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Rhizodeposits of *Trifolium pratense* and *Lolium perenne*: their comparative effects on 2,4-D mineralization in two contrasting soils

Liz J Shaw[a], Richard G. Burns[b,*]

[a]*Imperial College London, Wye Campus, Department of Agricultural Sciences, Wye, Kent TN25 5AH, UK*
[b]*School of Land and Food Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia*

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Abstract

Rhizosphere enhanced biodegradation of organic pollutants has been reported frequently and a stimulatory role for specific components of rhizodeposits postulated. As rhizodeposit composition is a function of plant species and soil type, we compared the effect of *Lolium perenne* and *Trifolium pratense* grown in two different soils (a sandy silt loam: pH 4, 2.8% OC, no previous 2,4-D exposure and a silt loam: pH 6.5, 4.3% OC, previous 2,4-D exposure) on the mineralization of the herbicide 2,4-D (2,4-dichlorophenoxyacetic acid). We investigated the relationship of mineralization kinetics to dehydrogenase activity, most probable number of 2,4-D degraders ($MPN_{2,4\text{-}D}$) and 2,4-D degrader composition (using sequence analysis of the gene encoding α-ketoglutarate/2,4-D dioxygenase (*tfd*A)). There were significant ($P<0.01$) plant–soil interaction effects on $MPN_{2,4\text{-}D}$ and 2,4-D mineralization kinetics (e.g. *T. pratense* rhizodeposits enhanced the maximum mineralization rate by 30% in the acid sandy silt loam soil, but not in the neutral silt loam soil). Differences in mineralization kinetics could not be ascribed to 2,4-D degrader composition as both soils had *tfd*A sequences which clustered with *tfd*As representative of two distinct classes of 2,4-D degrader: canonical *R. eutropha* JMP134-like and oligotrophic *α-proteobacterial*-like. Other explanations for the differential rhizodeposit effect between soils and plants (e.g. nutrient competition effects) are discussed. Our findings stress that complexity of soil–plant–microbe interactions in the rhizosphere make the occurrence and extent of rhizosphere-enhanced xenobiotic degradation difficult to predict.
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1. Introduction

Rhizoremediation, defined as the acceleration of organic pollutant breakdown in soil as a consequence of the enhanced biodegradative activity of rhizosphere microorganisms, is a property with potential for use in the clean up of contaminated soils (Siciliano and Germida, 1998). There are numerous studies (Shaw and Burns, 2003) and throughout) that present evidence for rhizosphere-enhanced biodegradation of a wide range of organic xenobiotics involving a large number of plant species. However, the mechanisms of rhizosphere-enhanced biodegradation are not fully understood although several have been postulated (Siciliano and Germida, 1998; Shaw and Burns, 2003). One suggestion concerns the role of chemicals released by plant roots (rhizodeposits) as natural analogs of xenobiotic catabolic pathways since it has been noted (Gilbert and Crowley, 1997; Siciliano and Germida, 1998; Dunning Hotopp and Hausinger, 2001; Singer et al., 2003) that some rhizodeposit components are structurally similar to xenobiotics or their metabolites.

The term rhizodeposit is used to define a spectrum of components ranging from simple exudate compounds to entire root fragments, released during sloughing of border cells and turnover of dead roots. It is known that both soil physicochemical properties and microbial community composition influence the quality and the quantity of rhizodeposition. For example, plant species growing in low nutrient environments may increase the concentration of nutrient-scavenging extracellular enzymes (e.g. phosphatases) or nutrient-solubilizing phenolics and organic

* Corresponding author. Tel.: +61 7 3365 2509; fax: +61 7 3365 1177.
E-mail address: r.burns@uq.edu.au (R.G. Burns).

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acids (Dakora and Phillips, 2002). Meharg and Killham (1995) have shown that *Lolium perenne* seedlings increase exudation of labelled C from 1% of that photosynthetically assimilated in the absence of rhizosphere microorganisms to up to 34% in the presence of microorganisms. In turn, soil type (Marschner et al., 2001) and the presence of plant roots (Marschner et al., 2001; Smalla et al., 2001) influence microbial community structure. Thus, the rhizosphere may be defined as a complex reciprocal relationship of soil, plant and microorganism with rhizodeposition both a driver and consequence of this interaction. It follows that the kinetics of xenobiotic biodegradation in the rhizosphere may be sensitive to such plant–soil–microbe interactions if specific components of rhizodeposition are key to rhizosphere-enhanced breakdown.

Shaw and Burns (2004, 2005) have shown that mineralization of the broad-leaved weed herbicide 2,4-dichlorophenoxyacetic acid (2,4-D) is enhanced due to the presence of legume rhizodeposits in an acidic (pH 4) sandy silt loam soil from Sourhope, Scotland. The rhizodeposit enhancement had legume (e.g. *Trifolium pratense, Lotus corniculatus, Medicago sativa*) specificity; no enhancement was recorded for non-legume species (e.g. the monocotyledon *Lolium perenne*). Our aim was to compare the legume *versus* monocotyledon rhizodeposit effect on 2,4-D mineralization kinetics recorded for Sourhope soil with that recorded for a second, neutral (pH 6.5) sandy loam soil. In the resulting soil and planting combinations, we related kinetics of 2,4-D mineralization to soil chemical and microbial properties.

2. Materials and methods

2.1. Soil and soil properties

The two different soils used were a brown forest soil from Sourhope Research Station in Scotland (see Shaw and Burns, 2004 for further details) and a garden soil (Boughton Lees, Kent, England). Sourhope (SH) soil had no known history of 2,4-D application whereas Boughton Lees (BL) soil had SBK Brushwood Killer (Vitax Ltd, Coalville, Leics, UK) at a rate of 1 ml m^{-2} (equivalent to 71, 35 and 15 mg m^{-2} of 2,4-D ethyl hexyl ester, mecoprop-P ethyl hexyl ester and dicamba, respectively) applied 9 months prior to sampling. Grid reference details and some soil properties are given in Table 1. The soils were collected from 10–40 cm depth, sealed in sterile polythene bags and transported to the laboratory where they were were sieved (<2.8 mm) and stored at 4 °C until use.

2.2. Plant growth

Plants were grown in boiling tubes (25 mm external diameter × 150 mm length) as described in (Shaw and Burns, 2004). Briefly, replicate tubes containing 12 g (dry weight equivalent) field moist soil were planted with 20 seeds per tube of either *Lolium perenne* or *Trifolium pratense* (Herbiseed, Twyford, England). As controls, additional tubes were left non-planted but were otherwise treated identically to the planted tubes. Tubes were kept at 20 °C under a light-dark cycle of 16 h light (4 200 *lux*) and 8 h dark. Tubes were weighed every 2 days and sufficient distilled water added to bring the weight to the initial value; no correction was made for increasing biomass of the plant when adjusting the water content. After 25 d from sowing, tubes were destructively sampled: shoots were excised and weighed and the roots chopped finely with a sterile scalpel and homogenised with the soil (i.e. the entire below-soil surface contents of the tube were defined as the rhizosphere and included rhizoplane and endorhizosphere microbial colonizers). Sub-samples were taken for biochemical, microbiological and 2,4-D mineralisation assays.

2.3. Soil biochemical and microbiological analysis

Soil dehydrogenase activity was determined using an unbuffered iodonitrotetrazolium chloride (INT; Sigma-Aldrich Co. Ltd, Gillingham, Dorest, UK) substrate solution and an assay adapted from Trevors (1984) and von Mersi and Schinner (1991), see Shaw and Burns (2004).

Soil sub-samples (0.5 g dry weight) were used as the basis for a 10-fold dilution series in the determination of most probable number of 2,4-D degraders ($MPN_{2,4\text{-}D}$) by assay of 2,4-D disappearance from inoculated mineral broth

Table 1
Selected physico-chemical properties of Sourhope (SH) and Boughton Lees (BL) soil. Data are mean ± standard error of the mean ($n \geq 3$)

Soil (GB grid reference)	Texture[a]	pH[b]	Total organic carbon (%)[c]	Ammonium-N ($\mu g\ g^{-1}$)[d]	Nitrate-N ($\mu g\ g^{-1}$)[e]	Phosphate-P ($\mu g\ g^{-1}$)[f]
BL (TR 025 471)	Sandy loam	6.53 ± 0.023	4.33 ± 0.08	208 ± 14	42.2 ± 3.2	104 ± 5
SH (NT 850 205)	Sandy silt loam	4.03 ± 0.01	2.84 ± 0.05	168 ± 20	26.0 ± 0.9	32.4 ± 1

[a] Soil Survey of England and Wales classification.
[b] 1:2.5 (w/v) soil: 10 mM $CaCl_2$.
[c] According to the method of Nelson and Sommers (1982).
[d] Ammonium was extracted using 2 M KCl and concentrations in extracts determined using a colorimetric method (Forster, 1995a).
[e] Nitrate was extracted using distilled water and concentrations in extracts determined using a colorimetric method (Forster, 1995a).
[f] Phosphate was extracted using 0.5 M $NaHCO_3$ and concentration in extracts determined using the ammonium molybdate-ascorbic acid colorimetric method (Forster, 1995b).

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