Multi-substrate induced respiration (functional capacity) in agriculturally degraded and intact restiad bogs: implications for carbon and nitrogen cycling

S.M. Lambie[1], J.L. Ratcliffe[2,3]

[1] Manaaki Whenua - Landcare Research, Hamilton, New Zealand
[2] School of Science and Engineering, University of Waikato, Hamilton, New Zealand
[3] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

SUMMARY

Natural peatlands provide ecosystem services such as carbon storage and habitat, which can be negatively affected (degraded) by the proximity of agricultural land due to lowered water table and increased nutrient deposition. We assessed peat biochemistry and microbial function in the dry, fluctuating and saturated zones of the peat deposits at Moanatuatua (degraded) and Kopuatai (intact) raised bogs in New Zealand to investigate the effects of adjacent agriculture on carbon (C) and nitrogen (N) cycling. Peat C and N density were elevated, due in part to greater bulk density, in the dry and saturated zones at Moanatuatua compared with Kopuatai. Functional capacity (multi-substrate induced respiration) at Moanatuatua was greater than at Kopuatai, and water-soluble C was at lower concentration but more degradable, indicating that microbes were C limited at Moanatuatua but N limited at Kopuatai. Greater microbial function at Moanatuatua infers C inputs may be more rapidly converted to gaseous or waterborne exports, and agriculturally affected peatlands may be more susceptible to losses of labile C. We conclude that proximity to agriculture is likely to have caused changes in chemical properties and altered microbial functioning of restiad bog and has important implications for C and N turnover within these peatland systems.

KEY WORDS: community level physiological profiles, microbial function, nutrient enrichment, peatland

INTRODUCTION

Peatlands comprise at least 3.8 million square kilometres of Earth's surface (Joosten 2009) and provide essential ecosystem services including biodiversity support and mediation of the global carbon (C) cycle (Zedler & Kercher 2005). Drainage for agriculture has been a major driver of peatland loss (Joosten & Clarke 2002, Zedler & Kercher 2005, McGlone 2009). The pace of wetland loss in New Zealand has been among the fastest in the developed world (Mitsch & Gosselink 2000), with only 10 % of the original area remaining (McGlone 2009, Ausseil *et al.* 2015). Approximately one-third of remaining lowland peat bogs (by area) are situated in the Waikato region (Ausseil *et al.* 2008) of Te Ika-a-Māui (North Island, New Zealand). These peatlands are predominantly derived from *Empodisma robustum* (*Restionaceae*), a rushlike vascular plant endemic to northern New Zealand (Wagstaff & Clarkson 2012). Although the majority of peatland in Waikato Region has been converted to agricultural use, remnants have escaped direct disturbance (McGlone 2009, Ausseil *et al.* 2015) and are now refuges for a number of rare species (de Lange *et al.* 1999, Hoare *et al.* 2006), important palaeo-climatological archives (Jara *et al.* 2017), and examples of an unusual peatland type not found elsewhere in the world (Wagstaff & Clarkson 2012).

Many remnants of restiad peatland have undergone drainage and, therefore, have deeper water tables than pristine bogs (Clarkson 2014, Ratcliffe *et al.* 2019). This is a cause of concern because peat forms under waterlogged anaerobic conditions with very slow decay of plant material, and water table depth is a key regulator of fundamental peatland processes (Holden *et al.* 2004). When a peatland is drained, the system shifts from a reducing to an oxidising state and the decay of accumulated plant material accelerates, which can shift some peatlands from sequestering C to becoming a source (Minkkinen *et al.* 1999, Joosten & Clarke 2002, Zedler & Kercher 2005, Hooijer *et al.* 2010). Degraded bogs tend to have highly fluctuating water tables due to the loss of water-holding capacity caused by the collapse of pore space as peat decays (Price *et al.* 2003), and water table fluctuations have been linked to the enhancement of peat C mineralisation (e.g. Kechavarzi *et al.* 2007, Reiche *et al.* 2009; Laine *et al.* 2013, 2014).

New Zealand bogs are naturally depleted in nitrogen (N) and phosphorus (P) (Luxton 1982,

Clarkson *et al.* 2004); however, remnant peatlands adjacent to agricultural land can undergo nutrient enrichment due to elevated atmospheric deposition (Pitcairn *et al.* 1998, Blyth *et al*. 2013, Tipping *et al.* 2014). Elevated N inputs, which can remove N limitation, may increase the rate of microbial degradation in peatlands (Bragazza *et al.* 2006, Currey *et al.* 2010, Song *et al.* 2013). C mineralisation is affected by changes in microbial community or function (Espenberg *et al.* 2018, Too *et al.* 2018) and vegetation (Chroňáková *et al.* 2019), and both microbial communities and vegetation can be altered by increased N inputs (Bubier *et al.* 2007, Peichl *et al.* 2018). Functional capacity, or multi-substrate induced respiration, provides a means for assessing microbial function in peatlands (Creamer *et al.* 2009). The fluctuating zone may have greater functional capacity and, therefore, greater C degradation than permanently dry and saturated zones in bogs (Artz *et al.* 2006, Preston *et al.* 2012, Lin *et al.* 2014).

Restiad bogs in New Zealand are unusual in that their peat-forming vegetation can tolerate a wide range of nutrient and hydrological conditions (Hodges & Rapson 2010). Therefore, to the best of our knowledge, these peatlands offer a unique opportunity to study the effects of altered water table regime and nutrient inputs without major changes to the peat-forming plant community. Similarly, these peatlands are ideal systems for investigation of whether the two dominant peat-forming plant species (*Empodisma robustum* and *Sporadanthus ferrugineus*) alter peat chemical or microbial community function. The objective of our work was to determine peat characteristics and microbial function in the dry, fluctuating and saturated zones of two restiad peatlands, one drainage-affected and the other almost intact, under two different peat-forming plants. We tested the hypothesis that agricultural pressure, from atmospheric nutrient inputs and water table lowering, would increase functional capacity and alter N cycling. We also examined the hypothesis that microbial function in the fluctuating zone would differ significantly from the dry and saturated zones and this would be correlated to peat chemical properties.

METHODS

Study sites

The Kopuatai and Moanatuatua bogs are situated in Waikato Region (Figure 1). The climate at both sites is similar, with mean annual temperature and precipitation 14.7 °C and 1269 mm for Kopuatai and 13.8 °C and 1121 mm for Moanatuatua (NIWA 2017).

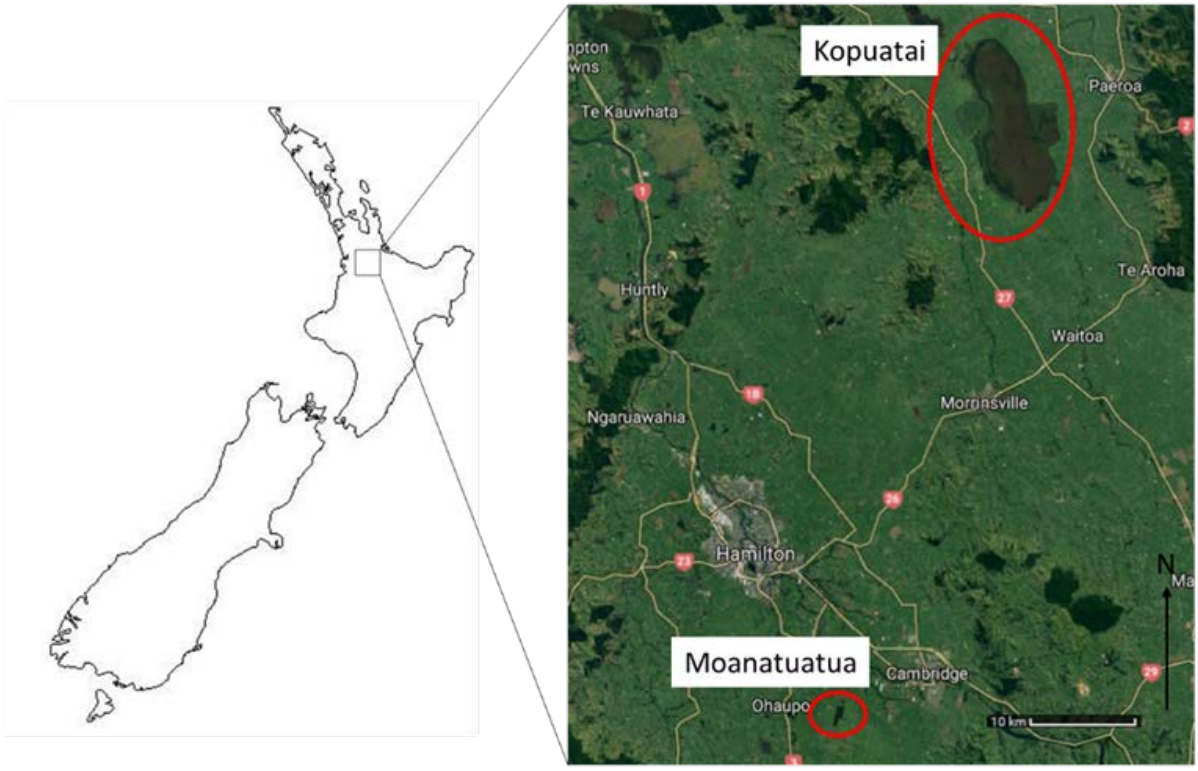

Figure1. Locations of the Kopuatai and Moanatuatua study sites in Waikato Region, Te Ika-a-Māui (North Island), New Zealand.

Kopuatai (175.55 °E, 37.79 °S) is an essentially intact (Clarkson *et al*. 2020) restiad peatland complex consisting of northern and southern ombrogenous domes. Peat formation began approximately 11,700 years cal. BP (Newnham *et al.* 1995). The site is 9,000 hectares in size and, although it is surrounded by agricultural land and drains, little evidence of effects on vegetation or hydrology can be seen beyond the edges, i.e. in the ombrotrophic areas of the peatland (Schipper *et al.* 1998). The vegetation at our sample points was dominated by the restiad peat-formers *Empodisma robustum* and *Sporadanthus ferrugineus* and, to a lesser extent, the sedges *Schoenus brevifolius* and *Machaerina teretifolia* as well as the fern *Gleichenia dicarpa.*

Moanatuatua (175.37 °E, 37.92 °S) is a drained bog around 114 hectares in size which has been highly negatively affected (degraded) by agricultural practices, including drainage and fertiliser applications, on surrounding land (Clarkson *et al.* 1999); with N increasing significantly in peat and both N and P increasing in foliage (Clarkson *et al.* 2020). The vegetation is currently dominated by *Empodisma robustum* and the ericaceous shrub *Epacris pauciflora*, with some patches of *Sporadanthus ferrugineus*.

Experimental design

Water table depth (below ground surface) was measured at 0.1 Hz for two years at both study sites using a Wl1000W probe (Hydrological services, NSW Australia) (Ratcliffe *et al.* 2019). These data were used to determine the depths and thicknesses of the dry, fluctuating and saturated zones (Table 1). The dry zone was characterised as rarely submerged, the fluctuating zone as containing the water table fluctuations, and the saturated zone as continuously within or below the capillary fringe of the water table. The depths and extents of these zones and, therefore, the sampling depths chosen, differed between the two sites (Table 1) but were deemed to be functionally equivalent. While we recognise that sampling at different depths was not ideal, this was unavoidable due to the significant differences in water table characteristics between Moanatuatua and Kopuatai.

Although *Empodisma robustum* and *Empodisma minus* are the principal peat-forming restiad species on mainland New Zealand, at latitudes north of 38 °S they can be succeeded by *Sporadanthus ferrugineu*s (Clarkson *et al.* 2004, Wagstaff & Clarkson 2012). While *Empodisma robustum* was the dominant restiad at both of our sites, Kopuatai had considerably more *Sporadanthus ferrugineus* than Moanatuatua (Clarkson *et al.* 2004). Each hydrological zone at each study site was sampled in four randomly selected areas under either *Emposdisma* or *Sporadanthus*. At Moanatuatua and Kopuatai, respectively, mean distances were 11 m and 23 m between *Empodisma* peat sampling points, 17 m and 426 m between *Sporadanthus* peat sampling points, and 13 m and 463 m between *Empodisma* and *Sporadanthus* peat sampling points.

Peat cores were taken using a cylindrical stainless steel corer (diameter 0.1 m, length 0.1 m) which was pressed into the peat at the depths indicated in Table 1. At each sampling point, at each of the three chosen depths a core sample was taken for bulk density (n = 24 per bog) and a separate sample was taken for microbial/biochemical analysis (n = 24 per bog). Each sample was removed from the corer and stored in a separate plastic bag at 4 ± 1 °C until required. Samples were not bulked before analysis, and each sample was treated as an independent replicate for the pertinent hydrological layer at each bog.

Peat biochemical characteristics

Bulk density was estimated using the dry weight of a known volume of peat after drying at 105 °C until moisture contents were constant (Päivänen 1969).

The peat samples taken for biochemical analysis were homogenised by cutting into 0.05 m cubes and hand mixing (Artz *et al.* 2006). A subsample of the mixed peat was then air dried at 35 °C, fine ground to a powder, and analysed for total C and total N contents using a combustion furnace (LECO TruMac, Saint Joseph, MI, USA). Peat pH was measured (Edge Multiparameter pH meter, Hanna Instruments, Rhode Island, USA) in a mixture of 5 g of peat with 20 ml of ultra-filtered water after incubation at 20 °C for 16 hours, following Schipper *et al.* (1998).

Table 1. The hydrological zones sampled at Kopuatai and Moanatuatua. 'Zone' indicates depth from the peat surface to the upper and lower boundaries of the zone.

Hydrological zones	**Kopuatai**		**Moanatuatua**	
	Zone (m)	Sampling depth (m)	Zone (m)	Sampling depth (m)
Dry	0–0.02	0–0.02	0–0.2	0–0.02
Fluctuating	0.02–0.1	0.03–0.05	0.2–0.6	0.4–0.5
Saturated	0.1–	0.4–0.5	0.6–	1.0–1.1

Anaerobically mineralisable N was measured as an indication of the amount of plant and microbially available N in the peat, using a method adapted from Schipper *et al.* (1998) and Blakemore *et al.* (1987). Five grams of wet peat were saturated with 50 ml of water, and the containers sealed and incubated for seven days at 40 °C before extraction with 50 ml of 4M potassium chloride (KCl) for one hour, so the equivalent extraction solution was 2M KCl. The extracts were gravity filtered through Whatman No. 42 filter papers. Corresponding non-incubated samples were extracted with 100 ml of 2M KCl. The amount of anaerobically mineralisable N was calculated from the difference in ammonium concentration between incubated and non-incubated samples. The non-incubated extracts were also quantified for nitrate concentration and the amount of mineral nitrogen present in the peat was calculated as the sum of nitrate and ammonium concentrations (QuikChem 8500 flow injection analyser, Latchat, Canada).

Water soluble C (WSC) was determined by a method adapted from Kalbitz *et al.* (2003). A mixture of 5 g of wet peat and 50 ml of ultra-filtered water was stirred three times over a 24-hour period while being incubated at 4 °C. The mixture was then filtered under vacuum through a 0.45 µm glass filter paper (GFF) to separate dissolved organic C (DOC) from particulate C, and DOC was quantified (Analytik Jena Multi-NC TOC Analyser, Jena, Germany). To determine the degradability of water-soluble C in the peat, the absorbance of the water extract at 280 nm (UV-160A, Shimadzu, Kyoto, Japan) was divided by the concentration of WSC (Kalbitz *et al.* 2003).

Because microbial function is directly affected by moisture content (Artz *et al.* 2006) and in order to enable comparisons between samples, prior to analysis for microbial biomass C (MBC), potentially mineralisable C (PMC) and multi-substrate induced respiration (MSIR), all peat samples were adjusted to the driest condition (lowest gravimetric moisture content) found amongst the samples collected. The peat samples were adjusted to 400 % of field gravimetric moisture content by slowly drying them at room temperature and assessing moisture content daily. The peat was then incubated in the dark, at 25 °C for seven days, to allow adjustment of the microbial community to the new moisture content (Degens *et al.* 2000).

Microbial biomass carbon (MBC) was determined by a method adapted from Schipper *et al.* (1998) and Preston & Basilio (2016). Briefly, 5 g of wet peat was weighed into a glass beaker and washed (fumigated) with 0.25 ml of chloroform and incubated at 25 °C for 24 hours in the dark. The peat was then extracted with 10 ml of 2M potassium sulphate for 30 minutes and filtered under gravity through Whatman No. 42 filter papers. The extraction was also completed for a parallel set of unfumigated samples, and the extracts of fumigated and unfumigated samples were analysed for total C content (Analytik Jena Multi-NC TOC Analyser, Jena, Germany). The difference in total C between fumigated and unfumigated samples and a k_{ec} factor of 0.41 were used to determine microbial biomass C (Schipper *et al.* 1998).

Potentially mineralisable C (PMC) in the peat material was measured by a method adapted from Semenov *et al.* (2008). Twenty grams of wet peat in a 100-mL plastic container was placed in a 2.2-L plastic container (Sistema, Auckland, New Zealand) with a glass beaker containing water to maintain humidity and another beaker containing 1M sodium hydroxide (NaOH) solution to trap carbon dioxide (CO_2) evolved from the peat. The 2.2-L container was sealed and incubated at 25 °C for 39 days. The CO_2 traps were refreshed after 7 and 23 days to ensure that saturation of the incubation container and trapping solution with CO_2 did not occur. CO_2 production was determined by back titration of the NaOH with 0.1M hydrochloric acid and a phenolphthalein indicator, after precipitation of carbonates with excess barium chloride (Saggar *et al.* 1999). PMC was estimated using 2 parameter exponential analysis where $f = a \times (1 - \exp(-bx))$, f is carbon mineralisation at time x (days), a is PMC and b is the decomposition constant (Hossain & Putely 2013).

Microbial functional capacity

Microbial functional capacity was assessed using multi-substrate induced respiration (MSIR). Although this method is widely used to assess the effects of perturbations (e.g. Degens *et al.* 2000, Artz *et al.* 2006, Preston *et al.* 2012), it has some limitations. The shorter incubation times may select for bacteria over fungi, and the pre-incubation and moisture adjustment may lead to alteration in microbial activity from that measured in the field. However, the method allows direct comparisons between samples collected at different times and sites (Campbell *et al.* 2003, Chapman *et al.* 2007).

After 7 days' pre-incubation at 25 °C, 5 g of wet peat (400 % moisture content) was applied with 10 ml of substrate at a C concentration of 1 mg ml^{-1} (C application rate 2 mg g^{-1}) (Preston *et al.* 2012). Ten substrates were selected from Artz *et al.* (2006) to represent common root exudates; a further two phenolic acids were also included to test the potential negative effect of phenolics on microbial processes (Kuder *et al.* 1998) making a total of 12 substrates. The selected substrates were glucose, galactose,

arabinose, xylose, sucrose, glycine, lysine, arginine, glutamic acid, benozoic acid, ferulic acid (phenolic acid) and couramic acid (phenolic acid). To determine background basal respiration, ultra-pure water (which did not contain any C) was applied at the same volume as the substrate. The peat and substrate were manually shaken to ensure thorough contact and incubated for 24 hours with 2M NaOH to trap CO_2. CO_2 production was determined by back titration of the trapping solutions with 0.1M hydrochloric acid and a phenolphthalein indicator after precipitation of carbonates with excess barium chloride (Saggar *et al.* 1999). Functional capacity was determined as the total amount of CO_2 produced, from all of the twelve substrates after subtraction of basal respiration, i.e. [($CO_{2(Substrate\ 1)}$ - basal respiration) + ($CO_{2(Substrate\ 2)}$ - basal respiration) + ($CO_{2(Substrate\ 3)}$ - basal respiration) … + ($CO_{2(Substrate\ 12)}$ - basal respiration)] (Artz *et al.* 2006).

Community-level physiological profiles (CLPP) are commonly used for the analysis of multi-substrate induced respiration data (Weber & Legge 2010). For CLPP analysis of the MSIR data, the datasets were normalised by calculating the difference between the respiration of each substrate and the basal respiration, then dividing this difference by the total CO_2 flux from all substrates (Banning *et al*. 2012, Bérard *et al.* 2014).

Statistical analyses

We tested the effect of hydrological zone on peat biochemical and microbial variables using two-way ANOVA with hydrological zone nested in site; and we determined differences between the hydrological zones within each site using Student-Newman-Keuls *post hoc* analysis. Two-tailed, two-sample, unpaired t-tests were used to determine differences between sites and vegetation within each measured factor.

Non-metric multidimensional scaling (NMDS) was used to assess CLPPs using substrate response in the MSIR assays. The normalised respiration response for each substrate was assessed using Euclidean distances, and NMDS ordinations were run using scaling of the least squares with ten starting configurations, primary tie assessment and 999 permutations. Two dimensions were plotted with reference to site and hydrological zone.

Linear regression modelling was used to assess relationships between soil chemical and physical characteristics, functional capacity and AMN. Akaike information criterion was used to determine the quality of multivariate regression models and which models were included in the analysis.

All analyses were conducted using Genstat 18 (VSN International, Hemel Hempstead, UK) and were considered to be statistically significant if $P < 0.05$.

RESULTS

Peat biochemical characteristics

There was no difference in soil properties under *Empodisma* and *Sporadanthus* vegetation (Table 2). There were, however, differences between the sites with reference to the hydrological zones (Table 3).

Table 2. Biochemical properties of peat under *Empodisma* and *Sporadanthus*, with no differentiation between hydrological zones or sites. AMN = anaerobically mineralisable nitrogen, dWSC = decomposability of water-soluble carbon, MBC = microbial biomass carbon, PMC = potentially mineralisable carbon, WSC = water-soluble carbon. Values in brackets represent the standard error of the mean ($n = 24$). Values with different letters within a row are significantly different ($P < 0.05$).

Property	*Empodisma*	*Sporadanthus*
pH	4.41 (0.09)a	4.35 (0.69)a
bulk density (g cm^{-3})	0.055 (0.06)a	0.055 (0.006)a
MBC (mg kg^{-1})	4378 (565)a	5311 (391)a
PMC (mg kg^{-1})	1095 (321)a	3975 (3525)a
AMN (mg kg^{-1})	245 (39)a	222 (39)a
mineral N (mg kg^{-1})	122 (19)a	79 (14)a
ammonium N^4 (mg kg^{-1})	115 (19)a	73 (14)a
total C (mg cm^{-3})	51.85 (0.78)a	52.65 (0.74)a
total N (mg cm^{-3})	1.28 (0.09)a	1.31 (0.07)a
C/N	44.44 (2.70)a	44.80 (2.13)a
WSC (mg kg^{-1})	1663 (303)a	1020 (157)a
dWSC (L mg^{-1} cm^{-1})	0.023 (0.002)a	0.026 (0.002)a

Table 3. Biochemical properties of peat in different hydrological zones at the Moanatuatua (degraded) and Kopuatai (intact) bogs. AMN = anaerobically mineralisable nitrogen, dWSC = decomposability of water-soluble carbon, MBC = microbial biomass carbon, PMC = potentially mineralisable carbon, WSC = water-soluble carbon. Values in brackets represent the standard error of the mean ($n = 8$). Values with different appended letters within a row are significantly different ($P < 0.05$).

Property	**Moanatuatua**			**Kopuatai**		
	Dry	Fluctuating	Saturated	Dry	Fluctuating	Saturated
pH	4.20 (0.09)abc	3.94 (0.06)a	4.17 (0.04)b	4.90 (0.12)e	4.66 (0.07)d	4.42 (0.05)b
bulk density (g cm^{-3})	0.100 (0.006)e	0.060 (0.003)cd	0.036 (0.002)b	0.052 (0.004)c	0.068 (0.003)d	0.014 (0.002)a
MBC (mg kg^{-1})	6023 (339)c	3408 (655)ab	3618 (674)ab	4922 (704)bc	3877 (445)ab	2374 (504)a
PMC (mg kg^{-1})	68 (49)a	336 (232)a	1908 (584)a	289 (355)a	278 (207)a	1855 (735)a
AMN (mg kg^{-1})	440 (57)c	117 (16)ab	16 (3)a	436 (62)c	242 (15)b	148 (39)ab
mineral N (mg kg^{-1})	28 (5)a	124 (20)b	9 (1)a	180 (40)b	135 (16)b	126 (14)b
ammonium N (mg kg^{-1})	21 (5)a	119 (19)b	4 (1)a	173 (40)b	128 (15)b	120 (14)b
total C (mg cm^{-3})	52 (3)d	32 (2)c	21 (1)b	25 (2)b	34 (2)c	7 (1)a
total N (mg cm^{-3})	1.39 (0.13)d	1.11 (0.08)c	0.54 (0.04)b	0.41 (0.03)b	0.65 (0.05)b	0.18 (0.03)a
C/N	38 (1)b	29 (1)a	39 (1)b	61 (2)d	53 (3)c	42 (3)b
WSC (mg kg^{-1})	479 (44)a	620 (61)a	332 (39)a	3015 (557)d	2236 (238)c	1366 (153)b
dWSC (L mg^{-1} cm^{-1})	0.036 (0.001)d	0.026 (0.003)c	0.028 (0.001)c	0.024 (0.002)bc	0.014 (0.002)a	0.018 (0.002)ab

Peat pH was lower in the dry and fluctuating zones at Moanatuatua (degraded) compared to Kopuatai (intact) but was the same between the two sites in the saturated zone (Table 3). Bulk density was greatest in the dry zone at the degraded site, and was also greater at the degraded site compared to the intact site for the dry and saturated zones, but there was no difference between the sites in the fluctuating zone (Table 3).

Microbial biomass C (MBC) was greatest in the dry zone at Moanatuatua, although not statistically greater than in the dry zone at Kopuatai. There were no significant differences between the sites with respect to MBC in the remaining zones (Table 3). Anaerobically mineralisable N (AMN) was also greatest in the dry zones at both sites, and did not differ between the sites. AMN showed no significant differences between equivalent hydrological layers in the two bogs, which was also the case for potentially mineralisable C (PMC). Compared with the degraded bog, mineral N concentrations at the intact bog were greater in the dry and saturated zones but not in the fluctuating zone, the majority of mineral N being in the form of ammonium (Table 3). Total C, total N and C/N were greater at Moanatuatua (degraded) than at Kopuatai (intact) (Table 3).

WSC decomposability (dWSC) in the dry zone was greater at the degraded site than at the intact site, and this was also the case for the fluctuating and saturated zones (Table 3) although the concentration of WSC was significantly greater at Kopuatai (intact) than at Moanatuatua (degraded).

Microbial functional capacity

Carbon dioxide (CO_2-C) fluxes did not differ between the two vegetation types for any of the substrates tested (Table 4). Also, CO_2-C fluxes did not differ between hydrological layers or between substrates within a hydrological layer (Table 5). However, despite the lack of differentiation between hydrological layer and vegetation treatments, functional capacity (defined as total substrate response) was greater at Moanatuatua than at Kopuatai (Figure 2a), and above zero at Moanatuatua but below zero at Kopuatai (Table 5). Between 50 % and 92 % of the substrate induced respiration was less than basal respiration at Kopuatai but only 9–17 % of the substrate induced negative respiration at Moanatuatua (Table 5). There were no differences in basal respiration between the sites (Figure 2b). NMDS analysis of community-level physiological profiles indicated no distinct patterns or separation between either the sites or the different hydrological zones (Figure 3). There were no effects of vegetation type.

The linear regression analysis between functional capacity and the assessed biochemical and physical properties of the peat was undertaken to determine which soil factors might influence microbial C and N cycling. This indicated only one weakly significant relationship between functional capacity and C/N, which explained 13 % of the variation in functional capacity (Figure 4).

Peat pH, bulk density, total C, WSC and MBC all had significant positive relationships with AMN

Table 4. Carbon dioxide (CO_2-C) fluxes (mg g^{-1}) after the addition of 12 carbon substrates and water, from peat under *Empodisma* and *Sporadanthus* vegetation, with no differentiation between hydrological zones or sites. Values in brackets represent the standard error of the mean ($n = 24$). There were no differences between the vegetation types for any of the substrates tested ($P < 0.05$).

Substrate	*Empodisma*	*Sporadanthus*
glucose	2.02 (0.65)	2.19 (0.48)
galactose	1.59 (0.41)	1.91 (0.48)
arabinose	2.89 (1.06)	2.10 (0.55)
xylose	1.35 (0.27)	1.46 (0.29)
sucrose	1.65 (0.46)	2.06 (0.30)
glycine	1.89 (0.36)	2.35 (0.46)
lysine	1.91 (0.56)	2.14 (0.42)
arginine	2.05 (0.46)	1.75 (0.55)
glutamic acid	1.70 (0.45)	1.60 (0.37)
benzoic acid	1.75 (0.50)	2.10 (0.59)
ferulic acid	1.72 (0.39)	1.31 (0.22)
couramic acid	1.08 (0.25)	1.32 (0.30)
water (basal respiration)	5.09 (0.73)	3.51 (0.46)

Table 5. Carbon dioxide (CO_2-C) fluxes (mg g^{-1}) after the addition of 12 carbon substrates and water, from peat in different hydrological zones at the Moanatuatua (degraded) and Kopuatai (intact) peatlands. Values in brackets represent the standard error of the mean ($n = 8$). The only statistically significant differences between hydrological layers observed for the two sites were for lysine; values with different letters are significantly different ($P < 0.05$). Values in bold were less than basal respiration (but differences were not statistically significant). Total substrate response is the sum of excess CO_2-C flux over basal respiration across all substrates, and again this did not differ between hydrological layers at these sites.

Substrate	**Moanatuatua**			**Kopuatai**		
	Dry	Fluctuating	Saturated	Dry	Fluctuating	Saturated
glucose	6.49 (1.76)	4.29 (1.52)	3.94 (1.03)	**3.28 (1.10)**	**3.13 (0.84)**	5.06 (0.86)
galactose	6.15 (1.52)	5.15 (0.97)	**3.28 (0.57)**	**4.12 (1.44)**	5.73 (1.36)	**3.59 (0.74)**
arabinose	7.81 (1.78)	6.35 (1.23)	6.56 (1.51)	**5.03 (1.30)**	5.11 (0.95)	**3.34 (0.88)**
xylose	**3.39 (1.06)**	4.64 (1.44)	4.20 (1.041)	**3.66 (0.96)**	**3.85 (0.79)**	4.67 (1.44)
sucrose	5.92 (1.59)	5.53 (1.04)	4.60 (0.93)	**4.95 (0.94)**	4.84 (0.82)	**3.49 (0.93)**
glycine	7.99 (1.22)	5.05 (1.13)	3.73 (0.54)	**5.45 (1.02)**	4.41 (0.78)	5.50 (1.37)
lysine	8.34 (1.57)b	3.48 (0.55)a	6.57 (0.80)ab	**4.38 (0.99)a**	**3.34 (0.81)a**	**4.82 (0.78)a**
arginine	7.43 (1.84)	6.77 (1.94)	3.74 (0.83)	**4.16 (0.88)**	**3.35 (0.75)**	**4.06 (1.23)**
glutamic acid	6.46 (1.51)	**3.45 (0.92)**	3.89 (0.38)	**4.89 (0.99)**	**3.46 (0.91)**	**3.65 (0.70)**
benzoic acid	6.37 (1.68)	4.75 (1.78)	4.46 (0.70)	**5.13 (1.23)**	**2.99 (0.79)**	**4.17 (1.11)**
ferulic acid	5.46 (1.57)	6.38 (1.85)	4.55 (0.49)	**3.43 (0.50)**	4.79 (1.00)	**3.81 (0.70)**
couramic acid	5.19 (1.60)	4.04 (1.36)	**2.83 (0.79)**	**4.03 (0.96)**	**3.64 (1.00)**	**1.90 (1.06)**
water (basal respiration)	4.73 (1.67)	3.45 (0.82)	3.53 (0.69)	5.87 (1.31)	3.90 (1.02)	4.33 (0.78)
Total substrate response	20.20 (9.31)	18.52 (10.16)	9.99 (9.33)	-17.89 (13.06)	1.78 (11.04)	-3.94 (5.53)

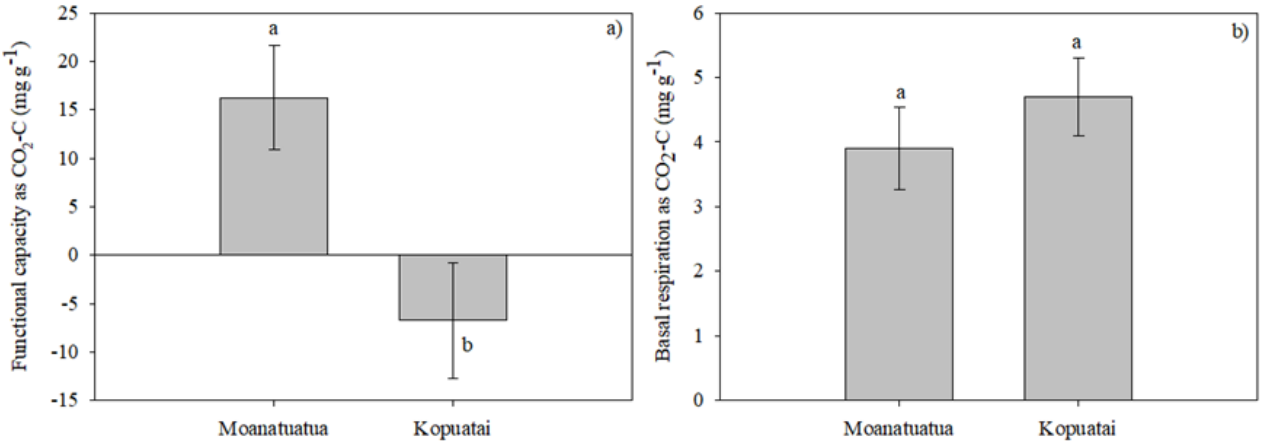

Figure 2. a) Microbial functional capacity and b) basal respiration at Moanatuatua (degraded bog) and Kopuatai (intact bog). Functional capacity was determined as total substrate respiration from multi-substrate induced respiration analysis. Error bars represent the standard error of the mean ($n = 24$) and bars with different letters within each panel are significantly different ($P < 0.05$).

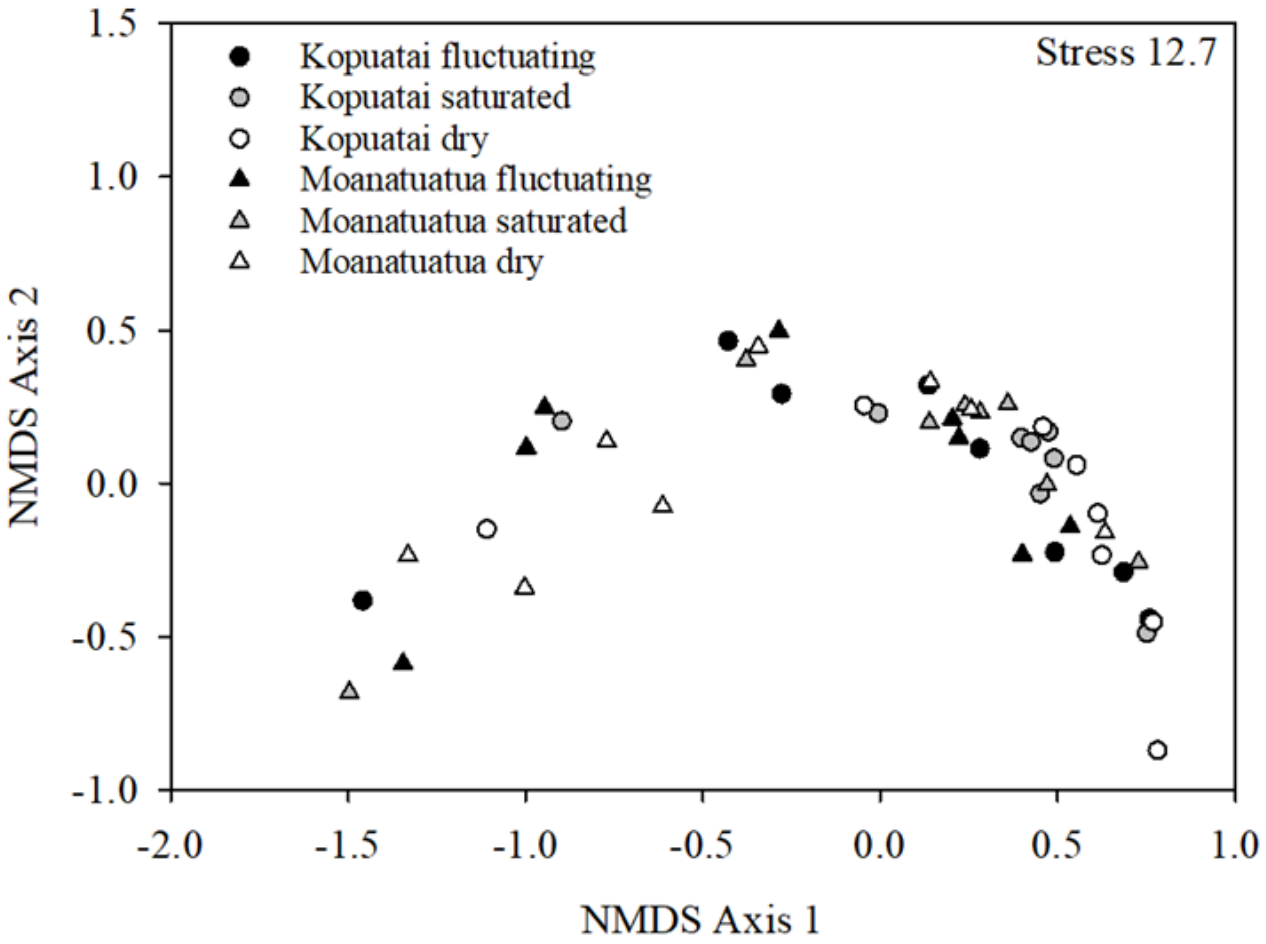

Figure 3. Two-dimensional non-metric multidimensional scaling (NMDS) plot of community-level physiological profiles in the dry, fluctuating and saturated zones at the Kopuatai and Moanatuatua peatlands. The stress value is a percentage.

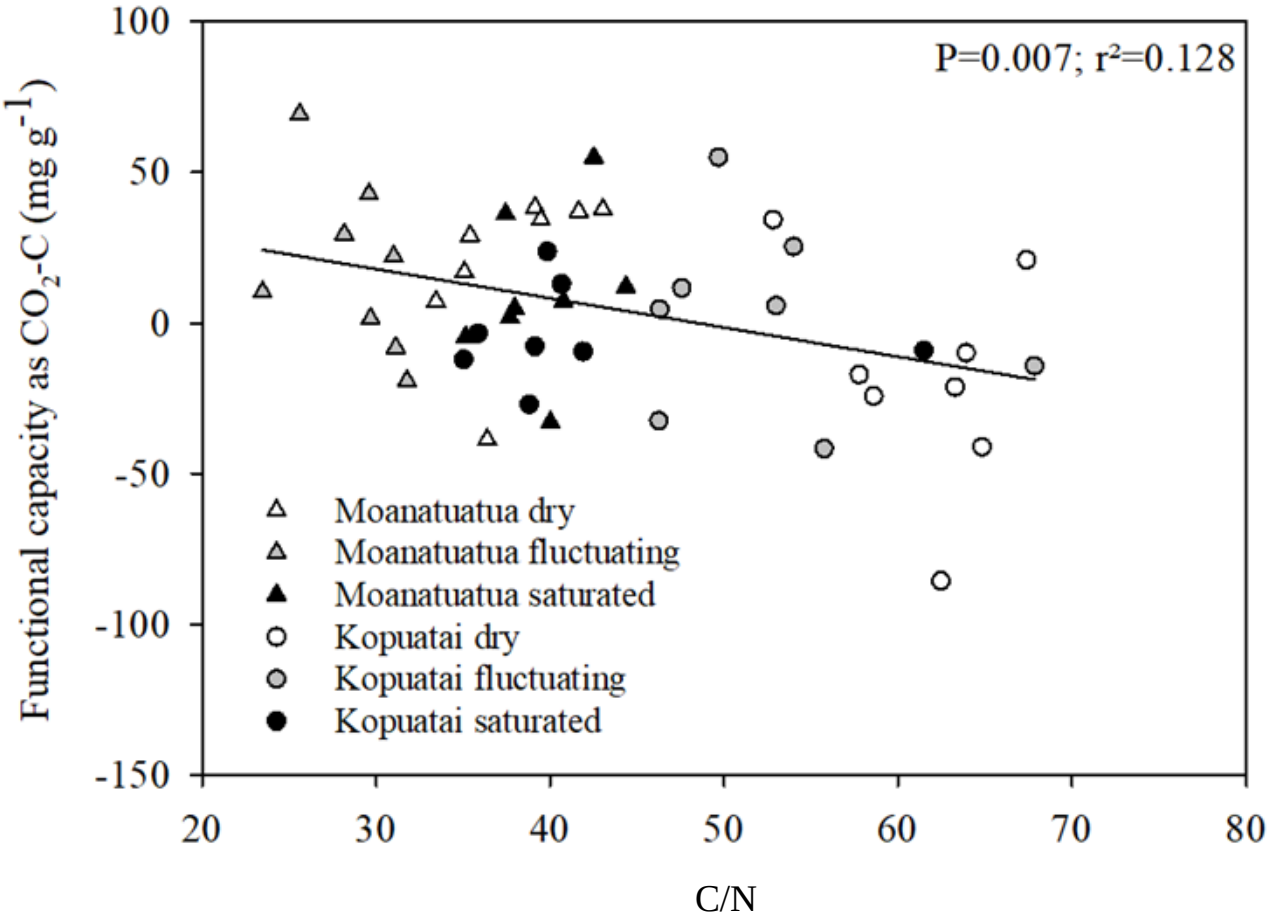

Figure 4. Linear regression analysis of functional capacity and C/N at the Kopuatai (grey circles) and Moanatuatua (black circles) peatlands.

(Figure 5), which explained variation ranging from 20 % to 33 %. Multivariate regression of combined pH and bulk density explained 66 % of the variation in AMN, and was the only multivariate combination that enhanced the single regression analyses.

DISCUSSION

Our assessment of biochemical and microbial factors in peat collected from different hydrological zones under *Epodisma* and *Sporadanthus* dominated vegetation in restiad bogs with contrasting agricultural pressures provided support for our hypothesis that the agriculturally affected Moanatuatua bog, with lower water table and elevated nutrients, would exhibit greater functional capacity than the intact Kopuatai bog. We also found support for the hypothesis that the fluctuating zone differs from the dry and saturated zones with respect to microbial function. The fluctuating zone also had some differences in chemical characteristics of the peat.

Bulk density was greatest in the dry and saturated zones at Moanatuatua compared to the equivalent zones at Kopuatai. Carbon density was also higher in these zones, most probably due to the higher bulk density. At Moanatuatua the lowest C/N value was seen in the fluctuating zone, which could reflect changes in plant composition or (perhaps more likely) the greater decay that can occur when peat undergoes rapid wetting and drying (Kuhry & Vitt 1996). Furthermore, CO_2 and DOC production can increase in peat undergoing alternating wet–dry cycles as would occur in fluctuating zones (Aerts & Ludwig 1997, Chow *et al.* 2006, Kechavarzi *et al.* 2007). However, we found no evidence to support this at Moanatuatua as, despite low C/N in the fluctuating zone, there was no discernible difference in mineralisable C or WSC compared to the dry and saturated zones.

Despite the increase in C density at Moanatuatua, there was a depletion of water-soluble C (WSC) compared with Kopuatai. N enrichment can increase C mineralisation by removing microbial N limitation (Bragazza *et al.* 2006, Wood *et al.* 2015) and by

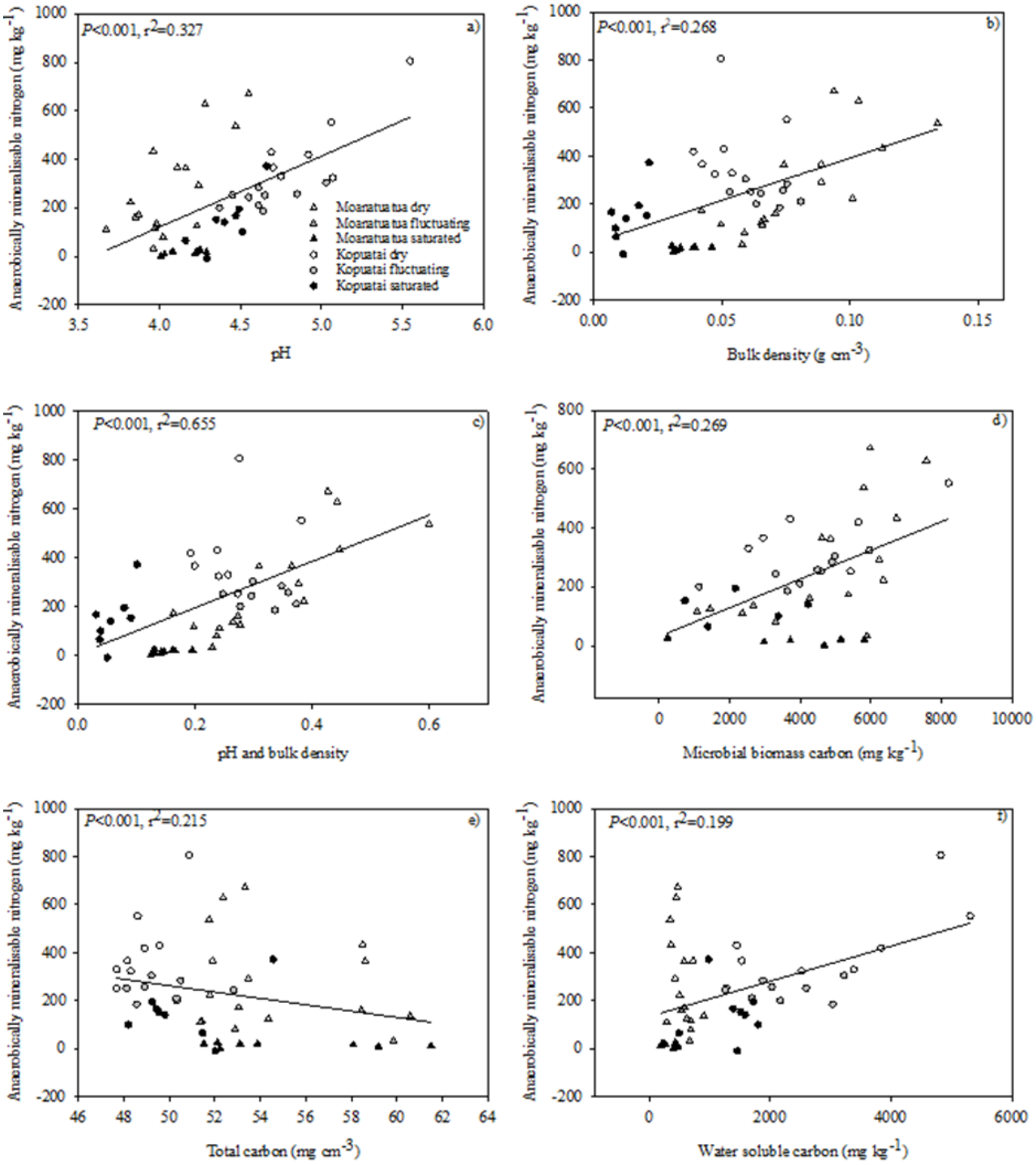

Figure 5. Linear regression analysis of anaerobically mineralisable nitrogen and a) pH, b) bulk density, c) pH and bulk density, d) microbial biomass carbon, e) total carbon and f) water-soluble carbon, at Moanatuatua (degraded peatland; triangles) and Kopuatai (intact peatland; circles).

enhancing enzyme activities (Pinsonneault *et al.* 2016), potentially contributing to higher turnover of peat and utilisation of WSC. Drainage can increase C export from peatlands in both aqueous and gaseous forms (Holden 2005, Worrall *et al.* 2006, Limpens *et al.* 2008, Hooijer *et al.* 2010, Frank *et al.* 2014, Hribljan *et al.* 2014, Laine *et al.* 2014) and this is consistent with greater ecosystem respiration from Moanatuatua, compared with Kopuatai (Ratcliffe *et al.* 2019). We therefore consider enhanced microbial utilisation to be the most likely explanation for reduced WSC. Moanatuatua also exhibited greater degradability of WSC, compared to Kopuatai, inferring that WSC would be more quickly

mineralised and potentially contribute to decreasing WSC. In a meta-analysis conducted by Vonk *et al.* (2015), increased N inputs were shown to increase the biodegradability of dissolved organic C in permafrost soils and aquatic sediments. Increases in N have been shown to enhance microbial respiration in some peatlands (Bragazza *et al.* 2006), and in more nutrient-rich sites peatlands tend to lose more C upon drying (Minkkinen *et al.* 2007, Sulman *et al.* 2010). Nitrogen enrichment can led to increased plant N contents, which can accelerate litter turnover (Morris 1991), and as vegetation N contents were higher at Moanatuatua than at Kopuatai (Clarkson *et al.* 1999), this may contribute to changes in WSC degradability. In contrast, Hribljan *et al.* (2014) reported that dissolved C was more recalcitrant in peat with a lowered water table under *Sphagnum*, however C inputs are likely to differ between the *Sphagnum* bogs they studied and the restiad peatlands in our study.

Previous measurements had indicated greater peat-N concentration at Moanatuatua than at Kopuatai (Clarkson *et al.* 2004), and it would appear that N enrichment has accelerated at Moanatuatua (Clarkson *et al*. 2020, Ratcliffe *et al*. 2020). Despite the higher total-N at Moanatuatua compared with Kopuatai, there was a significant depletion of ammonium in the dry and saturated zones. Decreased ammonium concentrations were also found by Björsne (2010) in a drained peatland compared to an undrained site, and were attributed to lower mineralisation. However, we found no support for this at Moanatuatua as AMN did not differ between the two sites. The fluctuating zone has been relatively well studied with respect to C cycling but has yet to be fully investigated with respect to N cycling, but it would appear that N mineralisation at Moanatuatua again differs between the fluctuating zone and the dry and saturated zones.

While Moanatuatua has experienced N enrichment and drainage, we found no indication of decreased N mineralisation (Table 2) compared with undrained peatland, as reported by Chapin *et al.* (2003) and Björsne (2010). In N rich peats, drainage can increase nitrification (Regina *et al.* 1996, Björsne 2010), generating nitrate that is leached to the saturated zone and subsequently lost as nitrous oxide (N_2O) via denitrification (Martikainen *et al.* 1993, Regina *et al.* 1996) or leaching, resulting in loss from the ecosystem (Daniels *et al.* 2012, Frank *et al.* 2014). However, Laine *et al.* (2013) found that fluctuations in the water table increased ammonium concentrations in previously undrained peat but showed no response in previously drained peat. The concentration of ammonium can be affected by seasonality (e.g. Sapek *et al.* (2007)), and it is particularly difficult to determine trends of ammonium concentrations in a one-off sampling. Therefore, we suggest further assessment of ammonium concentrations over time is required to more clearly elucidate the impacts of N enrichment and drying.

Moanatuatua had a greater, and above zero, functional capacity compared with a negative capacity at Kopuatai. This suggests that *r*-strategist microbes dominate at Moanatuatua, and respond rapidly to additions of easily degradable substrate, such as those from root exudates (Brouns *et al*. 2016). Negative functional capacity at Kopuatai occurred because substrate addition inhibited respiration. The reason for this was not identified within our work but may indicate increased stoichiometric stress for the *K*-strategists which predominate in near-pristine peatlands (Brouns *et al*. 2016).

Differences in functional capacity do not necessarily reflect differences in microbial composition (Preston *et al.* 2012). However, Moanatuatua has previously been found to contain a higher density of fungal decomposers than Kopuatai (Kuder *et al.* 1998). The MSIR technique used to determine functional capacity in these peats does not differentiate between bacterial-derived and fungal-derived C turnover; and whether the difference in fungal:bacterial ratio at the sites contributed to differing functional capacity is not known.

There was a very weak negative relationship ($r^2 = 0.128$) between functional capacity and C/N at our peatlands, suggesting that although N availability is probably not a primary driver of functional capacity, other factors that are known to correlate with C/N such as P availability or substrate quality may be the primary cause for the differences (Kuhry & Vitt 1996, Hamdan *et al*. 2012, Brouns *et al*. 2016). Furthermore, the rapid utilisation of C inputs, in concurrence with the substantial decrease in inherent WSC contents, may indicate C limitation at Moanatuatua, in contrast to Kopuatai, where higher WSC and a negative functional capacity would suggest that C alone is not limiting (e.g. Ye *et al.* 2014, Wyatt & Turetsky 2015).

Preston *et al.* (2012) found that peat pH was the best predictor of functional capacity, but we found no evidence of this at our sites. In fact, we found no evidence that any of the biochemical characteristics measured was a major predictor of functional capacity. Wakelin *et al.* (2014) found that phosphorus contents were correlated to functional capacity in pastures, pine forest and native forest soils, and may be a factor in peat bogs. Phosphorus contents at Moanatuatua are slightly elevated compared to Kopuatai (Clarkson *et al.* 2004) and may

have contributed to greater functional capacity at Moanatuatua but this requires confirmation. In contrast with functional capacity, AMN was predominantly predicted by peat pH and bulk density although the impact of P on AMN was not established within our work.

Community Level Physiological Profiles (CLPPs; Figure 3) are a visual representation of community-level functional capacity but showed no distinction between sites, vegetation types or hydrological zones in our study. This is in contrast to Fisk *et al.* (2003) and Yan *et al.* (2008), who found differences in CLPPs between plant species, vegetation types and peat depth. However, Yan *et al.* (2008) did not consider the hydrological conditions at each of their peat depths and it is difficult to determine how this may have affected their CLPPs. Artz *et al.* (2006) and Fisk *et al.* (2003) also suggest that CLPPs were related to the level of peat decomposition and the characteristics of the substrates available for microbial degradation, which requires further investigation at our sites. Clarkson *et al.* (2009) showed that *Sporadanthus* and *Empodisma* exhibit different mechanisms for N uptake, whereby *Empodisma* probably sources N predominantly from rainfall and *Sporadanthus* from peat degradation. However, whether these different mechanisms for sourcing N result in differing foliar N concentrations and litter degradation rates was not established. It is possible that the litter from our two restiad species were not sufficiently different for them to affect peat C and N cycling.

The mechanisms behind the differences in peat chemistry and microbial function between degraded and intact sites were not identified in our work. However, these could be elucidated by assessing microbial population dynamics and function in-situ over time, perhaps using a combination of water table depths, fertiliser applications and/or plant litter additions.

In conclusion, we found support for our hypothesis that pressure from agricultural practices increased functional capacity at drainage-affected Moanatuatua compared with the intact Kopuatai bog, but functional capacity showed at best only minor effects of the vegetation, soil biochemical and physical attributes measured. There is some indication that the two sites may differ with respect to microbial assemblage, which may be connected to differences in microbial function, but this requires further elucidation. The proximity to agriculture changed bog chemistry and biology which has important implications for C and N turnover in restiad peatland systems. In particular, the enhancement of functional capacity may decrease C sequestration in agriculturally affected peatlands due to a shift to a more dynamic microbial system which rapidly utilises new C inputs.

AUTHOR CONTRIBUTIONS

SL conceived the idea, contributed to experimental design and collection of field samples, undertook sample and statistical analysis, developed the manuscript and is lead author. JR contributed to experimental design, collection of field samples and development of the manuscript.

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Author for correspondence:
Dr Suzanne Lambie, Manaaki Whenua - Landcare Research, Private Bag 3127, Hamilton, New Zealand 3240.
Tel: +64 78593795; Fax: +64 78593701; Email: lambies@landcareresearch.co.nz