Grazing impacts on the spatial distribution of soil microbial biomass around tussock grasses in a tropical grassland

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Received 25 February 1999; received in revised form 11 June 1999; accepted 15 June 1999

Abstract

The role of grass tussocks in supporting soil microbial biomass (SMB) in grazed ecosystems is not fully understood, nor is the spatial distribution of SMB in response to different grass species. We undertook a study in 1997 that examined fine-scale distributions of SMB in grazed experimental paddocks located in the eucalypt woodlands of northern Queensland, Australia. Levels of SMB were determined on soil samples collected at seven locations along 60 cm transects in the vicinity of three species of tussock grass (Bothriochloa ewartiana, Chrysopogon fallax, Heteropogon contortus) and bare spaces, in replicate paddocks under five different grazing regimes. Data (n = 280) were analysed as a split-split plot in a randomised complete block. Slope position (block) and paddock management were the main plots, micro-patch type (tussocks and bare spaces) the split plot, and location around micro-patch the split–split plot. Paddock management, micro-patch, and location effects were significantly (p < 0.05) different, as were management location and micro-patch location interactions. The highest SMB levels were recorded at tussock centres on ungrazed (control) and lightly grazed paddocks, with lower levels recorded on degrading (15–27% reduction), and degraded/recovering (40–53% reduction) sites. Successively lower levels were noted from tussock centres outwards to the most distant locations (+30, −30 cm) with level of paddock degradation. High levels of SMB were noted around tussocks of B. ewartiana and C. fallax, while the lowest were recorded across bare patches (59% of levels for the above species). Heavy grazing reduced inputs of organic materials and carbon into the soil, thereby limiting resources available for microbial growth. Fine-scale monitoring of the plant–microbe–soil interface should be combined with large-scale measures of landscape response to properly describe degradation and recovery processes. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Grassland; Grazing pressure; Plant–microbe–soil interactions; Soil condition

1. Introduction

Perennial tussock grasses in the dry woodlands of northern Australia are patchily distributed within plant communities (Ash and McIvor, 1998). Although they comprise a minor segment of the total land area, grass tussocks play important roles in the capture and control of scarce nutrients and water, and contribute to ecosystem stability at larger spatial scales (Ludwig et al., 1994; Tongway and Ludwig, 1994,1997). Soil resources are concentrated in fertile patches in the
vicinity of plants, which enhances biological activity in soil close to plants, resulting in the development of fine-scale islands of fertility (Garner and Steinberger, 1989). The spatial and temporal persistence of perennial tussock grasses (and related soil biological activity) is important to landscape function and paddock productivity.

Large sections of the open eucalypt woodlands in northern Australia (covering 1,500,000 km²) have been overgrazed since the 1960s, following the advent of affordable feed supplements, improved animal husbandry, market downturns, and incorporation of Bos indicus bloodlines into cattle herds (Gardener et al., 1990; Tothill and Gillies, 1992). Excessive grazing causes the loss of basal area of perennial tussock grasses and ground cover, shifts in species composition, and decreased productivity (Gardener et al., 1990; Ash and McIvor, 1998). Soil characteristics (pH, water holding capacity, bulk density) are adversely affected (Bridge et al., 1983; Willat and Pullar, 1983; Tongway and Ludwig, 1997; Greenwood et al., 1998), as is biological activity within the soil profile (Holt et al., 1996a; Holt, 1997).

Soil microbial communities, which play important roles in nutrient cycles, rely on materials produced by plants as energy sources for growth and reproduction (Roper and Gupta, 1995; Young, 1998). They also produce exudates that contribute to the stability of soil micro-aggregates, thereby enhancing infiltration of water (Oades, 1993; Edgerton et al., 1995). Some vesicular-arbuscular mycorrhiza (VAM) fungi form partnerships with herbaceous species (both, grasses and forbs) and aid in water and mineral uptake by plants (Brundrett, 1991). Given the importance of grass tussocks to the conservation of soil resources in dry tropical Australia, grassland degradation via grazing pressure could also hinder the ability of herbaceous patches to support microbial activity (Tongway and Ludwig, 1997).

Studies have noted that heavy grazing reduces landscape-level measures of soil microbial biomass and macro-fauna in dry tropical ecosystems of Australia (Holt et al., 1996a; Holt, 1997). Changes in levels of microbial biomass at patch scales have also been defined (Holt et al., 1996b). However, the local influence of individual grass tussocks, or impacts of grazing pressure, on fine-scale spatial distribution of soil microbes are not known. Also, it is not known whether the impact of perennial tussock grasses on microbial activity is generic, or if species-specific effects on soil biological activity exist. Such information would help refine the understanding of grassland function and landscape processes in dry tropical Australia.

We undertook a study to define the impacts of management strategies and grazing histories on the spatial distribution of soil microbial biomass in zones around different species of perennial tussock grasses on a north Australian soil. An examination of the relationship between soil resources and microbial biomass was also included.

2. Materials and methods

2.1. Experimental area

Data were collected on experimental paddocks of the CSIRO Cardigan field site, north Queensland (20° 11'S; 146° 43'E), that comprised part of a study on the impacts of past grazing management (pre-1993) and utilisation of current year’s herbage on landscape condition (1993 through 1997). Grazing regimes were applied to sets of paddocks in initially excellent (S1) and deteriorated (S2) conditions, and herbaceous responses measured. Soils are described as Haplic Eutrophic Red Chromosols (oxic Paleustalfs and Haplustalfs) formed on the intrusive Ravenswood Granodiorite complex (Soil Survey Staff, 1994; Isbell, 1996). These soils are relatively infertile (Table 1), but of some agricultural importance for north Australia (Tothill and Gillies, 1992). The plant community is a dry tropical woodland with an overstorey dominated by Eucalyptus xanthoclada Brooker & A.R. Beau. and Corymbia erythrophloia (Blakely) K.D. Hill & L.A.S. Johnson trees (McIvor and Gardener, 1991). The herbaceous understory is a speargrass—desert bluegrass complex, with lightly grazed areas dominated by Bothriochloa ewartiana (Domin.) C.E. Hubb., Chrysopogon fallax S.T. Blake, Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult., and Themeda triandra (Forrskul.). Heavily grazed areas are dominated by Bothriochloa pertusa (L.) A. Camus (an invasive exotic stoloniferous perennial), Aristida spp., weedy forbs and annual grasses, and remnant B. ewartiana.
The climate is tropical, sub-humid, with an average annual rainfall (1985 through 1997) of 527 mm, 80% of which falls as monsoon rains during the wet season (November–April). Annual evaporation ranges from 1610 to 2206 mm (McIvor and Gardener, 1991).

### 2.2. Data collection

Data were collected in August through October 1997 from two replicate blocks, based on slope position (top of slopes; bottom of slopes), of paddocks under five combinations of grazing histories and herbage utilisation (Table 2). Initially excellent condition paddocks (S1) included: ungrazed control plots (S1-UG); lightly grazed following wet season deferment (S1-LG); and heavily grazed following wet season deferment (S1-HG). Prior to initiation of grazing regimes (1992), these paddocks were in similar condition (1250 kg/ha standing crop, 1.9% perennial tussock basal area). Two sets of initially degraded paddocks (135 kg/ha standing crop, 0.2% basal area) under historically heavy grazing (S2) were also included: degraded with continued heavy grazing without deferment (S2-HG); and degraded with light grazing pressure applied following wet season deferment (S2-LG). These paddocks were under heavy grazing pressure during the prior decade at commercial stocking rates used in the area, resulting in ≈75% utilisation of available herbage (A. Ash, personal communication).

Paddocks included in this study were representative of intact (S1-UG), conservatively grazed and productive areas (S1-LG), seasonally heavily grazed areas losing condition (S1-HG), degraded sites with little remnant productivity (S2-HG), and degraded sites regaining condition (S2-LG) under relaxed grazing.

### Table 1

General soil characteristics (±1 s.d.) of the CSIRO Cardigan research site, north Queensland, Australia

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Value ± Standard Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Chemical</strong></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>6.7 (0.2)</td>
</tr>
<tr>
<td>CEC (cmol/kg)</td>
<td>11.1 (2.2)</td>
</tr>
<tr>
<td>total N (%)</td>
<td>0.05 (0.02)</td>
</tr>
<tr>
<td>organic C (%)</td>
<td>0.82 (0.2)</td>
</tr>
<tr>
<td>bicarb. P (ppm)</td>
<td>8 (2)</td>
</tr>
<tr>
<td>available N (ppm)</td>
<td>6 (3)</td>
</tr>
<tr>
<td><strong>Physical</strong></td>
<td></td>
</tr>
<tr>
<td>gravel (%)</td>
<td>3 (1)</td>
</tr>
<tr>
<td>sand (%)</td>
<td>75 (3)</td>
</tr>
<tr>
<td>silt (%)</td>
<td>7 (2)</td>
</tr>
<tr>
<td>clay (%)</td>
<td>15 (3)</td>
</tr>
<tr>
<td>bulk density (Mg/m³)</td>
<td>1.58 (0.2)</td>
</tr>
</tbody>
</table>

* Physical characteristics (except bulk density), pH and CEC determined from data in McIvor and Gardener (1991). Remaining characteristics were determined on samples collected throughout the study site (B. Northup, unpublished data).

* Cation exchange capacity in NH₄OAc solution at pH 7.0.

* Total nitrogen extracted by micro-kjeldahl digest.

* Total carbon determined by Leco furnace.

* Bicarbonate available phosphorus extracted in 0.5 M NaHCO₃.

* NH₄⁺ and NO₃⁻ extracted in 2 M KCl.

The climate is tropical, sub-humid, with an average annual rainfall (1985 through 1997) of 527 mm, 80% of which falls as monsoon rains during the wet season (November–April). Annual evaporation ranges from 1610 to 2206 mm (McIvor and Gardener, 1991).
pressure. In this study, we defined degradation as loss of standing crop, basal area of perennial tussock grasses, and ground cover. Previous studies correlated such reductions with loss of productivity (Tothill and Gillies, 1992; McIvor et al., 1995; Ash and McIvor, 1998).

Soil samples were collected at points randomly located within each paddock. At each sample point, the closest of four micro-patches were located, including three perennial tussock grasses (Bothriochloa ewartiana [Boew], Chrysopogon fallax [Chfa], and Heteropogon contortus [Heco]), and bare spaces [Bare] without growing plants. Soil samples from the upper 75 mm of the profile were collected at seven points along transects that bisected the centres of micro-patches in an up-slope to down-slope orientation. Soil cores were collected at the centres (0 cm) and edges (±8 cm from centre) of plants. Two additional samples were collected, both up- (+20 and +30 cm) and down-slope (−20 and −30 cm) from the centre into neighbouring bare spaces. The above spacing was determined from the distance between sampled micro-patches and neighbouring up- and down-slope plants on the S1-UG paddocks, and retained across all paddocks. In bare spaces, samples were collected at the centre of the patch, ±8 cm either side of centre, and outward at the above intervals. Samples were collected from four randomly located units of each micro-patch within paddocks and bulked into composite samples representing soils at locations around tussocks and bare patches.

The above sampling arrangement was undertaken to include potential mechanisms of landscape function. Semi-arid Australian plant communities are thought to operate by trigger–transfer–reserve–pulse mechanisms (Tongway and Ludwig, 1997). Tussocks of native grasses are thought to interact with overland flow of water (and nutrients) from run-off zones following storm events. Intercepted resources are then incorporated into reserve pools in the vicinity of plants, which generate a pulse of growth, if thresholds are exceeded.

Standing crop, basal area and ground cover of paddocks were estimated on 200, 0.5 m² quadrats along fixed transects by BOTANAL procedures in June 1996 to describe vegetative responses to accumulated grazing effects (Tothill et al., 1992). BOTANAL is a double-sampling technique used to estimate herbaceous characteristics. Estimators first undergo training by visually estimating characteristic(s) and checking estimates by hand-measuring the traits. Data for a given site are then collected, and standards defined post-data collection by estimating and hand-measuring the characteristic(s) within a set of quadrats. These standards are then used to calibrate estimates by regression techniques.

2.3. Laboratory analyses

Soil samples were stored at 4°C following collection, during transport, and throughout processing at the laboratory. Samples were passed through a 2 mm sieve, and adjusted to 40% water holding capacity prior to analyses. Soil microbial biomass (SMB) was determined by assaying ninhydrin-reactive nitrogen (Amato and Ladd, 1988). Samples were fumigated under an atmosphere of chloroform for 10 days, extracted in 2 M KCl solution, and ninhydrin-reactive N colorimetrically determined. Microbial C (Cmic) was defined by multiplying N values by the conversion factor 21.

Soil resources were determined on 28 of the composite samples from one paddock receiving each grazing treatment to define soil condition and fertility. Percent soil moisture was described by weight loss after 12 h in a 105°C oven. Total nitrogen was determined by micro-Kjeldahl techniques, and total phosphorus was assayed by first igniting soil samples in a 550°C oven for 2 h and extracting with 0.5 M H₂SO₄ for 16 h (Olsen and Sommers, 1982; Rayment and Higginson, 1992). Both, N and P levels were assayed colorimetrically with an auto-analyser. Soil organic carbon (Corg) was described by low temperature (375°C for 20 h) ignition (Ball, 1964; Honeysett and Ratkowsky, 1989). Coarse organic material (roots and litter) was washed from a second set of soil samples collected at the same sites as those for SMB and nutrient analyses.

2.4. Statistical analysis

Soil microbial biomass was analysed as a split–split plot within a randomised blocked design, resulting in a model with fixed and random effects (Minitab, 1996). The blocks (B) and paddock management regimes (M), which were randomly assigned to paddocks in 1993, were the main effects. Micro-patches (P) were
the split plot, and location around micro-patches (L) the split–split plot. Split–split plots (L) were replications in space, and tested by the appropriate split-plot model (Steel and Torrie, 1980). The level of significance for all tests was set at $\alpha = 0.05$.

3. Results

3.1. Landscape characteristics

The S1-UG and S1-LG paddocks had larger amounts of basal area and standing crop than the S1-HG and S2-HG units after five years of grazing pressure (Table 3). The control paddocks had less bare ground than the grazed paddocks. The S2-LG paddocks had standing crops similar to S1-LG paddocks, but much less basal area.

3.2. Rainfall and evaporation

Rainfall during 1993 through 1997 was below the long-term average for the study site (Fig. 1). The lowest rainfall was recorded in 1993, and was only 45% of the average. Annual evaporation during 1993 through 1997 generally exceeded the long-term average of the site, and was threefold higher than the rainfall received.

3.3. Soil microbial biomass

Significant differences ($p < 0.05$) in main effects were noted for SMB responses to paddock management, type of micro-patch, and location around micro-patch (Table 4). The paddock management × location around micro-patches and micro-patch × location interactions were also significantly different. Only the significant interactions were considered further, since the main effects can only be understood in combination with other model elements.

The highest level of SMB was noted at micro-patch centres on S1-UG and S1-LG paddocks, followed by $-8$ and $+8$ cm locations in the control paddocks (Fig. 2). Micro-patch centres also had the highest SMB in the remaining management regimes followed by the $+8$ and $-8$ cm locations. Locations further from patch centres on the grazed paddocks had successively lower

<table>
<thead>
<tr>
<th>Paddock management</th>
<th>Vegetative characteristics</th>
<th>bare ground (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>standing crop (kg/ha)</td>
<td>basal area (%)</td>
</tr>
<tr>
<td>S1-UG</td>
<td>2278 (85)</td>
<td>2.1 (0.1)</td>
</tr>
<tr>
<td>S1-LG</td>
<td>1812 (92)</td>
<td>1.8 (0.2)</td>
</tr>
<tr>
<td>S1-HG</td>
<td>425 (65)</td>
<td>0.3 (0.2)</td>
</tr>
<tr>
<td>S2-LG</td>
<td>1353 (135)</td>
<td>0.8 (0.2)</td>
</tr>
<tr>
<td>S2-HG</td>
<td>56 (25)</td>
<td>&lt;0.1 (0.1)</td>
</tr>
</tbody>
</table>

* S1-UG = initial excellent condition, ungrazed controls; S1-LG = initial excellent condition, light grazing; S1-HG = initial excellent condition, heavy grazing; S2-HG = initial degraded condition, heavy grazing; S2-LG = initial degraded condition, light grazing.

* Standing crop, basal area, and bare ground were determined by BOTANAL procedures applied to 200, 0.5 m² quadrats per paddock (Tothill et al., 1992).
levels of SMB, as compared to S1-UG paddocks, with increasing level of grazing pressure. The +8 cm location in the grazed paddocks tended to have higher SMB levels than −8 cm (down-slope of centre) locations. Paddock-level SMB declined with intensity of grazing (S1-UG—S2-HG), and only improved slightly on the S2-LG paddocks.

Bothriochloa ewartiana (Boew) tussocks had the highest SMB of the micro-patches, across locations in all management regimes (Fig. 3). Chrysopogon fallax (Chfa) had the second highest levels across locations, followed by H. contortus (Heco). Micro-patch centres had the highest levels of SMB for the three tussock species, followed by +8 and −8 cm locations (e.g. tussock edges). Bare patches (Bare) had the lowest levels of SMB recorded across all locations except at −30 cm.

3.4. Soil resource status

Soil resource levels were generally lower in the paddocks under historic heavy grazing pressure (S2-HG, S2-LG), or currently being heavily grazed (S1-HG), except for total P (Table 5). On average, S2 paddocks had only 10% of soil organic material and 57% of carbon noted on the S1-UG site, while the S1-HG paddock had 45% and 73%, respectively. Total N was relatively consistent in S1 paddocks, while the S2 paddocks had 42% less than amounts recorded on the S1-UG site. The microbial-to-organic carbon ratio (Cmic:Corg) declined by 38% along the S1-UG to...
S2-HG trajectory, while the spatial distribution around tussocks remained similar; the highest ratios were noted near plant centres (Fig. 4). Total N and organic C on the S2-LG paddock improved only slightly, while soil organic material and the Cmic : Corg ratio were not different from the S2-HG paddock. Percent soil moisture was higher (38% to 44%) on S1 paddocks, as compared to the S2 units.

4. Discussion

Paddocks included in this study represented landscapes in a range of alternate conditions within the degradation and recovery continuum of dry tropical woodlands in north Queensland (Ash et al., 1994). Some paddocks were productive, with high standing crops and basal areas, while others were extremely unproductive. Vegetative attributes of paddocks were likely affected by both grazing pressure and drought conditions during the 1993 through 1997 time period. Precipitation during this period ranged from 45% to 98% of the long-term average. Plant communities on the initially excellent condition paddocks receiving little or no grazing exhibited short-term resilience to the drought conditions noted during the study, and which are common in dry tropical Australia (Gardener et al., 1990; Williams and Chartres, 1991). The S1-UG and S1-LG paddocks maintained productivity, given that standing crop and basal area did not decline below initial conditions after five years of applied treatments. Alternatively, vegetative attributes declined on the S1-HG paddocks (425 kg/ha standing crop, 0.3% basal area). Since these paddocks were in similar condition in 1993, degradation of the S1-HG paddocks was mostly due to grazing pressure. Reduced grazing pressure was also the likely reason for increases in standing crop on S2-LG paddocks.

Soil microbial biomass was reduced by even low levels of grazing pressure. Though the management regime for S1-LG paddocks had no major effect on herbaceous production, SMB levels at locations from the tussock edge outward were impacted. Reductions of 20–40% were noted, highlighting the sensitivity of microbial activity to grazing pressure (Holt, 1997). The likely cause of the declines in SMB on these

Table 5
Soil resource levels (± 1 s.d.) on paddocks under different management regimes at the Cardigan research site, north Queensland, in 1997; n = 28 per management regime

<table>
<thead>
<tr>
<th>Paddock managementa</th>
<th>Total N (mg/kg soil)</th>
<th>Total P (mg/kg soil)</th>
<th>Organic C (%)</th>
<th>Soil organic material (g/kg soil)</th>
<th>Cmic : Corg b</th>
<th>Soil moisture (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1-UG</td>
<td>608 (77)</td>
<td>91 (15)</td>
<td>1.14 (0.19)</td>
<td>4.33 (4.12)</td>
<td>0.032 (0.005)</td>
<td>1.40 (0.39)</td>
</tr>
<tr>
<td>S1-LG</td>
<td>589 (49)</td>
<td>89 (19)</td>
<td>1.04 (0.20)</td>
<td>3.74 (4.32)</td>
<td>0.027 (0.005)</td>
<td>1.37 (0.69)</td>
</tr>
<tr>
<td>S1-HG</td>
<td>569 (85)</td>
<td>81 (24)</td>
<td>0.83 (0.17)</td>
<td>1.95 (2.34)</td>
<td>0.024 (0.008)</td>
<td>1.28 (0.57)</td>
</tr>
<tr>
<td>S2-LG</td>
<td>414 (69)</td>
<td>93 (42)</td>
<td>0.71 (0.23)</td>
<td>0.59 (0.79)</td>
<td>0.021 (0.007)</td>
<td>0.78 (0.26)</td>
</tr>
<tr>
<td>S2-HG</td>
<td>352 (58)</td>
<td>131 (45)</td>
<td>0.61 (0.16)</td>
<td>0.37 (0.41)</td>
<td>0.020 (0.006)</td>
<td>0.79 (0.31)</td>
</tr>
</tbody>
</table>

a S1-UG = initial excellent condition, ungrazed controls; S1-LG = initial excellent condition, light grazing; S1-HG = initial excellent condition, heavy seasonal grazing; S2-HG = initial degraded condition, heavy grazing; S2-LG = initial degraded condition, light grazing.
b Ratio of microbial carbon to soil organic carbon.

Fig. 4. Ratio of microbial to organic carbon (μg Cmic/μg Corg) in soil (+1 s.e.) around grass tussocks on intact (S1-UG), degrading (S1-HG), and degraded (S2-HG) experimental paddocks of the Cardigan research site, north Queensland, in 1997.
lightly grazed paddocks was the slightly lower amounts of ground cover, and concomitant reductions in plant litter on the soil surface. It is also likely that minor declines in rooting activity and associated biomass of the tussocks, as in the defoliation responses of a C\textsubscript{4} tallgrass on Sandhills (north America) prairie (Engel et al., 1998), had an effect. We noted a 14\% reduction in soil organic material around the tussocks on S1-LG paddocks, which would limit sources of nutrients and energy required for microbial activity. Soil organic material on paddocks under the heavier grazing regimes was reduced by greater amounts. As such, the responses of plants, SMB and soil resources to perturbation are somewhat coupled, and highlight the need to consider biological activity and soil condition as integrated units when defining grazing impacts in north Queensland.

While we noted minor declines in plant vigour under light grazing pressure, some C\textsubscript{4} grasses in the Serengeti have exhibited small increases in root activity, crown biomass, and plant relative growth rates (McNaughton and Chapin, 1985; McNaughton, 1992). This divergence in response is likely related to plant morphology, and the inclusion of heavy grazing among the evolutionary pressures impacting Serengeti plant communities. The impacts of such plant responses on microbial biomass are not clear. However, it could be assumed that higher amounts of root growth, root exudates and litter production should supply more resources, and support greater levels of microbial activity. Conversely, tussock grasses in Australian ecosystems evolved mechanisms to deal with soil infertility, climatic variability and fire in the absence of large-scale intensive herbivory. The utilisation patterns of the landscape by native grazing animals (Macropodidae) generally tends to be more diffuse than that exhibited by cattle (Denny, 1982). As such, relatively minor but intensively applied grazing pressure from cattle will have some negative impact on the productivity of native Australian tussocks, and eventually inhibit microbial activity.

The ratio of microbial-to-organic carbon (C\textsubscript{mic} : C\textsubscript{org}) in soil has been proposed as a sensitive measure of soil health, since it represents a combination of microbial activity and key soil resource (Anderson and Domsch, 1989; Sparling, 1992). At the paddock scale, this ratio was lower on paddocks under heavy grazing pressure, and did not markedly improve in the recovering paddocks after five years of reduced grazing. Both microbial C and organic C within the soil decreased, with microbial C exhibiting the larger decline. This result was consistent with findings by Holt (1997), who noted that microbial carbon was more sensitive to grazing pressure than soil organic carbon. Our paddock-scale C\textsubscript{mic} : C\textsubscript{org} ratios were similar to those reported for tallgrass prairie (0.028) in the United States (Rice et al., 1994), C\textsubscript{3} grasslands (0.024) in Canada (Carter, 1986), and pampas grasslands (0.03) in Argentina (Alvarez et al., 1998). However, while the relationships between microbial and organic C were similar, levels of C\textsubscript{mic} and C\textsubscript{org} were two to six times higher than the amounts we noted.

While the paddock-scale C\textsubscript{mic} : C\textsubscript{org} ratios indicated landscape deterioration had occurred in heavily grazed paddocks, they did not describe initial impacts of the degradation process on microbial biomass and soil condition. Deterioration of soil quality (and hence reduction of soil microbial biomass) starts at finer spatial scales, as noted in the carbon ratio shift along the S1-UG → S1-HG → S2-HG trajectory (see Fig. 4). The largest changes were noted at 8 to 30 cm away from the tussock centres. This highlights the localised spatial and temporal responses of soil condition to management regimes, and the need to include finescale measurements of landscape condition in monitoring systems.

The degrading (S1-HG) paddocks may represent a potential threshold in landscape degradation, beyond which continued heavy grazing will reduce productive sites to a deteriorated condition. Significant declines (15–27\%) in microbial biomass were noted under the S1-HG regime, as were declines in organic C (28\%) and soil organic material (55\%) at the paddock scale. However, levels of total N and P were relatively high, and should help generate plant growth and induce re-invasion by perennial tussocks, if grazing pressure was reduced. Remnant tussocks will also be fed by larger run-off areas, increasing their input of water and nutrients (Tongway and Ludwig, 1997). Unfortunately, physical properties of the soil are also degraded under such grazing pressure, which limits infiltration of water and nutrients into the soil profile (Willat and Pullar, 1983). Recruitment of perennial grasses will also be low if sufficient time has elapsed for loss of the resident seed bank, a surface seal has developed, or
canopy cover is $<40\%$ (McIvor et al., 1995; Greenwood et al., 1998).

The low level of microbial biomass on S2-HG paddocks was indicative of the continued reduction in herbaceous productivity and loss of soil health with long-term heavy grazing. The deteriorated (S2-HG) paddocks had only 46%, 15%, and 33% of the organic C, soil organic material and total N, respectively, of the control paddocks. The loss of above and below-ground herbaceous materials removed the energy sources required for microbial growth, and limited the amounts of water and nutrients transferred into reserve pools for use in promoting biological activity (Williams and Chartres, 1991; Roper and Gupta, 1995; Tongway and Ludwig, 1997). Such a reduced input into reserve pools also limits the productive capacity of remaining plants, reducing future inputs of organic material into the soil, and inhibiting microbial growth. The S2-LG paddocks had microbial biomass levels similar to the degraded paddock. As such, they did not achieve recovery thresholds for microbial biomass during this study. Soils on these sites had not attained the reserves of organic matter and carbon required to encourage higher levels of microbial activity. Additional years of grazing at low levels coupled with wet season deferments will be required.

Drought conditions experienced in the years preceding this study likely affected soil microbial biomass. However, it is difficult to ascertain microbial responses under non-drought conditions. Increases in soil moisture in previously dry soil can either enhance and impede short-term microbial activity (Brock et al., 1984). Not only do microbes become metabolically active under improved moisture conditions, but bacterial cells can also be lysed, effectively reducing microbial activity for a time (Kieft et al., 1987). In this study (late dry season), soil in the immediate vicinity of plants held higher amounts of moisture than soil in other locations (1.4% to 2.3% vs. 0.6% to 1.3%). While these were only slight improvements, they likely enhanced levels of microbial biomass near plants. Higher levels of soil moisture close to plants would also be expected in the wet season, given the better soil conditions in these zones (Holt et al., 1996a). A separate study of seasonal effects conducted on the same paddocks as this study noted a 27% increase in microbial biomass following late wet season rains (B. Northup, unpublished data).

The distribution and amount of soil microbial biomass was also affected by species of tussock. Higher microbial biomass was found near B. ewartiana and C. fallax tussocks, compared to H. contortus and bare patches. Though not species-specific, Holt et al. (1996b) noted differences between patches of annual grasses, perennial tussocks and bare spaces in a study on north Queensland grass communities. The responses we noted were likely due to differences in plant morphology rather than genetic links (Groffman et al., 1996). Under light or no grazing, tussocks of all three species become large and leafy, with extensive root systems and large numbers of stems originating from the soil surface (Cameron, 1979). B. ewartiana and C. fallax tussocks had segments of living basal area spread through 8–25 cm diameter growth zones, depending on grazing pressure, filled with standing dead stems and litter (B. Northup, unpublished data). Conversely, H. contortus plants were smaller and less vigorous with 5–12 cm diameter growth zones and no standing dead stems or litter. As such, both B. ewartiana and C. fallax were more effective at capturing water and nutrients in run-off, and incorporating resources (transported and local) into the soil profile (Ludwig and Tongway, 1995). Such higher inputs would enhance both plant and soil microbial activity in the vicinity of the tussocks. The area around B. ewartiana and C. Fallax may also have larger reserves to respond to inputs, and hence produce larger growth pulses (Tongway and Ludwig, 1997).

Bare interspaces had their highest levels of microbial biomass at the down-slope end of patches. These sites represented zones where tussocks interacted with overland flow of water across interspaces, and caused the deposition of sediment and litter in run-off (Tongway and Ludwig, 1997). The remaining areas represented the sites which generated the run-off that enriched the down-slope tussocks. A separate study on the paddocks used in this study noted lower bulk densities (1.44 (+0.10) vs. 1.57(+0.09) Mg/m$^3$) in soils near tussocks than in bare interspaces (B. Northup, unpublished data). As such, soil closer to tussocks had better hydraulic conductivity, due to the combination of soil structure and biological activity, allowing greater infiltration of water and nutrients (Holt et al., 1996a).
Describing microbial biomass in soils is a complicated process that requires some technical expertise, and access to a soil analytical laboratory (Amato and Ladd, 1988). Also, variation in level of microbial biomass between different grass species adds to the level of complication. As such, it is not an entirely functional variable for regular measurement by land managers to describe landscape condition. However, soil microbial biomass is more sensitive to grazing pressure than other soil or vegetative characteristics, plays important roles in soil processes and landscape function, and should not be entirely discounted due to technical complications. A simplified sampling regime could be incorporated into larger-scale monitoring systems to supply the added sensitivity required to identify the initial stage of degradation. Microbial biomass could be measured (through arrangements with an analytical laboratory) in soil samples collected (by managers) near tussocks of one dominant grass species common to all landscapes, and compared to baseline conditions (e.g. good condition landscapes), or target levels for the plant community in question.

Our study indicates microbial biomass will be high and variable in native eucalypt woodlands with a diverse mix of healthy tussocks of the dominant native perennial grasses. Shifts in species composition of north Queensland grazing lands due to intensive grazing reduces the potential vegetative productivity of landscapes, limits the incorporation of scarce resources into soil and microbial activity, and ultimately the loss of nutrient cycle function and soil micro-structure (Oades, 1993; Roper and Gupta, 1995; Holt, 1997). Once a landscape becomes degraded, recovery of condition will require the application of light grazing regimes with seasonal deferments for long time periods (e.g. decades). Best management practices for Australian dry tropical woodlands should utilise conservative grazing systems that prevent landscape deterioration, thereby eliminating the need for expensive remedial techniques (Williams and Chartres, 1991; Ash et al., 1997).

At the paddock scale (the normal scale of management decisions), declines in soil organic material, organic carbon, and microbial biomass occurred under sustained grazing pressures. However, these values point to a short-coming in using measures of nutrient status or biological activity from larger spatial scales to indicate degradation in dry tropical Australia. Soil resources and microbial biomass are patchily distributed, and largely concentrated near tussocks. Due to their sensitivity, fine-scale measurements of soil condition around plants have a greater potential to define responses to management. By the time changes are noted at larger scales the landscape will already be degraded, since deterioration thresholds can not be detected at that scale of organisation. Monitoring of landscape condition in north Australia should incorporate plant-scale measures of grazing impacts at the plant–soil interface with large-scale indicators of vegetation responses, since the finer scales of organisation are more descriptive of soil health and productivity.

Acknowledgements

Data used in this manuscript was collected from paddocks that were part of the Australian Meat Research Corporation (MRC) funded project NAP3.205. The authors would like to express their appreciation to Malcolm Hodgen and Shelley Farr (CSIRO Land and Water) for their assistance in laboratory analyses, and to Andrew Ash, John McIvor, and Lynn Walker (CSIRO Tropical Agriculture) for comments on earlier drafts.

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