Clumped and isolated trees influence soil nutrient levels in an Australian temperate box woodland

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Abstract

Isolated paddock trees are a common feature of agri-pastoral landscapes in south-eastern Australia. We assessed the impact of trees on soil nutrients by examining (1) changes in soil nutrients under clumped and isolated (living and dead) trees at four microsites corresponding with increasing distance from the trunk (trunk, mid-canopy, drip line, open), and (2) changes with depth under trees growing in clearly-defined clumps. We detected significantly greater concentrations of organic C, and total N and S under trees growing in clumps compared with either isolated living or dead trees. Levels of soluble Ca^{2+}, K^+ and Mg^{2+}, pH, electrical conductivity (EC) and available P declined with increasing distance from the trees, but there were no significant trends for organic C, or total N and S. The concentration of most nutrients declined with depth, particularly at microsites close to the trunk, while pH increased with depth. We believe that differences in chemistry were largely driven by greater inputs of organic matter under the trees. This study reinforces the view that trees, whether scattered or in clumps, are important for soil nutrient conservation in agri-pastoral landscapes.

Introduction

Prior to European settlement, temperate box woodlands dominated by *Eucalyptus* spp. were widely distributed over gently undulating or hilly country in eastern Australia (Lunt, 1991; Prober, 1996; Prober and Brown, 1994; Prober and Thiele, 1993). Extensive vegetation clearance, primarily for agriculture, has left the majority of the original vegetation highly fragmented. Consequently, less than 0.01% remains unmodified, with the remainder found within a matrix of cropland and introduced pasture often disturbed by stock (Lunt, 1991; Prober and Thiele, 1995; Yates and Hobbs, 1997; Yates et al., 2000). This loss of trees has been associated with almost every aspect of land degradation in Australia (Bird et al., 1992), with degradation of remnants indicated by the early and rapid decline and death of trees, lack of tree recruit-

ment, loss of understorey species, rising water tables causing salinity and waterlogging, soil erosion, deterioration of soil structure, invasion by exotic plant species and an increase in unpalatable understorey species (Yates and Hobbs, 1997).

Clumped and isolated trees are important aesthetic features in the landscape and provide habitat for a wide range of invertebrate and vertebrate fauna (Law et al., 2000). They moderate the flow of water into the soil, and influence essential soil and ecological processes such as mineralisation and decomposition (Deans et al., 1999; Jackson and Ash, 2001; Yates et al., 2000). Studies of the effects of trees on soil properties in wooded and savanna ecosystems indicate higher levels of mineralizable nitrogen (N), and extractable phosphorus (P), potassium (K^+) and calcium (Ca^{2+}) in soils from below tree canopies compared with adjacent open grassland (Belsky, 1994; Belsky and Canham, 1994; Belsky et al., 1989; Bernhard-Reversat, 1982; Kellman, 1979; Weltzin and

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Coughenour, 1990). Within patches of tree-dominated savanna, concentrations of organic matter, total and available N, Ca^{2+}, K^+, P, sodium (Na^+) and sulphur (S) have been found to be highest adjacent to the tree trunks, decline with distance from the canopy, and reach their lowest concentrations in the open grassland (Belsky, 1994; Belsky and Canham, 1994; Belsky et al., 1989). The soils usually show a systematic and predictable variation, with a distinctive radial pattern around each tree (Amiotti et al., 2000). Soils also show clearly defined changes with depth, with rapid declines in nutrient concentrations with increasing depth (Ryan and McGarity, 1983; Schlesinger and Pilmanis, 1998). Depth effects often persist for many years after the tree has died. In grazed systems, improved fertility can result in increased herbage responses (Belsky, 1994), improved diet quality and feed intake (Jackson and Ash, 2001), and therefore higher animal productivity.

Soil chemical heterogeneity in woodlands results from the spatial and temporal effects of trees. Within woodlands, high root activity is linked to increased vegetative cover, which may increase the formation of macropores and therefore the stability of soil aggregates (Degens, 1997). Temperature and evapotranspiration are lower under tree canopies (Belsky, 1994; Belsky et al., 1989), and increased litterfall may prevent soil erosion by impeding water flow and enhancing absorption (Prinsley, 1992). Isolated trees have a greater root volume per tree than those within clumps, and therefore have the potential to intercept and pump larger volumes of subsurface water (Gibbons and Boak, 2000). Further, the root systems of scattered isolated trees can extend beyond the influence of the tree canopy, with their effects in savannas largely proportional to crown size (Joffre and Rambal, 1993; Zinke, 1962).

Although there is an extensive body of research on the role of trees in soil processes from tropical and subtropical savanna ecosystems (e.g. Belsky, 1994; Deans et al., 1999; Scholes, 1990), there are relatively few data from the temperate box woodlands of eastern Australia (see however Graham et al., 2004; Wilson et al., 2002). The present study aims to understand more about the impact of trees growing in clumps and isolated trees on surrounding soils. The aims of this study are threefold; (1) to examine the spatial variability of soil properties along a gradient extending from the canopy to open areas, (2) to determine whether these trends are consistent between trees growing within clumps, isolated dead and isolated living trees, and (3) to assess changes in soil nutrients with depth within a grove of clumped trees.

Materials and methods

The study area

The study was conducted at 'Mona Vale' in the Kyeamba Valley, approximately 15 km south-east of Wagga Wagga (35°09′36″ S, 147°27′35″ E) in the south-west slopes region of NSW, Australia. The general locality is underlain by slate and folded Ordovician metasediments, and overlain by younger alluvial deposits (McInerney and Smith, 1999). The study site is located on higher level terraces and valley slopes dominated by Quaternary alluvium associated with Kyeamba Creek and its terraces. The soils have been classified as Haplic Red Kurosols (Isbell, 1996) or Lixisols (FAO, 1998). The soils have a weakly pedal, sandy clay-loam A1 horizon, grading to a weakly pedal clay-loam A2 horizon to 0.3 m deep. The B horizon is typically a moderately pedal clay to depths of about 0.9 m.

The climate at Wagga Wagga, the nearest meteorological station, is warm temperate, with mean daily maximum and minimum temperatures in summer (January) of 31.3 °C and 16.1 °C respectively, and winter (August) of 14.3 °C and 3.6 °C or an annual average of 9.0 to 22.1 °C (Bureau of Meteorology, 2001). The area receives an average annual rainfall of 584 mm, which is winter dominant (Chen, 1997).

Kyeamba Valley has been used extensively for agriculture since the 1830s, initially for cropping. Consequently, about 7% of the original tree cover remains at the study site. Remnant patches of native vegetation and isolated trees of the box woodland communities, namely *Eucalyptus albens* Benth., *E. melliodora* A. Cunn. ex Schauer, *E. microcarpa* (Maiden) Maiden and *E. blakelyi* Maiden form, when intact, an open canopy within a matrix of improved pasture which is grazed by sheep and cattle, and that of cropped areas consisting mainly of wheat, oats, lucerne and canola. While an intact understorey is rare, the original woodland understorey would have been dominated by kangaroo grass (*Themeda australis* (R. Br.) Stapf, *Themeda triandra* Forssk.), and other perennial grasses (*Poa sieberana* Spreng, *Austrostipa* spp., *Austrodanthonia* spp.) (Prober and Thiele, 1993).

At the time of measurements the site at 'Mona Vale' was managed as a mixed farming property and

was lightly grazed by cattle and cross-bred Merino sheep on native unimproved pastures dominated by speargrasses (*Austrostipa* spp.), wiregrasses (*Aristida* spp.) and red grass (*Bothriochloa macra* (Steud.) S.T. Blake). Stocking rates vary from 1–2 sheep ha^{-1} depending on pastoral conditions. Some lower-lying paddocks had been sown to lucerne (*Medicago sativa* L.). Extensive replanting of native trees in large blocks or as long thin windbreaks has been carried out since the early 1990s in an attempt to reduce local groundwater levels.

Selection of sampling units

An area of approximately 300 ha consisting of six paddocks was selected at the property 'Mona Vale' for the study. We selected five *Eucalyptus melliodora* trees from two extensive patches of *E. melliodora* and *E. albens* spanning three paddocks. Trees were selected randomly by walking on a predetermined compass bearing and selecting the nearest tree based on generated random numbers. The selected trees were closely-spaced for this landscape (20–30 m between trunks) and for our study are termed 'clumped'. The five 'clumped' trees were of similar height and age, and at a similar position on the slope. The diameter of the crowns averaged 16.1 ($\pm$0.90 standard deviation) m across by 19.2 ($\pm$0.73) m tall, and the diameters at breast height (DBH) averaged 0.8 ($\pm$0.12) m. An additional five isolated living trees (termed 'isolated'), which were selected from the same and adjoining paddocks on the same soil type and similar slope, were not part of these large clumps. Tree dimensions averaged 19.3 ($\pm$1.93) m across, by 14.4 ($\pm$1.60) m tall, and 1.0 ($\pm$0.10) m DBH.

Five isolated dead trees (termed 'dead') were selected in the same or adjoining paddocks on the same slope and soil type. Average dimension of dead trees were 17.2 ($\pm$2.24) m across, by 13.8 ($\pm$1.02) m tall, and 0.9 ($\pm$0.10) m DBH. The crown diameters of dead trees were estimated from their branching structure. Landholders estimate that these trees died at least 25 years before the study. The isolated and clumped trees were estimated to be approximately 200–300 years old. Isolated and dead trees were selected on the basis that they were more than 150 m from the nearest tree, not close to a fence, track or watering point (dam or trough), of comparable size (and presumably age) as the clumped trees, and not in paddocks that had been

fertilised, or where lucerne (which fixes nitrogen) had been grown during the past 15 years.

Soil samples were taken from the surface layer (0–2 cm) at four microsites associated with each of five trees. The microsites were: adjacent to the trunk (termed 'trunk'), at the mid-canopy position, approximately 4–5 m from the trunk (termed 'mid'), at the edge of the canopy or drip line (termed 'drip'), and in the open. 'Open' sites were at least one canopy diameter away from the trunk of the tree being sampled or any other trees i.e. about 16–20 m crown separation. Because we needed to select trees containing a paired 'open' site with a minimum degree of crown separation, we restricted our selection of trees within clumps to those trees close to the edge of the clumps. This allowed us to find comparable open sites that were separated by at least one canopy diameter.

All trees and their associated soils were located within the midslope unit of the catchment. Soils were sampled along the contour to avoid any effects of different slopes, soil type or drainage, which might have influenced soil chemistry (Decker et al., 1999). At each of the five replicate trees, three samples were taken from approximately equal compass directions around the trunk (and averaged) from each tree configuration ($n = 3$) by microsite ($n = 4$) combination. These samples were bulked and a 500 g sub-sample taken for chemical analysis. For the study of soil chemistry with depth under the clumped trees, a 65 mm diameter auger was used to take two sub-samples (which were bulked) from four depths (0–2 cm, 5–10 cm, 20–25 cm and 40–50 cm) at each of the four microsites by five replicate clumped trees, resulting in a dataset of $n = 80$.

Because we were interested in changes in soil chemistry in the zone of maximum nutrient concentration, we restricted our measurements to the top 20 mm. Indeed, studies in woodland and grasslands worldwide have demonstrated that nutrients are concentrated at the surface and diminish rapidly with depth (e.g. Schlesinger and Pilmanis, 1998). Given that the sampled soil layer was only 20 mm deep, there was a possibility that litter and decomposing plant material would unduly contribute to the high soil nutrient concentrations. However to reduce any bias due to decomposing plant material, we carefully removed by sieving any organic material, dung, litter and comminuted organic material through a 2 mm sieve before soils were analysed.

Soil analysis

Soluble and exchangeable cation concentrations (Ca^{2+}, K^+, Mg^{2+} and Na^+) were measured using atomic absorption spectroscopy (Unicam 929 AAS) in 1:5 soil:water and 1:5 soil:NH_4Cl extracts. Organic carbon contents were measured using a modified Walkley-Black method (Nelson and Sommers, 1982), pH and electrical conductivity were measured in 1:5 soil-water extracts, while available phosphorus was determined colorimetricaly using a calcium lactate extractant ($C_6H_{10}CaO_6$) (Holford et al., 1985) on a Unicam 8625 UV/VIS spectrophotometer. Total carbon, nitrogen and sulfur were determined using high combustion on a LECO CNS-2000 CNS Analyser. Because of the strong correlations between total carbon and organic carbon for surface soils ($F_{1,58} = 762$, $R^2 = 0.928$) and soils at depth ($F_{1,78} = 434$, $R^2 = 0.846$), we report changes only for organic carbon.

Statistical analyses

Differences due to microsite and tree type (and their interactions), and microsite and depth (and their interactions) were tested using ANOVA with a split-plot design with two error terms. For the microsite and tree type study, the whole plots represented Tree Type, and the subplots were Microsites, and Tree Type*Microsite interactions. For the depth study, the whole plots were Microsites, and the subplots Depths and Microsite*Depth interactions. Data were tested for homogeneity of variance using Levene's Test (Minitab, 1997) and log_{10} transformed, where necessary to satisfy assumptions of ANOVA. Data are presented as back-transformed means. *Post-hoc* differences in means were tested using Least Significant Difference (LSD) testing.

A matrix comprising the values of each of the 14 soil attributes by 60 rows (three tree configurations; clumped, isolated and dead, each replicated 20 times i.e. five replicate trees by four microsites) was converted to a similarity matrix using the Bray-Curtis similarity coefficients contained within PRIMER (Vers. 4; Clarke and Warwick, 1994). This similarity matrix was subjected to non-metric Multi-Dimensional Scaling (MDS) using a PRIMER routine in order to determine whether surface soils from a particular tree configuration were chemically distinct. A further matrix which included only the clumped trees (14 soil attributes by 80 rows i.e. four depths by five replicate trees by four microsites) was similarly analysed. Hypothesis tests of differences between the depths and
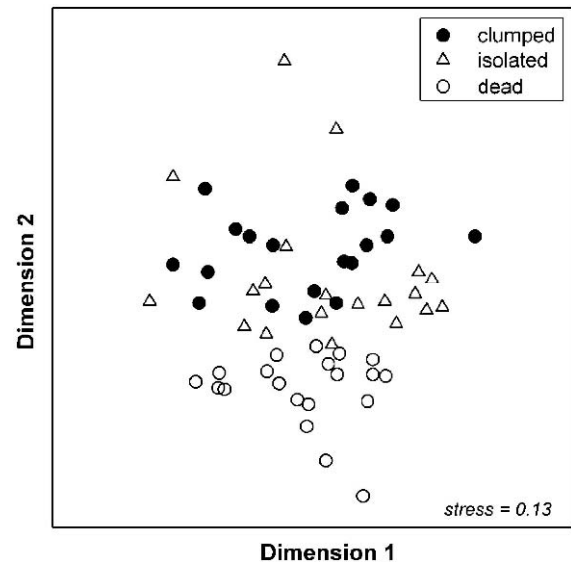

Figure 1. The first two dimensions of the non – metric MDS biplot based on 14 soil chemical properties showing the relative positions of the dead, isolated and clumped trees.

microsites, and tree configuration and microsites, 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 soil chemistry differed significantly between tree configurations, microsites or depths. The routine SIMPER was used to identify which of the soil attributes best described the dissimilarity between groups.

Results

Effects of isolated and clumped trees on soil chemical properties

Soil chemistry varied markedly between clumped, isolated and dead trees (Global $R = 0.279$, $P = 0.001$). The first dimension of the MDS biplot (Figure 1) was highly correlated with exchangeable Ca^{2+}, total N and organic C (Pearson's $r = 0.92$, 0.74, 0.72, respectively; $P < 0.05$) and the second dimension was positively correlated with soluble and exchangeable K^+ ($r = 0.82$, 0.80, respectively; $P < 0.05$).

There were clear differences in soil chemistry between tree configurations. Averaged across the four microsites, exchangeable Ca^{2+}, total N and S, and

Table 1. Mean (standard error of the mean - SEM) values of soil chemical properties from the surface 2 cm under three different tree configurations. Different letters within a row indicates a significant difference at $P < 0.05$

Soil property	Clumped		Isolated		Dead	
	Mean	SEM	Mean	SEM	Mean	SEM
EC (dS m^{-1})	0.35^a	0.04	0.38^a	0.08	0.41^a	0.09
pH (1:5 water)	5.77^a	0.11	5.99^a	0.12	6.88^b	0.10
Organic C (%)	12.5^a	1.3	7.4^b	0.70	5.8^b	0.70
Total N (%)	0.95^a	0.19	0.61^b	0.06	0.51^b	0.09
Total S (%)	0.074^a	0.008	0.058^a	0.006	0.041^b	0.025
Available P (mg kg^{-1})	59.8^a	7.7	51.9^a	11.5	47.2^a	15.3
Soluble cations (mg kg^{-1})						
• Ca^{2+}	70.8^a	14.2	187.8^b	40.0	146.4^b	26.1
• K$^+$	280.0^a	34.0	523.1^b	70.8	442.1^b	75.0
• Mg^{2+}	34.2^a	7.1	76.2^b	5.6	35.7^a	9.1
• Na$^+$	20.4^a	1.3	32.3^b	9.3	29.5^b	5.1
Exchangeable cations (mg kg^{-1})						
• Ca^{2+}	3580.1^a	254.3	2058.8^b	179.0	2914.0^c	293.6
• K$^+$	361.6^a	57.1	519.9^a	91.8	745.6^b	129.2
• Mg^{2+}	455.3^a	99.6	304.8^b	40.6	837.0^c	56.1
• Na$^+$	16.1^a	2.9	17.3^a	3.2	13.3^a	4.4

organic C contents declined markedly from clumped through isolated to dead trees ($F_{2,12} = 6.88$ to 8.10, $P < 0.05$), while pH and soluble Ca^{2+} and K$^+$ increased significantly from clumped to dead trees ($F_{2,12} = 6.7$, $P < 0.001$, $F_{2,12} = 3.5$, $P < 0.05$, $F_{2,12} = 16.1$, $P < 0.001$, respectively, Table 1, Figures 2 and 3). Significant differences in soluble and exchangeable Mg^{2+} did not correspond to any clearly-defined gradients (Table 1, Figure 3). Rather mean soluble Mg^{2+} was significantly greater under the isolated trees compared to the other two tree types ($F_{2,12} = 5.09$, $P = 0.025$) while exchangeable Mg^{2+} was greatest under dead trees compared with isolated or clumped trees ($F_{2,12} = 4.56$, $P = 0.034$). There were no significant differences in electrical conductivity, available P or exchangeable Na$^+$ between the three tree configurations ($P > 0.05$; Table 1, Figures 2 and 3).

Gradients in soil chemical properties from canopy to open areas

There were some clear trends in soil chemistry corresponding with increasing distance from the tree trunk. Multi-variate analyses (ANOSIM) revealed that microsites close to the trunk (trunk and mid-canopy) differed significantly in their chemistry from microsites furthest from the trunk (drip line and open; Global $R = 0.313$, $P = 0.01$). Averaged across the three tree configurations, electrical conductivity declined significantly with distance from the tree trunk ($F_{3,36} = 6.46$, $P < 0.001$), and pH was significantly higher adjacent to the trunk compared with the other three microsites ($F_{3,36} = 5.65$, $P < 0.01$), though this was only by about 0.6 pH units (Figure 2). Available P, and soluble Ca^{2+} and Mg^{2+} concentrations were significantly higher closer to the tree trunk (trunk and mid-canopy microsites) compared with more distant microsites (drip line and open microsites; $F_{3,36} = 4.30$, 7.45 and 3.56, respectively, $P < 0.001$, Figures 2 and 3).

Changes in nutrient concentrations with depth under clumped trees

Nutrient concentrations were typically highest at the surface, and declined markedly with depth, with significant differences between all depths (Global $R = 0.735$, $P = 0.01$) and a clearly defined gradient in depth along the first dimension of the MDS biplot. Increases in depth were associated with lower electrical conductivity ($F_{3,48} = 71.86$, $P < 0.001$). Significant changes in pH ($F_{3,48} = 5.51$, $P = 0.002$) did not correspond to a clearly-defined gradient down the
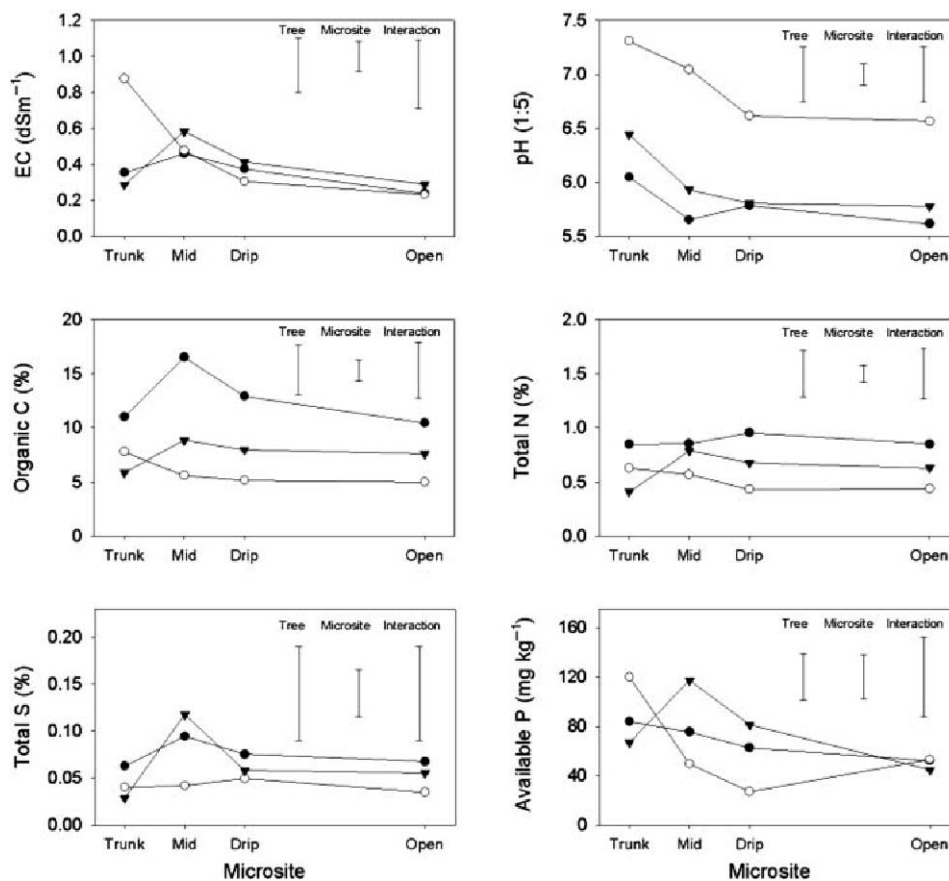
Figure 2. Mean values of soil chemical properties in relation to tree configuration and microsite for surface soils. The 5% LSD for tree, microsite and tree by microsite interactions are given. Closed circle = clumped, open circle = dead, triangle = isolated trees.

profile (Table 2). However, changes with depth for microsites close to the tree (trunk and mid-canopy) showed a pronounced increase in alkalinity with depth (Figure 4). Concentrations of organic C, total N and S, and available P were markedly higher at the surface and declined significantly with depth ($P < 0.001$; Table 2).

Concentrations of soluble Ca^{2+}, K^+ and Mg^{2+} and Na^+ were significantly higher at the surface compared with lower in the profile ($F_{3,48} = 59.7$, 83.8, 29.0 and 14.1, $P < 0.001$, respectively), and sometimes significant at intermediate depths. The greatest declines in soluble cations occurred in the top 2 cm of soil (Figure 4). Predictably, there were significant reductions in exchangeable cations (Ca^{2+}, K^+, Mg^{2+}, Na^+) with increasing depth ($F_{3,48} = 35.32$, $P < 0.001$; $F_{3,48} = 14.14$, $P < 0.001$; $F_{3,48} = 37.85$, $P < 0.001$ and $F_{3,48} = 21.6$, $P < 0.001$, respectively). There were significant depth by microsite interactions for all exchangeable cations ($F_{9,48} = 4.1–7.4$, $P < 0.023$;

Figure 4). These interactions can be explained by only slight changes down the profile under the drip line, but substantially greater reductions with depth for the other microsites.

Discussion

Three major findings resulted from our study of soil nutrients in relation to tree configuration in this agricultural landscape. Firstly, concentrations of organic C, N and S were substantially greater under trees growing in clumps compared with either isolated living or dead trees. Secondly, there were significant declines in soluble Ca^{2+}, K^+ and Mg^{2+}, pH, EC and available P with increasing distance from the trees, patterns which have been observed elsewhere (e.g. Wilson et al., 2002; Graham et al., 2004). However, no clearly-defined patterns were apparent with distance from the tree trunk for C, N and S. Thirdly, apart
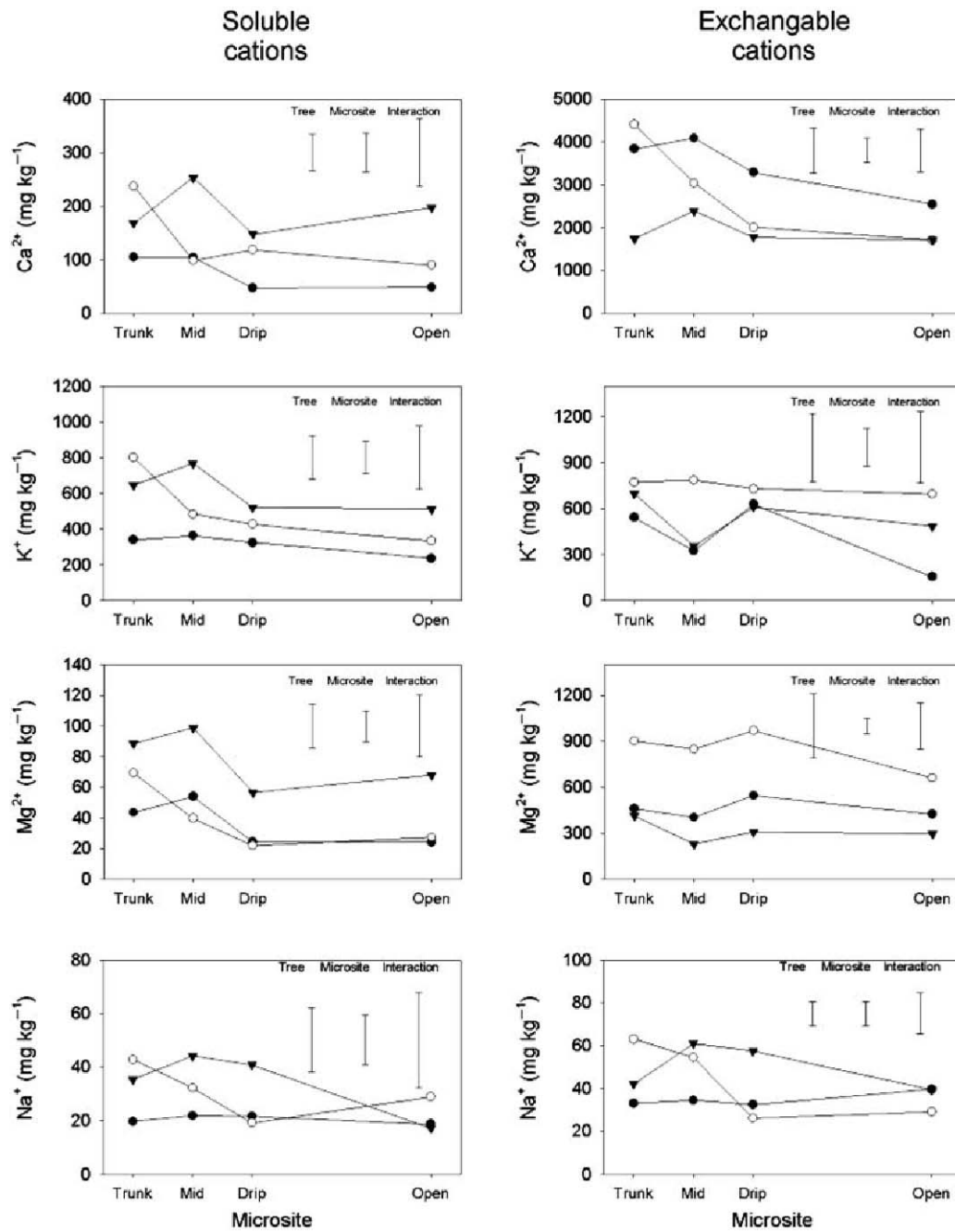
Figure 3. Mean concentrations of soluble and exchangeable cations in relation to tree configuration and microsite for surface soils. The 5% LSD for tree, microsite and tree by microsite interactions are given. Closed circle = clumped, open circle = dead and triangle = isolated trees.

Table 2. Mean (standard error of the mean - SEM) values of soil chemical properties with depth in the clumped trees only pooled across the four microsites. Different letters within a row indicates a significant difference at $P < 0.05$

Soil property	0–2 cm		5–10 cm		20–25 cm		40–50 cm	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
EC (dS m^{-1})	0.35[a]	0.04	0.16[b]	0.02	0.06[c]	0.01	0.05[d]	0.01
pH (1:5 water)	5.76[a]	0.11	5.57[b]	0.13	5.82[a]	0.14	5.84[a]	0.13
Organic C (%)	12.50[a]	1.25	4.58[b]	0.80	0.98[c]	0.10	0.61[c]	0.07
Total N (%)	1.060[a]	0.09	0.330[b]	0.06	0.061[c]	0.01	0.046[c]	0.02
Total S (%)	0.074[a]	0.008	0.032[b]	0.005	0.011[c]	0.001	0.008[d]	0.00
Available P (mg kg^{-1})	60.66[a]	7.56	18.37[b]	3.50	7.04[c]	1.36	1.89[d]	0.56
Soluble cations (mg kg^{-1})								
• Ca^{2+}	70.8[a]	14.2	58.1[a]	7.6	16.0[b]	2.4	11.2[c]	3.8
• K^+	280.0[a]	34.0	66.7[b]	12.0	57.8[b]	5.6	57.4[b]	5.5
• Mg^{2+}	34.2[a]	7.1	21.8[b]	2.1	14.5[c]	0.7	12.1[d]	0.9
• Na^+	21.1[a]	1.3	15.6[b]	1.3	13.7[b]	1.3	16.4[b]	1.7
Exchangeable cations (mg kg^{-1})								
• Ca^{2+}	1928.4[a]	363.8	1966.5[b]	332.7	981.1[c]	227.6	690.9[d]	160.2
• K^+	570.7[a]	83.9	529.1[a]	86.9	237.6[b]	33.4	288.5[b]	40.1
• Mg^{2+}	702.1[a]	98.2	392.1[b]	95.0	224.1[c]	51.8	314.3[b]	36.9
• Na^+	11.23[a]	3.8	9.4[b]	2.8	1.3[c]	1.2	1.2[c]	2.0

from pH which exhibited an initial decline to 10 cm and then a rapid increase, the concentration of nutrients generally declined with depth in the soil profile (Figure 4). Together these results extend the findings that trees increase soil fertility in savanna woodlands (e.g. Belsky, 1994; Belsky et al., 1989; Munzbergova and Ward, 2002; Scholes, 1990), and reinforce the view that trees, either scattered or in small clumps, are important for soil nutrient conservation in agricultural landscapes.

Effects of isolated and clumped trees on soil chemical properties

In our study, greater concentrations of exchangeable Ca^{2+}, and C, N and S were detected under clumped trees compared with either isolated living or dead trees (Table 1, Figures 2 and 3). High nutrient concentrations under clumped trees can be explained by the substantially greater concentration of organic C under clumped (12.5% C) compared with isolated live or dead (6.6% C) trees (Figure 2). Also, shaded conditions under trees growing closely in clumps may have been responsible for increased mineralisation rates and hence greater N pools under the clumped trees (Bird et al., 1992). Differences could also be attributed to the greater ability of clumped trees to capture nutrient-

laden, wind-blown sediments which when washed off the surface of the leaves would account for greater organic matter pools (Gersper and Holowaychuk, 1971; Rhoades, 1997).

Greater levels of some cations under dead trees (Figure 3) and substantial concentrations of phosphorus close to the trunk of dead trees (Figure 2) clearly cannot be explained by capture of nutrient-rich dust or decomposition of cation-rich leaf material. We attribute it however to the larger mass of decomposing organic matter, particular termite-infested bark, which we observed close to dead tree trunks. This resulted in a 47% greater C concentration at the trunk (7.8% C) compared with the other microsites (5.3% C; Figure 2).

Gradients in soil chemical properties from canopy to open areas

At Kyeamba, microsites closer to the tree trunks were associated with significantly higher EC and pH, and greater concentrations of soluble Ca^{2+} and Mg^{2+} (Figures 2 and 3). The highest concentrations of soluble Ca^{2+} and available P were found at the trunk and mid-canopy microsites, with lower concentrations at the drip line and in the open microsites (Figures 2 and 3). The bark of *Eucalypt* spp. is known to contain
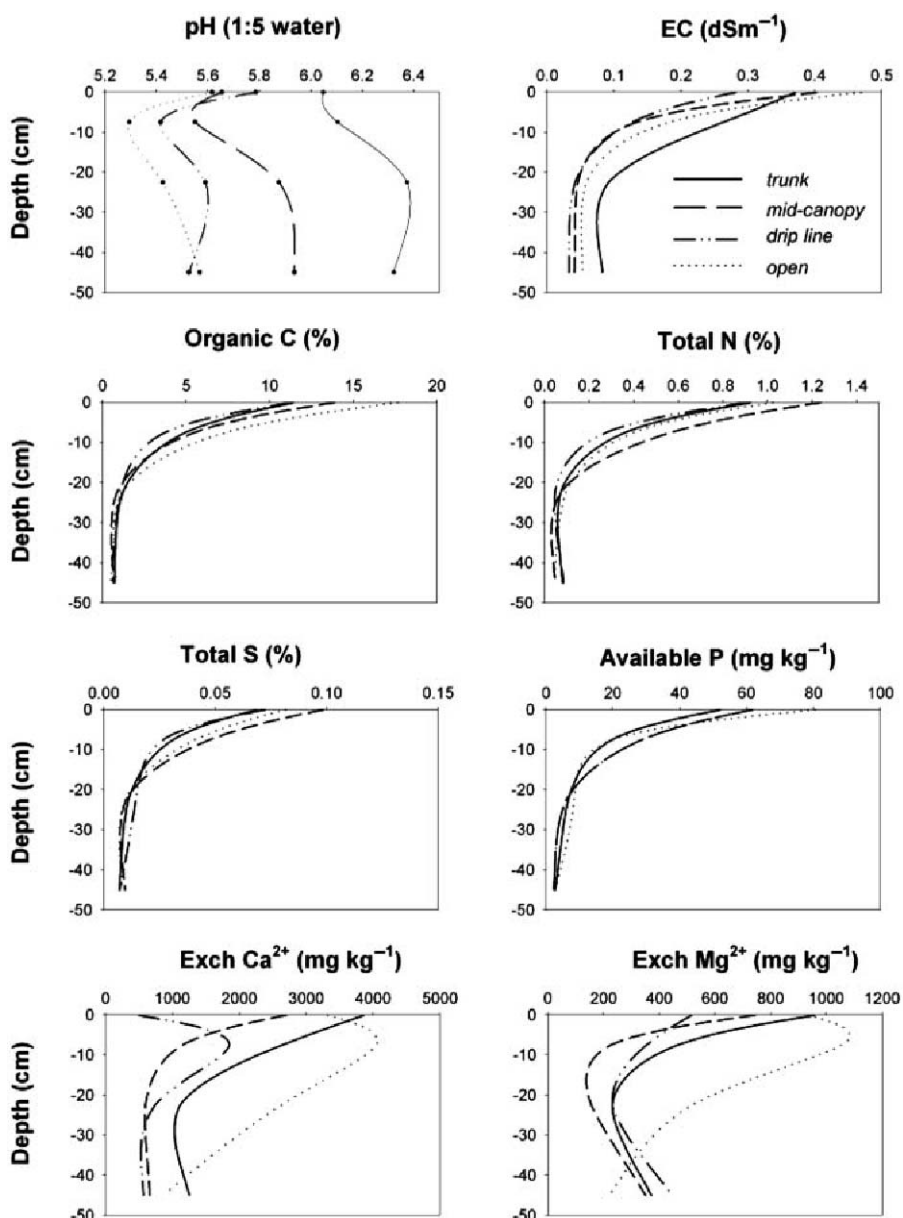
Figure 4. Mean values of soil chemical properties under clumped trees in relation to depth.

high concentrations of Ca^{2+} (B.W. Wilson, personal communication 2004), and bark shedding can lead to changes in the distribution of Ca^{2+} and other cations close to the trees (Weltzin and Coughenour, 1990).

Plants contain an excess of cations, and need to produce organic anions to maintain an internal charge balance (Noble et al., 1996). As calcium ions are relatively immobile within the leaf prior to leaf fall, Ca^{2+} often accumulates in leaf-rich litter close to the base of the trees (Mengel and Kirkby, 1982). Increases in

Ca^{2+} and Mg^{2+} close to the trunk in our study can be attributed to the buildup of organic matter, particularly C, at the base of the trees. Evidence from drier woodlands in eastern Australia indicate that significant gradients in exchangeable Ca^{2+}, Mg^{2+}, Na^+ and K^+ out from large *Eucalyptus intertexta* trees are attributable to the deposition and subsequent decomposition of up to 5.7 t ha^{-1} of litter as well as 3.5 t ha^{-1} of faeces beneath the tree canopies (Eldridge and Rath, 2002).

Under trees growing in clumps, the pronounced peak in C in the centre of the canopy, i.e. midway between the trunk and drip line microsites (Figure 2), suggests that leaf fall is greatest in the mid-canopy zone, possibly where it is protected from removal by stem flow processes or water from the drip line. It may also accumulate here after being scraped away from the centre of the tree by animals such as kangaroos which dig holes close to the tree trunks to regulate their body temperature during periods of heat stress (Eldridge and Rath, 2002).

Increases in pH close to the trunk (Figure 2) are likely due to greater concentration of cations, particularly Ca^{2+} and Mg^{2+}, which are 'biologically pumped' from depth by the trees and are deposited in leaf fall (Noble et al., 1996). Increasing levels of soil acidity with increasing distance from trees was only slight in our study (about 0.6 pH units), and has been reported in a range of studies (e.g. Beniamino et al., 1991; Boettcher and Kalisz, 1990; Crampton, 1982). The retention of trees is therefore likely to aid in the regulation of soil pH, mitigating against soil acidification problems in a landscape where acidic soils are an emerging land management issue (Gersper and Holowaychuk, 1971; Marcar, 1996; Noble et al., 1999).

Changes in nutrient concentrations with depth under clumped trees

Increases in depth were associated with reduced concentrations of most nutrients (Table 2, Figure 4), which is consistent with many studies from savanna and semi-arid grasslands (e.g. Rostagno et al., 1991; Schlesinger and Pilmanis, 1998). Concentrations of organic C, macro-nutrients such as N, P and S, and soluble cations were higher in the surface of the Kyeamba soils and declined markedly down the profile (Table 2, Figure 4). These declines were more pronounced at the mid-canopy and trunk microsites, providing support for the proposition of cation depletion by tree roots at depth (*sensu* Amiotti et al., 2000). The depth profiles for exchangeable and soluble cations demonstrate substantial declines in cation concentrations with depth (Figure 4). For the other soil properties however, there was sometimes an increase in nutrient concentration in the deepest parts of the profile, and this may have been related to proximity to parent material or buried soil layers.

Apart from chemical processes moderated by the trees themselves, the reductions in C, N, S, P and EC with depth (Table 2, Figure 4), and differences in Ca^{2+}, Mg^{2+}, EC and pH between microsites (Figures 2 and 3) could have been due to biotic factors such as the activities of soil biota below the canopy, canopy-inhabiting biota (e.g. birds and arboreal mammals), and sheep, cattle and kangaroos camping below the canopies for shade and shelter. In agricultural environments particularly, isolated trees tend to become foci of animal activity (e.g. Law et al., 2000) largely because there are few trees in these environments. Enrichment of soluble cations, which was greatest below isolated trees in our study (Table 1, Figure 3), is consistent with research from African savannas where many trees are large and isolated (Dean et al., 1999).

The combined effects of trees and resident soil and canopy biota would be expected to be more pronounced in the surface horizons which correspond to greater concentrations of both soil biota and organic matter. Studies from grazed open forests in eastern Australia have indicated that higher numbers of native macroarthropod species inhabit the soil beneath trees (Chilcott et al., 1997), improving physical and chemical conditions through the incorporation of litter and other organic materials into the soil (Vetaas, 1992). Microarthropods residing in litter below trees and shrubs are important regulators of mineralisation and decomposition processes (Elkins and Whitford, 1982). Although we have no empirical data on soil biota for the study site, we anticipate that resident populations would be more active in augmenting nutrient levels in the surface of sub-canopy soils.

Impact of tree removal on ecosystem processes

Despite increases in some exchangeable cations and P under dead trees (Figure 3), tree death appears to lead to a net loss in C, N and S which is exacerbated by reduced leaf and litter shedding and declines in animal detritus as fewer animals use dying trees for shelter (Dean et al., 1999). Despite these changes, the influence of trees on soil properties is likely to persist to some degree for many years after their death. For example, in a study of poisoned woodland trees in North Queensland, enhanced nutrient levels under trees remained for at least 10 years after their deaths (Jackson and Ash, 1998), probably due to the decomposition of the remaining organic material. Although we cannot say definitively how old the dead trees are in our study, they nonetheless play an important ecosystem service by concentrating cations at their base for a substantial number of years after their death.

Removal of trees has the potential to reduce available nutrients in the soil, and although grass yields may increase by at least 50% in some *Eucalypt* woodlands (McIvor and Gardener, 1995; Walker et al., 1986), the net effect is not always clearly defined (e.g. Jackson and Ash, 2001). Initial tree removal may result in increased short-term forage production, but is likely to lead to considerable losses of organic C and nutrients in the longer term (Dahlgren et al., 1997; Jackson et al., 1990).

The general perception by landholders in agri-pastoral areas of eastern Australia is that trees adversely affect agricultural production. However, consistent with other studies (e.g. Palm, 1995), this study has shown that paddock trees, whether alive or dead, have the potential to improve soil fertility. Our data from south-eastern Australia provide strong evidence that trees, particularly those in clumps, become zones of enhanced soil nutrients, analogous to 'islands of fertility' described for more arid systems (Belsky and Canham, 1994). While dead trees are routinely removed from the landscape, this study has shown that the effects of increased soil fertility remain long after their death, as well as providing important habitat benefits for hollow-seeking fauna.

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