schoenus caespititius</i>	HP					✓	✓	H7
Restionaceae								
<i>Chaetanthus tenellus</i>	HP				✓	✓	✓	H4
<i>Cytogonidium leptocarpoides</i>	HP				✓	✓	✓	H4
<i>Harperia confertospicata</i>	HP			✓	✓	✓	✓	H4
<i>Harperia lateriflora</i>	HP	✓	✓					H7
<i>Hypolaena fastigiata</i>	HP			✓	✓	✓	✓	H4
<i>Hypolaena pubescens</i>	HP	✓	✓	✓	✓	✓	✓	H4
<i>Lyginia barbata</i>	HP			✓	✓	✓	✓	H7
<i>Onychosepalum laxiflorum</i>	HP				✓	✓		H4
Dasygongonaceae								
<i>Lomandra hastilis</i>	HP			✓	✓	✓	✓	H7
<i>Lomandra micrantha</i>	HP			✓	✓	✓	✓	H4
<i>Lomandra nigricans</i>	HP			✓	✓	✓	✓	H4
Droseraceae								
<i>Drosera erythrorhiza</i>	G	✓	✓	✓	✓	✓	✓	H2
<i>Drosera macrantha</i>	G	✓	✓	✓	✓	✓	✓	H2
<i>Drosera</i> (pygmy species)	HP			✓	✓			H3
Anthericaceae								
<i>Laxmannia brachyphylla</i>	HP	✓	✓	✓		✓		H6
<i>Thysanotus patersoni</i>	G	✓	✓					H1
Asteraceae								
<i>Hypochaeris glabella</i>	E	✓	✓	✓			✓	H5
<i>Winter ephemeral</i>	E	✓	✓	✓				H3
Epacridaceae								

Continued

TABLE 1. *Continued*

Species	Life/growth form	A	B	C	D	E	F	Rooting morph.
<i>Andersonia simplex</i>	MS			✓	✓	✓	✓	W5
<i>Lysinema ciliatum</i>	MS					✓		W5
Mimosaceae								
<i>Acacia aemula</i>	LS			✓			✓	W5
<i>Acacia saligna</i>	T	✓	✓	✓	✓			W2
Papilionaceae								
<i>Chorizema cytisoides</i>	LS				✓	✓		W5
<i>Jacksonia spinosa</i>	TS				✓	✓	✓	W5
Aizoaceae								
<i>Carpobrotus</i> sp.	HP	✓	✓	✓				H6
Casuarinaceae								
<i>Allocasuarina humilis</i>	TS		✓	✓				W2
Colchicaceae								
<i>Burchardia congesta</i>	G	✓	✓	✓				H1
Dilleniaceae								
<i>Hibbertia gracilipes</i>	LS	✓	✓	✓	✓	✓	✓	W6
Haemodoraceae								
<i>Anigozanthos humilis</i>	G	✓	✓					H4
Loranthaceae								
<i>Nuytsia floribunda</i>	T					✓		W2
Phormiaceae								
<i>Dianella revoluta</i>	HP					✓	✓	H7
Pittosporaceae								
<i>Billardiera fusiformis</i>	CS					✓	✓	W5
Poaceae								
<i>Amphipogon turbinatus</i>	HP	✓	✓	✓	✓	✓	✓	H7
Santalaceae								
<i>Exocarpos sparteus</i>	TS			✓		✓		W4
Stylidiaceae								
<i>Stylidium repens</i>	HP	✓	✓	✓	✓	✓	✓	H6
Xanthorrhoeaceae								
<i>Xanthorrhoea latyphylla</i>	TS				✓	✓		W7

Codes for life and growth forms: T, tree; T(M), tree, mallee form; TS, tall shrub; MS, middle size shrub; LS, low shrub; CS, climbing shrub; HP, herbaceous perennial; G, geophyte; E, winter ephemeral. The key to rooting morphologies is shown in Table 2.

TABLE 2. *Classification of rooting morphologies of common species in transect*

(A) Woody species			
A	Deeply penetrating, stout tap-root	A1 Few fine (0.5–1 mm diameter) lateral roots	W1
		A2 Superficial spreading thick lateral roots	W2
		A3 Laterals (1–3 mm diameter) down most of tap-root	W3
B	Weakly developed tap-root not penetrating deeply	B1 Few long stout laterals	W4
		B2 Many laterals borne down tap-root	W5
C	Stem stock split, with most segments bearing tap- and lateral roots		W6
D	Tuberous stem base with many adventitious roots		W7
(b) Herbaceous species			
E	Root tuberous with fibrous feeding roots (<1 mm diameter)		H1
F	Stem tuberous, feeding roots on buried stem		H2
G	Fine shallow fibrous roots (<1 mm diameter)		H3
H	Rhizomatous shoot with adventitious roots		H4
I	Storage tap-root with fine feeding roots (<1 mm diameter)		H5
J	Stoloniferous shoot with adventitious roots		H6
K	Dense tufted shoot with fine fibrous roots		H7

The flora of parts of the reserve on the north-west side of the lake opposite the lunette was virtually identical to that of the transect, and many of the same suite of species were encountered in relic roadside verge vegetation in the general neighbourhood of the site.

It is not known how early stages of colonization of the lunette occurred, but, since playa lakes were reputedly moderately saline and sometimes gypsiferous when lunettes were forming (see Harper and Gilkes, 2004), pioneer species were likely to have been salt tolerant. Seasonally flooded mud flats of the lake are currently populated by paperbark (*Melaleuca cuticularis*), the chenopods (*Tegicornia uniflora* and *Salicornia quinqueflora*) and pig face (*Carpobrotus* sp.) – all halophytic species. The elevated rim of sand deposits on the landward margin of the lake carries a dense fringe of *Anarthria laevis* and *Lepidosperma* sp.1, with occasional tall tufts of *Cyathochaete avenacea*. Inland from this is a 200 m wide area of sand up to 2 m deep and vegetated by dense myrtaceous:proteaceous heath and patches of mallee eucalypts (see HW, Fig. 1C). All species in this area are commonly encountered in most zones of the study transect.

The lake at Chillinup is highly salinized, presumably due to incursion of salts displaced following clearing of adjacent land. The current lack of live tree cover and skeletons of dead woody species on the lake floor may therefore be an

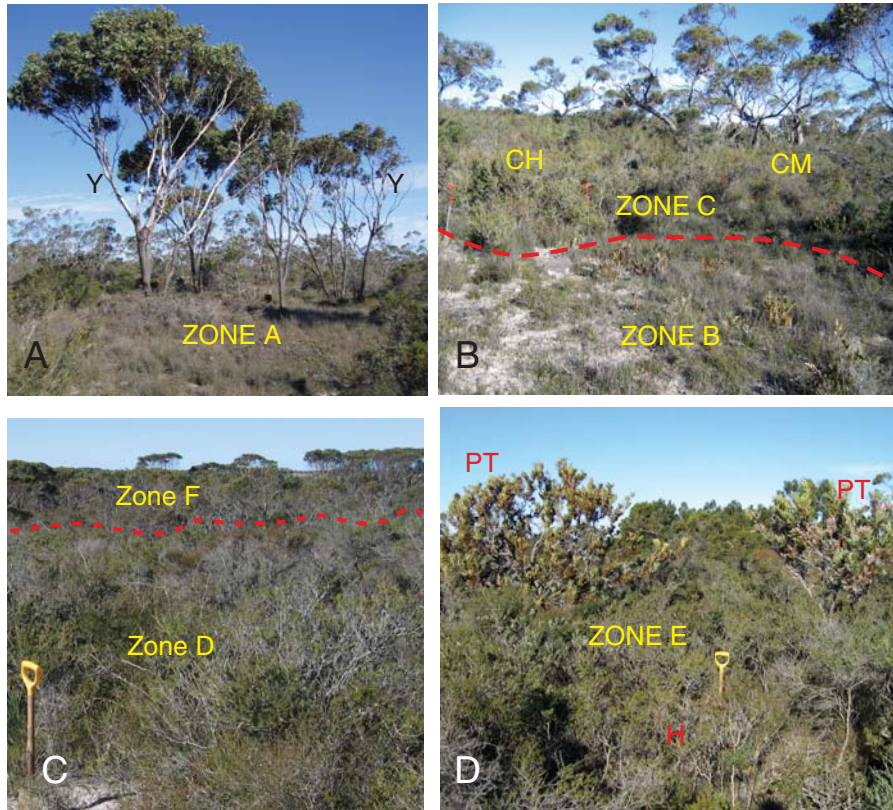


FIG. 4. (A) A grove of yates (Y) showing extremely sparse vegetation cover (Zone A) on superficial lateral root pavements of the trees. (B) Sparse vegetation colonizing superficial relict pavement (foreground, Zone B) with Zone C vegetation in the background comprising mixed heath (CH) and groves of mallee eucalypts (CM). Red dots demarcate the boundary between the two zones. (C) A general view of mixed myrtaceous:proteaceous heath (foreground, Zone D) with mixed mallee woodland (Zone F) in the background. Red dots mark the boundary between the two zones. (D) Zone E vegetation showing myrtaceous:proteaceous heath (H) interspersed with proteaceous tree species (PT).

artefact of modern agriculture. This would also apply to the incursion of salt-tolerant taxa along the lake margin.

Corroborating the above conclusion, several playa lakes well inside the Stirling Range National Park were recently examined. Each draws exclusively on runoff from pristine vegetation of the region, and lakes floors are well vegetated, in certain cases with large mature specimens of yate and paperbark. Flood lines on trunks suggest a seasonal flooding regime with no free-standing water during summer. Significantly, there was no evidence of salinization in these lakes, but the edaphic and floristic characteristics of the mixed mallee woodland/proteaceous heath on the surrounding dunes were essentially as described here for Chillinup.

The following comments apply to the five distinctive zones of vegetation in the transect.

Zones A and B. Species listed for these zones (see Table 1) were inhabiting superficial pavements under yate (Zone A, Fig. 4A) or superficial relict pavements not vegetated by eucalypts. The latter were identified by probing as Zone B (e.g. see foreground marked as B in Fig. 4B). Ground cover in both zones was exceptionally sparse (5–8%), consisting principally of dwarf herbaceous perennials, ephemerals and geophytes, accompanied by a scattering of mostly low-growing woody shrubs. The zone showed 30 common species, with nine not found elsewhere in the transect. These were classified as

‘shallow platform specialists’, and five of these (*Harperia lateriflora*, *Gahnia ancistrophylla*, *Lepidosperma* sp.1, *Melaleuca suberosa* and *Conothamnus aureus*) proved to be reliable indicators of superficial pavements elsewhere in the reserve and beyond. Other species, notably the monocotyledons *Mesomelaena stygia* and the dwarf woody shrubs *Hibbertia gracilipes*, *Banksia repens* and *Banksia arctotides*, were well represented in Zones A and B, and also widely across the transect.

Zone C. This zone included open woodland of mallee (mostly *E. pleurocarpa* and *E. decipiens*, CM, Fig. 4B) interspersed with dense myrtaceous:proteaceous heath (CH, Fig. 4B), the latter overlying non-paved deep sand. The zone extended from the mid-proximal up to the crest of the dune and slightly beyond. The flora was diverse, containing 48 of the 74 species listed for the transect. Tree-free zones of heath were dominated by *Melaleuca striata* and a range of other myrtaceous shrubs. Prominent proteaceous species were *Lambertia inermis*, *Petrophile* spp. and *Banksia* spp. Ground cover of the heath was rated at 70–80% compared with a value of <50% for paved areas under mallee. Vigour and density of most of the tall shrubs of the heath were considerably reduced when occupying understoreys of mallee.

Zone D. This zone, marked D in the foreground of Fig. 4C, embraced the upper part of the gently sloping distal face of

the dune and mostly comprised dense scrub heath dominated by *M. striata*, accompanied by a wide variety of woody myrtaceous and proteaceous shrubs. The ground flora of mostly monocotyledonous species was sparse. The scattering of small-sized mallees (*E. pleurocarpa* and *E. decipiens*) in this zone generally lacked pavements and their understoreys were almost as prolific and species rich as in the general body of heath.

Zone E. This relatively narrow strip (Fig. 4D) along the southern side boundary of the transect showed a dense ground cover of 80–90% and contained essentially all shrub and understorey components of Zone D. It also carried stands of trees of mostly proteaceous taxa (PT, Fig. 4D) (*Banksia attenuata*, *B. baxteri*, *B. coccinea* and *L. inermis*). Mallee eucalypts were growing poorly in the zone, and in most cases lacked pavements. Heath was not noticeably suppressed except under the dense canopies of the proteaceous trees.

Zone F. This consisted of an almost continuous area of open mallee woodland (*E. decipiens* and *E. pleurocarpa*) – see background marked F in Fig. 4C. Understoreys varied in ground cover from 30 to 60% and were generally less species rich than in Zones D and E. As in Zone C, vigour of *M. striata* and other shrubs was noticeably reduced under mallees. This applied particularly to the understoreys of the dense groves of *E. pleurocarpa* and occasional trees of yate which occupied a sizeable depression towards the south-east corner of the zone.

Finally, considering the flora of the transect as a whole, a group of ‘generalist’ species was identified which occurred at moderate density in all zones of the transect (see Table 1). These comprised two stem tuberous geophytes (*Drosera erythrorhiza* and *D. macrantha*) a small grass (*Amphipogon turbinatus*), the semaphore sedge (*Mesomelaena stygia*), the dwarf trigger plant (*Stylidium repens*) and two ground-hugging dwarf shrubs, *B. repens* and *H. gracilipes*.

Information from the deep profiles exposed by the cutting through the dune

Aeolian beddings, clay pavements and soil profiles were remarkably well preserved considering that the dune had been deposited >10 000 years ago and that the land had been cleared for farming 50 years previously. As shown in the montage photograph of the north-facing wall of the cutting (Fig. 5A and details in Fig. 5B–F), double or single layers of columns ran closely parallel to the surface contour of the proximal side of the dune. Five distinctive, horizontally adjoining zones (see Fig. 5A, Zones 1–5) were identified along the whole face of the cutting, the four of these closest to the lake containing one or more clay pavement layers, and the fifth (Zone 5) lacking such structures.

Zone 1, closest to the lake (Fig. 5B), showed a layer of closely abutting round-topped columns (UL) of large diameter and strongly haematitic colour. This lay directly on top of a second layer (LL) of narrower prismatic columns of browner colour. The columns of the upper layer closely resembled those found under yate in the flora reserve. Attached to the

bottom of the lower layer were discontinuous, narrow bands of silcrete (Si) overlying a 1 m thick layer of bleached sand (BS). The latter graded progressively into a basal mineralized layer.

Zone 2 included the remaining area of the profile occupied by an upper layer of large columns (UL, Fig. 5C). These became of decreasing size and increasingly separated from one another and from the underlying pavement as one progressed from proximal (left of picture) to distal ends of the zone. The morphology of the lower layer of small columns (LL) was essentially as seen in Zone 1. Lenses of silcrete (Si) underlay these columns, and horizontally segregated fine layerings of iron were visible in the lower regions of the sand profile below (labelled FeL in the insert to Fig. 5D and in Fig. 5E). Clay percentages and bulk densities down this profile were $17 \pm 3\%$ and $1.57 \pm 0.01 \text{ mg m}^{-3}$, respectively, for the younger still-developing top columns, compared with $2 \pm 1\%$ and $1.52 \pm 0.01 \text{ mg m}^{-3}$ for the sand between the two pavement layers. Corresponding values were $29 \pm 2\%$ and $1.68 \pm 0.03 \text{ mg m}^{-3}$ for the top of the lower columns and $3 \pm 1\%$ and $1.53 \pm 0.01 \text{ mg m}^{-3}$ for sand down to 3 m depth below columns.

Zone 3 (Fig. 5D) bore no evidence of large columns, but the lower layer of finer columns (LL) continued in a fully formed and closely packed condition. Again, the columns graded down into lenses of silcrete (Si). The underlying sand substrate of this zone was approx. 5 m deep and iron layerings were scattered through its lower regions. Clay values and bulk densities of this pavement were essentially the same as that recorded in Zone 2. Aboriginal artefacts were encountered in undisturbed aeolian bedding at varying depths (see example AT, Fig. 5D). Some of these were at 4 m below the surface, attesting to the relatively recent age of the lunette system. The inset to Fig. 5D shows an ancestral root channel shrouded in calcium carbonate (Ca) and the horizontally segregated iron layerings (FeL) typically encountered in all paved parts of the cutting face.

Zone 4 extended up to and a short distance beyond the dune crest. The layer of fine columns (LL, Fig. 5E) continued, but individual columns became of progressively smaller size, less regular shape and increasingly separated from one another towards the distal end of the zone. A silcrete layer was absent, but horizontally segregated iron layers (FeL, Fig. 5E) were prominent below the region of columns, just as they were below columns in Zones 2–4. The inset to Fig. 5E is a close-up of nascent column (NC) formation showing bio-mineralization surrounding clusters of fine eucalypt roots.

Zone 5 (Fig. 5F) encompassed the long pavement-free stretch along the distal side of the dune, with sand depth of 6 m at its proximal end grading down to <1 m at the distal end furthest from the lake. Laterally extensive podzolization within this layer was evident as a non-mineralized (eluviated) horizon (E) above a layer mildly enriched with sesquioxides (Se). This whole region of the face of the cutting was presumed to have carried heath vegetation prior to clearing for agriculture. Clay percentages and bulk densities down the profile changed only slightly with depth, namely within the range 2–4% for clay and $1.48\text{--}1.50 \text{ mg m}^{-3}$ for bulk density.

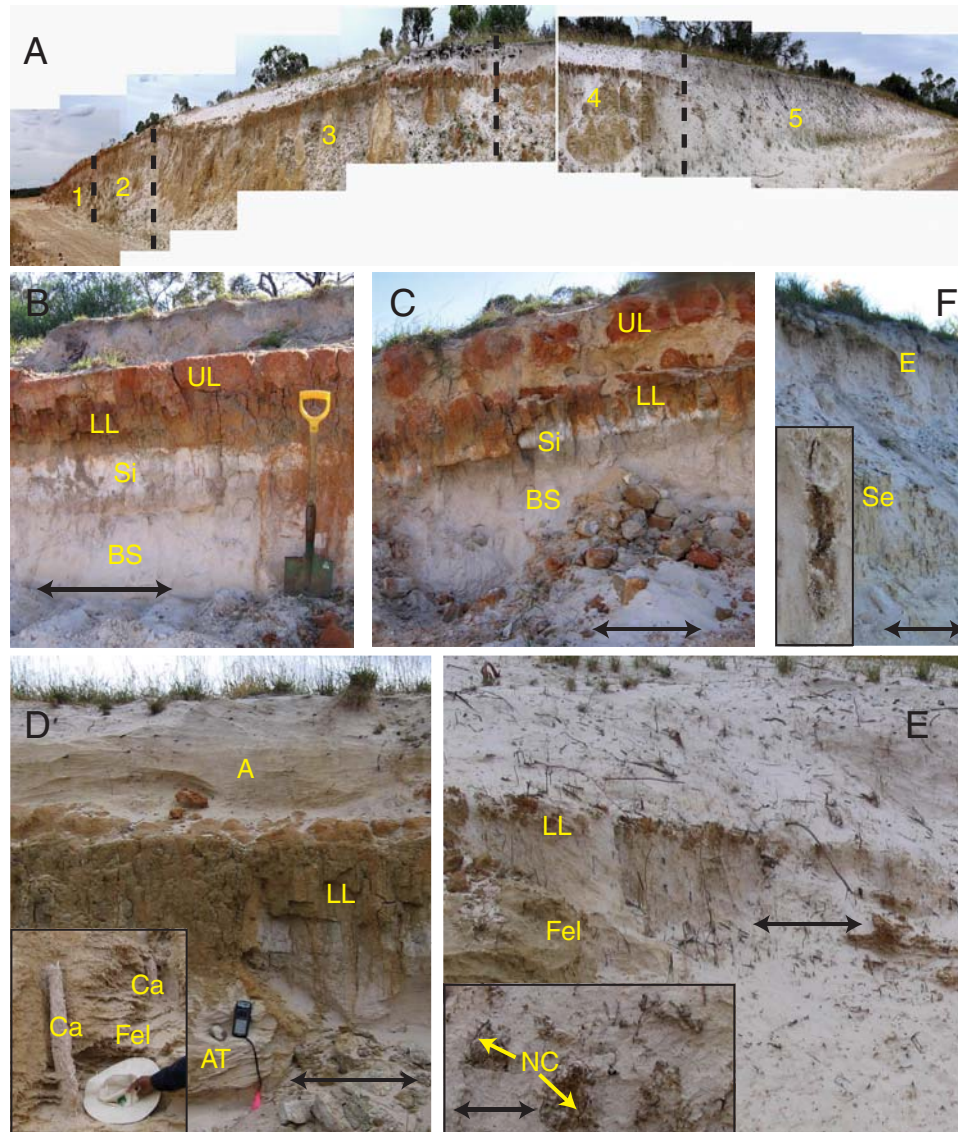


FIG. 5. (A) General fish-eye view of the northern face of the 200 m cutting through the lunette showing five zones: the first four, closest to the lake, carry double or single pavements formed by eucalypts, the fifth is pavement free and was previously vegetated by proteaceous heath. (B) The mid region of Zone 1 of the cutting showing a red upper layer of columns (UL) welded onto each other and onto a lower brown layer of columns (LL). Si, silcrete layer; BS, layer of bleached sand. (C) Zone 2 showing upper columns separated from each other and from the underlying lower pavement. Letter designations are as in (B). (D) Zone 3 of the cutting profile with single pavement (LL) straddled by wind-etched aeolian sand beddings visible in A and C horizons. An aboriginal artefact (AT) can be seen in the C horizon. The inset shows calcium carbonate precipitations (Ca) around ancestral root channels and horizontal iron layerings (FeL). (E) Attenuating lower layer (LL) of columns of decreasing size from left to right of the photograph. Horizontally segregated iron layerings (FeL) are visible below the pavement. The inset shows bio-mineralization around clumps of fine roots at sites of nascent column formation (NC). (F) Pavement-free zone originally occupied by myrtaceous:proteaceous heath showing podzolization as an eluviated upper horizon (E) above a sesquioxide enriched layer (Se). Note the Fe precipitations surrounding the descending root channels in the latter layer (detailed in the inset of a 5 cm long Fe-encased root). All scale bars in principal figures (A–E) are 0.5 m. The scale bar in the inset to (E) is 1 cm.

Despite substantial decomposition and oxidization of root materials since the time of clearing, there was still evidence of well-defined relic root channels descending through the sand layers of the dune. Some of these were outlined by intense accumulations of iron (see FeA in Fig. 5F). Some of the larger channels (RC, Fig. 5F) were tracked all the way down to the lacustrine substrate, suggesting that eucalypts and some of the larger shrubs and trees of the heath would have had access water and minerals from basement regions of the dune.

DISCUSSION

The presence of intractable pavements of clay in the upper B horizon of soils vegetated by mallees and other eucalypts is a well known feature across broad expanses of semi-arid parts of Australia (Chartres, 1985; Chittleborough, 1992), and the constraints which apply when duplex (texture contrast) soils of such type are cleared for agriculture (Rengasamy, 2002) are well known to farmers, agronomists and soil scientists. Parallel investigations of the calcretes and silcretes

which frequently underlie these pavements have also been undertaken (Butt, 1983; Milnes and Hutton, 1983; Anand *et al.*, 1997), albeit with considerable dispute as to modes of origin and inter-relationships.

In a recent review (Verboom and Pate, 2006a), seal-like clay pavements under eucalypts are listed as one of a broad range of outcomes in which soils can be modified structurally and chemically by plants and their microbial partners. These are detailed and discussed under the 'Phytotarium concept' advanced in the same review.

Earlier studies at Lake King (Verboom and Pate, 2006b) showed that shallow clay pavements were associated specifically with the lateral root platforms of mallee eucalypts and typically overlay complex profiles of ancient origin above the bedrock. Where mallee woodland was invading areas previously occupied by myrtaceous:proteaceous heath, the clay pavement produced by the mallee was overprinting the ferricrete (laterite) left behind by the heath. As a further complication, pavements in the lateral root catchment of one species of mallee (*Eucalyptus flocktoniae*) proved to be calcareous throughout, whereas those of a closely co-habiting species (*E. scyphocalyx*) were calcareous only in their lower layers.

The intimate spatial relationships between pavements and lateral root platforms of eucalypts observed at Lake King were essentially similar to those described here for the young dune system at Chillinup. In all cases, top layers of pavements were of high bulk density and clay content, consistent with biogenically formed clays having occluded spaces between the quartz sand grains of the original profile. However, morphologies of pavements at Lake King were planiform and composed of large interlocking irregular blocks, whereas those at Chillinup were made up of closely packed, vertically aligned clay columns. The reasons for such biotypical variations between and within sites remain unclear, and further study is obviously required across a broad range of mallee species before reaching conclusions regarding the factors and influences determining pavement morphologies.

As a further difference between the two sites, the numbers of small 'sinker' roots descending from laterals and penetrating through underlying pavements tended to be far greater at Lake King than at Chillinup. Again one cannot say why such variation exists, nor what such differences might mean in terms of water and nutrient relationships within the respective systems.

To test whether the differences in depths to pavement surfaces between yate and the mallees at Chillinup might apply generally, a soil and vegetation database from regional surveys conducted by the Western Australian Department of Agriculture was sourced. This showed a significant difference ($P < 0.001$) between mean depth to pavements, namely 20.8 ± 1.1 for yate vs. 31.5 ± 1.1 for blue mallee (no data available for *E. decipiens*). Assuming that differences of this kind applied widely across a range of eucalypts, one would suppose that areas of cleared land originally occupied by species of mallee which had formed shallow pavements would be generally less tractable for agricultural purposes than would areas with a legacy of more deeply located pavements.

The single-layered pavements at Chillinup were generally located close to the surface of the deposit of aeolian sand.

However, in certain areas, a second large-columned pavement had been laid down on top of a small-columned version. This double layer, well displayed in both the reserve and cutting through the dune, provided the first well-authenticated case where the signature layer formed by one eucalypt was succeeded by a second one of differing morphology, and probably involving another eucalypt species. The cutting revealed that the later-formed pavement petered out halfway up the slope, whereas the lower older one continued upwards before attenuating just beyond the dune crest. The state of preservation and high bulk density of this lower layer rendered it unlikely that appreciable amounts of minerals had been scavenged from its structure when the succeeding phase of eucalypt growth was constructing its signature pavement.

Another somewhat unexpected finding was the extent of mineralization and reworking of profiles in the relatively short time of the Holocene. Where heath vegetation had been present before clearing, the lower sand profile showed weakly podzolized layers, just as have been encountered elsewhere in deep sands carrying such vegetation (see Pate *et al.*, 2001). However, the telling feature for Chillinup is that these changes are taking place in an unequivocally recent setting. The younger upper pavement in the profile of the cutting at this site is strongly red coloured (possibly ferrihydrite) compared with the browner (goethitic) coloration of the older lower pavement, while the most intense red condition was encountered in nascent columns of developing pavement. Similar colour changes have been recorded when ferrihydrite precipitates age to goethitic or haematitic minerals (see Cornell and Schwertmann, 2003).

It is generally known that understoreys of mallee vegetation are considerably less biodiverse and prolific than those of heath or open, non-eucalypt woodlands occupying the same rainfall zone. Such effects have been mostly interpreted as due to underlying differences in soil profiles, but this certainly does not apply to Chillinup where depauperate understorey vegetation overlying pavements grows side by side with dense heath growing on pavement-free areas.

Just as was observed at Lake King, a small number of specialized taxa, including certain large shrub species, colonize pavements at low density. The tap-roots of some of these shrubs penetrate down below a pavement, while their far-reaching laterals extend across and even reach out beyond the paved area. Root systems of this nature would be expected to access water and nutrients throughout the year. Nevertheless, most pavement specialist species at Chillinup are shallow-rooted herbaceous monocotyledons where drought resistance, slow growth rates and inordinately low nutrient requirements are likely to be paramount to long-term survival (see case studies of seasonal growth and nutrition of Restionaceae by Meney and Pate, 1999).

Pavements overlain by shallow A horizons, such as seen under mallees at Lake King and yate at Chillinup, exert a noticeably more repressive effect on biodiversity and vigour of understoreys than is observed for more deeply located pavements of mallees at Chillinup. Differences of this sort have previously been attributed to constraints of underlying ancient soil types. Perhaps such cases should be re-examined to determine whether intractable layers, engineered biotically by previous generations of eucalypts and other taxa, might

be held responsible. Were this so, new understanding might be gained on how different phytotaria compete in time and space and how the long-term evolutionary dynamics of such situations generate the mosaics of vegetation now visible within and between ecosystems. Issues such as these are addressed generally by Habets *et al.* (2006), Lehmann (2007) and Verboom (2007).

The recent colonization of lunettes in the South Stirlings area was pictured to have involved invasion by a set of species already commonly present in neighbouring areas. This pre-supposes that there has been a long and relatively stable history of heath and woodland vegetation in the region, as indeed suggested from the fossil pollen studies of Itzstein-Davey (2004) and Atahan *et al.* (2004). Nevertheless, as seen at Chillinup, there is still a well defined sorting out of invading species, and mostly in accordance with dune aspect and topography, depth of deposited sand and abilities or otherwise of species to withstand competition for nutrients and water in paved regions of the dune. Here, one might well find the forces shaping competition between contrasting phytotaria, and ultimately generating the complex mosaics and spiral waveforms of vegetation already described in floristic surveys and radiometric studies of older landscapes in the region (see Verboom and Pate, 2003; Verboom, 2007).

So far, all studies have demonstrated a consistent association between certain eucalypts and clay pavements, and an equally faithful relationship between certain cluster root-bearing Proteaceae and lateritic podsols. One can therefore read from the highly characteristic footprints left behind by these causal relationships to predict vegetation histories of cleared or uncleared landscapes. Examples of this approach are seen in the contemporary lateral facies changes described here for Chillinup and earlier for cleared landscapes at Merridin and Belka (Verboom and Pate, 2006a). Similarly, chronosequences of layers attributable to different or the same classes of vegetation should permit one to unravel the vegetation histories of stacked paleosols, as described for Kalannie (Verboom and Pate, 2006b), for deep coastal sands of the Gnararra Mound near Perth, Western Australia (R. Froend, pers. comm.) and for certain sites in Eastern Australia (e.g. see Walker *et al.*, 1981). These latter instances attest not only to the longevity of footprint layers in profiles but also to the limited extent to which their structural integrity is affected by succeeding phases of vegetation.

It is interesting to speculate whether the clay pavements formed by certain Australian eucalypts are unique structural entities in ecological and functional terms, or whether counterparts might be present in semi-arid systems elsewhere in Australia or overseas. A case in point might well be the South African legume *Colophospermum mopane* (Leguminosae) which appears to bioengineer distinctive 'sodosolic' pavements, especially under 'mallee' forms of this species (W. Verboom, unpubl. obs.). According to Khomo and Rogers (2005), ecosystems involving this key species have expanded greatly in area over 50 years, indicating that pavements and their effects on understoreys can be generated surprisingly rapidly.

Important questions remain concerning the agencies through which mineral elements essential to pavement formation are

sourced by eucalypts at Chillinup, and the underlying chemical and microbiological processes which implement construction of such extensive and durable structures. It is most unlikely that sufficient aluminium and iron would have been sourced from the surrounding quartzitic sand at Chillinup and equally unlikely that aerial depositions of the same elements would have been available in appreciable quantities while pavements were forming during the relatively wet Holocene. Earlier opinions on the subject (see Stace *et al.*, 1968; Hubble *et al.*, 1983; Chittleborough, 1992) suggest that such materials are likely to have been synthesized *in situ* from reworked resident and imported constituents.

It is thought that the most likely scenario is that pavement construction at Chillinup involves tap-root-mediated uplift of minerals from water tables perched on the mineral-rich lacustrine basement of the dune profile. The minerals in question would then be delivered via the ascending xylem stream to sites of pavement construction in extending regions of the lateral root system. Hydraulic lift of this nature is well authenticated for woody species, including mallee eucalypts (K. Brooksbank, pers. comm.), and occurs particularly at night when the shoot is not a transpiring sink for water (see references listed and discussed by Verboom and Pate, 2006a).

Were such mining of deeply located mineral resources to be the *sine qua non* for pavement construction, one should be able to detect a strong positive relationship between their development and access to mineralized ground water. This has yet to be fully tested at landscape scale, particularly in relation to the distribution of pavement-forming mallees and other eucalypts vs. heath-type vegetation. Some of the issues alluded to in this paragraph are currently being addressed at Chillinup and will hopefully form the substance of a further research paper.

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