Soil Biology & Biochemistry 42 (2010) 260–269

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Rates of *in situ* carbon mineralization in relation to land-use, microbial community and edaphic characteristics

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ARTICLE INFO

Article history:
Received 5 June 2009
Received in revised form
26 October 2009
Accepted 29 October 2009
Available online 10 November 2009

Keywords:
Soil microbial communities
Root exudates
Low molecular weight compounds
Fungal-to-bacterial ratios
Land-use
Rhizosphere
Carbon cycling
Decomposition

ABSTRACT

Plant-derived carbon compounds enter soils in a number of forms; two of the most abundant being leaf litter and rhizodeposition. Our knowledge concerning the predominant controls on the cycling of leaf litter far outweighs that for rhizodeposition even though the constituents of rhizodeposits includes a cocktail of low molecular weight organic compounds which represent a rapidly cycling source of carbon, readily available to soil microbes. We determined the mineralization dynamics of a major rhizodeposit, glucose, and its relationship to land-use, microbial community and edaphic characteristics across a landscape in the southeastern United States. The landscape consists of cultivated, pasture, pine plantation, and hardwood forest sites ($n = 3$). Mineralization dynamics were resolved in both winter and summer using an *in situ* ^{13}C-glucose pulse-chase approach. Mineralization rates of the labeled glucose decline exponentially across the 72 h measurement periods. This pattern and absolute mineralization rates are consistent across seasons. An information-theoretic approach reveals that land-use is a moderately strong predictor of cumulative glucose mineralization. Measures assessing the size, activity, and/or composition of the microbial community were poor predictors of glucose mineralization. The strongest predictor of glucose mineralization was soil-extractable phosphorus. It was positively related to glucose mineralization across seasons and explained 60% and 48% of variation in cumulative glucose mineralization in the summer and winter, respectively. We discuss potential mechanisms underlying the relationship between soil phosphorus and glucose mineralization. Our results suggest that specific soil characteristics often related to land-use and/or land-management decisions may be strong predictors of glucose mineralization rates across a landscape. We emphasize the need for future research into the role of soil phosphorus availability and land-use history in determining soil organic carbon dynamics.

1. Introduction

Much of our understanding regarding the cycling of plant-derived carbon (C)-compounds has been developed from studies that examine leaf litter decomposition (Melillo et al., 1982; Couteaux et al., 1995; Aerts, 1997; Gholz et al., 2000; Harmon et al., 2009). However, leaf litter is not the only plant-derived input of C to terrestrial systems. Of growing interest is the role that rhizodeposits play in ecosystem level C-processes (van Hees et al., 2005; Pollierer et al., 2007; Hogberg et al., 2008; Phillips et al., 2008). Rhizodeposits are in part composed of low molecular weight organic C (LMWOC) compounds, such as sugars (mono- and disaccharides), amino acids, and organic acids (Rovira, 1969; Grayston et al., 1997; Dakora and Phillips, 2002). These compounds represent a highly labile, rapidly cycling, form of C which is immediately available to the soil microbial community for growth, maintenance and respiration and so their impact on C dynamics may be large (van Hees et al., 2005; Hogberg et al., 2008). Furthermore, the degree to which rhizodeposition interacts with the microbial community is likely to influence ecosystem C-sequestration, with increases or decreases in soil organic C pools expected under differing input rates of LMWOC

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doi:10.1016/j.soilbio.2009.10.026

compounds (Bradford et al., 2008a,b; Blagodatskaya et al., 2009). Less well understood is how variation in land-use, microbial community and edaphic characteristics will impact the mineralization rates of such rhizodeposits.

Overall there is the expectation that the size, activity, and composition of the soil microbial community will influence the mineralization rates of LMWOC compounds (van Hees et al., 2005; Fierer et al., 2007; Allison and Martiny, 2008; Green et al., 2008; but see Kemmitt et al., 2008). An increase in the size and/or activity of the microbial community is expected to increase mineralization (van Hees et al., 2002; van Hees et al., 2005; Six et al., 2006). The influence of composition, on the other hand, is less clear. Compositional changes in the soil microbial community, associated with broad distinctions in life history strategies, are likely to have the greatest impact on mineralization dynamics. For example, a phylogenetic distinction might posit that communities dominated by bacteria will have greater mineralization rates than those dominated by fungi (Bardgett and McAlister, 1999; Six et al., 2006).

It is also feasible that microbial communities which have previously been exposed to a specific LMWOC compound will subsequently influence the future mineralization of that compound (Saggar et al., 2000). This expectation is similar to the hypothesis of 'home-field advantage', which was developed to explain differences in litter decomposition rates not accounted for by climate and/or litter quality (Hunt et al., 1988; Gholz et al., 2000; Ayres et al., 2009; Strickland et al., 2009a). The hypothesis suggests that communities pre-exposed to a given leaf litter are likely to mineralize that litter more rapidly than communities for which that litter is novel (Gholz et al., 2000; Ayres et al., 2009). Although the underlying mechanisms for home-field advantage may differ for mineralization rates of litter and LMWOC compounds, the scenario suggests that communities which derive the bulk of their C from LMWOC compounds may have greater mineralization rates than communities deriving their C from another source (Saggar et al., 2000; Stevenson et al., 2004). Based on this possibility, the mineralization rates of LMWOC compounds may be dependent on the plant community and factors such as land-use/land-cover, season, and nutrient availability (Grayston et al., 1997; Warembourg et al., 2003; van Hees et al., 2005). For example, where the dominant plant cover is grass (e.g. pastures), inputs of LMWOC compounds may be a more important C source than in forests, explaining higher mineralization rates of these compounds in herbaceous communities (Stevenson et al., 2004). Similarly, these inputs may vary with both season and the nutrient demands of the plant itself (Nguyen, 2003; Bais et al., 2006). Finally, factors typically related to soil C dynamics, such as temperature, moisture, pH, soil texture and nutrient availability, may all influence mineralization rates of LMWOC compounds (Saggar et al., 2000; Fierer and Jackson, 2006; Yuste et al., 2007; Bradford et al., 2008a,b). Specifically, each of these factors has been related to effects on the activity and/or composition of the soil microbial community but their effect on the mineralization rates of LMWOC compounds is lacking (van Hees et al., 2005).

One of the key constituents of LMWOC compounds is glucose (Dakora and Phillips, 2002; Nguyen, 2003; van Hees et al., 2005). Glucose is likely to be found in the rhizodeposits of nearly all plant species under an array of environmental conditions and is also found in the leachates of forest floor litter (Dakora and Phillips, 2002; Nguyen, 2003; van Hees et al., 2005). In light of the significance of glucose as a rhizodeposit and leachate-constituent, microbial mineralization of glucose has been widely studied. As early as the 1980s researchers have been adding glucose to soil and tracking the resulting mineralization dynamics. Notably, Voroney et al. (1989) found that the initial mineralization of glucose was rapid but that a large proportion (~25%) of it was later stabilized in the system, presumably as microbially-derived products. Research has shown that the mineralization of this compound is often dependent on its concentration and when using concentrations more typical of those found *in situ*, mineralization of glucose has been shown to follow Michaelis–Menten type kinetics (van Hees et al., 2005; van Hees et al., 2008; Schneckenberger et al., 2008). Soil microbial communities respond rapidly to glucose additions, even when these additions are in trace amounts, suggesting that at least certain components of the microbial community may be adapted to it and/or LMWOC compounds in general (De Nobili et al., 2001; Jones and Murphy, 2007; Hanson et al., 2008; Hoyle et al., 2008). Lab-based studies of this phenomenon have demonstrated that this adaptation may be contingent on the source environment of the microbial community, with microbes from grasslands responding more rapidly than those from forests (Jones and Murphy, 2007). Such studies have added greatly to our understanding of the microbial response to glucose but few studies have assessed these dynamics in intact soil systems under field conditions. One exception to this is Boddy et al. (2007), who found that glucose mineralization was more rapid in the field than in the lab; this was attributed to an intact microbial community *in situ* associated with the rhizosphere. Less well understood is whether the mineralization of glucose (or other LMWOC compounds) can be generalized across a landscape in much the same way that leaf litter decomposition has been (Barlow et al., 2007; Madritch and Cardinale, 2007). That is, are there characteristics across space and time that likely explain variation in the mineralization rates of glucose *in situ*?

The objective of our study was to determine the landscape-level controls on glucose mineralization rates via the comparison of multiple, ecologically relevant models to provide a greater mechanistic understanding of mineralization dynamics of LMWOC compounds across a landscape. To accomplish this we amended soils with small amounts of ^{13}C-labeled glucose and tracked its resultant mineralization, in both the summer and winter, across a representative rural landscape of the southeastern United States (see Richter et al., 1999; Richter and Markewitz, 2001). We expected that the size, activity, and composition of microbial communities, all of which could be considered potential determinants of glucose mineralization rates, would vary markedly. Our primary expectation was that either one or all three of these microbial community characteristics, and/or land-use, would be a major determinant of *in situ* glucose mineralization rates. More specifically, we expected, due to likely differences in microbial community characteristics and rhizospheric inputs, that mineralization rates would be related to plant cover (i.e. herbaceous vs. forest). To investigate these expectations we used an information-theoretic approach (Burnham and Anderson, 1998) which permitted the comparison of a suite of ecologically relevant models (i.e. models arrived at *a priori* and based on relevant and justifiable ecological theory [see Burnham and Anderson, 1998]) in order to determine the probable best model, in addition to the most important model parameter (or variable), for explaining variation in glucose mineralization *in situ*. This regression approach allowed us to compare multiple linear models but without the shortcomings associated with many frequentist model selection techniques (Stephens et al., 2007; Bolker, 2008). We assessed a secondary set of models that, in addition to microbial community characteristics and land-use, included a suite of soil characteristics that have been speculated to influence glucose mineralization (e.g. texture).

2. Materials and methods

2.1. Site descriptions

Sites used in this study were located in, or adjacent to, the Calhoun Experimental Forest (CEF), which is managed by the USDA

Forest Service and located in the Southern Piedmont physiographic region (approximately 34.5°N, 82°W) of northwestern South Carolina, USA (Gaudinski et al., 2001; Callaham et al., 2006). The acidic Ultisol soils at these sites are classified as fine, kaolinitic, thermic Typic Kanhapludults of the Appling, Cecil, Hiwassee, and Madison series (Lauber et al., 2008; Grandy et al., 2009). All sites are on uplands with minimal slope and on interfluves from similar bedrock, thus attempting to control native soil characteristics, geomorphology, and geology. Sites were within 30 km of each other and each represented one of four land-use practices common to the region (Lauber et al., 2008; Grandy et al., 2009): annual row-crop agriculture, cattle pasture, old-field pine forest, and oak-hickory forest ($n = 3$ in all cases).

Management regimes for both the cultivated and pasture sites have been in place for at least the past 40 years. The cultivated sites are managed by the South Carolina Department of Natural Resources as wildlife fields with annual crop rotation between corn (*Zea mays*), millet (*Panicum miliaceum*), wheat (*Triticum* sp), sorghum (*Sorghum* sp), sunflowers (*Helianthus annuus*), and fallow using conventional tillage practices. During the winter sampling (start date: 30th November 2006) two of the three cultivated sites were fallow while the other (site name: Cultivated 3) was planted in winter wheat. In the summer sampling (start date: 12 June 2007), cultivated sites were planted with corn (Cultivated 1), sunflowers (Cultivated 2), and wheat/corn (Cultivated 3). Pasture sites are dominated by rye (*Lolium* sp) and Bermuda grass (*Panicum dactylon*) and are, more or less, continuously cattle-grazed. Both cultivated and pasture ecosystems are fertilized and limed. Two of the pine plantations (i.e. Pine 1 and 3) are ~50 years old and consist of an overstory of loblolly pine (*Pinus taeda*) with an understory of oak (*Quercus* sp) and hickory (*Carya* sp) species. The other pine plantation (i.e. Pine 2) is a 10-year old loblolly pine monoculture. These pine forests are all growing on old fields previously cultivated for cotton and have therefore been fertilized and limed but not during the growth of pine. The hardwood sites are mature oak-hickory stands, ~75 years of age. One hardwood plot (i.e. Hardwood 2) is grazed by cattle and has little understory vegetation. Average bulk density (for depth 0–7.5 cm) ± 1 S.E. was 1.23 ± 0.15, 1.66 ± 0.10, 1.32 ± 0.09, and 1.16 ± 0.17 g cm^{-3} for cultivated, pasture, pine, and hardwood land-uses, respectively.

This replicated land-use design allowed us to explore how variation in both the contemporary and historical management of these sites drove differences, which might be expected to influence glucose mineralization, in soil properties and microbial communities (Richter et al., 1999; Richter and Markewitz, 2001). Differences in dominant plant cover per land-use could also be a significant determinant of glucose mineralization (e.g. Stevenson et al., 2004). It was our goal to select sites representative of the land-use practices and land-use legacies of this region, enabling a practical insight into the relationship between *in situ* glucose mineralization and soil chemical, physical and microbial community characteristics. It should be noted though that this is not a controlled study of land-use classifications but is a comparative study of sites that share many natural similarities but that contrast greatly in their land-use practices and land-use legacies.

2.2. ^{13}C-glucose pulse-chase

To determine glucose mineralization rates across sites and seasons, we conducted a ^{13}C-glucose pulse-chase experiment in both the winter and summer. The pulse-chase was conducted by making additions of 99 atom% ^{13}C-labeled glucose and tracking its mineralization as $^{13}CO_2$. This was accomplished by randomly placing two (analytical repeats) PVC collars (15.4 cm dia., inserted 5 cm into the soil) in a 5 m^2 land-use sub-plot. Within each collar small plants, if present, including grass in the pasture sites were removed by clipping at the soil surface and any surface litter material was also removed. Collars were removed at the end of the winter pulse-chase and placed again at different random locations within the same sub-plot at the beginning of the summer pulse-chase. Water (1 l) was added to each core 24 h prior to sampling in order to minimize soil-moisture stress and make water potential comparable between sites. Soil CO_2 efflux rates were determined using a closed-chamber approach (e.g. Bradford et al., 2001), where CO_2 concentrations were determined at the start and end of a 45 min capping period. We conducted a pilot study to determine the appropriate capping time and found that headspace CO_2 concentrations increase linearly from 0 to 45 min and flux rate estimates only begin to decrease after 60 min. Headspace samples were taken with 20 ml SGE gas syringes, transported to the laboratory in 12 ml Exetainers (previously evacuated), and then CO_2 concentrations were determined using an infra-red gas analyzer (IRGA; Li-Cor Biosciences, Lincoln, NE, USA, Model LI-7000). A second sample was analyzed using continuous flow, isotope-ratio mass spectrometry (IRMS; Thermo, San Jose, CA, USA) to determine the $\delta^{13}C$ value of the CO_2 in the sample. The initial headspace sampling provided the natural abundance values for the isotope mixing equations (see below). After this initial sampling, 1 l of 2.5 mM ^{13}C-labeled glucose solution (99 atom%) was added to the collars and permitted to drain. The capping procedure was repeated post addition at 2, 5, 24, 48 and 72 h, permitting a negative exponential 'decay' of ^{13}C label to be tracked in the soil CO_2 efflux, from which cumulative mineralization rates were estimated. The amount of C added to each collar was relatively small: <25 μg C g dry wt $soil^{-1}$, which is <0.0001% of the total soil carbon (from 0 to 7.5 cm depth in a 15.4-cm dia. PVC collar). We recognize that this methodology may underestimate the absolute amount of glucose mineralized to CO_2 due in part to lateral diffusion of the glucose through the soil leading to its mineralization outside of the collar. We expect though that the impact of this on the relative differences between plots was minimal even if there was an impact on the absolute amounts given that key variables such as soil moisture and texture were unrelated to glucose mineralization (see Results). Furthermore, preliminary tests of the hydrological consequences of our method indicate that the glucose solution likely penetrated the soil to a depth no greater than 10–15 cm and lateral diffusion was minimal across the CEF soils.

The contribution of ^{13}C-labeled glucose to soil respiration was estimated using isotope mixing equations. The amount of glucose-derived CO_2 was calculated as follows (*sensu* Ineson et al., 1996): $C_{glucose\ derived} = C_{total} \times (\delta^{13}C_{after} - \delta^{13}C_{before})/(\delta^{13}C_{glucose} - \delta^{13}C_{before})$, where C_{total} is the total amount of C respired, $\delta^{13}C_{after}$ is the $\delta^{13}C$ value of the respired C after glucose was added, $\delta^{13}C_{before}$ is the $\delta^{13}C$ value of respired C before glucose was added (i.e. the natural abundance value), and $\delta^{13}C_{glucose}$ is the value for the glucose itself. Values were calculated per PVC collar but for the statistical analyses the mean of the two analytical replicates for each plot (per season) were used; in effect treating the pair of values as 'experimental repeats' and not replicates.

2.3. Determination of microbial community structure and soil characteristics

During both the summer and winter pulse-chase, we collected ten individual A horizon soil cores (8 cm dia., 0–7.5 cm depth) from each site using a stratified random approach. Soil cores were taken from areas adjacent (i.e. within 10 m) to the pulse-chase plots in each land-use. Soils were sieved (4 mm), homogenized, and stored at +5 °C until analyzed. Analyses included those used to assess the soil microbial community and key soil characteristics expected to

influence the mineralization of glucose. Mean values per land-use for both sets of characteristics are presented in Supplementary Table 1.

We used three common methods to determine the size, activity, and composition of microbial communities. These included a modified chloroform fumigation-extraction (CFE) method to assess microbial biomass, substrate-induced respiration (SIR) as an estimate of activity (Wardle and Ghani, 1995), and determination of fungal-to-bacterial dominance via qPCR to estimate composition. All measures of microbial community size, activity, and composition were determined for both the winter and summer pulse-chase.

The modified CFE method as described in Fierer and Schimel (2002, 2003) was used to estimate microbial biomass C. Briefly this was estimated as the flush of DOC following fumigation with ethanol-free chloroform. Raw values are reported for microbial biomass C; no correction factors were used and so we refer to this as microbial cytoplasm C. The SIR method used follows Fierer and Schimel (2003) whereby soil slurries are incubated, after a 1 h pre-incubation with excess substrate (i.e. autolyzed yeast extract), for 4 h at 20 °C. After the 4-h incubation, SIR is determined via infrared gas analysis of headspace CO_2 concentrations using a static incubation technique (Fierer et al., 2005a).

The composition of the microbial community was assessed as the relative abundance of fungi-to-bacteria. We determined these ratios using the quantitative PCR (qPCR) method described by Fierer et al. (2005b) and Lauber et al. (2008). Briefly, DNA was isolated from soil (kept at −80 °C until use) using the MoBIO Power Soil DNA Extraction kit (MoBio Laboratories, Carlsbad, CA) with modifications described in Lauber et al. (2008). Standard curves were constructed to estimate bacterial and fungal small-subunit rRNA gene abundances using *E. coli* 16S rRNA gene, or the *Saccharomyces cerevisiae* 18S rRNA gene, according to Lauber et al. (2008). Ratios of fungal-to-bacterial gene copy numbers were generated by using a regression equation for each assay relating the cycle threshold (Ct) value to the known number of copies in the standards. All qPCR reactions were run in quadruplicate. Notably qPCR gives a relative measure of fungal-to-bacterial dominance due to large variability between taxa in the ratio of gene copy numbers to cellular biomass and should not be taken to indicate biomass ratios. Additional details, including the specific qPCR reaction conditions and primer details, are provided in Lauber et al. (2008).

In addition to measures aimed at determining the size, activity, and composition of the soil microbial community we also identified and determined several soil characteristics that are likely to influence the mineralization of glucose both directly and indirectly. These included in the same 7.5-cm deep samples, soil pH, soil temperature and moisture, soil texture, soil organic material C:N ratio, and extractable P. Soil pH, moisture, and temperature were determined for both the winter and summer pulse-chase. Soil texture, C:N, and extractable P were determined on 7 September 2006 as differences between sites with regards to these variables are expected to be much greater than that expected across seasons (Richter et al., 2006).

Soil pH (1:1, soil:H_2O by volume) was measured with a bench-top pH meter. Soil temperature (determined at 7.5 cm depth) and moisture (determined across 0–10 cm depth) were determined at each pulse-chase measurement using hand-held moisture and temperature probes. The average of both was estimated for the entire 72 h period of both the summer and winter pulse-chase. Soil texture was estimated using a simplified version of the hydrometer method as described by Gee and Or (2002). Soil C:N was determined using an NA1500 CHN Analyzer (Carlo Erba Strumentazione, Milan, Italy) and extractable P was measured on an Alpkem auto-analyzer (OI Analytical, College Station, TX) using Murphy-Riley chemistry after extraction with Mehlich I double-acid (H_2SO_4–HCl) using a 1:4 mass:volume ratio (Kuo, 1996).

2.4. Statistical analyses

Linear mixed-effects models (Pinheiro and Bates, 2000) were used to examine the relationships between glucose mineralization and soil microbial community characteristics (i.e. size, activity, and composition), land-use, and select soil characteristics. For this approach microbial community characteristics, land-use, soil characteristics, and season (when applicable) were treated as fixed effects. Site identity was included as a random effect to account for repeated sampling (i.e. season). Cumulative glucose mineralization was $\log_e$-transformed to conform to assumptions of homoscedasticity (verified using model checking). Parameter estimates were calculated using restricted maximum likelihood. However, models compared using the information-theoretic approach were constructed using maximum likelihood estimates as the fixed effects of these models varied (MacNeil et al., 2009). Further assessment of model fit was done using linear regression within a given season (i.e. the same linear model was fit to either data gathered in the winter or summer). Finally, analyses were also conducted which examined the effect of land-use on cumulative glucose mineralization and mineralization dynamics. We analyzed cumulative glucose mineralization using a linear mixed-effects model where land-use and season were treated as fixed effects and site identity was treated as a random effect to account for repeated sampling across seasons; land-use and season were allowed to interact in this model. Land-use was further examined within each season using ANOVA with land-use as a discrete variable and the Tukey method was used to assess differences between means. We analyzed the mineralization dynamics across the 72 h period using a linear mixed-effects model where land-use, season, and time since glucose addition were treated as fixed effects and site identity was treated as a random effect to account for repeated sampling across the 72 h. Time was treated as a continuous variable and all three variables were allowed to interact. Mineralization dynamics were also analyzed within a given season using a similar mixed-effects model except in this case there was no fixed effect of season. All analyses were conducted using the freeware statistical package R (http://cran.r-project.org/).

Model selection and comparison was conducted using an information-theoretic approach (Burnham and Anderson, 1998). This approach allows the comparison of multiple linear models and is developed from classical multiple regression. It was developed to overcome limitations of the classical approaches, such as nesting and selection in a stepwise fashion (Burnham and Anderson, 1998; Stephens et al., 2007). That is, in classical multiple regression all the models in a candidate set cannot be compared simultaneously but via an information-theoretic approach they can (Burnham and Anderson, 1998; Stephens et al., 2007; Bolker, 2008). It also allows for the determination of 'parameters of interest' within a suite of models allowing, in this case, for the robust determination of potential controls on mineralization. We initially compared models which related soil microbial community characteristics and land-use to cumulative glucose mineralization. This resulted in a set of 30 candidate models plus an additional intercept only model (see Supplementary Table 2 for the full model list). Land-use was also included in this candidate set as a single parameter and in combination with season. Model parameters were only included as additive terms in order to both keep the number of candidate models manageable and because there was no *a priori* rationale for the inclusion of interactions. Akaike's information criterion for small sample size (AICc) was used as the model selection criterion (Burnham and Anderson, 1998). Model comparisons are based on the difference in AICc (Δ_i) with models $<$ 2 AICc units apart considered nearly indistinguishable (Burnham and Anderson, 1998). Models $>$ 10 AICc units from the model with the minimum

AICc value have no support (Burnham and Anderson, 1998). We also calculated Akaike weights (ω_i) which allowed us to quantify the support for one model relative to another, calculate the 95% confidence set of models, and determine the importance of a given model variable (Burnham and Anderson, 1998). The last of these was calculated as the $\Sigma\omega_i$ for all models containing the variable in question (Burnham and Anderson, 1998).

In addition to the initial 30 candidate models we also looked at the role of specific soil characteristics. We determined *a priori* that pH, the interaction between soil temperature and moisture, silt + clay content, soil organic matter C:N ratio, and extractable P might influence glucose mineralization via effects on the microbial community. Each of these was included as an additive variable in models containing microbial community characteristics as well as a single factor and as an additive factor with season (see Supplementary Table 2 for the full model list). This resulted in a total of 110 candidate models (plus an intercept only model) that included the original 30 candidate models. Model selection for this set of candidate models was conducted in the same manner as described above.

3. Results

3.1. Temporal dynamics and cumulative mineralization of glucose

Overall the addition of glucose caused relatively little if any change in total soil respiration within a land-use, regardless of season (Supplementary Fig. 1). The amount of glucose respired as $^{13}CO_2$ declined across the 72 h measurement period with the highest mineralization values recorded ~2 h after the addition of glucose and the lowest values occurring at ~48 or ~72 h (Fig. 1). This change in glucose mineralization rates across time was highly significant ($F_{1, 96} = 278.93$; $P < 0.0001$) and an interaction between these temporal dynamics and season was detected ($F_{1, 96} = 5.27$; $P < 0.05$). This interaction was likely explained by the similar mineralization rates regardless of season at the 2 and 5 h measurement periods but greater mineralization rates in the winter at the 24, 48, and 72 h measurement periods. It is worth noting that glucose mineralization rates tended to be similar across seasons in spite of the fact that total soil respiration was greater in the summer when compared to the winter (Fig. 1, Supplementary Fig. 1). Land-use was also a significant factor impacting glucose mineralization rates ($F_{3, 8} = 9.89$; $P < 0.01$) and this was consistent for both the winter ($F_{3, 8} = 10.08$; $P < 0.01$) and summer ($F_{3, 8} = 9.57$; $P < 0.01$) (Fig. 1a,b). In general we noted that pasture and cultivated sites typically had higher glucose mineralization rates across 72 h than did pine and hardwood sites, although this pattern was clearer in the summer than in the winter (Fig. 1).

Overall, land-use had a significant influence on cumulative glucose mineralization ($F_{3, 8} = 10.34$; $P < 0.01$). Neither season effects ($F_{1, 8} = 0.45$; $P = 0.52$), nor an interaction between season and land-use ($F_{3, 8} = 1.36$; $P = 0.32$), were observed for cumulative mineralization. Generally, cumulative mineralization was higher in pasture sites while both the pine and hardwood sites tended to be lower (Fig. 1). The cultivated sites were not as easily generalized given that cumulative mineralization tended to be lower in the winter when compared to the summer. Additionally, during the summer there was a large degree of variation associated with this land-use, likely due to differences in crop cover between the three sites (see Methods and Discussion). The high variation in cultivated sites in the summer may explain why the land-use effect on cumulative glucose mineralization (Fig. 1c,d) was not consistent across seasons. That is, in the winter a clear land-use effect was noted ($F_{3, 8} = 18.22$; $P < 0.001$) but this was not true for the summer ($F_{3, 8} = 2.64$; $P = 0.12$), where larger error variances were observed (compare Fig. 1c and d). The large variation in cumulative glucose mineralized across cultivated sites may also explain why the temporal data (Fig. 1b) revealed a statistically significant land-use effect but the cumulative data (Fig. 1d) did not.

Relatively little of the added glucose was recovered as CO_2 and this was true regardless of season or land-use. The amount of C recovered as CO_2 ranged from a low of 0.57% (Hardwood 3 in the winter) to a high of 4.29% (Cultivated 3 in the summer) and across all land-uses and both seasons averaged 1.93%. This suggests that approximately 95–99% of the added glucose-C remained within the soil system. Of course, given that we did not begin tracking the mineralization of glucose until 2 h after its addition, and the fact that some of the respired glucose may not have been captured by our chamber method (see Methods), the actual amount of C remaining may have been lower. However, low recovery rates of glucose-C as CO_2 are typical when glucose solutions are added to soils at low vs. high concentrations (Boddy et al., 2007).

3.2. Glucose mineralization and its relationship to microbial community structure and land-use

We initially set out to determine the importance of land-use and the size, activity, and composition of the microbial community as they relate to cumulative glucose mineralization *in situ*. In order to do this we utilized an information-theoretic approach to assess a series of 30 candidate models (Burnham and Anderson, 1998). Given that land-use was significantly related to cumulative glucose mineralized (Fig. 1), it is not surprising that the best model (i.e. lowest AICc) included land-use as the sole explanatory variable (Table 1). The probability that this model was the actual best model in this set was 53% suggesting moderate support for this outcome. However, a model which only included an intercept term was within 2 AICc units of the top model suggesting that it was also a plausible top model candidate (Table 1). Furthermore, the evidence ratio (i.e. $\omega_1/\omega_2 = 1.89$) when comparing these two models is ~2 and we must then assume a high level of model selection uncertainty (Burnham and Anderson, 1998). Additionally, all of the remaining models, including those that accounted for the size, activity, or composition of the microbial community, were >4 AICc units from the top model indicating that there was overall considerably less support that any of these models was the 'actual' best model (Burnham and Anderson, 1998). In fact when calculating the importance of each model parameter, we found that the size, activity, and composition of the microbial community were all relatively unimportant in the prediction of glucose mineralization ($\omega_i < 0.10$ for all 3; Fig. 2a) while land-use was only moderately important ($\omega_i = 0.55$; Fig. 2a). Parameter estimates for models within the 95% confidence limit are reported in Supplementary Table 3.

3.3. Glucose mineralization and its relationship to microbial community structure, land-use, and soil characteristics

Given that only marginal support for any one model or model parameter was found in the initial candidate set, we decided to explore the relationship between several key soil characteristics at our sites and the cumulative mineralization of glucose. We found that the best model (i.e. lowest AICc) in this candidate set included soil P concentrations as the sole explanatory variable (Table 2). The probability that this model was the actual best model in this set was 73% suggesting moderately strong support for this outcome. In fact no other model was within 2 AICc units of this model and in comparison to the second ranked model in this set, the evidence ratio was 10.11. This suggests that given this set of candidate models it is fairly certain that this model is the top model. Further supporting this is the fact that no other models were <4 AICc units

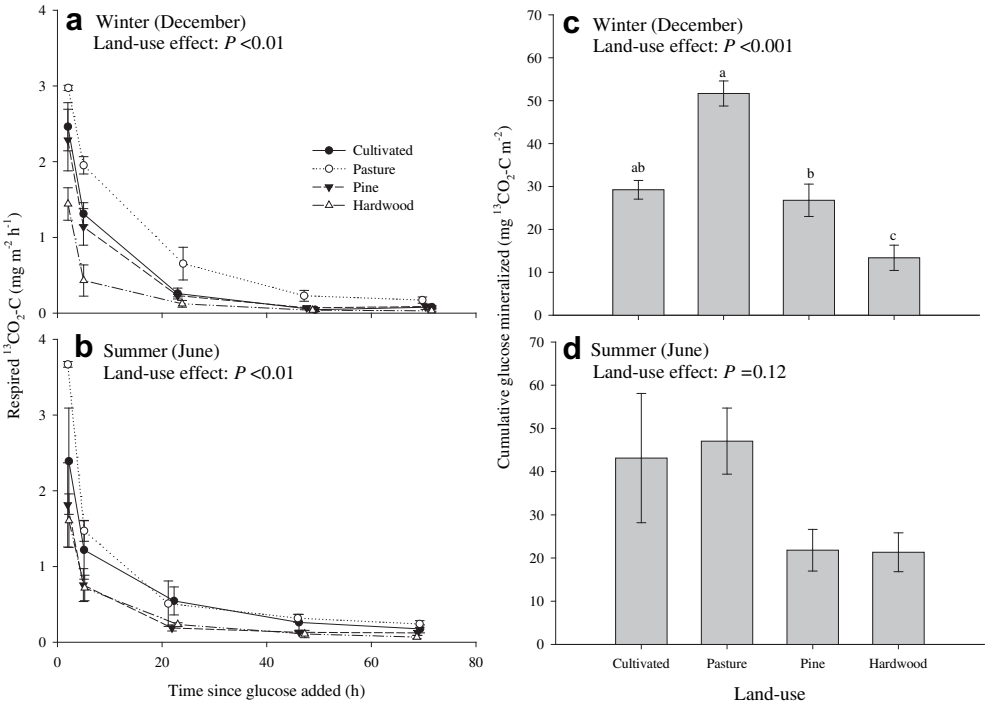

Fig. 1. Results of the ^{13}C-glucose pulse-chase conducted during the winter (December 2006) and summer (June 2007) associated with land-use. Panels a and b show glucose mineralization dynamics across 72 h for each land-use. Land-use differences were detected for these dynamics across seasons ($P < 0.01$) and during both the winter ($P < 0.01$) and summer ($P < 0.01$). Panels c and d show the cumulative amount of glucose mineralized during the entire 72-h period. Although there was a significant land-use effect across seasons on cumulative glucose mineralization ($P < 0.01$) this was not consistent within seasons. That is, a statistically significant land-use effect was observed in the winter ($P < 0.001$) but not in the summer ($P = 0.12$) for cumulative amounts. Values are means ± S.E. per land-use ($n = 3$) and letters in panel c indicate significant differences between land-uses based on pair-wise comparisons. Note that mineralization dynamics and cumulative values were roughly equivalent for a given land-use regardless of season.

from this model which indicates that there was overall considerably less support for any of the other 109 models (Burnham and Anderson, 1998). Parameter estimates for all models within the 95% confidence limit are reported in Supplementary Table 4.

We also found that soil-extractable P was the most important model parameter and was significantly related to land-use ($F_{3,\ 8} = 9.53$; $P < 0.01$). This is not surprising given that soil P was both the sole parameter in the top model and was also found in all of the other top models (i.e. all models within 10 AICc units of the top model). Soil P also had an extremely high weight of evidence ($\omega_i = 0.99$; Fig. 2b), again demonstrating its importance as an indicator of cumulative glucose mineralization. No other parameter was found to be as important. In fact all other model parameters were >10 times less likely to be as important as soil P (Fig. 2b). Soil P and cumulative glucose mineralized, after accounting for variation among plots, were positively related ($\beta = 0.48 \pm 0.09$; $F_{1,\ 10} = 30.04$; $P < 0.001$). Regression analysis found that this was generally consistent across seasons (Fig. 3) with soil P explaining 60 and 48% of the variation in cumulative glucose mineralized in the winter and summer, respectively (Fig. 3).

Table 1
The 10 best models (i.e. ΔAICc < 10) of the initial 30 candidate models considered which explain cumulative ^{13}C-glucose mineralized across 72 h ($^{13}CO_2$).

Model	K	log(L)	AICc	Δ_i AICc	ω_i	Evidence ratio	Rank
$^{13}CO_2$ = Land*	**6**	**−7.08**	**40.15**	**0.00**	**0.53**	**1.00**	**1**
$^{13}CO_2$ = 1*	**3**	**−16.38**	**41.42**	**1.27**	**0.28**	**1.89**	**2**
$^{13}CO_2$ = MicC*	4	−15.73	44.47	4.32	0.06	8.65	3
$^{13}CO_2$ = F:B*	4	−16.25	45.51	5.36	0.04	14.57	4
$^{13}CO_2$ = SIR*	4	−16.36	45.72	5.57	0.03	16.18	5
$^{13}CO_2$ = MicC + SIR	5	−14.67	47.90	7.75	0.01	48.24	6
$^{13}CO_2$ = MicC + Seas.	5	−14.82	48.21	8.06	0.01	56.16	7
$^{13}CO_2$ = Land + MicC	7	−6.29	48.98	8.83	0.01	82.73	8
$^{13}CO_2$ = MicC + F:B	5	−15.39	49.36	9.21	0.01	99.92	9
$^{13}CO_2$ = Land + Seas.	7	−6.82	50.04	9.89	0.00	140.35	10

The table shows the number of parameters (K), maximized log-likelihood (log(L)), AICc, AICc differences (Δ_i AICc), Akaike weights (ω_i), evidence ratio (ω_1/ω_n), and the model rank. In bold are the best top models in this candidate set (ΔAICc < 2). Models within the 95% confidence interval are denoted with an * and parameter estimates for these models are given in Supplementary Table 3. All models had plot as a random effect in order to account for repeated sampling at the plot level.
SIR = substrate-induced respiration, a measure of microbial activity; MicC = microbial biomass C as determined via CFE, a measure of the size of the microbial biomass; F:B = fungal-to-bacterial dominance as determined via qPCR, a measure of community composition; Seas. = Season, either winter or summer when the pulse-chase experiment was conducted; Land = land-use.

4. Discussion

In this study we amended four land-uses representative of a rural upland landscape with ^{13}C-labeled glucose and tracked its mineralization across the course of 72 h in both the summer and winter in order to determine what factors were related to the mineralization of this common LMWOC compound in soils. We expected that cumulative mineralization would be related to land-use and/or the size, activity, or composition of the soil microbial community. We also evaluated a second set of putative explanatory variables related to specific soil characteristics. We expected that these soil characteristics either alone or in combination with microbial community characteristics would affect cumulative glucose mineralization. Both of these sets of variables were examined using an information-theoretic approach that allowed us to determine the probable best model as well as the most important individual parameter for explaining glucose mineralization. The approach, when applied to evaluate and compare potential explanatory variables for which there is an established mechanistic rationale detailing why they might cause variation in a response

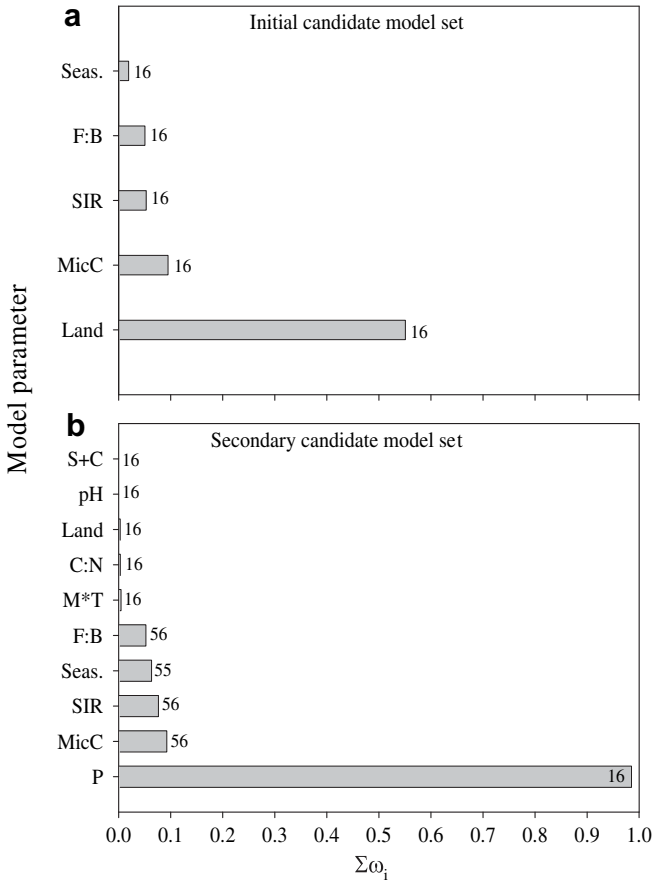

Fig. 2. The relative importance of variables from the primary (a) and secondary (b) set of candidate models which explain cumulative glucose mineralized. Relative importance was determined via the sum of Akaike weights ($\sum\omega_i$) for the models in which a given variable was present. The closer to 1 a variable is the more important it is in this given set. Numbers to the right of each bar indicate the number of models that a given variable was in (e.g. land-use was in 16 of the candidate models).

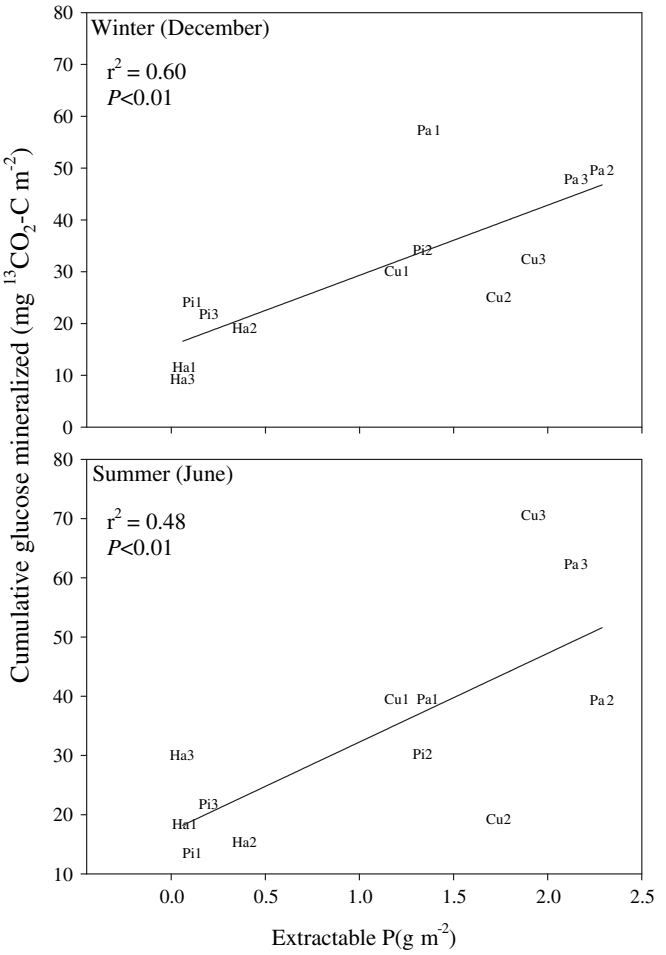

Fig. 3. The relationship between cumulative glucose mineralized and soil P for the winter (a) and summer (b). Notably this relationship was very similar in both the winter ($y = 0.51x + 2.73$) and summer ($y = 0.45x + 2.90$). Cumulative glucose mineralized was $\log_e$-transformed in the regression analysis but untransformed values are shown here. Each symbol represents a specific plot with Cu1-3, Pa1-3, Pi1-3, and Ha1-3 representing the individual sites ($n = 3$) in the cultivated, pasture, pine, and hardwood land-uses, respectively.

variable, generates ecologically relevant, regression models (see Burnham and Anderson, 1998). Our overarching objective was to advance the understanding of factors that influence the *in situ* mineralization of LMWOC compounds across landscapes.

Across the course of 72 h we found that glucose mineralization rates decreased exponentially and this pattern was consistent across land-use and season (Fig. 1a and 1b). Such results are similar to the findings of an array of lab-based studies (Bremer and Vankessel, 1990; Bremer and Kuikman, 1994; Hoyle et al., 2008; van Hees et al., 2008; Schneckenberger et al., 2008), as well as the findings of field-based studies where relatively high concentrations of glucose have been applied (Voroney et al., 1989). The mineralization dynamics observed in this study where similar to those observed by Boddy et al. (2007), one of the few *in situ* studies which simulated glucose additions at amounts and concentrations comparable to those expected under root exudation. This may suggest that across a wide array of settings the mineralization dynamics of glucose and, perhaps other LMWOC compounds, follow a predictable pattern.

Of the glucose added, we found that as much as 4% was recovered as CO_2 meaning that ~96% of glucose-derived C remained in the soil. This is not an uncommon occurrence, with comparable studies such as Voroney et al. (1989) finding that ~25% of a large glucose addition remained after 7 years and Boddy et al. (2007) finding that ~70–80% of a small glucose addition remained after 48 h. It is worth noting that our recovery of glucose-derived CO_2 is at the low end of most lab-based studies (Jones and Murphy, 2007; Schneckenberger et al., 2008). This may simply be due to the fact that our method did not enable us to capture the total flux of CO_2

Table 2
The 6 best models (i.e. ΔAICc < 10) of the initial 104 candidate models considered which explain cumulative ^{13}C-glucose mineralized across 72 h ($^{13}CO_2$). Parameter estimates for each of these models is given in Supplementary Table 4.

Model	*K*	log(L)	AICc	Δ_i AICc	ω_i	Evidence ratio	Rank
$^{13}CO_2$ = P*	**4**	**−8.10**	**29.20**	**0.00**	**0.73**	**1.00**	**1**
$^{13}CO_2$ = P + MicC*	5	−7.63	33.83	4.63	0.07	10.11	2
$^{13}CO_2$ = P + SIR*	5	−7.84	34.26	5.06	0.06	12.53	3
$^{13}CO_2$ = P + Seas*	5	−7.87	34.30	5.10	0.06	12.82	4
$^{13}CO_2$ = P + F:B	5	−8.06	34.68	5.48	0.05	15.50	5
$^{13}CO_2$ = P + MicC + SIR	6	−5.52	37.04	7.84	0.01	50.31	6

The table shows the number of parameters (*K*), maximized log-likelihood (log(L)), AICc, AICc differences (Δ_i AICc), Akaike weights (ω_i), evidence ratio (ω_1/ω_n), and the model rank. In bold are the best top models in this candidate set (ΔAICc < 2). Models within the 95% confidence interval are denoted with an * and parameter estimates for these models are given in Supplementary Table 4. All models had plot as a random effect in order to account for repeated sampling at the plot level.
SIR, MicC, F:B, Land, and Seas. are the same as in Table 1. P = extractable phosphorous.

but this should not impede our ability to make relative comparisons (see Methods). On the other hand, given that there are currently very few studies examining the *in situ* mineralization of realistic concentrations of glucose (Boddy et al., 2007), our results may prove to be the norm. Future research will determine if this is the case. In light of such findings, it has been suggested that relatively large amounts of added/exuded glucose are cycled through the microbial biomass and may to some degree be stabilized as microbial byproducts in the soil organic matter (Voroney et al., 1989). However, such processes may be slow and occur over decadal time scales (Richter et al., 1999). The stabilization (or not) of LMWOC in SOC sinks is an area requiring considerably more research attention, given the importance of these compounds to C dynamics in soils.

We found that land-use affected the cumulative amount of glucose mineralized (Fig. 1c,d). Like temporal mineralization dynamics (Fig. 1a,b), we found that pasture sites typically had greater cumulative glucose mineralization than did pine or hardwood sites. These results concur with those of Stevenson et al. (2004), who showed, using lab-based catabolic response profiling, that grassland soils are typically associated with greater glucose mineralization than forest soils. Cumulative glucose mineralized in the cultivated sites was on average lower in the winter than in the summer and this was likely due to the presence of established crop cover in the summer. Specifically, cumulative mineralization in the cultivated sites in summer was often comparable to cumulative values for pastures. In the winter two of the cultivated sites were fallow and the third (Cultivated 3) had freshly sprouted winter wheat. Interestingly, variation in mineralization rates across cultivated sites in the summer was high (Fig. 1d) and this variation may be due to differences in crop species cover. However, the role of plant-cover species identity in regulating mineralization dynamics of LMWOC compounds is relatively unexplored (see Paterson et al., 2007).

The best explanatory model in the primary set of models analyzed using the information-theoretic approach contained land-use as the sole parameter (Table 1). Land-use was also found to be the most important parameter for the prediction of cumulative glucose mineralization (Fig. 2a). Surprisingly, all models containing parameters related to the size, activity, or composition of the microbial community were likely poor predictors of cumulative glucose mineralization and overall they were not important parameters (Table 1, Fig. 2a). A possible explanation for the overall lack of importance for all of these model variables may be the high functional redundancy in the microbial community with regards the mineralization of glucose (Jones and Murphy, 2007; Hanson et al., 2008). However, we only used one method each to determine the size, activity, and composition of the microbial communities. Although these methods are commonly and widely employed, they are coarse and may not be indicative of the actual characteristics of the microbial community involved in the mineralization of glucose. Future research will need to assess the role of methodology as it pertains to measures of the microbial community that might explain glucose mineralization dynamics *in situ*.

Land-use and land-management regimes are likely to transform soil systems in many ways and this is apparent at the CEF (Richter and Markewitz, 2001). Research at these sites has demonstrated that a suite of edaphic properties (e.g. soil P, texture) are affected by both the contemporary land-use as well as the legacy of land-management decisions (Richter and Markewitz, 2001; Richter et al., 2006; Lauber et al., 2008; Grandy et al., 2009). For example, Richter et al. (2006) demonstrates across the same landscape that soil P is strongly influenced by management history such as fertilization, even for decades after it was last practiced. Notably, we found that soil P was a parameter of major importance in explaining cumulative glucose mineralization; it was over 10 times more important than any other parameter considered in the entire model set (Fig. 2b). Soil P was positively related to cumulative glucose mineralized and this was consistent across both the winter and summer (Fig. 3). These results may suggest that both past and present land-use/management decisions ultimately influence ecosystem C dynamics through influences on underlying variables including soil P. Saggar et al. (2000), using a lab-based study of pasture soils with different fertilizer input histories, observed that glucose mineralization was positively related to soil P concentrations. They suggested that this occurs because the microbial biomass becomes less efficient at utilizing C-compounds as soil P becomes limiting. Similarly, Cleveland and Townsend (2006) found that when labile C (i.e. leached from litter) was plentiful then P-availability was the primary control on its mineralization under both field and lab conditions. There is also the likelihood that increasing P-availability increases overall plant biomass, including root biomass (Saggar et al., 1997, 2000), leading to a shift in microbial community composition towards organisms geared to the mineralization of LMWOC compounds like glucose. A recent study conducted with soils from our CEF sites demonstrated that the decomposition of recalcitrant leaf litter material decreased as soil P increased (Strickland et al., 2009b). Together these studies, and our new results, suggest that soil P may be an indicator of shifts in the microbial community from (under higher P) organisms which specialize in utilizing LMWOC compounds to those (under lower P) which utilize more complex substrates such as leaf litter. This may be similar to distinctions relating certain components of the microbial community to *r*- and *K*-strategists (Fierer et al., 2007; Blagodatskaya et al., 2009). Alternatively, soil P may simply be co-correlated with characteristics of the soil microbial community that determine C dynamics. For example, it has been shown that soil P is related to the relative abundance of different microbial taxa (Lauber et al., 2008). Increased resolution beyond the level of fungal-to-bacterial dominance may provide more relevant indices of community composition when attempting to predict glucose mineralization (e.g. Hanson et al., 2008).

In conclusion, it was the goal of this study to determine the *in situ* mineralization of the common rhizodeposit and leachate-constituent, glucose, and its relationship to land-use, soil microbial community and edaphic characteristics across a landscape. Surprisingly no measure of the microbial community was related to glucose mineralization. However, soil P and land-use were predictors of glucose mineralization. Given that land-use and soil P are intimately related at these sites, there is the indication that land-management decisions which impact soil P may in turn lead to altered mineralization rates of LMWOC compounds (Richter and Markewitz, 2001; Richter et al., 2006). This is not likely a trivial matter given that a large proportion of the Earth's soils are similar to the low P Ultisols at our sites and that many of these same soils are apt to be or are already impacted by management decisions which increase soil P (Richter and Markewitz, 2001). Such management decisions may lead to increased mineralization of LMWOC compounds, altering ecosystem C-cycling and C source-sink dynamics. Future studies, both field and laboratory based, will need to address these possibilities and decipher the underlying mechanisms that explain the relationship between soil P and C dynamics. Such studies will further our understanding of the factors which control the cycling of belowground plant-C inputs and may ultimately lead to an understanding of LMWOC compound dynamics comparable to our current understanding of leaf litter dynamics.

Acknowledgements

We gratefully acknowledge funding from the Andrew W. Mellon Foundation to N.F. and M.A.B., and to M.A.B from the Office of

Science (BER), U.S. Department of Energy. We thank Tom Maddox in the Analytical Chemistry Laboratory of the Odum School of Ecology, Univ. of Georgia, for element and isotope analyses; Jimmy Blackmon for field assistance; and Mr. Jack Burnett for access to his property. We also thank two anonymous Reviewers whose comments significantly improved this manuscript.

Appendix. Supplementary information

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.soilbio.2009.10.026.

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