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RESEARCH ARTICLE

Organic matter decomposition in mountain peatlands: effects of substrate quality and peatland degradation

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Abstract

Background and Aims Peatlands occupy only 3% of Earth's terrestrial lands but store about one-third of global soil carbon. However, these large carbon stocks are currently under threat due to peatland degradation, where altered hydrological balance could enhance peat oxidation; thus releasing large amounts of CO_2 into the atmosphere. We investigated the interactive effects of substrate quality, peat depth and peatland degradation on the decomposition rate of organic matter in peatlands by way of a field incubation experiment.

Methods We incubated high-quality fresh peat and a lower-quality degraded peat substrate at three different depths (5, 15, and 30 cm) in two (intact and degraded) mountain peatlands for 18 months. Our results indicated that there is a significant interactive effect of substrate quality, peat depth, and peatland type on the peat decomposition rate.

Results The fresh peat showed significantly higher decomposition rates than the degraded peat substrate, likely due to the high percentage of bioavailable carbon in the fresh moss substrate. In the degraded peatland, fresh peat at 30 cm showed no mass loss during the incubation period, likely due to the high-water table creating anaerobic conditions. The fresh peat incubated in the intact peatland showed a higher decomposition rate than the same substrate incubated in the degraded peatland due to the comparatively lower water table in the intact peatland.

Conclusions Our findings indicate that the quality of the substrate being decomposed and the depth of the water table act as the main factors affecting the decomposition rate in mountain peatlands.

Keywords Water table depth · *Sphagnum* · Decomposed peat · Acrotelm · Aerobic decomposition · Bioavailable carbon

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Introduction

Peatlands are a type of wetland ecosystem that play an important role in the global carbon cycle. These ecosystems occupy less than 3% of Earth's terrestrial landscape (Xu et al. 2018) but store between 500 – 600 Pg of carbon, which accounts for one-third of global soil carbon (Poulter et al. 2021; Yu et al. 2010). Intact peatlands have an imbalance between carbon fixation via primary production and respiratory losses of carbon (Moore 1989), due to slow organic matter decomposition rates (Jackson et al. 2009; Malmer 1986; Yule 2010). The slow decomposition rates in peatlands have been attributed to cold temperatures in alpine and high latitude peatlands, high water table levels (water-saturated conditions) and consequent anoxia, high acidity, reduced activity of extracellular enzymes, low nutrient availability, decay-resistant litter types, and lack of availability of corresponding electron acceptors for microbial respiration (Andersen et al. 2013; Belyea 1996; Brouns et al. 2014; Clymo 1984; Fenner and Freeman 2011; Freeman et al. 1996; Knorr and Blodau 2009; Laiho 2006; Limpens et al. 2008; Philben et al. 2015; Williams and Yavitt 2003). The organic matter decomposition process, defined as the breakdown of organic matter through the metabolic activity of saprotrophic organisms that release gases (CO_2 and CH_4) or dissolved organic matter into the soil solution as decomposition products, plays a major role in carbon dynamics in all wetland ecosystems and is an ongoing process (Clymo 1984). The rate at which the organic matter decomposes is important as it affects the net carbon storage in peatlands and the rate of nutrient release and therefore, the amount of nutrients available for plant growth which in turn, affects primary production (Clymo 1984; Laiho 2006).

Among the major factors affecting organic matter decomposition rates in peatlands, substrate quality or the extent of decomposition of organic materials plays a major role (Laiho 2006; Pankratov et al. 2011). The ratio of alkyl carbon to O-alkyl carbon is considered a sensitive index for measuring extent of decomposition of organic material (assuming a common vegetational origin) (Baldock et al. 1997; Grover and Baldock 2012). From a chemical point of view, fresh litter, such as fresh *Sphagnum* moss litter, is very different from older, partly decomposed peat substrate (Gibson 2023). Fresh *Sphagnum* moss litter has a relatively high percentage of easily decomposable, cellulose compounds and is relatively depleted in macronutrients such as nitrogen (N), phosphorus (P), and sulphur (S) (Van Breemen 1995), while mature, partially decomposed *Sphagnum* peat has a relatively high concentration of chemically complex, lignin-like recalcitrant compounds (Grover and Baldock 2012; Hilasvuori et al. 2013; Laiho 2006). Furthermore, the decomposition process of *Sphagnum* moss produces pectin-like compounds including uronic acid and sphagnan that have tanning properties, which immobilize the extracellular enzymes influencing the decomposition process (Børsheim et al. 2001; Hájek 2009; Hájek et al. 2010).

Studies have found that the decomposition rate of organic matter changes with the changing vertical depth of the peat (Beer and Blodau 2007; Bonaiuti et al. 2017). *Sphagnum* decomposition can be conceptualised as occurring in two phases: in the first phase climate, nutrient and carbon availability of the substrate and the solubility of constituent components control the decomposition rate (Verhoeven and Liefveld 1997). In the second phase, lignin-like recalcitrant compounds control the peat decomposition rate (Van Breemen 1995; Verhoeven and Liefveld 1997). The first phase of decomposition occurs in the upper aerated layer (acrotelm) of the peatland, which is the principal matter and energy exchange site (Ingram 1978). About 80–90% of the easily decomposable organic matter dry mass is estimated to be lost at a fast rate in this first phase (Clymo 1984; Frolking et al. 2001; Malmer and Holm 1984). The remaining recalcitrant organic matter is incorporated into the deeper, waterlogged, anaerobic layers (catotelm) below the water table level, where slow anaerobic decomposition causes additional carbon loss through methanogenesis and sulphate reduction (Clymo 1984; Wieder et al. 1990). The C:N ratio of peat increases with increasing peat depth, due to differential loss of carbon, mainly as CO_2 and CH_4, occurs compared to nitrogen (Drollinger et al. 2019; Wang et al. 2015). Furthermore, the oxygen availability as the primary terminal electron acceptor decreases with increasing peat depth (Boonman et al. 2024), while the availability of alternative electron acceptors including nitrate (NO_3^-), manganese (Mn(IV)), ferric iron (Fe(III)), or sulfate (SO_4^{2-}) are limited in peatlands (Boonman et al. 2024; Dettling et al. 2006). As a

result, a vertical gradient of abiotic environmental factors such as temperature, moisture and substrate quality, combined with biotic factors such as soil biota community composition, occurs in peat soil profiles (Beer and Blodau 2007; Bonaiuti et al. 2017; Krab et al. 2010; Wright et al. 2009). Furthermore, seasonal fluctuations of the water table lead to changes in the position of the boundary between aerobic and anaerobic layers (Zhou et al. 2020), thus affecting peat microbial activity and decomposition rates at different depths (Brake et al. 1999; Strack and Waddington 2007).

The rate of organic matter decomposition in peatlands is also affected by the peatland's degradation status (Strack et al. 2008), such that the vulnerability of organic matter to decomposition can increase with the increasing degree of decomposition and decreasing soil organic carbon content (Säurich et al. 2019). Disturbances resulting from anthropogenic activities such as human-induced drainage, land-use changes, peat extraction and dry conditions associated with climate warning (Preston et al. 2012, Blodau and Moore, 2003, Laiho 2006, McCarter and Price, 2014) can alter the hydrological and physicochemical properties of peatlands. Changing peatland properties can in turn accelerate organic matter decomposition rates and subsequent CO_2 emissions and carbon loss as dissolved organic carbon (Beer et al. 2008, Strack et al. 2008, Meunpong et al., 2020, Jauhiainen et al., 2005). The decomposition rate of fibrous peat can be accelerated by increasing temperature and oxygen availability, enhanced nutrient supply and decreasing C:N ratio (Frolking et al. 2001, Pichan and O'Kelly, 2012, Pichan and O'Kelly, 2013). As a result, degraded peatlands can rapidly release stored carbon into the atmosphere (Freeman et al. 2001). Once the decomposition rate exceeds net primary production, the peatland becomes a net carbon source to the atmosphere (Laiho 2006). Some studies have recognised that peatlands dominated by *Sphagnum* moss species have a particularly effective mechanism for restricting enzyme-mediated decomposition, where oxygen constraints associated with waterlogging suppress the activity of phenol oxidase enzymes (Beer et al. 2008; Freeman et al. 2001). However, drainage induced water table drawdown, for example due to severe drought, could disrupt this balance, thus enabling carbon loses as CO_2 to the atmosphere (Fenner and Freeman 2011; Freeman et al. 2001).

The individual and interactive effects of peatland degradation, substrate quality, and the changing environmental conditions and microbial communities with peat depth on the peat decomposition process are of particular interest to understanding the carbon cycle in peatlands and how it may be affected by climate change-induced environmental changes. Nevertheless, given the complex nature of the decomposition process, the interactive effects of these factors on peat decomposition rates remain poorly understood. Furthermore, the peat decomposition process in degraded peatlands is more complex than in intact peatlands, due to unstable underlying processes in degraded peatlands. To the best of our knowledge, this study is one of the first to investigate the on-site peat decomposition rate in two representative intact and degraded peatlands. To our knowledge it is also the first to do so in an Australian mountain peatland, which have been understudied in comparison with boreal and temperate peatlands elsewhere. Therefore, we aimed to investigate the interactive effects of peat depth, substrate quality, and land-use related peatland degradation on the peat decomposition rate of *Sphagnum* moss-dominated mountain peatlands. To this end, we conducted a long-term field incubation experiment by incubating mesh bags filled with substrate of differing quality (fresh and degraded peat substrate) in an intact and a degraded peatland, at three different depths. We hypothesised that: i) fresh peat will decompose faster than degraded peat substrate, ii) the rate of decomposition will decrease with increasing peat depth due to changing environmental conditions, and iii) the peat incubated in the degraded peatland will decompose faster than the peat incubated in the intact peatland.

Materials and methods

Site description

Two peatland sites, one intact and one degraded (~ 10 km apart), were selected from the Bogong High Plains of the Alpine National Park, Victoria, Australia. The Bogong High Plains is an elevated plateau of about 120 km^2 and consists of alpine and subalpine landscapes with mosaics of peatland, closed and open heathland, tussock grassland, and snow gum forest ecosystems (McDougall and Walsh 2007). The

Bogong High Plains are primarily underlain by gneiss and schist with some volcanic outcrops and isolated pockets of fluvial deposits along the major river courses (Morand 2005). Australian alpine peatlands are typically *Sphagnum* moss (*Sphagnum cristatum*) dominated ecosystems and form where groundwater seeps to the surface (Wahren et al. 1999). These peatlands are characterized by treeless, closed heath vegetation with hummock, hollow, and lawn formations. Other major species in peatlands include *Dracophyllum continentis* (previously: *Richea continentis), Empodisma minus, Baeckea gunniana,* and *Astelia alpina*. *Empodisma minus* is also a peat forming plant species, especially a maker of relic peat in some mountain peatland systems (Clarkson et al. 2004).

The sites have a sub-polar oceanic climate (Cfc; Köppen Climate Classification) with cool summers and cold, snowy winters (Beck et al. 2018). The temperature of the sites varies between a mean annual maximum of 9.5 °C and a minimum of 2.7 °C (BOM 2023). The average annual precipitation of the sites is 2434 mm, with the majority of this being snowfall. The highest snowfall occurs from June to October, with typically three months of continuous snow cover. Alpine ecosystems in the study area have a long seven-month growing season, from the end of September snowmelt to late April (Venn and Morgan 2009).

The post-European colonisation, anthropogenic disturbance history of the region is one dominated by cattle grazing and fire, with tourism, invasive floral and feral faunal incursions and climate change now adding to pressures on these ecosystems (McDougall and Walsh 2007). All of the Bogong High Plains were subjected to cattle grazing from early 1800's until 1994 (Lawrence 1995), with most parts still grazed until the summer of 2004/2005 (McDougall 2007). Frequency of fires in Bogong High Plains has increased in recent years; fires burned across the Bogong High Plains in 1926 and 1939 and some parts were burned in 2003 (McDougall 2007), 2006, and 2019 (Tolsma 2020).

Intact peatland site

The intact peatland, known as Heathy Spur 1 (HS-1) (-36°51′44''S, 147°19′15″ E, 1765 m a.s.l), is a 5-ha valley peatland that developed in a poorly drained, low relief plateau. The peatland system receives water from several exposed groundwater sources, and discharge of these sources ranges from seepage to sustained annual flows (Silvester 2009). The peat layer is mainly peaty organosols of thickness ranging from 75–120 cm (Gunawardhana et al. 2021) with underlying Ordovician meta-sedimentary rocks, Devonian granites, and minor Tertiary basalts (Vandenberg et al. 2004). A cross-section of the peatland to a 30 cm depth is shown in Fig. 1a. The peatland had a 62% *Sphagnum* coverage in 2018 (TERN 2018), and the average canopy height of the vegetation during the peak growth stage is 0.3 m (Gunawardhana et al. 2021). The peatland has been subject to fires in the distant past, but as per the vegetation and peat soil

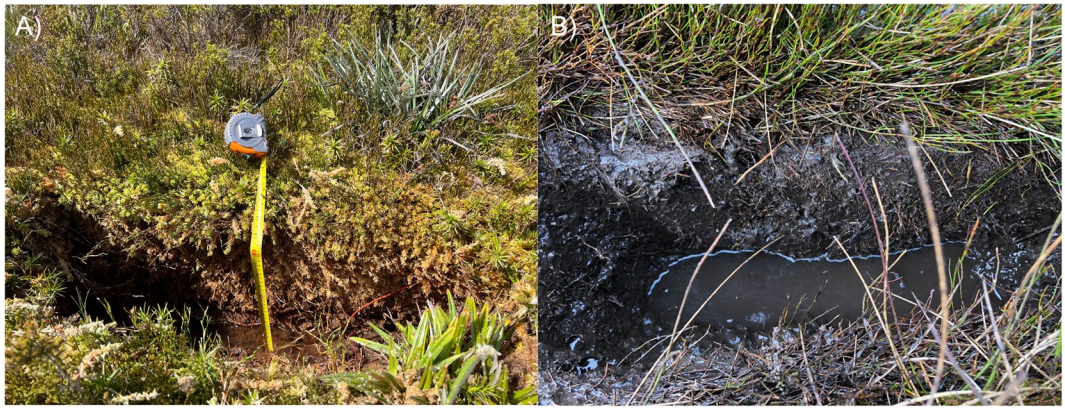

Fig. 1 Cross-sections of one of three replicate pits dug in (a) intact and (b) degraded peatlands. Each pit was 30 cm in depth from the peat surface and water table of both peatlands is visible in the images

metric survey by Whinam et al. (2003), the peatland is currently considered to be in intact condition.

Degraded peatland site

The degraded peatland, known as Cope Saddle Hut peatland, (36° 55′ 40.4″ S 147° 15′ 35.6″ E, ~ 1654 m a.s.l) lies in a valley bottom on the Bogong High Plains. The peatland is located in the headwaters of a stream catchment that supplies water to the Bundara River and is underlain by metamorphic migmatite rocks. A later intrusion of small Paleogenic basalt through the migmatite layer restricts the downward water flow, creating the peatland. The peatland is approximately 7 ha in area and is bordered by two aqueducts on the east and west sides, which divert water flow to a nearby reservoir (Pretty Valley Dam) for hydroelectricity generation. In addition, a walking track and a gravel road for management vehicles also run through the peatland, restricting water flow into and through the peatland. The majority of the Cope Saddle Hut peatland comprises degrading peatland and the peat in these sections is mainly dark, moderately decomposed fibrous material (Fig. 1b). The vegetation is mostly dominated by *R. continentis* and *E. minus* species with a low abundance of *Sphagnum* moss. The sections of the peatland that are closer to the road are dominated by grass species such as *Poa* spp. Peat depth at this site varies between 10 – 50 cm. There are some intact peatland sections with *Sphagnum*-dominated hummocks, mainly in the centre of the peatland, where the peat depth can reach up to 120 cm.

Field incubation experiment

The field incubation experiment was carried out by incubating mesh bags containing peat of two different substrate qualities (fresh and degraded) at 5, 15, and 30 cm depths in the intact peatland and in the degraded peatland for 18 months. Monitoring the mass-loss of organic matter is one of the simplest yet most effective methods to determine the overall decomposition rate of organic matter in a peatland (Haraguchi et al. 2002). In this method, mesh pore size should be large enough for microbial decomposers to enter but small enough to retain the peat material (Bragazza et al. 2008); we used mesh bags with pore size of 200 µm. The mass loss of the organic material inside the mesh bag represents the *in-situ* decomposition rate (Domisch et al. 2000; Haraguchi et al. 2002; Latter et al. 1997), while the use of different substrate types can help elucidate the effect of substrate quality on decomposition rate (Laiho 2006).

The two peat types used in the incubation experiment were collected from the 0 – 5 cm layer of the Cope Saddle Hut peatland. The fresh substrate was collected from *Sphagnum* moss hummocks of the peatland, while the degraded peat substrate was collected from areas with degrading peat moss. Three random samples of each substrate type were collected, and two composite samples (one for fresh and one for degraded peat substrate) were prepared by mixing 250 g of peat from each set of three random samples (Online Resources, Fig. S1). Leaves, roots, and other large identifiable pieces of plant material were removed during the sample preparation, and aggregates > 10 mm were broken into < 5 mm pieces. The fresh substrate was cut into < 20 mm pieces using clean scissors, and a sub-sample from both substrates was stored below 4 °C prior to allow quantification of the initial water content and oven dry mass (Online Resources 1). We measured 5 ± 0.005 g of substrate into each rectangular nylon mesh bag (5.8×7 cm). The open end of each bag was folded and manually sewn closed with nylon thread. A second nylon thread was attached to one corner of each mesh bag and tied to a numbered wooden stake to aid identification and later retrieval. Seventy-two mesh bags were prepared for each of the two substrate types, totalling 144 bags.

In the Heathy Spur-1 peatland and the degraded sections of the Cope Saddle Hut peatland, we dug pits ($70 \times 15 \times 30$ cm) with minimal disturbance to the long-side edge and marked 5, 15, and 30 cm depths. Four small cuts were made on either side of each depth-marking stake (total 24 cuts), and the mesh bags were inserted horizontally into each cut without coming into contact with each other (Fig. 2). The fresh peat mesh bags were incubated on the one side of the pit and the degraded peat mesh bags were incubated on the other side (Fig. 2). Three replicate pits were prepared in each peatland (Table 1), and the pits were back-filled with the removed peat.

The mesh bags were all buried at the beginning of winter (May 2021) and were retrieved at four different times: November 2021 (total incubation time = 5 months over winter and spring); January 2022 (total incubation time = 8 months over

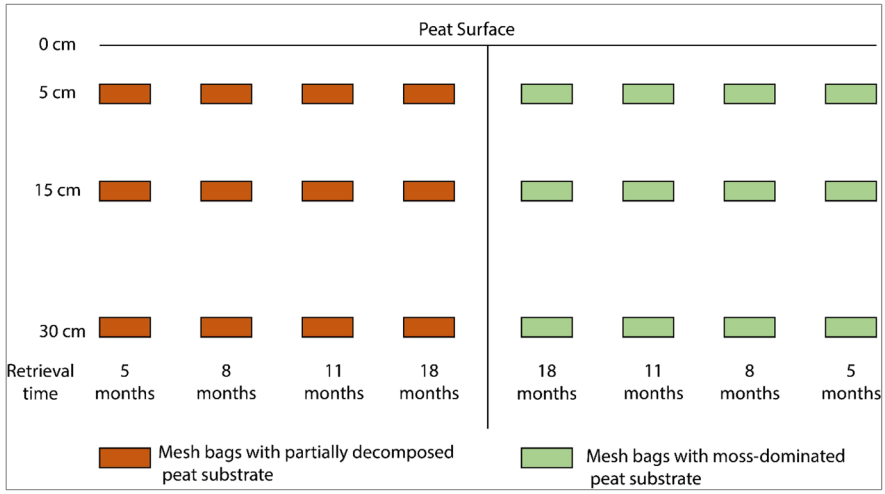

Fig. 2 Experimental design of the buried field mesh bags in a pit. Three replicate pits were made in each peatland (intact and degraded). Each coloured symbol marks the depth and time at which 9 bags were retrieved (3 replicate bags from each of the three pits)

Table 1 The total peat soil depth at the places of three replicate pits in the intact and degraded peatland

Peatland	Replicate pit	Peat depth (cm)
Intact Heathy Spur-1	A	60
	B	70
	C	120
Degraded Cope Saddle Hut	A	43
	B	35
	C	30

winter, spring, and summer); April 2022 (total incubation time = 11 months over winter, spring, summer, and autumn); and November 2022 (total incubation time = 18 months over winter, spring, summer, autumn, and a second winter and spring). At each time, a set of 6 mesh bags, three fresh peat and three degraded peat, were retrieved from each replicate pit (Fig. 2). Controls (mesh bags containing 3 g ashless filter paper cut into < 10 mm pieces) were buried at the same depths in November 2021 and retrieved after 5 months in April 2022 (Online Resources, Table S1). The purpose of incubating control mesh bags was to confirm that there was a weight loss due to decomposition, rather than the leaching of materials. Upon retrieval, mesh bags were put in separate zip lock bags and transported and stored below 4 °C prior to measuring dry weight loss in the laboratory.

The mesh bags were thoroughly cleaned in the laboratory using forceps, scientific delicate-use wipes, and a small paintbrush to remove plant roots and any peat attached to the outside of the bags. We removed the nylon threads from the mesh bags and oven dried them at 105 °C for 24 h. Nine out of 144 mesh bags were removed from the analysis as they increased in mass compared to their initial weight; likely due to roots growing into the bags or silt moving through the mesh and getting trapped inside. While it is possible that influx of silt could occur in any mesh bag without resulting in a net weight gain (Belyea 1996) it was assumed that the observed mass loss in all other bags was not impacted by slit influx. The stored 5 g subsamples of the initial peat substrates were oven dried at 105 °C for 24 h to determine the amount of dry mass (W_0) in 5 g of fresh peat substrate. The decomposition rate of the peat substrates (and control) mesh bags was calculated using the following equation.

$$DR = \frac{\left(\frac{(W_i - W_b) - (W_o - W_b)}{W_i - W_b} \times 100\%\right)}{D}$$

where DR is the decomposition rate of the peat substrate (% dry mass loss/day), W_i is the oven-dry weight of the initial substrate (g), W_b is the weight of the empty mesh bags, W_0 is the oven-dry weight of the mesh bags after field incubation (g), and D is the number of days of field incubation.

Measurements of the water table depth

The depth of the water table was measured in each replicate during the initial peat incubation as well as each mesh bag retrieval occasion, using a tape

measure to measure the distance between the peat surface and the top of the water table. During both the initial mesh bag incubation and subsequent meh-bag retrieval occasions, the water table depths of all the replicate pits were measured prior to mesh bag incubation and retrieval, respectively. Given the design of our experimental setup, where the t4 mesh bag was set in the centre of the pit and t1 at the end, we only had to re-excavate the two corners of each pit for mesh bag removal. This way, we were able to minimise the disturbance to peat soil and remaining mesh bags.

Carbon chemistry of the peat substrate

The carbon chemistry of two sub-samples each of fresh peat and degraded peat was analysed by solid state Cross Polarisation Magic Angle Spinning ^{13}C Nuclear Magnetic Resonance (CP/MAS NMR) spectroscopy using an Agilent 500 MHz spectrometer (Agilent, USA). The NMR spectrum was integrated over eight spectral regions and the signal intensities within these regions were combined to determine the contribution of eight carbon functional groups. The NMR data processing, including phasing, baseline correction, and spectra integration, was conducted using the Advanced 1D NMR 12 Processor software (ACD, Version 12). We calculated the alkyl/O-alkyl ratio by dividing the area of the alkyl region (0 – 45 ppm) by the area of the O-alkyl region (45–110 ppm). The alkyl/O-alkyl ratio is a parameter that is widely used to characterize peat soils as it represents the extent of decomposition, where the organic material has a common vegetational origin (Baldock et al. 1997; Grover and Baldock 2010; 2012).

Statistical analysis

We used multivariate permutational ANOVA (PERMANOVA, (Anderson 2001) to investigate the effects of site (intact vs degraded, fixed effect), substrate quality (fresh vs degraded peat, fixed effect), depth (5 vs 15 vs 30 cm, fixed effect) and time (5 vs 8 vs 11 vs 18 months, fixed effect) on the decomposition rate of peat samples. The rate of dry mass loss per day was tested using a four-way interactive term including site, substrate quality, depth, and time. Pair-wise tests were conducted to investigate the effects of significant terms in the main four-way test. PERMANOVA is a non-parametric multivariate statistical permutation test, used to test the simultaneous response of one or more variables to one or more fixed and/or random effects. It uses an analysis of variance (ANOVA) experimental design for the analysis on the basis of any resemblance measure, using permutation methods (Anderson et al. 2008). We used PERMANOVA to accommodate the experimental design having four factors and unequal sample size between replicates. The analysis was conducted using PRIMER (V6) & PERMANOVA + (Massey University, Auckland, New Zealand) software. We did not use any data transformation techniques, given the normally distributed nature of the data set ($P = 0.15$, Shapiro–Wilk test), and we used 999 permutations for the analysis with Type III (partial) sums of squares. The permutation method used was permutation of residuals under a reduced model and we used Euclidean distance as the resemblance measure for all tests. We applied a significance level of 0.05 for all the tests. The pair-wise tests were also conducted using 999 permutations with Type (III) partial sums of squares under a reduced model, while fixed effects were summed to zero in the interactions. We also calculated decay constant (k) values for both fresh and degraded substrate incubated at each 5, 15, and 30 cm depths in both intact and degraded peatlands.

Results

Changes in peat decomposition rate with time

The results of the field incubation demonstrate that the decomposition rate was significantly affected by the interaction between site, substrate type and time ($P = 0.003$, Online Resources, Table S2). The decomposition rate of the fresh peat in the intact peatland gradually declined over time, with the decomposition rate during the first five-month incubation period (which included a winter and spring snow melt event) being significantly higher than in the other incubation periods ($P = 0.001$, Online Resources, Table S3 – S8) (Fig. 3A). In contrast, the decomposition rate of degraded peat incubated in the intact peatland did not change during the entire 18-month incubation period. In the intact peatland, the fresh peat decomposed

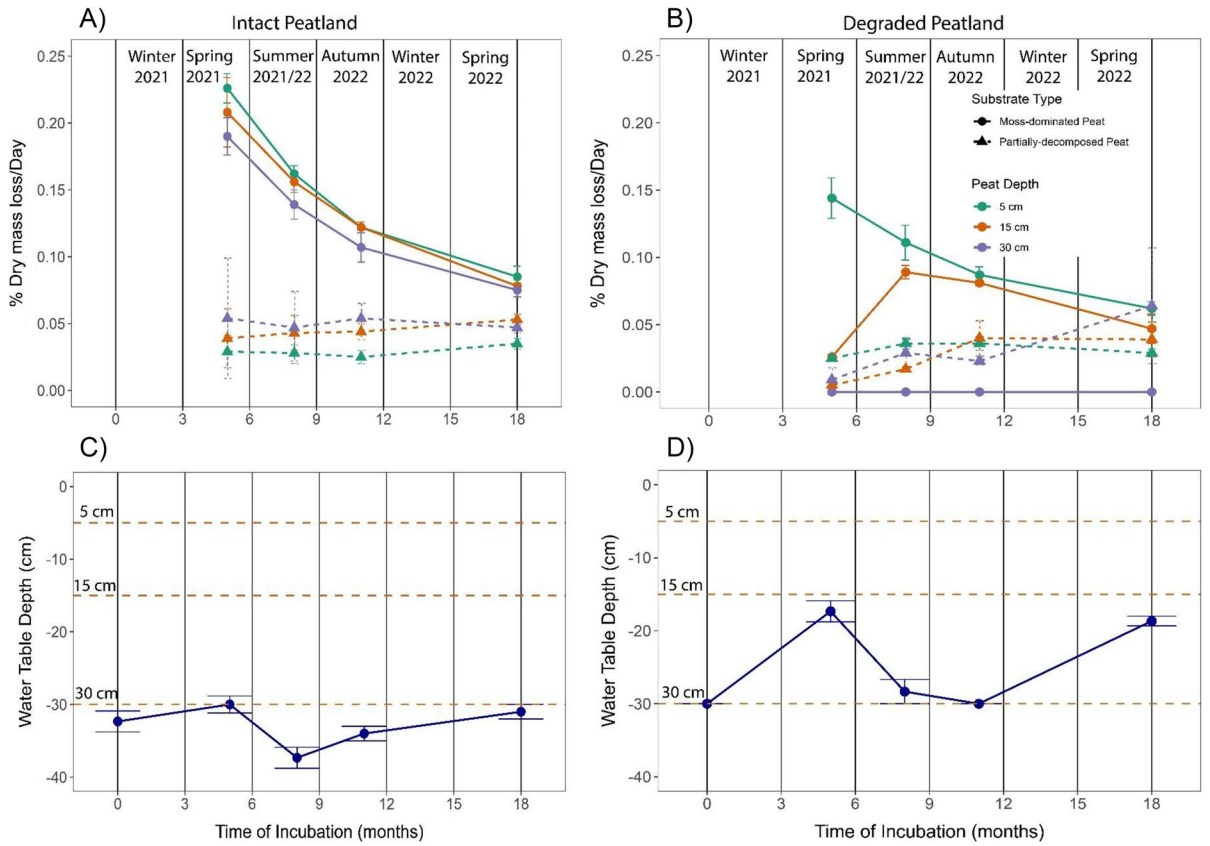

Fig. 3 Decomposition rate of fresh and degraded peat in intact (A) and degraded (B) peatlands with incubation time at each incubation depth, shown as mean values with standard error bars. The water table depth measured at the time of incubation and each retrieval time for intact (C) and degraded (D) peatlands, shown as mean values (of all three replicates) with standard error bars

significantly faster than the degraded peat throughout the incubation period ($P=0.001$) (Fig. 3A).

In the degraded peatland, the fresh peat at 30 cm depth did not decompose at all during the 18-month incubation period (Fig. 3B). The decomposition rate of the fresh peat at 5 cm depth gradually declined with time, while at 15 cm depth, the decomposition rate was slowest during the first incubation period (Fig. 3B). The decomposition rates of degraded peat in the degraded peatland were significantly slower during the first incubation period than during all subsequent incubation periods (Fig. 3B). Fresh peat in the degraded peatland decomposed significantly faster than decomposed peat during the first three incubation periods. However, in the fourth incubation period, the decomposition rate of fresh peat slowed to comparable rates to the degraded peat ($P=0.7$) (Fig. 3B).

In the intact peatland, the fresh peat decomposed significantly faster than the same substrate incubated in the degraded peatland throughout the incubation period ($P=0.001$ for all incubation periods). However, the degraded peat substrate decomposed at a similar rate in both the intact and the degraded peatland throughout the incubation period ($P=0.33$, 0.31, 0.41, and 0.86 for 5, 8, 11, and 18-month periods, respectively) (Fig. 3).

The water table was both closer to the surface and more variable in the degraded peatland (Fig. 3D) than in the intact peatland (Fig. 3C). In the intact peatland, the water table remained between 30 and 38 cm below the surface throughout the incubation period, with the lowest water table observed in summer (Fig. 3C). In the degraded peatland, the water table varied between 17 and 30 cm below the surface, with maximums each spring (Fig. 3D).

Average peat decomposition rate

The results of the field incubation demonstrate that the average decomposition rate over the whole 18-month incubation was significantly affected by the interaction between site, substrate quality and depth ($P=0.005$, Table S2). Particularly noteworthy is that, in the intact peatland, fresh peat decomposed significantly faster than the degraded peat at all three depths (Fig. 4A). The fresh peat incubated in the intact peatland had significantly different decomposition rates at 5 and 30 cm depths ($P=0.005$), while the rate of decomposition did not differ between 5 and 15 cm or between 15 and 30 cm depths ($P=0.29$ and 0.18 respectively) (Fig. 4A). The degraded peat incubated in the intact peatland decomposed at significantly different rates between 5 and 15 cm depths ($P=0.02$), but not between 5 and 30 cm or between 15 and 30 cm depths ($P=0.23$ and 0.84, respectively). The calculated k values support these results (Online Resources, Table S10, Fig. S2 and S3).

In the degraded peatland, the fresh peat incubated at 5 cm depth decomposed significantly faster than the same substrate incubated at 15 and 30 cm depth (Fig. 4B). The fresh peat incubated at 15 cm depth decomposed significantly faster than that incubated at 30 cm depth, where no decomposition occurred (Fig. 4B). In contrast, the rate of decomposition of the degraded peat was not significantly different between the three depths in the degraded peatland (5 and 15 cm $P=0.3$, 5 and 30 cm $P=0.9$, 15 and 30 cm $P=0.7$) (Fig. 4B). Furthermore, the fresh peat decomposed significantly faster than degraded peat at 5 and 15 cm depth in the degraded peatland ($P=0.001$ and 0.003 respectively), while at 30 cm depth, degraded peat substrate decomposed significantly faster than the fresh peat, which did not decompose at all ($P=0.001$) (Fig. 4B).

In the intact peatland, the fresh peat decomposed significantly faster than the fresh peat incubated in the degraded peatland at all three depths ($P=0.05$, 0.05, and 0.03 at 5, 15, and 30 cm depths respectively) (Fig. 4). In contrast, the degraded peat substrate decomposed at the same rate in the intact peatland and in the degraded peatland at 5 and 30 cm depth ($P=0.6$ at 5 cm and $P=0.4$ at 30 cm), while at 15 cm, the degraded peat substrate decomposed somewhat faster in the intact peatland ($P=0.013$) (Fig. 4). All control mesh bags showed a weight loss after incubation (Online Resources, Table S1), confirming there is a weight loss due to decomposition, rather than leaching.

Characterisation of peat substrate quality

The ^{13}C NMR results showed that there was more O-alkyl carbon in the fresh substrate than in the degraded substrate. Furthermore, the amount of aromatic carbon (including Aryl and O-aryl carbon) considerably increased from fresh to degraded peat, while carbonyl and amide carbon and ketone carbon was also higher in degraded peat than fresh peat (Online Resources, Table S9). The alkyl/O-alkyl ratio of the fresh peat was smaller (0.14) than the alkyl/O-alkyl ratio of the degraded peat (0.44), clearly demonstrating the difference in substrate quality.

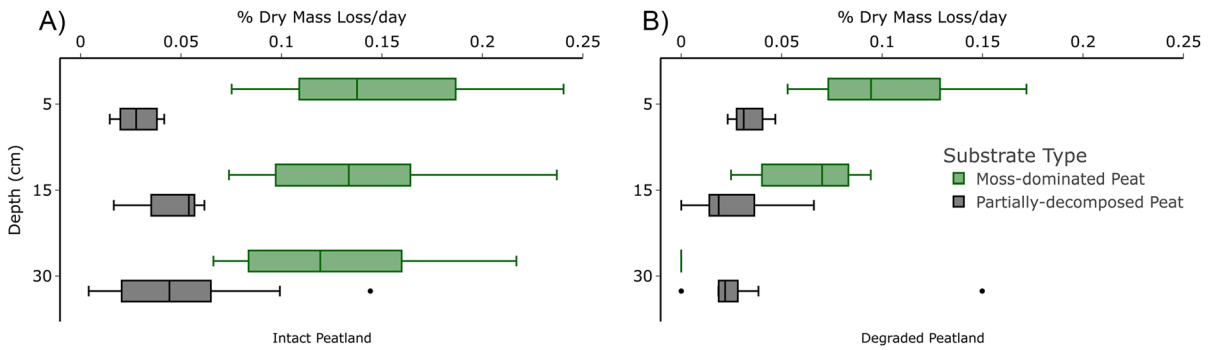

Fig. 4 Average decomposition rates of fresh peat substrate and degraded peat substrate incubated at 5, 15, and 30 cm depth in A) the intact peatland and B) the degraded peatland over the 18 month incubation period (n = 135). Each bar represents the average decomposition rate of all the mesh bags that were incubated at each depth throughout the entire incubation period

Discussion

Effects of peatland degradation status on the peat decomposition rate

In contrast to our hypothesis that peat incubated in the degraded peatland would decompose faster than the peat incubated in the intact peatland, the fresh peat decomposed significantly faster in the intact peatland than in the degraded peatland. This could be due to the difference in water table depth (Gorecki et al. 2021; Lieffers 1988) and peat structure (Drzymulska 2016; Sinsabaugh 2010) between intact and degraded peatlands. All the mesh bags incubated in the intact peatland were above the water table throughout the incubation period (Fig. 3) and were within the *Sphagnum* moss layer that has high porosity (low bulk density) (Treby and Grover 2023) and favourable environmental conditions such as oxygen for aerobic microbial decomposition (Clymo 1984; Lieffers 1988; MacFarlane and Williams 2015). In contrast, the degraded peatland was devoid of a high porosity *Sphagnum* moss layer due to anthropogenic disturbances, and therefore, the mesh bags were incubated within a moderately decomposed and dense peat layer (Jayasekara et al. In preparation) with high bulk density (Treby and Grover 2023). Moreover, the water table of the degraded peatland varied between 17 – 30 cm below the surface (Fig. 3), creating anaerobic conditions that would have prevented aerobic peat decomposition (Fenner and Freeman 2011; Freeman et al. 2001) at the 15 and 30 cm incubation depths, while in the intact peatland all 3 depths were likely aerobic as they were above the water table. Previous studies have shown that, microbial richness at an intact peatland acrotelm was higher than in the degraded peatland acrotelm in the Victorian Alps, which was attributed to *Sphagnum* moss being a more labile carbon substrate and the intact peatland vegetation providing more root exudates for microbial activity (Birnbaum et al. 2023). Given that peat incubated in the intact peatland likely experienced more favourable conditions for decomposition (Birnbaum et al. 2023; Grover and Baldock 2010; Treby and Grover 2023) than in the degraded peatland, it is not surprising that the decomposition rate of fresh peat at the intact peatland was higher than the degraded peatland. Similar to our study, Grover and Baldock (2010) observed more decomposition in peat incubated *in-situ* in an intact peatland (termed bog peat) than peat incubated in a degraded peatland (termed dried peat), attributed to the combined effects of environmental conditions and substrate quality. They also found a significant effect of depth and substrate quality but no interaction between these two variables within the intact peatland (Grover and Baldock 2010). In contrast to our study, both Lieffers (1988) and Domisch et al. (2000) observed faster rates of peat decomposition in degraded peatlands than in intact peatlands, attributed to a lower water table in the degraded peatland.

Effects of substrate quality on the peat decomposition rate

Fresh peat decomposed significantly faster than degraded peat in both the intact peatland and in the degraded peatland, confirming that our first hypothesis was correct. This is likely due to the differences in substrate quality, particularly the percentage of labile carbon, between the two substrates. *Sphagnum* moss contains more O-alkyl carbon, primarily as cellulose, that is readily decomposed in soils, while alkyl carbon is selectively preserved (Baldock and Preston 2006). Our ^{13}C NMR analysis showed a higher percentage of O-alkyl carbon in the fresh substrate (80%) than in the degraded peat substrate (54%) (Online Resources, Table S9). A lack of labile carbon limits heterotrophic microbial activity in decomposed peat substrates, reducing the rate of decomposition (Beer and Blodau 2007; Bonaiuti et al. 2017; Wright et al. 2009). According to Chimner and Ewel (2005), fresh organic materials decompose faster while recalcitrant organic materials decompose slower and contribute more to the peat formation process. Grover and Baldock (2012) also observed higher O-alkyl carbon in fresh peat (termed bog peat) compared to degraded peat (termed dried peat) in an Australian alpine peatland. Furthermore, Limpens and Berendse (2003) observed higher mass loss in young *Sphagnum* stems than in old stems, which they attributed to high N availability in the young *Sphagnum* stem substrate.

In our study, the fresh peat decomposed significantly faster during the first incubation period than in the subsequent incubation periods. The amount of bioavailable carbon in substrate is highest at the beginning of the incubation, and other studies have found that microbes rapidly decompose bioavailable

carbon within a short time (Haraguchi et al. 2002; Latter et al. 1997; Turetsky et al. 2008). Once the labile carbon has been consumed, the remaining recalcitrant carbon is consumed by microbes more slowly over a long period of time (Laiho 2006), at which stage environmental factors such as temperature and water availability become the main factors controlling the decomposition rate (Nikonova et al. 2019; Turetsky et al. 2008). Similar to this work, Latter et al. (1997) observed rapid peat decomposition during the early stages of incubation, attributed to nutrient release from substrate being at a maximum at the beginning of an incubation. Haraguchi et al. (2002) also observed a rapid dry mass loss during the first month of the incubation period, suggesting that labile compounds are available for microbial utilization immediately after mesh bag placement within the peatland. Nikonova et al. (2019) suggests that the rapid decomposition observed during the first year of their incubation experiment was due to a high percentage of water soluble and easily hydrolysable substances in fresh substrates, which are consumed first by microbes.

We found that the rate of decomposition of the degraded peat substrate did not change significantly over time or between the intact and degraded peatland environments. This finding is attributed to the recalcitrant nature of the degraded peat, as documented in our NMR results and work by others on similar peatlands (Grover and Baldock 2010; 2012). Degraded peat lacks labile carbon for microbial decomposition (Serk et al. 2022) and therefore substrate quality acts as a limiting factor for microbial decomposition (Grover and Baldock 2010). The slow decomposition rate of the degraded peat substrate indicates that the recalcitrant organic material that remains in these degraded peatlands is now relatively stable. In addition, the very low decomposition rates of the degraded peat in the intact peatland indicates that even under favourable environmental conditions such as high oxygen availability and the surrounding high-quality (base-rich) organic materials of the intact peatland (Aerts 1997; Grover and Baldock 2010), the low bioavailability of the substrate acts as a limiting factor for peat decomposition. This finding aligns with the proposition by Aerts (1997) that the main controls of the rate of decomposition shift from climatic at a global scale to substrate quality at regional scales.

Effects of changing peat depth on the peat decomposition rate

Our second hypothesis, that the rate of decomposition will decrease with increasing peat depth due to changing environmental conditions, was confirmed by our results in the degraded peatland but contradicted by our results in the intact peatland, and this is attributed to water table depth. In the intact peatland, the decomposition rates of both fresh and degraded peat did not differ with depth and the reason behind this could be that all three burial depths were within the intact peatland acrotelm (Birnbaum et al. 2023; Grover and Baldock 2010). The acrotelm of the intact peatland by definition has good oxygen supply (Liu et al. 2016) and a recent study on a similar Australian alpine peatland found high microbial abundance and diversity in the acrotelm (Birnbaum et al. 2023), which would facilitate rapid aerobic decomposition of peat substrates (Liu et al. 2016). These favourable environmental conditions for aerobic microbial decomposition exist throughout the acrotelm (Clymo 1984; Freeman et al. 1996). Furthermore, in *Sphagnum* peatlands elsewhere, the highest microbial diversity has been observed above 30 – 40 cm depth (Lamit et al. 2017; Lin et al. 2014). Similar to our study, Belyea (1996) observed similar dry mass losses down to around 20 cm depth in two peatlands, attributed to the similar environmental conditions such as oxygen supply and high microbial abundance and diversity. In addition, Wiedermann et al. (2017) observed rapid cellulose and *Sphagnum* decomposition with a lowering of the water table, while Williams and Yavitt (2003) observed more rapid peat decomposition above the water table, which both attributed to favourable environmental conditions. Moreover, Moore et al. (2007) observed decreased decomposition rates from 10 to 30 cm depth, as mesh bags at 10 cm were above the water table while mesh bags at 30 cm depth were below the water table in their study.

In the degraded peatland, fresh peat substrate incubated at 30 cm depth did not measurably decompose during the incubation period, which is likely due to the mesh bags being below the water table. The water table in the degraded peatland varied between 17 – 30 cm during the incubation, thus mesh bags buried at 30 cm depth were below the water table throughout the incubation period. The mesh bags buried at 15 cm

depth mirrored the effects of water table depth, where the decomposition rate increases with the lowering of the water table (Fig. 3). Anoxic conditions inhibit aerobic microbial activity and facilitate slow anaerobic microbial activity (Belyea 1996; Fenner and Freeman 2011; Freeman et al. 2001; Frolking et al. 2010). According to Moore et al. (2007), mesh bags incubated at 10 cm depth and below the water table for the whole incubation period only had a very small mass loss due to inundation. Furthermore, findings by Schellekens et al. (2012) showed little cellulose decomposition under water inundated and anaerobic conditions. In addition, Nikonova et al. (2019) also observed low decomposition rates in mesh bags incubated near the water table level in a bog, attributed to regularly changing anaerobic and aerobic conditions resulting from water table fluctuations.

The degraded peat incubated at 30 cm depth in the degraded peatland did loose mass during the incubation period and this could be due to abiotic processes (rather than biotic decomposition) such as leaching (MacDonald et al. 2018). Inundation could cause transportation of soluble materials away from buried mesh bags (MacDonald et al. 2018) and physical erosion of particles finer than the mesh, due to bulk water movement through the mesh bag that could transport small peat particles (Belyea 1996; Clymo and Mackay 1987). Limpens and Berendse (2003) also observed evidence of physical leaching during their incubation study, due to water movement or consumption or removal by soil invertebrates. It is possible that the degraded peat lost some fine particles through the mesh and thus the observed mass loss may not be due to biologically-mediated decomposition within the bag (Cotrufo et al. 2010; MacDonald et al. 2018). Clymo (1965) demonstrated that physical losses due to erosion of particles out of mesh bags from *Sphagnum* moss substrate was minimal, which could explain why mass loss was not observed in the fresh substrate.

Implications for peatland management

Overall, our results indicated that degraded peat decomposes more slowly than fresh peat, while higher water table levels in the degraded peatland further reduce the decomposition rate. These results have implications for peatland conservation and restoration. Raising the peatland water table in degraded peatlands either by blocking drainage ditches or constructing bunds or terraces, is a common hydrological restoration method in peatland management (Price et al. 2003; Zak and McInnes 2022). While some investigations into the effects on peat decomposition rates of such restoration have identified that artificially elevated water table levels reduce peat decomposition rates and CO_2 emissions (Planas-Clarke et al. 2020; Tarvainen et al. 2012), other studies have observed no difference (MacDonald et al. 2018) or enhanced decomposition rates (Basiliko et al. 2007). These observed differences in decomposition rates may be related to differences in how soon the studies were conducted after the restoration was first applied, the level of degradation prior to applying restoration, or differences in peat substrate quality, nutrient availability, or microbial biomass and activity (Basiliko et al. 2007; Kareksela et al. 2015; Lucchese et al. 2010; Schimelpfenig et al. 2014). However, our study suggests that increased water table levels are effective in reducing the decomposition rate of degraded peatlands and thus have the potential to reduce CO_2 emissions from degraded mountain peatlands (Planas-Clarke et al. 2020; Schimelpfenig et al. 2014). Therefore, we suggest that elevation of water table levels could be effective in minimising decomposition rates and reducing CO_2 emissions from degraded mountain peatlands.

Conclusions

In conclusion, we found that substrate quality and the depth of the water table are the two most important factors affecting the rate of peat decomposition in intact and degraded *Sphagnum* moss mountain peatlands. We suggest that further research could usefully explore the interactive effects of changing substrate quality, temperature, and moisture regimes on peat decomposition rates, in order to better understand the fate of mountain peatlands and manage the restoration and conservation of these important carbon, water and biodiversity resources as the climate continues to change.

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Author Contributions The conceptualisation and design of this study was mainly done by Charuni Jayasekara, Samantha Grover and Catherine Leigh. Material preparation, data collection, and analysis were performed by Charuni Jayasekara, under the supervision and advise from Samantha Grover, Catherine Leigh, Jeff Shimeta, and Ewen Silvester. The first draft of the manuscript was written by Charuni Jayasekara, and all authors commented on all versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated and analysed during the current study are available in the Online Resources provided and further information can be obtained from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no competing interests to declare that are relevant to the content of this article.

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