

THE LIFE AND TIMES OF TREE ROOTS: ELEMENTAL DYNAMICS IN THE RHIZOSPHERE OF CO-OCCURRING TREES IN A MIXED-SPECIES DRY SCLEROPHYLL FOREST.

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INTRODUCTION

The rhizosphere is a narrow zone of the soil or regolith that is under the direct influence of plant roots. The root alters the physical, chemical and biological properties in the rhizosphere through concomitant processes of growth, nutrient uptake and organic anion exudation (Bertin *et al.*, 2003, Curl & Truelove 1986, George *et al.* 2002, Hinsinger *et al.* 2003, Jones 1998, Jones *et al.* 2003). Many studies on the role of roots on regolith geochemistry focus on understanding and improving nutrient uptake (and crop yield) in agricultural and forestry settings (e.g., Hinsinger *et al.* 2003, Shaw 1960a, van Hees *et al.* 1996, Vance *et al.* 2003, Zoyza *et al.* 1997). So, while roots are recognised pedogenic agents there remains little understanding of the actual implications they have for mineral weathering and pedogenesis in the rhizosphere (see Ryan *et al.* 2001, Waisel *et al.* 1991). This study is part of a much broader research project (Little & Field 2003) focused on understanding root-mediated weathering by combining field and laboratory methods with a knowledge of plant physiology, microbiology, and chemistry and mineralogy in soils and regolith in the fine-scale environment of the rhizosphere (Figure 1).

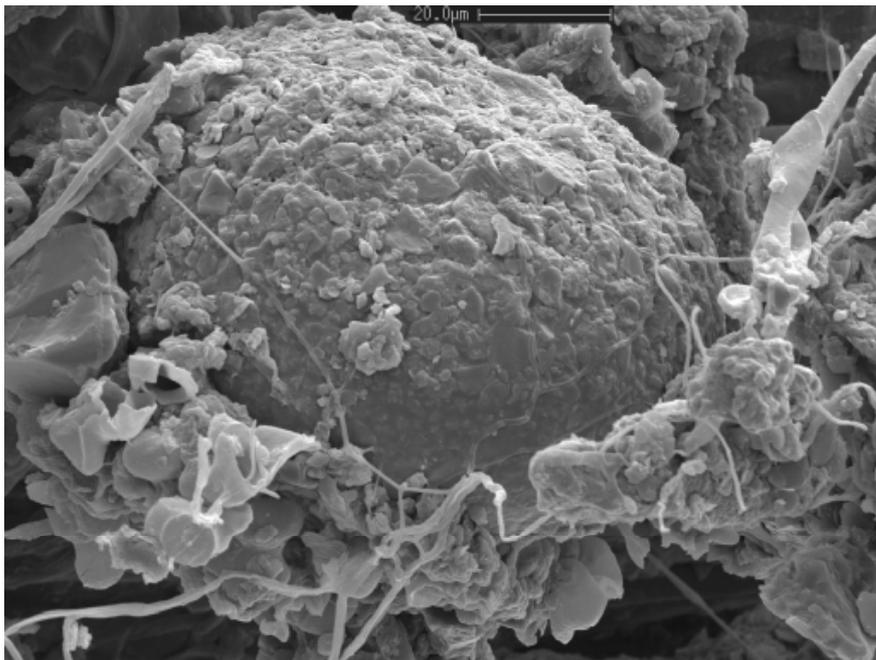


Figure 1: Scanning Electron Microscope (SEM) image of mycorrhizal fungi in the *Acacia falciformis* rhizosphere mining scarce mineral nutrients from soil aggregates, with silicon (Si) and iron (Fe) concretions accumulating around the fungal strands.

There are several major components to the research. Here we present results from a preliminary study of rhizosphere characteristics of two adjacent but very different individual trees, *Eucalyptus mannifera* and *Acacia falciformis*, by geochemical analysis of different soil fractions and with a special emphasis on the relationship between roots and soils beneath the *A. falciformis*.

THE SITE

The study site is located approximately 9 km northeast of Bungendore, New South Wales, in a warm-temperate mixed-species dry sclerophyll forest. Specifically, the site is situated on the east-facing lower-mid slope of some undulating to rolling low hills on highly weathered Devonian metasediments. The parent materials consist mainly of fine-grained quartz (ca. 70%), with minor occurrences of albite, orthoclase and muscovite mica weathering to interstratified illites and vermiculites, and kaolinite, with amorphous materials (sesquioxides and soil organic matter) making up ca. 20% of the bulk soil materials. *Eucalyptus mannifera*

and *A. falciformis* commonly occur in the landscape as co-dominant tree species. The soils are shallow Haplic Brown Chromosols (Isbell 1996), Dy 2.21 (Northcote 1971), or Yellow Podzolic soils (Stace *et al.* 1968), generally with a shallow (*E. mannifera*) to moderately thick (*A. falciformis*) sandy loam A₁ horizon, overlying a sandy clay (*A. falciformis*) to light clay (*E. mannifera*) B₂ horizon. Table 1 provides a summary of soil properties at the site.

Table 1: Summary table, showing Bulk Density (g/cm³), Soil Moisture Content (wt. %), Soil Organic Matter Content (% DWt), Cation Exchange Capacity (CEC (mM⁺ kg⁻¹) B – Bulk soil; R – Rhizosphere), field pH, texture and thickness (cm) of the A₁ and B₂ soil horizons beneath two co-occurring *Eucalyptus mannifera* and *Acacia falciformis* trees.

	<i>Eucalyptus mannifera</i>		<i>Acacia falciformis</i>	
	A ₁ horizon	B ₂ horizon	A ₁ horizon	B ₂ horizon
Thickness (cm)	5	10	25	10
Field Texture	Sandy loam	Light clay	Sandy loam	Sandy clay
Bulk Density (g/cm ³)	1.23	1.38	1.12	1.26
Porosity	0.54	0.48	0.58	0.52
Soil Moisture Content (wt. %)	8.37	6.88	8.11	5.48
Field pH	4	6	3.5	4.5
Soil Organic Matter (% DWt)	5.79	3.39	7.32	3.97
Organic Carbon (% DWt)	3.42	2.00	4.32	2.30
CEC (mM ⁺ /kg)	22.6	14.3	B 44.7	R 55.0 B27.2 R 33.8

METHODS

Soil and fine root samples were collected from pits dug at 0.5 m from the base each of the adjacent *E. mannifera* and *A. falciformis* trees using 50 mm diameter bulk density cores. Two samples were collected from the A₁ and B₂ soil horizons respectively, placed into separate polyethylene sample bags and labelled, so a total of four samples were collected from each soil pit. The field pH was estimated for each horizon using an INOCULO soil pH test kit. The field texture and thickness (cm) of the A₁ and B₂ horizons were described as well as the nature of the boundary between the two.

Laboratory procedures

We prepared the samples to determine baseline physical and chemical properties of the fine roots, rhizosphere and bulk soils:

- Mineralogy was determined using powder X-Ray Diffraction techniques;
- Soil Organic Matter (SOM) content was determined using a Loss on Ignition technique;
- Bulk soil, rhizosphere and root samples were prepared for analysis of total chemical content using a nitric-perchloric acid (HNO₃, HClO₄) digest. Solutions were analysed using an Inductively Coupled Plasma – Atomic Emission Spectrometer (ICP-AES);
- Rhizosphere and bulk soil samples were prepared for analysis of ammonium acetate (NH₄COOH, AAC) extractable and water (H₂O)-soluble elements. Three aliquots of either 25 mL of 1M AAC or deionised H₂O was added to extract elements from 1 g soil and solutions were pooled. The samples were acidified to ca. 1% nitric acid (HNO₃) for analysis using ICP-AES.
- We calculated Cation Exchange Capacity (CEC) for the bulk and rhizosphere soils using the sum of the AAC extractable Al³⁺, Ba²⁺, Ca²⁺, Fe^{2+/3+}, K⁺, Mg²⁺ and Na⁺ concentrations (see Table 3);
- Element concentrations (mg/kg or g/kg of oven dried weight) were normalised and reported as element:aluminium ratios to examine element mobility through the rhizosphere with respect to a potentially immobile and toxic element.

At this stage all interpretations are purely observational and no statistical significance is implied from the data.

RESULTS AND DISCUSSION

The results of major and trace elemental analysis of the different soil fractions collected from the regolith (bulk soil, rhizosphere and fine root; Table 2) provide clear evidence that mineral-elements are influenced by fine tree roots (see also Zoysa *et al.* 1997). The highly leached and weathered nature of the landscape have, over time, led to the development of soils deficient in most biologically important mineral elements (Table 2).

Element dynamics in bulk soils, rhizosphere and fine roots

The patterns of accumulation or depletion were most evident when the total and AAC extractable element concentrations were examined together in the rhizosphere of the *Acacia falciformis*. Table 2 shows that Al and Fe concentrations dramatically decline from the *A. falciformis* and *E. mannifera* rhizosphere towards the fine roots. The Al concentration in the root and rhizoplane is a factor of 1/10 the rhizosphere concentration, and the <3 mm roots contain only 1/50 of the Al compared to the rhizosphere and bulk soils. The change in Fe concentrations is at least as dramatic.

The biologically important elements Ca, K and Mg also exhibit interesting rhizosphere dynamics in what are highly leached and weathered soils. Calcium and K are particularly deficient in these soils (compare Tables 2 and 3), though for different reasons. Nearly 80% and 25% of the total Ca in the A₁ soil horizons beneath the *A. falciformis* and *E. mannifera*, respectively, can be accounted for by AAC extractable forms, indicating that it is recycled through organic materials in the A₁ horizon and that little Ca is contained in the parent materials. These results strongly suggest that Ca is being recycled by both species through litter fall and its resultant decomposition. More dramatic is the two- to five-fold increase in Ca concentrations from the rhizosphere to the root for the *A. falciformis*, which is strong evidence that the fine roots of both species are actively scavenging for this vital element.

In contrast the total K concentrations are relatively high, only a small fraction (1/20 to 1/50) appears to occur on exchange complexes with the soils indicating the small but significant proportion of K in the parent materials. Potassium-cycling also tends to be internal so the K that is taken up by the fine roots is likely to be stored there before being translocated directly to young foliage to maintain physiological processes there, and also be re-translocated from senescing leaves to actively growing leaves as a tight K-conservation measure.

Table 2: total chemical composition of the fine root, rhizosphere soil and bulk soil compartments in the soil profiles beneath two adjacent, but very different trees (determined using ICP-AES); *denotes previously unpublished data provided by Leonard (2004, work in progress); RP – rhizoplane.

Tree species	Sample	Horizon	Al	Fe	Ca	K	Na	Mg	Ba	Cu	Mn	Sr	Zn
			g/kg	g/kg	g/kg	g/kg	g/kg	g/kg	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg
<i>A. falciformis</i>	Soil	A ₁	12.5	7.8	0.6	2.5	0.2	1.0	61	6	36	12	15
	Rhizosphere		17.2	11.5	0.8	5.0	0.3	1.4	100	11	56	14	43
	Fine root + RP	B ₂	9.2	4.2	2.4	3.1	0.5	1.2	80	17	66	37	31
	*< 3 mm root		0.2	0.1	3.3	4.0	0.7	0.5	14	20	49	29	53
	Soil		20.8	13.8	0.5	5.5	0.2	1.6	99	2	54	10	16
	Rhizosphere		22.6	11.3	0.6	5.9	0.3	1.7	115	5	62	12	21
	Fine root + RP		8.5	3.2	1.4	2.0	0.5	1.4	99	8	25	33	27
<i>E. mannifera</i>	Soil	A ₁	19.4	9.8	0.6	4.9	0.2	1.4	104	13	60	10	21
	Rhizosphere		20.9	17.1	0.6	5.8	0.4	1.6	204	13	883	11	35
	Fine root + RP	B ₂	5.3	2.3	2.3	3.4	0.5	1.4	75	8	149	22	19
	Soil		27.0	13.2	0.3	6.7	0.2	1.8	125	3	60	8	30
	Rhizosphere		29.4	24.7	0.3	7.2	0.3	2.2	200	3	89	9	32
	Fine root + RP		10.6	2.8	1.3	2.2	0.6	1.3	250	14	30	22	41
	*< 3 mm root		0.8	0.3	4.0	7.0	0.8	1.2	28	18	98	28	53

The results are less clear for the *E. mannifera*, however there is still good evidence that the fine roots of this tree were involved in actively scavenging for elements, especially Ca, K and Mg, indicated by relatively high root concentrations of the elements, but the rhizosphere dynamics are yet to be elucidated. In contrast there is relatively little AAC extractable Al or Fe in either the bulk soils or rhizosphere of either of the trees (Table 3), despite the high total concentrations, reflecting their abundance as structural components in soil minerals and/or that mechanisms are employed by fine roots to regulate movement of these elements through the rhizosphere (Curl & Truelove 1986, Waisel *et al.* 1991).

Element: Aluminium ratios

The purpose of this part of the research was to clarify the apparent accumulation and depletion patterns observed for major and minor inorganic elements in the rhizosphere of the *A. falciformis*. Table 4 shows that the apparent rhizosphere dynamics seen in Tables 2 and 3 are much clearer when the elements were

normalised to aluminium (Al).

Table 3: Ammonium Acetate (AAC) extractable cation content of the bulk soils and rhizosphere under *Acacia falciformis*.

Horizon	Compartment	Al g/kg	Fe g/kg	Ca g/kg	Na g/kg	K g/kg	Mg g/kg	Ba mg/kg	Cu mg/kg	Mn mg/kg	Sr mg/kg	Zn mg/kg
A ₁	Soil	0.04	0.03	0.4	0.08	0.08	0.1	20	2	9	7	5
	Rhizosphere	0.04	0.03	0.6	0.1	0.09	0.2	23	2	12	9	3
B ₂	Soil	0.04	0.02	0.2	0.06	0.05	0.1	14	2	2	3	3
	Rhizosphere	0.04	0.02	0.2	0.08	0.08	0.2	14	2	3	3	3

Table 4: Table showing element:aluminium (Al) ratios for 1M-ammonium acetate extractable major and minor rock forming mineral elements for rhizosphere and bulk soil compartments, and the total root content, under *Acacia falciformis*. *denotes previously unpublished data provided by Leonard (2004, work in progress).

Sample	Hor	Fe:Al	Ca:Al	K:Al	Na:Al	Mg:Al	Ba:Al	Cu:Al	Mn:Al	Sr:Al	Zn:Al
Soil	A ₁	0.75	10.0	2.00	2.0	2.5	0.50	0.05	0.225	0.175	0.125
Rhizosphere		0.75	15.0	2.25	2.5	5.0	0.50	0.05	0.300	0.225	0.075
* < 3 mm root		2.20	16.5	2.00	3.5	2.5	0.05	0.10	0.250	0.150	0.270
Soil	B ₂	0.50	5.0	1.25	1.5	2.5	0.35	0.05	0.050	0.075	0.075
Rhizosphere		0.50	5.0	2.00	2.0	5.0	0.35	0.05	0.075	0.075	0.075

There were a number of observations made of elements in AAC-extractable forms with respect to aluminium in the rhizosphere of the *A. falciformis*:

- Sodium (Na), K and Mg, and Mn accumulated in the rhizosphere of the A₁ and B₂ horizons, showing the relative mobility of these elements with respect to Al and their importance for biological functions;
- AAC-extractable forms of Ca and Sr accumulated in the A₁ horizon rhizosphere only, indicating the deficient nature of the parent materials with respect to Ca and a tight Ca-cycle through litter fall and its subsequent decomposition in the surface horizons;
- Some depletion of Ca may occur in the B₂ horizon despite the low concentrations, suggesting that most Ca required by the *A. falciformis* is recycled through the A₁ horizon. Elevated fine root Ca:Al in the B₂ horizon suggest that fine roots in deeper horizons actively scavenge for this element throughout the soil profile;
- Zinc (Zn) was depleted with respect to Al in the A₁ horizon rhizosphere, but elevated ratios of Zn:Al in the fine roots suggests active uptake here;
- Iron (Fe), Ba and Cu concentrations did not alter with respect Al in the rhizosphere of the *A. falciformis* throughout the soil profile.

Clearly most elements accumulated in the A₁ horizon rhizosphere with respect to Al, indicating that biologically important are more mobile in this horizon, probably as a result of tight nutrient cycling through processes of stem flow and canopy through fall, but probably more importantly as a result of rapid recycling of these elements through litter fall and its subsequent decomposition.

CONCLUSIONS AND FUTURE DIRECTIONS

The soils are highly leached and weathered, and as a result are deficient in many biologically important elements, especially Ca. While the adjacent eucalypt and acacia take up a suite of similar nutrients, the location of uptake varies and there is evidence that uptake of Al and Fe in particular is at least likely to be highly regulated by the trees. The results are promising, and warrant further investigations into the rhizosphere, and root weathering in these co-occurring tree species; *E. mannifera* and *A. falciformis*.

This study showed differences in the biogeochemistry of fine roots, and rhizosphere and bulk soil, indicating the large effects plants can have on soil geochemistry and element mobility throughout the life of a tree. Good evidence of elemental rhizosphere dynamics can be seen on examination of the bulk soil, rhizosphere soil and <3 mm root compartments (Table 2 and Table 3), and is further supported by the patterns of accumulation and depletion for the AAC-extractable forms of mineral elements with respect to Al (Table 4).

For the *A. falciformis* it is apparent that rhizosphere activity is greatest in the surface, organic rich horizons where nutrient elements are in much greater abundance and in forms more readily plant accessible than those usually observed in the deeper mineral horizons. Evidence is also present for uptake of elements such as Ca, Mg and Sr in the B₂ horizons beneath both trees, where these elements are more likely to occur in inorganic forms.

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