PERGAMON

Soil Biology & Biochemistry 32 (2000) 189–196

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Decreases in organic C reserves in soils can reduce the catabolic diversity of soil microbial communities

Bradley P. Degens[a, b,*], Louis A. Schipper[a], Graham P. Sparling[a], Maja Vojvodic-Vukovic[a]

[a]*Landcare Research, Private Bag 3127, Hamilton, New Zealand*
[b]*Ecosystems Research Group, Department of Botany, The University of Western Australia, Nedlands, WA 6907, Australia*

Accepted 30 July 1999

Abstract

An understanding of the main factors influencing microbial diversity in soils is necessary to predict the effects of current land-use trends on terrestrial diversity. We used microbial catabolic evenness as a measure of one component of soil microbial diversity. Catabolic evenness was assessed by measuring the short-term respiration responses of soil to a range of simple organic compounds. Differences in catabolic evenness between pasture and other land-uses on matched soils were related to differences in organic C pools (total organic C, microbial biomass C, and potentially mineralizable C). This approach enabled comparison of land-use effects on organic C pools in relation to catabolic evenness without the effects of soil type. In general, microbial catabolic evenness was greatest in soils under pasture and indigenous vegetation (range: 19.7–23.3), and least in soils under cereal/maize/horticultural cropping (range: 16.4–19.6). Soils under mixed cropping land-uses had catabolic evenness that ranged between these extremes (range: 17.7–20.5), but under pine forestry there was no characteristic level of evenness (range: 15.1–22.3). Catabolic evenness correlated poorly with the absolute values of soil organic C pools ($r^2 < 0.36$). However, across a range of paired comparisons between pasture and other land-uses, greater differences in microbial catabolic evenness corresponded with greater differences in organic C ($r^2 = 0.76$) and, to a lesser degree, with differences in microbial biomass C ($r^2 < 0.45$) or potentially mineralizable C ($r^2 < 0.13$). Therefore, land-uses that deplete organic C stocks in soils may cause declines in the catabolic diversity of soil microbial communities. Although the implications of this for microbial processes are unknown, maintenance of soil organic C may be important for preservation of microbial diversity.

Keywords: Microbial functional diversity; Catabolic response profiles; Land use; Soil organic matter; Microbial biomass; Potentially mineralizable organic C

1. Introduction

Fundamental determinants of biological diversity have been extensively researched in aquatic and above-ground terrestrial ecosystems, but are inadequately understood for the below-ground component of terrestrial ecosystems (Giller et al., 1997; Trevors, 1998). Unlike studies of plant and animal communities, it has not been possible to make unbiased assessments of species diversity for soil microbial communities using current culture-based, molecular and biochemical methods (Zak et al., 1994; Trevors, 1998). Furthermore, it has not been possible to interpret the functional diversity of microbial communities from community structure (Giller et al., 1997; Degens, 1999), as can be determined for higher organisms (Körner, 1993; Gitay and Noble, 1997). This limitation exists largely because soil microorganisms can be present in soil, but not necessarily functionally active (van

* Corresponding author at Ecosystems Research Group, Department of Botany, The University of W.A., Nedlands, WA 6907, Australia. Fax: +61-8-9380-7925.
E-mail address: bdegens@cyllene.uwa.edu.au (B.P. Degens).

0038-0717/00/$ - see front matter
PII: S0038-0717(99)00141-8

Table 1
USDA great soil group, land-uses and general soil properties (pH, organic C content and soil texture) of soils analysed to determine microbial catabolic evenness

Soil taxonomy suborders[a]	Land-uses sampled	pH[b]	Organic C (mg g^{-1} soil)	Soil texture
Aquepts	2 grass pastures	5.4–5.6	45–57	silt loams
	1 horticultural cropping (vegetables)	6.2	27	
	1 indigenous Podocarp dominated forest	4.9	85	
Humults	1 grass pasture	5.7	52	clay loam
	1 horticultural cropping (vegetables)	6.2	34	
Ochrepts	1 grass pasture	6.0	63	clay loam
	1 indigenous Podocarp dominated forest	4.5	74	
	2 mixed maize cropping/pastures	5.5–5.8	36–37	
Psamments	3 grass pastures	5.8–6.1	26–65	sand–loamy sand
	2 commercial *Pinus radiata* forest	4.9–5.9	3–9	
	1 indigenous broadleaf forest	5.5	25	
Saprists	1 grass pasture	4.1	200	peat loam
	1 indigenous *Dacrycapus dacryoides* forest	5.6	260	
Udands	4 grass pastures	5.9–6.5	101–109	silt loams
	1 maize cropping	6.2	60	
	1 nonarable horticulture (orchard)	5.2	36	
	4 effluent-irrigated grass pastures	5.8–6.1	101–118	
Vitrands	2 grass pastures	5.8–5.9	59–80	sandy loam
	4 commercial *Pinus radiata* forest	4.8–5.4	42–52	
Xererts	2 grass pastures	6.1–6.6	51–70	clay
	4 mixed cereal or vegetable cropping/pasture	6.4–7.0	34–46	
	1 horticultural cropping (vegetables)	7.1	24	

[a] Soil Survey Staff, 1992.
[b] pH determined in 1:2.5 ratio of soil to deionised water.

Veen and Heijnen, 1994; Meikle et al., 1995; Trevors, 1998). Direct measurements of functional diversity in soil microbial communities are likely to provide information more relevant to the functioning of soils than species diversity (Zak et al., 1994; Trevors, 1998).

The functional diversity of microbial communities includes the range and relative expression of activities involved in such functions as decomposition, nutrient transformations, plant growth promotion/suppression and various soil physical processes influenced by microorganisms (Giller et al., 1997). The diversity of decomposition functions performed by heterotrophic microorganisms represents one component of microbial functional diversity. Here, we directly measure the diversity of decomposition functions by assessing the variation (evenness) in catabolic response profiles (Degens and Harris, 1997; Degens, 1998a, b; 1999). Although it is generally accepted that diversity is composed of two components (richness and evenness, Magurran, 1988), we are constrained to measuring catabolic evenness because it is impractical to measure the immense richness of microbial catabolic functions in soils. Catabolic response profiles are determined by measuring the short-term utilization of a range of readily available substrates that have been added to soils (Degens, 1998a, b; 1999; Degens and Vojvodic-Vukovic, 1999). The short assay time captures the catabolic patterns of active microorganisms, rather than those in resting or dormant states. Therefore, the assay provides a measure of a component of the catabolic functional diversity in soil.

Despite widespread recognition that land-use can influence microbial diversity in soils (Wardle, 1995; Pankhurst et al., 1996; Insam and Rangger, 1997; Kennedy and Gewin, 1997), there have been no broad-scale assessments of any components of microbial functional diversity in soils or the factors that influence this diversity (Pankhurst et al., 1996; Giller et al., 1997; Kennedy and Gewin, 1997). Such information is essential before any investigation of whether conventional land-uses could compromise the resilience or stability of nutrient cycling processes through effects on microbial functional diversity.

Our objective was to determine the effects of land-use on microbial catabolic diversity and whether these effects were related to pools of organic C in soils. It is well established that the availability of organic C regulates the turnover and activities of heterotrophic microbial communities in soils (Jenkinson and Ladd, 1981; Wardle, 1992; Sparling, 1997). We hypothesized that land-use can decrease community catabolic diversity by causing decreases in different organic C pools in soils, as indicated by total organic C, microbial biomass C and potentially mineralizable C. To eliminate

the underlying influence of soil type on organic pools and microbial catabolic diversity, we compared differences in these properties between pasture and other land-uses on the same soil types in the same geographic location.

2. Materials and methods

2.1. Soils and land-uses

A range of soils with varying land-uses were sampled from across New Zealand (Table 1). The soils had formed from on a diverse range of parent materials, including volcanic tephras, marine dune deposits, glacial out-wash, loess and alluvial deposits. The land-uses were classified as either: long-term (10–60 yr) agricultural pasture, long-term arable cropping (including horticultural, maize and cereal cropping), indigenous vegetation (forest and heathland communities), abattoir effluent treated pasture, commercial *Pinus radiata* plantation, long-term non-arable horticulture or a mixed history of pasture/cropping rotations. The pastures (Table 1) were dominated by a mixture of perennial grasses and clovers (*Trifolium* sp.), whereas the indigenous vegetation consisted of either kahikatea dominated forest (*Dacrycarpus dacrydioides*), mixed podocarp–broadleaf forests (*Dacrydium cupressinum*, *Prumnopitys taxifolia*, *Dacrycarpus dacrydioides* and *Leptospermum scoparium*) or *Dracophyllum* heathland (Table 1).

To factor out the effects of soil type, we compared differences in organic C pools with differences in catabolic evenness across a range of paired land-use comparisons. Each comparison consisted of pasture in close geographical proximity (0.1–0.5 km) to another land-use (Table 1) on pedologically matched soils (Schipper and Sparling, 1998, personal communication). The soils were matched on the basis of soil series and soil classification, slope, elevation, landform, annual precipitation, parent material and soil drainage class (Milne et al., 1995). Land-use comparisons were obtained for each great soil class in Table 1, but it was not possible to obtain all combinations of land-uses on each soil type. Only a single comparison was available at most sites, but at some sites it was possible to obtain multiple combinations of land-uses. Pasture sites were used as reference soils and compared with other nearby land-uses to determine whether apparent declines in organic C pools corresponded with declines in catabolic evenness. Long-term pasture sites (10–60 yr) were considered suitable reference soils because this land-use generally involves large inputs of organic C into soils (Wardle, 1992; Sparling, 1997) and is widely available on most soil types.

Moist top-soils (0–100 mm depth) were collected along 30 m transects across each of seven land-uses within the same year during the active growing season (spring–early summer). Within each land-use, a total of 25 cores (25 mm diameter) were randomly sampled from within each of five plots (5×5 m) along the transect to obtain a total of 125 cores/transect. This conformed with the approach used in a nation-wide soil quality programme (Schipper and Sparling, 1998, personal communication). On sloping areas, the transects were aligned perpendicular to the slope. The 125 core samples from each land-use were bulked and mixed before analysis to obtain one sample per site. All samples were sieved (4 mm mesh) and then conditioned at a moisture potential of -5 kPa and 25°C for 7 d before conducting measurements. The soils were stored for no more than 5 d at 5°C until analysed.

2.2. Analysis of microbial catabolic evenness and organic C pools

Microbial catabolic evenness was determined by measurement of the short-term respiration responses of soils after addition of solutions of 25 different simple organic compounds (Degens and Harris, 1997; Degens, 1998b). The various substrates were added as 2 ml solutions to 1 g equivalent dry weight of soil in McCartney bottles sealed with Vacutainer stoppers (Degens and Harris, 1997). A no-substrate control treatment, where only deionised water was added to the soils, was also conducted to determine whether each substrate caused a respiration response above basal respiration. CO_2 efflux from each sample was measured using an infrared gas analyser (Model LI-6252, LI-COR, Lincoln, NE) after incubation of the bottles for 4 h at 25°C (Degens and Harris, 1997). During the incubation, all bottles were vigorously mixed using a vortex mixer for 15 to 20 s at 1 to 1.5 h after substrate addition and then before sampling the head space gas for CO_2 analyses.

The substrates used in the assay were: eight amino acids (L-arginine, L-asparagine, D-glucosamine, L-glutamic acid, L-glutamine, L-histidine, L-lysine, L-serine), two carbohydrates (D-glucose, D-mannose), and 15 carboxylic acids (L-ascorbic acid, citric acid, fumaric acid, gluconic acid, α-ketobutyric acid, α-ketoglutaric acid, α-ketovaleric acid, DL-malic acid, malonic acid, pantothenic acid, quinic acid, succinic acid, tartaric acid, uric acid and urocanic acid; see Degens, 1998b; Degens and Vojvodic-Vukovic, 1999). These substrates were those giving the greatest discrimination between soils as determined by Degens and Harris (1997) and Degens (1998b). Previous investigations showed that amino acid and amine solutions at 15 mM, carbohydrate solutions at 75 mM and carboxylic acid solutions at 100 mM gave generally maximum respiration

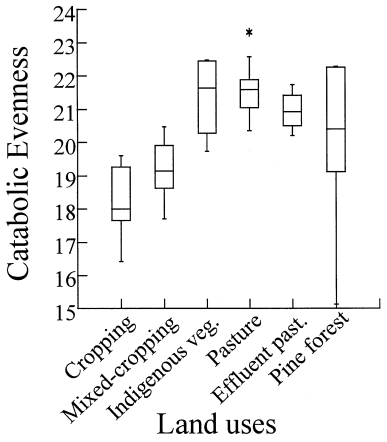

Fig. 1. Box plots of microbial catabolic evenness (Simpson–Yule index) in soils under different land-uses. Data for soil under nonarable horticultural cropping were combined with other cropping data. The centre bar shows the median value and the box hinges show the interquartile range. Values significantly (95%) greater or less than 3 times the interquartile range are displayed as asterisks (SYSTAT, 1992). Maximum evenness = 25. High evenness values indicate little variation in catabolism of substrates, whereas low evenness values indicate large variation in catabolism of substrates.

responses across soil types (Degens and Vojvodic-Vukovic, 1999). All solutions were adjusted to between pH 5.8 and 6.0 before addition to soil (Degens, 1998b).

As outlined above, catabolic diversity is composed of two components: richness and evenness. Richness in this case was the number of substrates used by organisms, whereas evenness was the variability of substrate use across the range of substrates tested. For all soils tested here, richness was not different between the soils because there was a response (above the no-substrate treatment) to all substrates. It was therefore appropriate to concentrate on catabolic evenness. Catabolic evenness (E) was calculated using the Simpson–Yule index: $E = 1/\sum p_i^2$, where p_i is the respiration response to individual substrates as a proportion of total respiration activity induced by all substrates for a soil (Magurran, 1988). Using this formula, the maximum achievable evenness (where all substrates respond equally) was 25. Similar patterns were also obtained by other evenness indices such as the coefficient of variation of substrate responses or deriving evenness from the Shannon–Weaver index (Magurran, 1988).

Microbial biomass C was determined on field-moist soil using the fumigation-extraction method (Vance et al., 1987). Potentially mineralizable C (organic C availability) was determined using a closed-jar system, incubated for 7 d at 25°C (Alef, 1995). Samples were air-dried and ground before analysis of total organic C by LECO 2000 CNS combustion furnace (Blakemore et al. 1987).

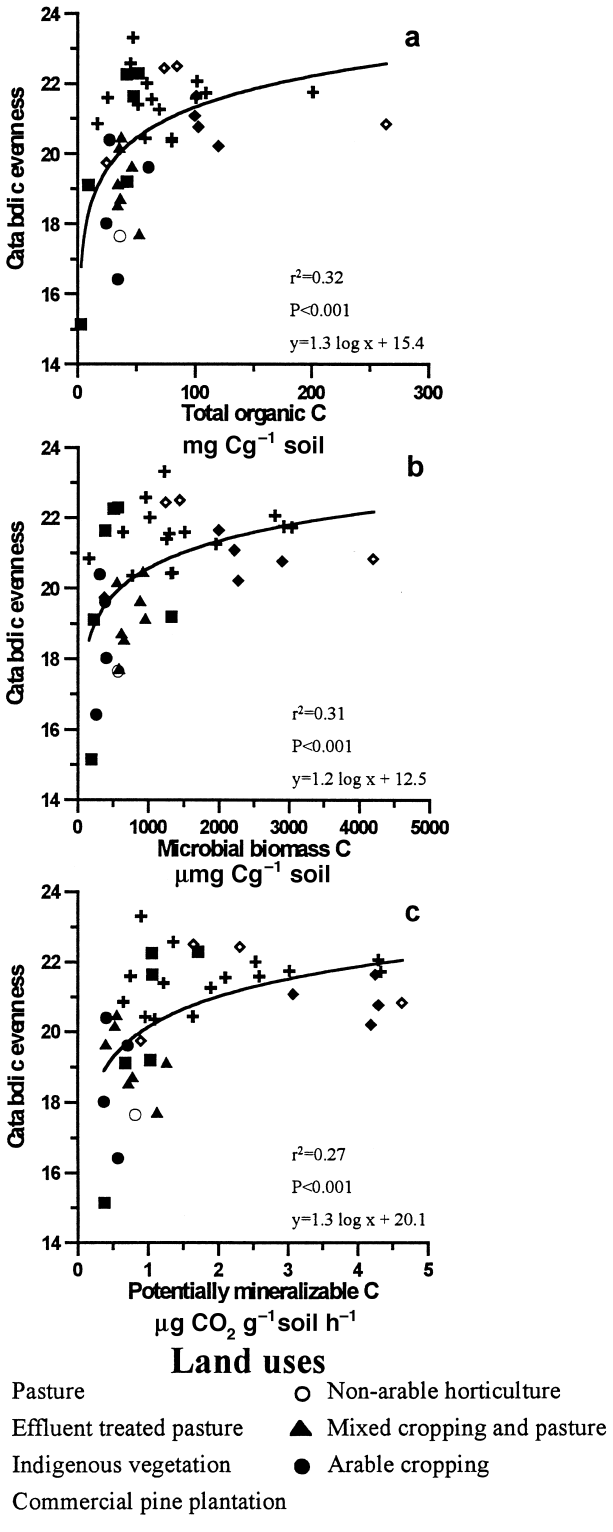

Fig. 2. Catabolic evenness (Simpson–Yule index) of soil microbial communities in relation to (A) total organic C, (B) microbial biomass C and (C) potentially mineralizable C across a range of soils and land-uses (n = 41).

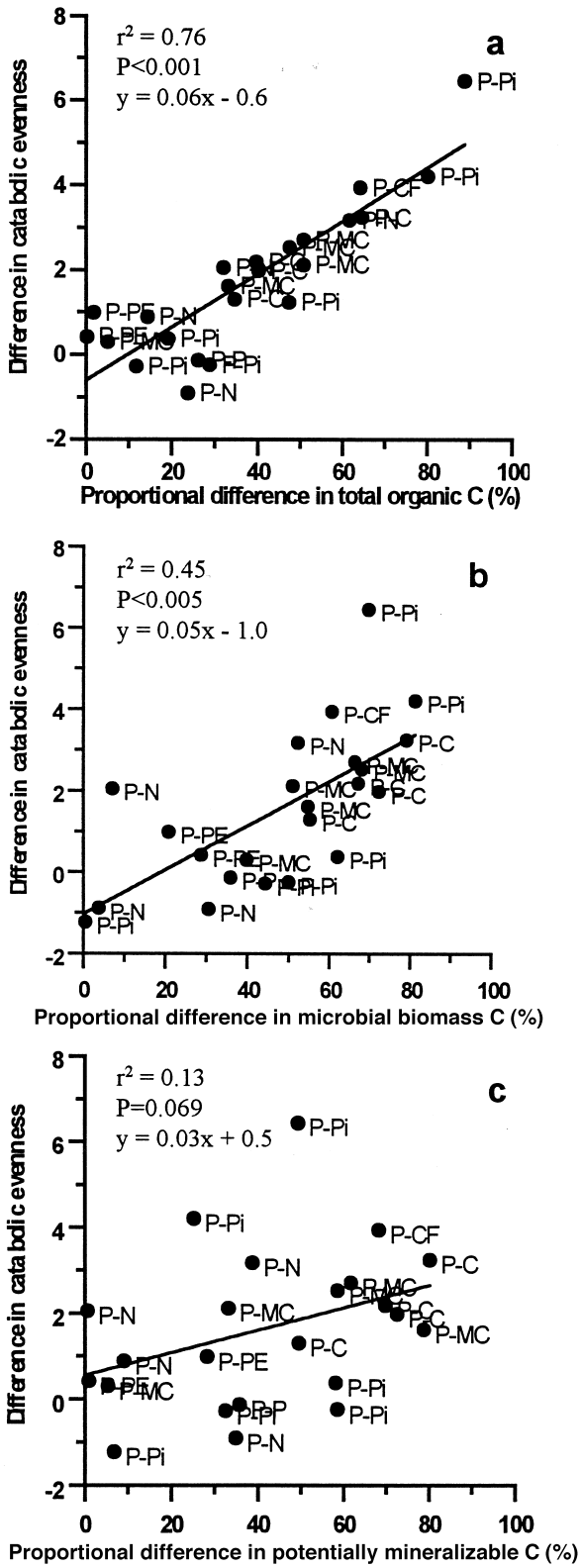

Fig. 3. Relationship between differences in microbial catabolic evenness (Simpson–Yule index) and proportional differences in (a) total organic C, (b) microbial biomass C and (c) potentially mineralizable C for paired land-uses on matched soil types ($n = 23$). Comparisons were made between pasture (P) and either indigenous vegetation (N), effluent treated pasture (PE), commercial *Pinus radiata* plantation (Pi), nonarable horticulture (CF), mixed cropping and pasture rotations (MC) or arable cropping (C). Greater differences occurred where the comparison land-use contained much lower soil properties than pasture.

2.3. Data analyses

Catabolic evenness data in different land-uses were analysed by one-way ANOVA followed by Bonferroni pairwise comparisons (SYSTAT, 1992). Linear regression analyses were determined using SYSTAT Version 7.0 (SYSTAT, 1992). For each paired comparison, proportional differences in soil organic pools were calculated as: (pasture minus comparison land-use)/pasture × 100. These data were then used to evaluate relationships between differences in soil organic C pools and differences in evenness. In using this approach, spatial differences in organic C pools between pasture and other land-uses were assumed to also occur temporally if the soil under pasture was converted to the other land-uses.

3. Results

Catabolic evenness was greater ($P < 0.05$) for soils under pasture, effluent treated pasture and indigenous vegetation than for soils under cropping (Fig. 1). For soils under cropping, the catabolic evenness averaged 18.2 (range: 16.4–19.6) whereas under pasture, effluent treated pasture, and indigenous vegetation, evenness averaged 21.5 (range: 20.4–23.3), 20.9 (range: 20.2–21.7) and 21.4 (range: 19.7–22.5), respectively. Soils under mixed cropping had catabolic evenness that was between these land-uses (mean: 19.2, range: 17.7–20.5) being not different from cropping, but significantly less than pasture soils ($P < 0.05$). In contrast, there was no characteristic level of catabolic evenness for soils under pine forest (mean: 19.9, range: 15.1–22.3; Fig. 1). Evenness under pine was as great as under pasture on some soil types, but could be below the evenness found in cropped soils on other soil types. The consistently high levels of evenness in soils under pasture confirmed that these soils were a suitable reference point for comparison of the effects of other land-uses on catabolic evenness.

There were positive, but weak correlations between catabolic evenness and organic C pools (Fig. 2). These correlations were determined across a range of soil types with total organic C ranging from 3 to 260 mg C g^{-1} soil, microbial biomass C ranging from 192 to 4206 μg C g^{-1} soil and potentially mineralizable C ranging from 0.4 to 4.6 μg C g^{-1} soil h^{-1}. The paired site comparisons removed the effects of soil type and simultaneously reveal more meaningful relationships between catabolic evenness and organic C pools (Fig. 3).

The differences in microbial catabolic evenness between land-uses were significantly correlated with differences in total organic C ($r^2 = 0.76$; Fig. 3). Where land-use resulted in greater deficits in organic C, relative to pasture, there were correspondingly greater declines in catabolic evenness. Cropping and pine forestry, on some soils, consistently resulted in the largest differences in organic C and catabolic evenness (Fig. 3). In contrast, organic C in land under indigenous vegetation or effluent irrigation differed only slightly from that in pasture and were similarly associated with only small differences in catabolic evenness. Differences in the more available organic pools, such as microbial biomass C or potentially mineralizable C, were only weakly correlated with declines in catabolic evenness ($r^2 = 0.45$ and $r^2 = 0.13$, respectively; Fig. 3). This contrasted with the strong correlations between microbial biomass C and total organic C ($r^2 = 0.78$, $P < 0.001$) and between potentially mineralizable C and total organic C ($r^2 = 0.49$, $P < 0.001$). Microbial quotients (microbial biomass C: total organic C) or eco-physiological quotients (potentially mineralizable C: microbial biomass C) calculated from the data were not correlated with either catabolic evenness ($P > 0.1$), even when differences in evenness were compared with differences in these quotients for the 23 paired sites.

4. Discussion

Our results provide evidence that a generalized relationship exists between organic C pools and microbial catabolic diversity in soils. We suggest that land-uses causing comparable proportional depletions of organic C may also cause the same proportional losses of microbial catabolic diversity. Despite acknowledging the importance of organic resources in the dynamics of soil microbial communities, individual studies of paired soils have not reported links between any components of microbial diversity and organic C pools (Wardle, 1995; Pankhurst et al., 1996; Insam and Rangger, 1997). This is largely because there have been no previous broad-scale investigations of microbial diversity in different soils under a range of land-uses. In using a short assay time and compounds able to be rapidly degraded to assess catabolic response profiles, the differences we have found between soils may only reflect particular microbial groups; probably the actively growing or fast responding organisms. Despite this, it is clear that changes in the catabolic response profiles revealed information about the functional diversity of microbial communities which is linked with changes in organic C pools.

Losses in microbial catabolic evenness were greater where there was greater depletion of soil organic C, possibly due to the reduced quality of organic matter in soils with low amounts of organic C. The more readily decomposable organic C fractions are generally lost preferentially when soil organic C decreases as a result of land-use (Cambardella and Elliott, 1992; Bremer et al., 1994; Carter and Stewart, 1996). These fractions support a significant proportion of the heterotrophic microbial biomass in soils (Ladd et al., 1996; Chotte et al., 1998), and their loss could conceivably decrease microbial catabolic evenness through disproportionate declines in some catabolic functions. There are no clear reasons why differences in catabolic evenness correlated less with differences in the more labile pools of organic C (microbial biomass and potentially mineralizable C) than with differences in total organic C pools. It was possible that there was greater error associated with estimation of the more labile organic C pools because these can be temporally more variable than total organic C. In contrast, catabolic diversity may be a more stable property of microbial communities, as indicated by Degens and Vojvodic-Vukovic (1999).

The strong relationship between differences in total organic pool size and differences in evenness emphasised that *changes* in the relative size of organic C pools, rather than the *total* sizes, has greater significance for evenness. Weak correlations between total organic pool sizes and catabolic evenness probably resulted from modifying influences of soil type. The soils with low catabolic evenness (cropping, some pine forests and mixed cropping) also characteristically contained smaller organic pools compared with other soils, but not invariably less than in soils with high evenness. Soils with high evenness (long-term pasture or indigenous forest) could contain a broad range of organic pool sizes. By considering differences in organic pool sizes within soil types, this recognizes that small absolute decreases in total organic C between land-uses in, for example, a sandy soil (from 20 to 10 mg C g^{-1}) have greater effects on diversity than similar absolute decreases (e.g. from 100 to 90 mg C g^{-1}) in a clay soil.

The implications of decreases in microbial catabolic evenness are not known, but may affect soil ecosystem functioning. Treatment of soil to reduce microbial catabolic diversity can reduce the capacity for the soil to decompose organic matter, although not always (Degens, 1998a). Studies of classical community diversity have found that processes performed by communities with reduced species diversity can be more variable (McGrady-Steed et al., 1997; Naeem and Li, 1997) and less resilient to environmental stresses (Tilman and Downing, 1994). Reductions in heterotrophic catabolic evenness may also result in less resilient or more unstable microbial decomposition function (particularly in response to normal environmental stresses such as seasonal temperature or moisture extremes). If this is the case, land-uses resulting in losses of organic C from soils may generate soils that

are less resilient to stresses or disturbances. This adds further to the importance of maintaining organic C stocks in soils, which, once lost, can take decades to restore (Jenkinson et al., 1987; Paustian et al., 1997).

The method we employed might appear to impose some limitations on the scope of catabolic diversity able to be assessed in soils. The substrates used in the assay consisted of carboxylic acids, amino acids and a few carbohydrate compounds, initially selected from a range of 83 substrates on the basis that they provided the greatest discrimination between soils (Degens and Harris, 1997; Degens, 1998b). It is possible that substitution of more polymeric, phenolic and carbohydrate compounds may improve the discriminatory power of the catabolic diversity method. However, the current set of 25 substrates was clearly sufficient to derive a useful index of a component of microbial diversity that could scale the effects of a range of land-uses across different soils. Furthermore, we have not attempted to determine which substrates were responsible for the differences in catabolic evenness between soils because little interpretation can currently be placed on this.

Catabolic evenness shows potential to be an indicator of a component of microbial diversity that can be applied across soil types. Our results show that the catabolic evenness of soils under different land-uses fell within generalized ranges. For soils with an unknown history of land-use, a preliminary assessment of catabolic diversity can be compared with evenness under other common land-uses. Values of evenness greater than 21 may be considered favourable, whereas values less than 18 may be of concern since these can be correlated with large declines in organic C. Although a single index inherently captures only a few characteristics of a catabolic response profile, such an index can be particularly useful for rapid evaluation of at least a component of microbial diversity.

Acknowledgements

We thank Wim Rijkse and Allan Hewitt for assistance in collection of the soils and Stephanie Degens, Brian Daly and Keitha Giddens for assistance with laboratory analyses. Thanks also to Gary Barker, Bruce Clarkson, Jake Overton, Bruce Burns and Kevin Tate for comments on the manuscript during preparation. This work was supported by a Hayward Postdoctoral fellowship from the New Zealand Foundation for Science, Research and Technology.

References

Alef, K., 1995. Soil respiration. In: Alef, K., Nannipieri, P. (Eds.), Methods in Applied Soil Microbiology and Biochemistry. Academic Press, London, pp. 214–219.

Blakemore, L.C., Searle, P.L., Daly, B.K., 1987. Methods for chemical analysis of soils. New Zealand Soil Bureau Scientific Report No. 80, Lower Hutt.

Bremer, E., Janzen, H.H., Johnston, A.M., 1994. Sensitivity of total, light fraction and mineralizable organic matter to management practices in a Lethbridge soil. Canadian Journal of Soil Science 74, 131–138.

Cambardella, C.A., Elliott, E.T., 1992. Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Science Society of America Journal 56, 777–783.

Carter, M.R., Stewart, B.A., 1996. Structure and Organic Matter Storage in Agricultural Soils. CRC Press, London.

Chotte, J.L., Ladd, J.N., Amato, M., 1998. Sites of microbial assimilation and turnover of soluble and particulate ^{14}C-labelled substrates decomposing in a clay soil. Soil Biology & Biochemistry 30, 205–218.

Degens, B.P., 1998a. Decreases in microbial functional diversity do not result in corresponding changes in decomposition under different moisture conditions. Soil Biology & Biochemistry 30, 1989–2000.

Degens, B.P., 1998b. Microbial functional diversity can be influenced by the composition of simple organic substrates added to soil. Soil Biology & Biochemistry 30, 1981–1988.

Degens, B.P., 1999. Catabolic response profiles differ between microorganisms grown in soils. Soil Biology & Biochemistry 31, 475–477.

Degens, B.P., Harris, J.A., 1997. Development of a physiological approach to measuring the metabolic diversity of soil microbial communities. Soil Biology & Biochemistry 29, 1309–1320.

Degens, B.P., Vojvodic-Vukovic, M., 1999. A sampling strategy to assess the effects of land use on microbial functional diversity in soils. Australian Journal of Soil Research 37, 593–601.

Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.-M.N., Swift, M.J., 1997. Agricultural intensification, soil biodiversity and agroecosystem function. Applied Soil Ecology 6, 3–16.

Gitay, H., Noble, I.R., 1997. What are functional types and how should we seek them? In: Smith, T.M., Shugart, H.H., Woodward, F.I. (Eds.), Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, pp. 3–19.

Insam, H., Rangger, A., 1997. Microbial Communities: Functional Versus Structural Approaches. Springer, Berlin.

Jenkinson, D.S., Ladd, J.N., 1981. Microbial biomass in soil: measurement and turnover. In: Paul, E.A., Ladd, J.N. (Eds.), Soil Biochemistry, vol. 5. Marcel Dekker, New York, pp. 415–471.

Jenkinson, D.S., Hart, P.B.S., Rayner, J.H., Parry, L.C., 1987. Modelling the turnover of organic matter in long-term experiments at Rothamsted. INTECOL Bulletin 15, 1–8.

Kennedy, A.C., Gewin, V.L., 1997. Soil microbial diversity: present and future considerations. Soil Science 162, 607–617.

Körner, Ch., 1993. Scaling from species to vegetation: the usefulness of functional groups. In: Schulz, E.-D., Mooney, H.A. (Eds.), Biodiversity and Ecosystem Function. Springer, Berlin, pp. 117–140.

Ladd, J.N., van Gestel, M., Jocteur-Monrozier, L., Amato, M., 1996. Distribution of organic ^{14}C and ^{15}N in particle-size fractions of soils amended with ^{14}C, ^{15}N-labelled glucose/NH_4, and legume and wheat residues. Soil Biology & Biochemistry 28, 893–905.

Magurran, A.E., 1988. Ecological Diversity and Its Measurement. Croom Helm, London.

McGrady-Steed, J., Harris, P.M., Morin, P.J., 1997. Biodiversity regulates ecosystem predictability. Nature 390, 162–165.

Meikle, A., Amin-Hanjani, S., Glover, L.A., Killham, K., Prosser, J.I., 1995. Matric potential and the survival and activity of a

Pseudomonas fluorescens inoculum in soil. Soil Biology & Biochemistry 27, 881–892.

Milne, D.B., Clayden, B., Singleton, P.L., Wilson, A.D., 1995. Soil Description Handbook, Revised ed. Manaaki Whenua Press, Lincoln, New Zealand.

Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. Nature 390, 507–509.

Pankhurst, C.E., Ophel-Keller, K., Doube, B.M., Gupta, V.V.S.R., 1996. Biodiversity of soil microbial communities in agricultural systems. Biodiversity and Conservation 5, 197–209.

Paustian, K., Andrén, O., Janzen, H.H., Lal, R., Smith, P., Tian, G., Tiessen, H., Van Noordwijk, M., Woomer, P.L., 1997. Agricultural soils as a sink to mitigate CO_2 emissions. Soil Use and Management 13, 230–244.

Soil Survey Staff, 1992. Keys to Soil Taxonomy, 5th ed. In: SMSS Techical Monograph, no. 19. Pocahontas Press, Virginia.

Sparling, G.P., 1997. Soil microbial biomass, activity and nutrient cycling as indicators of soils health. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R. (Eds.), Biological indicators of soil health. CAB International, New York, pp. 97–119.

SYSTAT, 1992. Systat for Windows: Statistics Version 5. Systat, Evanston.

Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. Nature 367, 363–365.

Trevors, J.T., 1998. Bacterial biodiversity in soil with an emphasis on chemically contaminated soils. Water, Air and Soil Pollution 101, 45–67.

van Veen, J.A., Heijnen, C.E., 1994. The fate and activity of microorganisms introduced into soil. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R., Grace, P.R. (Eds.), Soil Biota: Management in Sustainable Farming Systems. CSIRO Australia, Adelaide, pp. 63–71.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biology & Biochemistry 19, 703–707.

Wardle, D.A., 1992. A comparative assessment of the factors which influence microbial biomass carbon and nitrogen levels in soil. Biological Reviews 67, 321–358.

Wardle, D.A., 1995. Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. Advances in Ecological Research 26, 105–185.

Zak, J.C., Willig, M.R., Moorhead, D.L., Wildman, H.G., 1994. Functional diversity of microbial communities: a quantitative approach. Soil Biology & Biochemistry 26, 1101–1108.