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Ecosystem wicks: Woodland trees enhance water infiltration in a fragmented agricultural landscape in eastern Australia

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Abstract Since European settlement, *Eucalyptus* box woodlands have been substantially modified by agricultural practices, and in many areas in southern Australia are now restricted to scattered or clumped trees. We report here on a study to examine the impact of trees on water flow (infiltration) in an agricultural landscape with substantial areas of extant native vegetation. We examined infiltration through coarse- and fine-textured soils within four landscape strata, the zones below *Eucalyptus melliodora* and *Callitris glaucophylla* canopies, the intertree zone dominated by perennial grasses and a landscape homogenized by cultivation and dominated by annual crops. We measured sorptivity, the early phase of water flow, and steady-state infiltration with disc permeameters at two supply potentials. These different potentials enabled us to separate infiltration into (i) flow through large (biopores) and small pores and (ii) flow through small pores only where biopores are prevented from conducting water. On the fine-textured soils, both sorptivity and steady-state infiltration were significantly greater (approximately fivefold) under the timbered strata compared with the grassy slopes or cultivation. Differences were attributable to the greater proportion of macropores below the tree canopies compared with the nontimbered strata. The lack of a significant difference on the coarse-textured soils, despite their macropore status, was attributed to differences in surface litter and plant cover, which would maintain continuous macropores at the surface and thus conduct large amounts of water. The tendency of slopes covered by cryptogamic crusts and grasses to shed run-off and for the trees to absorb substantial quantities of water reinforced the important ecological service provided by trees, which moderates large run-off events and captures small amounts of water leaking from the grassy patches. In the absence of these 'ecosystem wicks', run-off would find its way into regional groundwater and contribute to rising salinity.

Key words: carbon, ecosystem engineering, eucalypt, infiltration, isolated tree, macroporosity, semiarid woodland.

INTRODUCTION

Woodlands dominated by *Eucalyptus* spp. such as yellow box (*Eucalyptus melliodora*), white box (*Eucalyptus albens*), grey box (*Eucalyptus microcarpa*) and poplar box (*Eucalyptus populnea*) once occupied extensive areas of temperate southern Australia, occurring as a continuous belt along the western side of the Great Dividing Range (Yates & Hobbs 1997). Since European settlement however, these woodlands have undergone extensive modification (Harrington *et al.* 1979) and now exist as a series of fragmented remnants of varying size, shape and quality within a largely agricultural matrix dominated by annual crops and introduced pasture species (Prober & Thiele 1995; Yates & Hobbs 1997).

Vegetation clearance, a major structural change in this agricultural region, has resulted in substantial changes in landscape function at both regional and local scales. These changes include, but are not limited to, declining soil fertility, increased erosion and increasing salinization resulting from rising groundwater tables (Robertson 1996). This dramatic change in landscape structure has also resulted in major changes in biodiversity including loss of overstorey and understorey flora, declines in many faunal taxa and invasion by exotic species (Bird *et al.* 1992; Prober & Thiele 1995; Yates & Hobbs 1997; Yates *et al.* 2000). Trees within the remaining woodland fragments are typically in poor health. They have a low viable seed output (Burrows 2000) and rarely recruit because of the loss of seedlings from grazing, competition from exotic pasture species and active suppression by farming practices (Sheahan 1998; Ozolins *et al.* 2001). In many areas, isolated trees are in the order of 200–500 years old (Kile 1981). Clumped and isolated trees

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are important aesthetic features and provide habitat for a wide range of invertebrate and vertebrate fauna (Law *et al.* 2000; Fischer & Lindenmayer 2002a,b). Trees also influence essential soil and ecological processes such as mineralization of nutrients and infiltration of rainfall (Old *et al.* 1981; Breckwoldt 1983; Wylie & Landsberg 1987; Campbell *et al.* 1988; Jackson & Ash 1998; Deans *et al.* 1999; Yates *et al.* 2000).

Loss of trees can be directly linked to changes in local and regional hydrology (Walker *et al.* 1993; Hobbs & Cramer 2003). Vegetation clearance increases the incidence of rising water tables by impacting directly on the hydrological balance between inputs of rainfall and outputs of evapotranspiration. In general, replacement of woodlands with annual, shallow-rooted, generally winter-growing crops and pastures has resulted in increased groundwater recharge and rising water tables. Rising water tables can mobilize salts stored in the unsaturated soil horizons, transporting the salts to the ground surface and resulting in the onset of dryland salinization (Butler 1958; Bell 1999).

Little is known about the impact of large eucalypts on surface hydrology at the patch and sublandscape scale within the temperate agricultural zone of eastern Australia. Further, little is known about the ways in which soils and vegetation influence the fate of rainfall once it reaches the soil surface, and therefore little is known about the implications that changes in land use and vegetation would likely have on landscape function. The aim of our study was to learn more about the role of eucalypts, the dominant biological elements, on water infiltration within two soil types. We recognized four strata or zones in the landscape: (i) the zone under large *Eucalyptus* trees or (ii) *Callitris* pines; (iii) the gently sloping intertree matrix dominated by perennial tussock grasses, annual forbs and cryptogamic crusts; and (iv) formerly vegetated areas that have been cleared for dryland agriculture and are dominated by annual crops and pastures. Soil chemical analysis and soil surface analysis were used to characterize differences among these zones.

Our objective was to test four hypotheses about the way that water moves within this landscape in relation to the four landscape strata:

1. Given that trees are known to be sites of enhanced meso-faunal (e.g. arthropod, earthworm, termite) activity (Chilcott *et al.* 1997; Deans *et al.* 1999; Munzbergova & Ward 2002), we predicted that measures of soil water flow (in terms of ponded infiltration and ponded sorptivity – see definitions below) would be substantially greater under the trees, would diminish exponentially from trees through the grassy matrix and would be least on the cultivated soils;
2. When a negative pressure or tension is applied to the soil, water flow is restricted to the tiny, non-biological pores in the soil termed matrix pores (Perroux & White 1988). We predicted that when measurements are made under tension, and the large biopores (macropores) are bipassed, there would be no differences in water flow between the strata;
3. Similarly, when these biopores are prevented from conducting water, there would be no difference in water infiltration between coarse- and fine-textured soils, and;
4. Strong links have been established between water infiltration through soils, and surface measurements of litter cover, vegetation cover, soil coherence, microtopography and soil texture (Tongway & Hindley 1995). We predicted therefore that differences in these attributes between strata would explain differences in infiltration between the strata.

We tested these hypotheses by examining sorptivity and steady-state infiltration under both tension and ponding at sites within the four landscape strata using disc permeameters at two tensions, and by characterizing the surface of the soil.

METHODOLOGY

Study sites

The study was conducted in the Riverina area of south-eastern New South Wales, Australia within an area bounded by Oaklands in the north, Corowa in the east and Mulwala in the west (35°50′S, 146°00′E). The village of Savernake was the approximate centre of the study area. The climate is temperate, with a long-term average annual rainfall of 476 mm (Bureau of Meteorology 1975). Approximately 18% more rain falls in the six winter months (April–September) compared with the six summer months. Average maximum temperatures are about 30°C in summer and 16°C in winter.

The geology of the area is predominantly Quaternary alluvium, broken up by folded Upper Ordovician rock outcrops and thinly covered bedrock on the upper slopes and crests of hills and ridges (Beattie 1972). The Quaternary deposits comprise extensive, level to locally depressed plains of clays and clay loams, traversed by discontinuous low ridges associated with the levees of prior streams. Superimposed on the plains are three smaller units: (i) sand ridges and lunettes to 10 m high dominated by well-sorted loams and sandy loams; (ii) rocky outcrops of shallow, stony loams on exposed granites or metasediments to 20 m in relief; and (iii) shallow depressions and lowlands of cracking grey clays (Butler 1958; Kent *et al.* 2002).

Our study was confined to the plain (fine-textured) and sand ridge (coarse-textured) units of the landscape. The dominant soils on the plains are hard, alkaline, red duplex soils commonly referred to as red brown earths (Dr 2.3, Northcote 1966) or Red Chromosols (Isbell 1996). These soils have a brownish, loamy A horizon changing abruptly to a reddish-brown blocky clay B horizon at depths of about 30 cm. The surface soils of the sand ridges are generally loose, greyish-brown, neutral red earths (Gn2, Northcote 1966) or Kandosols (Isbell 1996), gradually becoming finer (higher clay content) with depth (Northcote 1966).

The study area lies within the former extensive cover of grassy-box woodlands in the eastern part of the New South Wales wheat–sheep belt (Moore 1970). On the fine-textured soils, vegetation on the study sites was dominated by grey box, yellow box, buloke (*Allocasuarina leumannii*) and white cypress pine (*Callitris glaucophylla*), and supported a diverse but sparse shrubby understorey of *Acacia*, *Eutaxia*, *Dodonaea* and some *Maireana* species. The groundstorey comprised a moderate cover of native perennial grasses (e.g. *Austrodanthonia* and *Austrostipa* spp.) and introduced annual grasses (e.g. barley grass *Hordeum leporinum* and wild oats *Avena* spp.). The overstorey vegetation at the sites with coarse-textured soils was dominated by grey box, yellow box, white cypress pine and Blakely's red gum (*Eucalyptus blakelyi*), and a diverse shrub and groundcover dominated by *Acacia*, *Hibbertia*, *Eragrostis* and *Austrostipa* (Freudenberger & Stol 2002). A more detailed description of the vegetation is given in the study by Kent *et al.* (2002).

Site selection

The aim of the study was to examine differences in water infiltration between the four landscape strata within two different soil types. Within each soil type we selected three sites supporting remnant vegetation for detailed infiltration measurements. Four strata were selected within each of these three sites. These were termed: (i) '*Eucasphere*'; (ii) '*Callitrisphere*; (iii) 'grassy slope' (see descriptions below); and (iv) 'cultivated'. The first three strata were located within fenced remnants that were rarely grazed by domestic livestock but more regularly by kangaroos as determined by a sparse scatter of kangaroo dung. The fourth stratum, in an adjacent paddock, consisting of a surface that had been regularly cultivated for at least 50 years.

Three replicate locations of each of the four strata were randomly selected at each of the six ($n = 3$ coarse-textured, $n = 3$ fine-textured) sites. We selected trees of a similar height and canopy diameter, and avoided trees showing obvious evidence of disturbance below the canopy. We acknowledge that soil hydrology can vary over small spatial scales, but considered three subsamples per soil type to be feasible and appropriate. The 'grassy slope' strata were selected within an area of homogeneous grass cover at least 10 m from the edge of the nearest tree canopy. The cultivated strata were selected as close as possible to the remnant patch containing the other three strata, usually at distances of less than 30 m. As land to be cultivated is typically chosen in a nonrandom manner from the landscape, the cultivated strata within this survey could not be considered to be selected completely randomly.

Description of the landscape strata

'*Eucasphere*': The zone of maximum litter accumulation extending a few metres beyond the drip line around the bole of generally mature *Eucalyptus* spp. trees. These trees had canopies up to 15 m in diameter and trunks up to 900 mm diameter at breast height (d.b.h.). The soil surface was characterized by a moderately dense and extensive (up to 100% cover) layer of leaves, twigs and organic material with a high degree of incorporation within the surface soil. *Eucaspheres* supported a sparse and variable cover of vascular plants, depending on the soil type.

'*Callitrisphere*': The area below the canopy of mature *C. glaucophylla* trees extending to distances of approximately 3 m from the trunk. The soil surface was characterized by a deep (up to 15 cm thick) layer of pine needles in various stages of decomposition. Observation of the pine litter indicated that it was often water-repellent because of the presence of large quantities of fungal hyphae (Bond & Harris 1964). Tree canopies were up to 8 m in diameter, and trunks up to 450 mm d.b.h. The surface below the canopy was typically shaded and devoid of vascular plant cover except for occasional *Einadia nutans* ssp. *nutans* or *Rhagodia spinescens* subshrubs, which tolerate low light levels.

'Grassy slope': Slopes and flats up to 50 m between trees, and with slopes of 1–2% characterized by extensive areas of perennial grass tussocks separated by bare or cryptogam-covered interspaces with a variable cover of annual and perennial forbs. The soils generally supported a high population of ants and termites, as indicated by the presence of nests, and the interspaces were generally stable, uneroded and protected by biological soil crusts (cryptogams) or physico-chemical crusts with a variable cover of unincorporated litter.

'Cultivated': Broad undulating plains up to 1.5 km between patches and strips of woodland that have been cleared and regularly cultivated for 50–150 years. The soil surfaces ranged from a physically sealed and crusted surface to a slightly open surface morphology with a massive sandy fabric (coarse-textured soils) or sandy-to-earthy fabric (fine-textured soils). Litter cover was generally sparse and variable depending on the particular cropping rotation.

Measurement of soil hydrological properties

Soil consists of a matrix of organic matter, mineral material and pores of various size and shape, which are filled with air or water. Large soil pores, termed macropores, which are generally greater than 0.75–1.00 mm in diameter, are important in the transfer of water and nutrients through the soil (Bouma 1992). In the absence of cracking in soils of a high clay content, macropores are biotic in nature and formed by plant roots and soil fauna (Lee & Foster 1991; Lavelle *et al.* 1997). Smaller pores, termed micropores or matrix pores, also occur between individual mineral grains and soil particles, but are not generally formed by soil biota.

In simple terms, water infiltration occurs in two distinct phases. 'Sorptivity' is the early 'wetting up' phase of infiltration, approximately 2–10 min after water is applied. During this period water enters the soil in response to gradients in water potential influenced by soil dryness and capillary (pore) structure (White 1988). The sorptivity phase is largely governed by the forces of attraction between soil and water molecules. As the soil wets up, gravitational forces become more important (White 1988) and, after long time periods, a steady state is reached when the flow rate from a source of water stabilizes over time. This steady-state flow rate or steady-state infiltration, is governed by capillarity, gravity, the area of the disc permeameter in contact with the soil and the pressure at which the water is supplied to the soil surface (CSIRO 1988). These properties can be measured relatively simply with disc permeameters, portable infiltration devices, which measure the flow of water through the soil at a range of pressures or supply potentials.

Water flow through the soil depends on the combination of macropores and matrix pores. When a negative pressure or tension is applied to the soil using the disc permeameter, water is prevented from entering macropores, and therefore the influence of matrix pores on sorptivity and steady-state infiltration can be assessed independent of the effect of macropores. Similarly, when infiltration is measured with a positive pressure, flow through both macropores and matrix pores is assessed. Thus by varying the pressure on the disc permeameter, it is possible to isolate water flow between either small pores only, or small and large pores together.

In September 2001 we assessed both sorptivity (mm $h^{-0.5}$) and steady-state infiltration (mm h^{-1}) through the soil using two pressures or supply potentials: –40 mm tension, which measured only matrix pore flow, and +10 mm tension, which measured flow through all pores (Perroux & White 1988). The ratio of sorptivity under ponding (+10 mm) to sorptivity under tension (–40 mm) is a measure of the relative importance of macropores to total water flow (White 1988). This is an informative measure, as macropores are indicative of healthy, highly conductive soils, and a loss of ecosystem function in terms of water flow can be attributed, in a large part, to a loss of this macroporosity.

The permeameters were placed between the canopy edge and the trunk (for *Eucasphere* and *Callitrisphere*), or between individual grass tussocks (for the grassy slope stratum). On the cultivated soils, the permeameters were placed between windrows that had been created by previous cultivation. All of the 'cultivated' soils were fallow at the time of measurements, that is, they did not support actively growing crops, but had been cultivated during the previous year. The cultivated soils had a sparse cover of crop residue, annual grasses and broad-leaf weeds. The ponded and unsaturated permeameters were placed alongside each other (but about 70 cm apart) within each replicate at each site. Infiltration was measured at three locations at each of the four strata at each of the six sites (i.e. two soil types each with three sites, by four strata, by three replicates; $n = 72$).

The permeameter at –40 mm supply potential was placed on a thin bed of sand to provide a uniform contact with the soil surface. The ponded (+10 mm) permeameter was placed on a steel ring of 220 mm internal diameter, which was gently pressed into the soil to a depth of about 7–10 mm, and sealed with soil along the outside edge to prevent leakage of water. The permeameters were run for approximately 30 min by which time steady-state had been achieved. At each supply potential, sorptivity was calculated according to the method of Wooding (1968) (see Cook & Broeren 1994), and steady-state infiltration according to White (1988).

Soil surface attributes

We compared the empirical infiltration data obtained with the disc permeameters with soil surface indices of infiltration originally derived for arid landscapes (see Tongway & Hindley 1995). We did this in order to examine the relationship between infiltration and soil surface features as one means of exploring possible reasons why infiltration might differ between landscape strata.

We characterized five attributes of the soil surface at each disc permeameter site: microtopography, crust coherence, soil surface texture, litter cover and vegetative cover. Surface microtopography was defined as the vertical distance between the lowest and highest points on the surface in the quadrat and was placed into five classes, that is, <5 mm, 5–8 mm, 8–15 mm, 15–25 mm, >25 mm. Crust coherence is a measure of the force required to disrupt the soil surface with an object equivalent to the diameter of a pencil, and assesses the degree to which the surface has the capacity to resist stress immediately upon wetting, or to reform after wetting (Tongway 1995). Crust coherence classes were scored as sandy (single grained) (score 1), break on touch (2), moderately hard pressure (3), significant pressure, hard and brittle (4), nonbrittle and flexible or self-mulching (clay aggregates) (5). Increasing number equates with increasing predisposition to hardsetting. Soil texture was determined in the laboratory using the bolus method of Northcote (1979) and soils were placed into one of the following groups: sand, loam, clay loam or clay. Further, at each permeameter site, both vascular plant cover and litter cover were visually estimated as 0%, <10%, 10–25%, 25–50% or >50%. For litter cover, a further class was added to include 100% cover but a very deep (>2 cm) litter layer. The score given to each of the five attributes was such that a higher score equated with a healthier microsite (in terms of the potential to accept infiltrating water). A more detailed description of this method is given in the study by Tongway and Hindley (1995) and on the web (http://www.cse.csiro.au/research/Program3/efa/index.htm). For each stratum within which infiltration measurements were made, we scored each of the five surface attributes within small (0.5 m^2) quadrats.

For each stratum at each of the six sites, the individual scores for each of the five attributes were summed and expressed as a percentage of the maximum possible score. The resulting infiltration index was plotted against empirical measures of sorptivity and steady-state infiltration to examine how well it corresponded with measured infiltration rates and to assist us in accounting for differences in infiltration between strata.

Soil analyses

Soil samples were taken from the top 20 mm of the soil at each stratum at each of the six sites ($n = 24$) and bulked before a 500-g subsample was selected. Soluble cation concentrations (Ca^{2+}, K^+, Mg^{2+} and Na^+) were measured using atomic absorption spectroscopy (Unicam 929 AAS, Technomatic-Unicam, Portsmouth, NH, USA) in 1 : 5 soil : water and 1 : 5 soil : NH_4Cl extracts. Organic carbon content was measured using a modified Walkley–Black method (Nelson & Sommers 1982), pH and electrical conductivity were measured in 1 : 5 soil : water extracts. Total carbon, nitrogen and sulphur were determined using high-temperature combustion in an oxygen stream using a LECO CNS-2000 CNS Analyser (LECO Corporation, St Joseph, MI, USA).

Statistical analyses

Differences in infiltration parameters and soil physical and chemical properties between the two soil types each with three individual sites were examined using a Generalized Linear Model with 'sites' ($n = 6$) random, and the four levels of 'strata' fixed. The two-way ANOVA was performed on $\log_{10}$ or arcsine transformed data in order to stabilize the error variance from each of the individual one-way ANOVAs (Minitab 1997).

A matrix comprising the scores for each of the five soil surface attributes (by the four strata for each site by soil type; $n = 24$) was converted to a similarity matrix using the Bray–Curtis similarity coefficients contained within the PRIMER (Version 4) statistical package (PRIMER-E Ltd, Plymouth, UK; Clarke & Warwick 1994). This similarity matrix was subjected to nonmetric Multidimensional Scaling (MDS) using one of the PRIMER routines in order to determine whether surfaces from a particular stratum were characterized by distinct surface features. Hypothesis tests of differences between the four strata, defined *a priori*, were performed using ANOSIM, which is comparable to a distribution-free two-way ANOVA (Clarke 1993). Using a number of random permutations on the similarity matrix, ANOSIM produces a test statistic (Global *R*) with a significance level, which we used to determine whether the soil surface differed significantly between the four strata. The routine SIMPER was used to identify which of the soil surface features best described the dissimilarity between groups.

RESULTS

Infiltration parameters

There was a significant site effect on sorptivity under ponding ($F_{4,12} = 3.45$, $P = 0.043$). This was attributed to significantly greater sorptivity at one of the three coarse-textured sites compared with the three fine-textured sites, which was greater than sorptivity at the two remaining coarse-textured sites.

Pooled across all sites and landscape strata, there were no significant effects of soil type for any of the measures of infiltration ($P > 0.05$). Similarly, pooled across sites and soil type there were no effects of landscape stratum ($P > 0.05$). However, for both sorptivity under ponding and steady-state infiltration under ponding there were significant soil × stratum interactions ($F_{3,12} = 6.63$, $P = 0.007$; $F_{3,12} = 7.23$, $P = 0.005$ respectively). Multiple comparison tests revealed that steady-state infiltration was substantially greater (approximately fivefold) in the *Eucasphere* and *Callitrisphere* compared with the grassy slope and cultivated strata, but only on the fine-textured soils (Fig. 1). Further, on the fine-textured soils, sorptivity under ponding was significantly greater in the *Eucasphere* and *Callitrisphere* compared with the grassed and cultivated strata (Fig. 2). On coarse-textured soils however, there

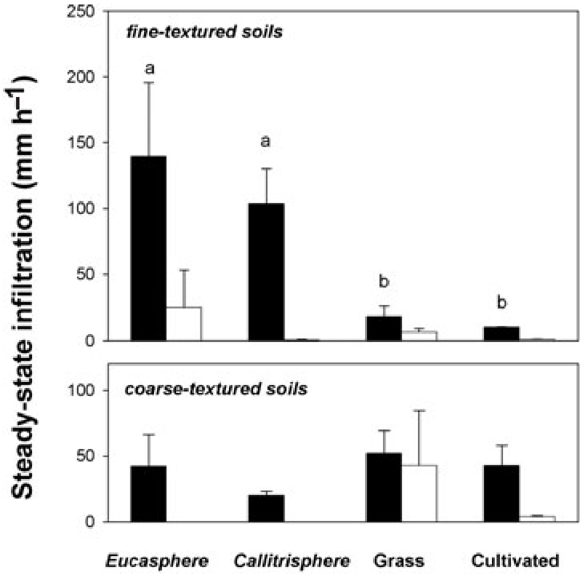

Fig. 1. Mean (± SEM) steady-state infiltration under ponding and tension on fine-textured and coarse-textured soils in relation to the four landscape strata. For infiltration under ponding or tension, different letters indicate a significant difference at $P < 0.05$, and bars without letters are not significantly different. There were no significant stratum effects on the coarse-textured soils. Note the differences in scale on the y-axes. (■) Ponding; (□) Tension.

were no significant differences in sorptivity or infiltration between landscape strata.

Indices of macroporosity

As indicated above, the ratio of sorptivity under ponded (+10 mm) to unsaturated (–40 mm) conditions is a useful measure of the degree to which the soil is dominated by macropores (White 1988). These pores are the most sensitive to changes in management (e.g. trampling or overgrazing), and the larger the ratio the greater the macropore effect on infiltration. A ratio of 1.0 indicates a completely degraded, macropore-free soil, with the movement of water through the upper soil profile restricted to matrix or micropores (<0.25 mm in diameter).

Pooled across both soil types, there were highly significant effects of stratum on the ratio of ponded to unsaturated sorptivity (Table 1). In both soil types the ratio under *Eucasphere* and *Callitrisphere* was significantly greater than that for the grassy slopes or for cultivation ($F_{3,12} = 10.82$, $P = 0.001$ for $\log_{10}$ transformed data). This indicated the preponderance of macropores under trees compared with soils between native grass tussocks or in the cultivated paddocks. However, there were no significant differences in the ratios between the soil types ($P > 0.05$). On the coarse-textured soils, sorptivity ratios were five times greater in the *Eucasphere–Callitrisphere* compared with the grassy slope–cultivated strata. On the fine-textured soils, ratios for sorptivity were approximately seven times greater in the *Eucasphere–Callitrisphere* compared with the grassy slope–cultivated strata.

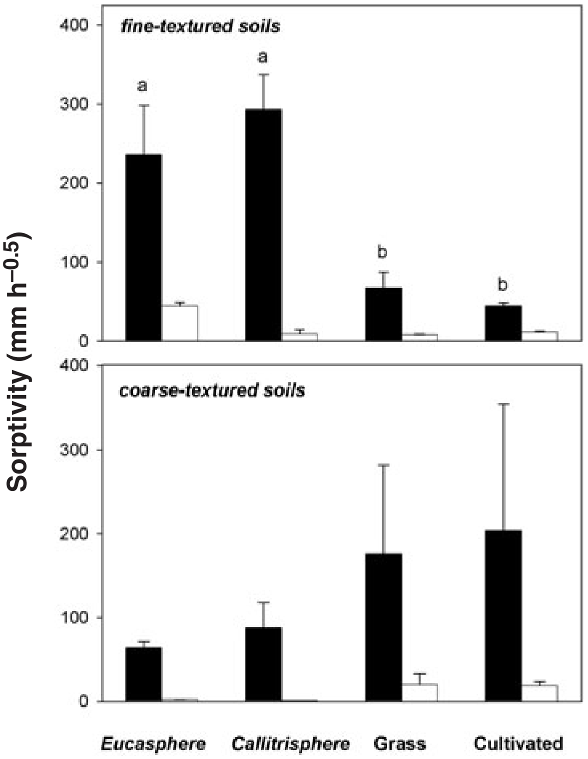

Fig. 2. Mean (± SEM) sorptivity (initial wetting) under ponding and tension on fine-textured and coarse-textured soils in relation to the four strata. For ponded or tension infiltration, different letters indicate a significant difference at $P < 0.05$. Bars without letters are not significantly different. (■) Ponding; (□) Tension.

Infiltration and soil surface condition

The infiltration index, comprising the scores for soil surface attributes influencing infiltration, ranged from 37.5% to 70.8% (Fig. 3). For the fine-textured soils alone we could detect no meaningful relationship between measured sorptivity under ponding and the infiltration index score ($P = 0.08$). However, increases in the infiltration index were associated with increases in steady-state infiltration ($P = 0.05$, $R^2 = 0.24$, $n = 12$). Further, when one extremely water-repellent site on a cryptogam-dominated soil (steady-state infiltration = 4.6 mm h^{-1}) was excluded from the analyses, a highly significant relationship between measured infiltration and the infiltration index was detected ($P = 0.003$, $R^2 = 0.64$, Fig. 3).

Table 1. Mean soil physical and chemical properties of the four strata by soil type

		Stratum			
Properties	Soil type	*Eucasphere*	*Callitrisphere*	*Grassy slope*	*Cultivated*
Sorptivity ratio†	Fine	46^{a}	57^{a}	11^{b}	4^{b}
	Coarse	48^{a}	61^{a}	14^{b}	8^{b}
Organic carbon (%)	Fine	7.05^{a}	7.44^{a}	2.82^{b}	1.04^{b}
	Coarse	4.18^{a}	4.50^{a}	2.23^{a}	1.10^{a}
Total carbon (%)	Fine	8.67^{a}	9.19^{a}	3.30^{b}	1.32^{b}
	Coarse	4.72^{a}	4.93^{a}	2.52^{a}	1.14^{a}
pH (1 : 5 water)	Fine	6.09^{a}	5.97^{a}	5.92^{a}	5.54^{a}
	Coarse	5.95^{a}	5.81^{a}	6.13^{a}	5.72^{a}
EC (dS m^{-1})	Fine	111.23^{a}	139.67^{a}	58.78^{a}	57.53^{a}
	Coarse	67.60^{a}	155.20^{a}	81.05^{a}	50.17^{a}
Calcium (p.p.m.)	Fine	54.17^{a}	51.81^{a}	69.23^{a}	19.25^{a}
	Coarse	43.44^{a}	31.86^{a}	30.33^{a}	13.16^{a}
Magnesium (p.p.m.)	Fine	18.43^{a}	16.62^{a}	15.35^{a}	33.60^{b}
	Coarse	42.83^{a}	12.34^{b}	14.67^{b}	25.19^{c}
Sodium (p.p.m.)	Fine	24.68^{a}	10.84^{a}	14.89^{a}	14.70^{a}
	Coarse	27.28^{a}	22.75^{a}	16.83^{a}	30.25^{a}
Potassium (p.p.m.)	Fine	78.81^{a}	81.13^{a}	61.04^{a}	52.29^{a}
	Coarse	53.13^{a}	84.38^{a}	49.42^{a}	38.83^{a}
Total sulphur (%)	Fine	0.04^{a}	0.02^{ac}	0.02^{ac}	0.01^{bc}
	Coarse	0.02^{a}	0.02^{a}	0.01^{a}	0.004^{b}
Total nitrogen (%)	Fine	0.55^{a}	0.25^{ab}	0.27^{ab}	0.08^{b}
	Coarse	0.25^{a}	0.30^{a}	0.31^{a}	0.05^{b}

†Refers to the ratio of saturated (+10 mm) to unsaturated (–40 mm) sorptivity.
For a particular soil type, different letters within a row indicate a significant difference in that attribute at $P < 0.05$.

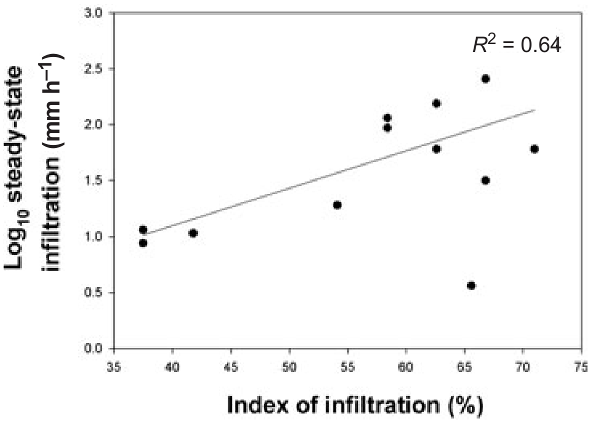

Fig. 3. Relationship between the index of infiltration (%) and log$_{10}$ steady-state infiltration under ponding for the fine-textured sites only and omitting one site with infiltration = 4.6 mm h^{-1}.

Analysis of similarities (ANOSIM) indicated a strong significant difference among the four strata in relation to the make-up of their soil surfaces (Global $R = 0.725$, $P = 0.001$) as well as significant differences between soil types (Global $R = 0.346$, $P = 0.003$). Predictably, there were substantial differences between cultivated, grassy slopes and the timbered (*Eucasphere*, *Callitrisphere*) strata, but within the timbered areas, the *Eucasphere* and *Callitrisphere* strata did not differ from each other (Fig. 4). Litter cover and foliage cover accounted for about half of the cumulative dissimilarity between the three groups of strata, with litter cover declining from timbered (*Eucasphere* and *Callitrisphere*) to cultivated strata, and maximum cryptogam and foliage cover at the grassy strata and declining elsewhere. About half of the difference between soil types was attributed to a greater litter and foliage cover on the fine-textured soils compared with the coarse-textured soils.

Effect of soil type

In general, there were a greater number of significant differences among the fine-textured soils compared with the coarse-textured soils. Averaged across all strata and paddocks, fine-textured soils contained approximately 40% more total carbon (5.6% C) compared with the coarse-textured soils (3.3% C; $F_{1,4} = 11.26$, $P = 0.0028$).

On the fine-textured soils there were significantly higher levels of both organic carbon and total carbon in the timbered (*Eucasphere–Callitrisphere*) strata compared with the grassy slopes and cultivated strata (Table 1). Similarly, total sulphur and total nitrogen levels were significantly lower, and soluble magnesium concentrations significantly higher, in the cultivated

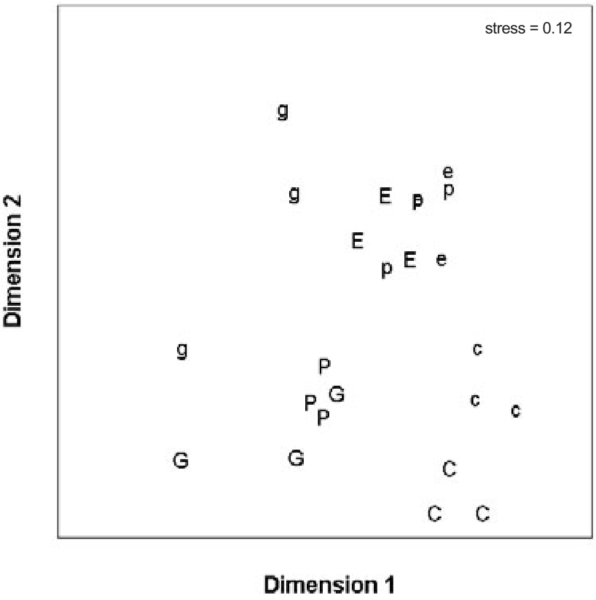

Fig. 4. The first two dimensions of the nonmetric MDS biplot based on soil surface characteristics showing the relative positions of *Eucasphere* (E, e), *Callitrisphere* (P, p), grassy slope (G, g) and cultivated (C, c) strata. Upper-case letters indicate fine-textured sites and lower-case coarse-textured sites. Note the wide separation in grassy strata between the two soil types.

strata compared with the *Eucaspheres* ($P < 0.05$, Table 1).

On the coarse-textured soils, there were some ill-defined trends in magnesium, but these did not correspond to a gradient from the timbered to cultivated strata. As in the fine-textured soils, total sulphur and total nitrogen concentrations were significantly lower in the cultivated soils compared with the *Eucasphere* soils (Table 1).

DISCUSSION

Based on previous studies we had four *a priori* hypotheses: (i) water infiltration rates should be higher under trees than on grassy slopes or on cultivated soils; (ii) when biopores are bipassed there would be no difference in water flow among the strata; (iii) the impact of trees on water flow under tension would be similar on fine- and coarse-textured soil; and (iv) differences in surface cover and condition would explain differences in infiltration among the strata.

The results clearly supported our first hypothesis that infiltration rates are substantially higher under trees than on intertree grassy slopes or on cultivated soils, but only on the fine-textured soils (Figs 1,2). Sorptivity (the initial wetting-up phase) and steady-state infiltration rates under the tree canopies were significantly greater than rates at the noncanopy strata. Measurements of sorptivity under tension, where water is restricted to small matrix pores and macropores are unable to conduct water, supported our second hypothesis, that soil macroporosity drives the differences between timbered and nontree strata.

Increased infiltration under trees and shrubs has been demonstrated in a range of low rainfall environments. Scholte (1989) showed that the rate of infiltration under shrubs was 20 times greater than adjacent nonshrub surfaces, while greater flow under woody plants can be attributed to differences in macropores (Devitt & Smith 2002). Greene (1992) demonstrated 10-fold greater infiltration rates in mulga (*Acacia aneura*) groves compared with adjacent sparsely grassed run-off slopes. *Eucalyptus* trees have an extensive network of horizontal roots, allowing them to scavenge for moisture from many metres beyond their canopy (Tunstall & Walker 1975; Johns *et al.* 1984) as well as from depth. Our results indicated only about a sevenfold greater increase in infiltration between timbered and nontimbered (grassy) sites (Figs 1,2), lower than values reported for other systems. Nevertheless, the results highlighted the importance of woody plants for enhancing infiltration, and extended the concept of trees as ‘ecosystem wicks’ to low rainfall agricultural landscapes.

Increased infiltration under trees is also linked to increased soil nutrient concentrations. Studies of wooded and savanna ecosystems worldwide have demonstrated elevated concentrations of carbon, mineralizable nitrogen and extractable P, K and Ca in soils below trees compared with adjacent open grassland (Kellman 1979; Bernhard-Reversat 1982; Eldridge & Wong in press). Concentrations also declined rapidly with distance from the trunks (Belsky *et al.* 1989). Soil nutrient differences also likely exist between the soil types as some nutrients are more strongly adsorbed onto soils with a higher clay content (Schlesinger & Pilmanis 1998). In our study, the carbon content of fine-textured soils (7%) was significantly greater than on coarse-textured soils (4%, Table 1). These fine-textured soils would likely be associated with higher levels of soil forming processes (Rostagno *et al.* 1991), invertebrates and soil mineralization, resulting in greater soil stability and resilience after disturbance.

The effect of preventing flow through soil macropores was consistent between the two soil types, supporting our third hypothesis. Infiltration under tension was uniformly low across both soil types and was significantly less than infiltration under ponding for both soil types (Figs 1,2). However, the effect of soil type on ponded infiltration was not consistent. Greater infiltration under trees was only recorded in the fine-textured soils. The statistically significant interaction between soil texture and ponded infiltration suggested that trees have a different biological effect on infiltration depending on soil texture. Infiltration under tension essentially measures the capacity of water to pass through the soil body while bypassing large biologically derived pores. Thus the greater infiltration under trees on fine-textured soils is likely attributed to a much higher density of biologically derived macropores and possibly differences in soil surface condition.

As indicated above, the ratio of sorptivity under ponding to sorptivity under tension is related to the area of macropores and structural voids in the soil, and the length of large pores and capillaries (White 1988). There were no apparent differences in the ratios of sorptivity under ponding to sorptivity under tension between fine- and coarse-textured soils, but clearly large differences for the cultivated and grassy strata (4–14) compared with ratios for the timbered strata (46–61; Table 1). In more degraded rangelands near Cobar, ratios of 1–2 are more typical (Eldridge 1993). Our greater ratios for 'macropore-free' sites of the order of 4–8, even under cultivation, suggested that there were some macropores present, but not of the same extent as under the trees.

We therefore cannot attribute differences in infiltration between soil types to differences in macroporosity alone. Differences in infiltration were likely attributed to variations in surface cover, which allowed the fine-textured soils to accept more water than the coarse-textured soils. The highly significant relationship between steady-state infiltration and the index of infiltration suggested that increasing values of those soil surface attributes used to derive the infiltration index were associated with increasing infiltration (Fig. 3). This was supported by the multivariate analyses that indicated about half of the difference between soil types was attributed to greater litter and foliage cover on the fine-textured compared with the coarse-textured soils. We suggest that the greater cover of vegetation and litter on the finer soils was responsible for maintaining the surface integrity of macropores, and, despite the fact that macropore status was similar overall between both soil types, that the fine-textured surface allowed a greater ingress of water and thus substantially greater volumes of infiltration compared with the coarse-textured surfaces. The implication of these results is that fine-textured soils are probably able to maintain continuity of macropores to the surface to a greater extent than coarse-textured soils, resulting in greater overall infiltration.

Compared with fine-textured soils, coarse-textured soils have a poorer ability to retain water when wet because of a combination of larger matrix pore sizes with shorter path lengths (D. J. Tongway pers. comm. 2003). On these soils, values of sorptivity under ponding showed the opposite trend to steady-state infiltration, with the magnitude and variability increasing from timbered to cultivated strata (Fig. 2). Low rates of sorptivity, the initial wetting-up phase, could have been attributed to a number of factors. Water repellency is common under *C. glaucophylla* canopies because of large populations of fungal hyphae, which are known to repel water (Bond & Harris 1964). Even after the soil wetted up after the sorptivity phase, steady-state infiltration was typically quite low. Fine material is low in these sandy soils (<10% clay), resulting in structurally poor surface horizons. However, even low levels of silt and clay are sufficient to block matrix pores, inducing crusting and restricting water flow (Eldridge *et al.* 2000). Crusting is exacerbated by low levels of plant and litter cover on the coarse-textured soils resulting in structural breakdown after raindrop impact (Tao *et al.* 2001).

Landscape structure and infiltration

The marked differences in infiltration capacity between the timbered and grassy strata suggested to us a patterning of the Savernake landscape into two distinct geomorphic zones: (i) water-shedding grassy slopes and (ii) water-catching timbered groves (see Ludwig & Tongway 1995). Ponded infiltration under the eucalypts on fine-textured soils exceeded 140 ± 60 mm h^{-1}, far in excess of any likely maximum rainfall for the area (Pilgrim 1998). On the grassy slopes, cryptogamic crusts create a patchwork of small run-off zones (Eldridge 1993) separated by individual grass tussocks, which function as localized sites for water accumulation. During small rainfall events, grass tussocks capture most of the run-off water (Bochet *et al.* 2000), which is generated off the relatively water-repellent cryptogamic crusts. At the scale of individual grass tussocks, cryptogams provide an ecological service by redistributing rainfall and organic material to productive grassy patches without contributing to sediment yields. At the broader landscape scale, run-off generated from intense storms is likely to be captured in the timbered strata, which have the capacity to absorb substantial volumes of run-off. Our infiltration measurements indicated that *Eucalyptus* trees are capable of soaking up substantial quantities of surface run-off, functioning as 'ecosystem wicks' during high rainfall events.

During less intense rainfall events however, trees are also likely to capture surface run-off generated from the cryptogamic surfaces which is not captured by grasses, that is, 'ecosystem leakage' *sensu* Ludwig *et al.* (1994) and Shachak *et al.* (1998). Redistribution of water from the grassy patches could therefore be finding its way into deep drainage and contributing to local and regional recharge. However, roots of eucalypts typically draw water from depths greater than 20 m and are able to transpire water from depths normally out of reach by grasses and even shrubs (Stirzaker *et al.* 1999). Consequently much of this infiltrated water finding its way through timbered mounds is prevented from reaching and recharging groundwater (Walker *et al.* 1993).

Notwithstanding that tree density is substantially higher in the Savernake area compared to other areas of south-eastern Australia, dryland salinity is still a major threat. On cropping land in the mallee landscapes further west, recharge rates are typically in the order of 2–23 mm h^{-1} for coarse-textured soils and 0–8 mm h^{-1} for fine-textured soils (Leys *et al.* 1994). The maintenance of functional, run-on–run-off patches at Savernake where water is channelled below the trunk and ultimately absorbed by trees may be delaying the rise of water tables, which are still relatively deep (24 m) compared to nearby alluvial soils. Vegetation clearance has totally obliterated the key landscape function of run-on–run-off by removing the trees, destroying ecosystem patchiness and reducing the number and size of sinks available for capturing of surface flows. On sloping country, and in the absence of timbered sinks, excess run-off leads to uncontrolled soil movement in the form of rilling and gullying. Under traditional cropping practices these landscapes become increasingly arid, with water ponding on flat slopes and depressions as a result of low levels of infiltration. In terms of water movement, the long-term prognosis of excessive tree removal in these environments is a breakdown in landscape patchiness, increased landscape instability and eventually increased accession to the water table.

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