BOREAL ENVIRONMENT RESEARCH 23: 221–235
ISSN 1797-2469 (online)

Helsinki 17 August 2018

Using the Tea Bag Index to characterize decomposition rates in restored peatlands

Erin MacDonald[1], Martin E. Brummell[2,*], Aneta Bieniada[1], James Elliott[1], Alexandra Engering[1], Tasha-Leigh Gauthier[1], S. Saraswati[1], Sabrina Touchette[1], Laurence Turmel-Courchesne[3] and Maria Strack[1]

[1)] *Department of Biological Sciences, University of Alberta, 116 St & 85 Ave, Edmonton, Alberta T6G 2R3, Canada*
[2)] *Department of Geography and Environmental Management, University of Waterloo, 200 University Avenue, West Waterloo, Ontario N2L 3G1, Canada(*corresponding author's e-mail: martinbrummell@gmail.com)*
[3)] *Département de Phytologie, Université Laval Pavillon Paul-Comtois 2425, rue de l'Agriculture Québec, Québec G1V 0A6, Canada*

Received 19 Aug. 2017, final version received 6 Apr. 2018, accepted 6 Apr. 2018

MacDonald E., Brummell M.E., Bieniada A., Elliott J., Engering A., Gauthier T.-L., Saraswati S., Touchette S., Turmel-Courchesne L. & Strack M. 2018: Using the Tea Bag Index to characterize decomposition rates in restored peatlands. *Boreal Env. Res.* 23: 221–235.

Peatlands characteristically accumulate organic matter due to low decomposition rates, but peatland disturbance alters local physicochemical conditions often resulting in loss of soil organic matter and emission of CO_2. Restoration may reduce peat oxidation, but traditional measurements of decomposition are time-consuming. The Tea Bag Index (TBI) is a simple, standardized method to measure decomposition rates in soils. We used the TBI to measure decomposition rate at four restored peatland sites across Canada that were used for peat extraction or disturbed by oil extraction (former well-sites), comparing to undisturbed and unrestored sites. We measured environmental conditions including soil temperature, water table position and peat pH from May to August 2016. Litter bags were buried for one year alongside tea bags at one site for a direct comparison of decomposition rates between the methods. There were no significant differences for TBI decay constant (k_{TBI}) between treatments of restored, unrestored or undisturbed sites across the whole data set, but some differences were found among treatments within the same peatland site for sections restored at different times in the past. Soil temperature, pH, and water table were not significantly related to k_{TBI}, but were negatively correlated with the stabilization factor (S). The k_{TBI} and litter bag k were significantly different but positively correlated. The TBI is not easily comparable to traditional litter bags, but is less costly in both time and money, and may be used in conjunction with additional parameters to determine decomposition patterns with potential for use as a metric for evaluating restoration outcomes.

Introduction

Decomposition is the breakdown of organic material completed through the metabolic activity of saprotrophic organisms that may release decomposition products as gases, such as CO_2, or as dissolved organic matter into soil solution (Laiho 2006). Decomposition is important for

Editor in charge of this article: Sari Juutinen the storage and recirculation of nutrients within ecosystems (Didion *et al.* 2016), and is strongly regulated by environmental conditions such as temperature, substrate and moisture availability (Laiho 2006). Peatlands have waterlogged conditions that often inhibit microbial activity and reduce the rate of decomposition, leading to the accumulation of organic matter (Belyea 1996, Freeman *et al.* 1996). Local conditions including water content, temperature, and pH play large roles in determining decomposition rates (Preston *et al.* 2012), which can be altered by landscape disturbance such as peatland extraction.

Peatlands represent important soil carbon stocks, but many peatlands around the world have been disturbed by resource exploration and extraction (Strack *et al.* 2016). Disturbances to peatlands can alter hydrological and physiochemical conditions, usually accelerating the rate of organic matter decomposition and increasing the release of carbon dioxide (CO_2) to the atmosphere (Lucchese *et al.* 2010). Ecological restoration is the process of assisting the recovery of a disturbed ecosystem (Clewell and Aronson 2007), and by comparing biogeochemical functioning of natural, restored, and unrestored peatland sites, restoration has been demonstrated to ameliorate some of the negative effects of disturbance (Nwaishi *et al.* 2015, Strack *et al.* 2016). As decomposition of plant material is a key process for the release of CO_2 in terrestrial soils (Davidson and Janssens 2006), assessing rates of decomposition post-restoration can provide information on the return of peatland function. Generally, natural peatlands act as a source of methane (CH_4) but a sink for CO_2, both of which are potent greenhouse gases. Methanogenesis, the bacterial production of CH_4, proceeds under anaerobic conditions typical of peatlands, though the total amount and radiative forcing of CH_4 is often outweighed by net carbon sequestration (Bridgham *et al.* 2013, Page and Baird 2016). Decomposition processes in peatlands are expected to include release of CH_4 and marginal amounts of CO_2, though we do not include direct measurements of these gas fluxes.

A common method for estimating decomposition rates is to use litter bags, which are mesh bags filled with plant material that are buried, retrieved, and weighed to determine the residual mass loss over a specific time, often two years or more (Moore 1984, Moore and Basiliko 2006). Litter bags are typically filled with local vegetation, which can hinder comparison between study sites due to the ambiguity of environmental conditions versus litter characteristics (Keuskamp *et al.* 2013), since vegetation characteristics affect measured rates of decomposition comparable to shifting environmental factors (Straková *et al.* 2012, Péli *et al.* 2016, Wiedermann *et al.* 2017). Additional characteristics such as the amount of litter used, length of burial and litter bag construction can vary greatly between studies, further complicating cross-site comparisons. Furthermore, litter bag construction is time-consuming and difficult to scale up to larger studies, so Keuskamp *et al.* (2013) have proposed the Tea Bag Index (TBI) as a method to solve these issues by using a widely available, standardized and pre-constructed tea bags.

The TBI allows for the compilation of decomposition rates that are directly comparable across sites by using commercially produced tea bags as a substitute for litter bags (Keuskamp *et al.* 2013). The TBI uses green tea, a more labile material that decomposes at a faster rate, as well as rooibos tea, a more recalcitrant material (Keuskamp *et al.* 2013). The difference in decay between the two tea types allows the TBI to estimate the decomposition rate constant (k_{TBI}) from a single burial time interval of approximately 90 days, which is a much shorter time period compared to the two or more years recommended for traditional litter bags (Moore 1984, Moore and Basiliko 2006, Keuskamp *et al.* 2013). An additional parameter, the stabilization factor (S), is included to account for any deviation from the actual decomposition rate that may occur when labile material stabilizes into more recalcitrant material (Keuskamp *et al.* 2013). Measuring k_{TBI} and S will provide insight into decomposition rates at post-restoration peatlands and may act as a simple metric of restoration outcome that could be easily deployed by land managers.

The objectives of this study are to: (1) estimate the decomposition rates of restored peatlands using the TBI while also contributing to the global map of k_{TBI} and S values, (2) evaluate potential environmental controls (water table position, soil temperature, peatland type, peat pH) on TBI estimated parameters, (3) compare the k_{TBI} results with decomposition rates determined by the traditional litter bag method, and (4) determine if the TBI can identify differences between peatland restoration treatments that may be used to evaluate restoration success. We hypothesized that decomposition rates would be lowest at natural sites due to functioning peat accumulation, intermediate at restored sites due to wetter conditions, and highest at the unrestored sites due to dry and disturbed conditions. We also hypothesized that patterns of TBI estimated decomposition rates would be similar to those measured with traditional litter bags.

Materials and methods

Study sites

This study includes four disturbed peatlands across Canada, with two peatlands in the province of Alberta, one in Manitoba, and one in Quebec. Three of the four peatlands had peat extracted for horticultural purposes, while one peatland in Alberta had a mineral soil pad installed to support oil extraction. All four peatlands were restored following disturbance and are described in greater detail below. The ecosystem-scale restoration process generally involves levelling the peatland, then filling or blocking the drainage ditches to allow accumulation of precipitation to raise the water level. A common re-vegetation method is to transfer donor material from the top 10 cm of a nearby natural (i.e., undisturbed) peatland, following the moss layer transfer technique (Rochefort *et al.* 2003, Graf *et al.* 2012). Sites were assessed for pre-disturbance status as either ombrotrophic bog or minerotrophic fen by using aerial photographs that predate peat extraction land clearing, where available. A space-for-time analog was used where photos were not available, by using adjacent natural areas to examine peat characteristics. Both methods followed the classification guidelines for peat with high contents of graminoid litter judged to be derived from a fen, while peat dominated by *Sphagnum*-derived material indicated a bog. The differences between bogs and fens is evident in environmental characteristics such that bogs are disconnected from local groundwater, have lower pH and lower available nutrients than fens (Bourbonniere 2009), where fens receive at least some nutrient-rich groundwater and support more vascular plants (Chimner *et al.* 2017).

The Bois-des-Bel (BDB) peatland (47.9671°N, 69.4285°W) is a forested bog located in the Bas-Saint-Laurent region of Quebec. An 11.5 ha section of the peatland was drained in 1972, extracted for horticulture from 1973 to 1980, then abandoned until 1999. Restoration was started in fall 1999 and completed in fall 2000 for approximately 7.5 hectares of the peatland. A 1.8 ha section was left unrestored (BDBU) and was separated from the restored area (BDBR) by a buffer strip. The natural (i.e. undisturbed) (BDBN) portion of the Bois-des-Bel peatland was located approximately 2 km away from the restored site.

The Seba Beach (SB) peatland (53.458°N, 114.884°W) is a bog/fen complex located near Seba Beach, Alberta. The peatland complex had approximately 30 ha that were restored in 1991 (SB1991), 2009 (SB2009), and 2012 (SB2012) following extraction. For restoration, the ditches were filled with peat (or simply blocked, as at SB1991) and donor material was added from a nearby treed ombrotrophic bog for re-vegetation. Extraction, but not restoration beyond blocked ditches, was completed at the unrestored site (SBU); some spontaneous re-vegetation has occurred in the form of scattered *Eriophorum vaginatum* individuals growing on bare peat and invasion of the site at the edges by young birch (*Betula papyrifera*). A natural (i.e. undisturbed) forested bog nearby was used as the natural site (SBN). All sites at Seba Beach were considered bogs pre-disturbance based on the use of *Sphagnum* peat for horticultural peat extraction.

The Peace River (PR) peatland (56.397°N, 116.890°W) is a forested, moderately-rich fen located near Peace River, Alberta. A mineral well-pad was placed on top of the peatland for oil extraction, but drilling never occurred. Approximately 1.4 ha of the peatland was restored in 2012 (PRR) by removing the well-pad and inverting the underlying peat, then donor material collected from nearby fens was added on top. As the entire well-pad was restored, there was no unrestored treatment at this site, but nearby natural (i.e. undisturbed) bogs and fens were used as the natural sites (PRN).

The South Julius (SJ) peatland (49.931°N, 96.238°W) is a shrubby, rich fen located near Elma, Manitoba. The peatland was drained and the surface was levelled, removing the previous vegetation, but commercial extraction never occurred. Approximately 8 ha of the peatland was re-wetted by filling and blocking the drainage ditches in 2006 (SJR). A disturbed, but unrestored site (SJU) was included, a site that resembles the unrestored site at Seba Beach and consists mainly of bare peat, as well as a natural (i.e. undisturbed) sedge-dominated rich fen (SJN).

Tea Bag Index

The TBI uses Lipton green tea (EAN: 87 22700 05552 5) and rooibos tea (EAN: 87 22700 18843 8) in tetrahedron synthetic bags, with a side length of 5 cm and a mesh size of 0.25 mm (Keuskamp *et al.* 2013). The tea bags were labelled and the initial weight was recorded to 0.001 g using an analytical balance. Tea bags were not dried before weighing. Pairs of tea bags (one green and one red bag constitute a replicate) were shipped to the study sites and buried at a depth of approximately 8 cm below peat surface. Determining the height of the ground surface in a peatland can be difficult, thus tea bags were placed 8 cm below the apparent line of transition from green living material to brown, probably non-living material. There were 17 replicates buried in BDB, 20 in PR, 29 in SB, and 20 in SJ (Table 1). The tea bags were buried in late May or early June 2016, and then retrieved after approximately 90 (67 to 100) days in August or September 2016. The tea bags were removed and stored frozen at –20 °C until they were shipped back to the University of Waterloo for analysis, except at BDB where bags were dried in the on-site facility using the same procedure. Following the procedure described in Keuskamp *et al.* (2013), thawed tea bags were dried in an oven at 60 °C for 48 hours, and any remaining soil or other foreign particles were removed. The bags were re-weighed and the mass loss was calculated based on the initial weight. Stabilization factor (*S*) and decomposition rate constant (k_{TBI}) were calculated using the program provided by TBI research team (available from http://www.teatime4science.org).

While the decomposition rate calculated by the TBI is based on the mass lost from the tea bags during their time in the ground (Keuskamp *et al.* 2013), the stabilization factor may not be as easily understood. Briefly, *S* accounts for the transformation of some components of the tea bags from fast-decomposing molecules into slow-decomposing molecules; these components are said to be stabilized (Prescott 2010, Keuskamp *et al.* 2013). High values of *S* indicate

Table 1. Sites and their mean (SE) soil temperature, water table depth, and peat pH. n.m. = not measured. BDB pH data from (Strack *et al.* 2015) and SB Natural from Murray *et al.* 2017.

Site and pre-disturbance peatland type	Site (*n*)	Soil temperature (°C)	Water table depth (cm)	Mean
BDB	Natural (6)	18.5 (0.08)	–18.7 (1.0)	4.13 (0.39)
Bog	Unrestored (5)	n.m.	n.m.	6.06 (0.22)
	Restored (6)	19.2 (0.08)	–48.1 (1.7)	5.86 (0.52)
SB	Natural (6)	14.8 (0.42)	–32.4 (2.8)	4.34
Bog	Unrestored (5)	17.5 (0.48)	–35.6 (4.3)	n.m.
	1991 (3)	17.0 (0.52)	–6.4 (1.5)	n.m.
	2009 (4)	15.8 (0.33)	–14.3 (2.4)	5.25
	2012 Wet (6)	14.6 (0.28)	–11.7 (1.4)	5.02 (0.07)
	2012 Dry (5)	16.9 (0.76)	–45.3 (2.4)	4.53 (0.32)
PR	Natural (8)	13.1 (1.0)	–1.3 (2.0)	5.63 (0.16)
Fen	Restored (12)	17.8 (0.59)	–9.6 (1.2)	5.62 (0.06)
SJ	Natural (10)	19.2 (0.47)	8.6 (0.94)	6.74 (0.11)
Fen	Unrestored (4)	18.3 (0.44)	–11.6 (1.2)	6.29 (1.07)
	Restored (6)	18.1 (0.62)	20.2 (1.2)	6.37 (0.20)

inhibition of decomposition, typically attributed to factors such as low pH or anoxia that are expected to slow decomposition of the tea.

Environmental conditions

The soil temperature was measured biweekly from May to August 2016 using an Omega HH200A temperature probe at depths of 5 and 10 cm below the soil surface at individual burial sites in PR, SB, and SJ. These soil depths were measured as part of the measurements of greenhouse gas fluxes also undertaken at these sites; the mean of the two measurements was used to estimate soil temperature at the position of the tea bags. At BDBR and BDBN, thermocouple wires were installed at a depth of 5 cm below the soil surface to measure soil temperature hourly in combination with an automatic data logger (CR1000, Campbell Scientific, Edmonton, Canada). The water table was measured biweekly from May to August 2016 at individual burial sites in PVC wells in all treatments from PR, SB, and SJ, but only from the restored and natural sites at BDB. Peat was collected from SB2009, SB2012, PR, and SJ at positions within a few metres of the buried tea bags then prepared for pH analysis by adding 5 g of field-wet peat to 10 ml of deionized water, shaking for 1 minute and allowing the mixture to settle for 1 hour. The pH was measured using a Pocket Pro+ Multi 2 Tester (Hach, Loveland, CO, USA) that was calibrated following the manufacturer's instructions before it was inserted into the peat solution. Estimates of pH at BDB and SBN were taken from Strack *et al.* (2015) and Murray *et al.* (2017), respectively.

Litter bags as comparison

At SB2012, traditional litter bags were buried alongside the tea bags to compare methods. The litter bags were prepared using nylon screen with a nominal mesh size of 1 mm, side length of approximately 9 cm, filled with 4–6 g of plant material collected from the site and dried in an oven at 60 °C for at least 24 hours. The litter bags were filled with one of four plant species that were common at SB2012: *Agrostis scabra*, *Calamagrostis canadensis*, *Carex canescens,* and *Eriophorum vaginatum*. The initial weight of the bag with the plant material was recorded. Triplicate bags for each plant species were buried at two sample sites that were previously estimated to be either wet or dry (Brummell *et al.* 2017), for a total of 24 litter bags. The litter bags were buried at a depth of 5–8 cm below the soil surface and were retrieved after one year on 22 August 2016. The litter bags were then shipped to the University of Waterloo and stored at –20 °C until analysis. The litter bags were dried in an oven at 60 °C for 48 hours and any remaining soil or foreign particles were removed. The final weight of the litter bags was recorded and the mass loss was calculated based on the initial weight of the plant material. The annual decomposition rate constant k (Olson 1963) for the litter bags was calculated using a single exponential decay function $k_t = \ln(M_i/M_f)$, where k is the estimated decomposition rate, M_i is the initial mass of the plant material, M_f is the mass of the plant material remaining after burial, and t is the time (in years) (Olson 1963, Moore 1984, Hagemann and Moroni 2015, Péli *et al.* 2016). The mean decomposition rate for the litter bags was calculated for each plant type in both the wet and dry section, and then expressed as a rate of mass loss per day to compare to the decomposition rate estimated from the TBI.

Statistical analysis

All statistical analysis considers type I errors and F values from the ANOVA command completed using R version 3.2.2 (R Development Core Team 2013). A difference (correlation) was considered significant at $p < 0.05$. In order to account for repeated measures within each peatland site, we evaluated the effect of restoration treatment and peatland type (i.e., bog *vs*. fen) on TBI derived k and S using a linear mixed effect model in the package *nlme* (Pinheiro *et al.* 2016) with site as a random factor. Differences between groups were evaluated using the package lsmeans (Lenth 2016) with Tukey correction for pairwise comparison. Differences between sites or restoration treatments within a site were evaluated using one-way ANOVA with *post-hoc* Tukey's HSD pairwise comparisons. The assumptions for parametric tests were assessed using a Shapiro-Wilk test to determine normality and a Bartlett test for homogeneity of variances. A Welch two-sample *t*-test was used to evaluate differences in water table depth between the wet and dry areas at SB2012.

A linear regression model was used to evaluate controls on mean k_{TBI} and S including the environmental conditions of mean soil temperature, pH, water table depth, as well as pre-disturbance peatland type (i.e. ombrotrophic bog or minerotrophic fen), with treatment as an additional categorical variable in addition to interaction effects between the environmental conditions and the treatment. As environmental conditions were not always available for each teabag burial location, we used an average value for each treatment within each site. Therefore, there were no repeated measures within each treatment and so simple linear regression was used.

Litter bag and tea bag decomposition rates were compared using linear regression following assessment of assumptions using the same tests as applied to the tea bag analyses. ANOVA was used to determine any interactive effect between the water table depth and the plant species with the decomposition rate.

Results

Tea bags

The mass lost from the green tea bags ranged from 46.5% to 84.0%, with the mean (SE) of 69.1% (0.8%) for all sites (Table 2). As expected, there were lower losses from the rooibos tea bags, which ranged from 18.3% to 40.8%, with a mean of 29.5% (0.5%) for all sites. SJ had the highest mean mass loss for both green and rooibos tea, despite being buried for an average of 75 days instead of the full 90 days. Mean mass loss from green tea and rooibos tea was lowest in PR and in BDB, respectively.

The TBI decomposition rate constant (k_{TBI}) ranged from 0.003 to 0.02 d^{-1}, with the mean (SE) of 0.01 (0.003) d^{-1} for all sites and treatments. The TBI stabilization factor (S) ranged from –0.075 to 0.435 with a mean of 0.138 (0.012) for all sites and treatments (Fig. 1).

The mean k_{TBI} was not significantly different among restoration treatments (GLM: $F_{2,80}$ = 0.473, p = 0.62) across the whole data set or among treatments at most sites (BDB: $F_{2,14}$ = 0.18, p = 0.83; PR: $F_{2,18}$ = 0.17, p = 0.67; SJ: $F_{2,17}$ = 3.14, p = 0.06). There was a significantly higher k_{TBI} at SJ than all other sites. At SB, the year restoration was completed was significant for explaining differences in k_{TBI}. SB2009 k_{TBI} was significantly higher than SB natural, SB unrestored, and SB2012 ($F_{4,24}$ = 11.13, p < 0.001; Fig. 2A), but was not significantly different from SB1991. The peatlands SB, BDB and sections of PR were classified as bogs and k_{TBI} was lower, but not significantly different than at fen sites PR and SJ ($F_{1,81}$ = 1.50, p = 0.224).

The mean S was significantly higher at unrestored sites than both restored and natural at all

Table 2. Mean (SE) values (n = 3) of mass lost from litter bags and calculated decomposition rate (k) from the two sample areas of wet (mean water table depth –18 cm) and dry (mean water table depth –33 cm) at SB2012.

Plant material	Wet area		Dry area		Total	
	Mass loss (%)	k (d^{-1})	Mass loss (%)	k (d^{-1})	Mass loss (%)	k (d^{-1})
Litter bags						
Agrostis scabra	42.65 (2.93)	0.0015 (0.0001)	48.53 (3.09)	0.0018 (0.0002)	45.59 (2.3)	0.0016 (0.0001)
Calamagrostis canadensis	53.26 (3.38)	0.002 (0.0002)	53.13 (4.10)	0.002 (0.0003)	53.19 (2.3)	0.002 (0.0001)
Carex canescens	61.44 (1.86)	0.0026 (0.0001)	44.51 (3.52)	0.0016 (0.0002)	52.98 (4.1)	0.0021 (0.0002)
Eriophorum vaginatum	47.12 (3.38)	0.0017 (0.0002)	37.66 (7.97)	0.0013 (0.0004)	42.39 (4.4)	0.0015 (0.0002)
Mean (SE)	51.12 (2.47)	0.002 (0.0001)	45.96 (2.75)	0.0017 (0.0001)	48.5 (1.88)	0.0018 (0.0001)
TBI						
Green tea	62.61 (2.52)	n.a.	63.72 (3.25)	n.a.	63.17 (1.85)	(*see* mean)
Rooibos tea	22.43 (2.2)	n.a.	20.64 (2.56)	n.a.	21.53 (1.56)	(*see* mean)
Mean (SE)	42.52 (9.10)	0.007 (0.001)	42.18 (9.80)	0.006 (0.001)	42.35 (6.38)	0.006 (0.0008)

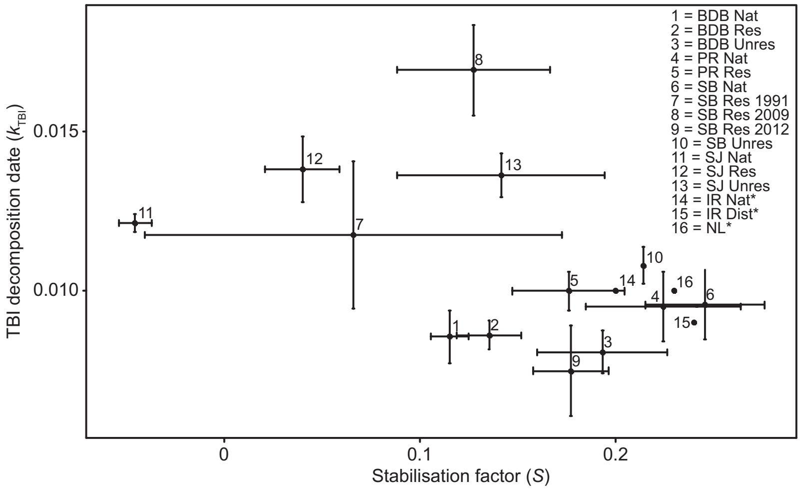

Fig. 1. The mean decomposition rate constant and the stabilization factor for each treatment at all sites with bars showing standard error. * Data points estimated from Keuskamp *et al.* (2013) for peatlands in IR = Ireland, Natural and Disturbed, and NL = Netherlands and are shown to illustrate the range in variation for temperate and boreal wetlands already reported. Other values reported by Keuskamp *et al.* (2013) for tropical wetlands and non-wetland ecosystems would fall outside of the axes of this figure.

sites ($F_{2,80}$ = 5.34, p = 0.007; Fig. 2B). *S* was significantly different between sites ($F_{3,82}$ = 17.07, p < 0.001), where SJ was lower than all other sites. *S* was also significantly lower at fen sites compared to bogs ($F_{3,81}$ = 8.95, p = 0.004).

Environmental conditions

There were no significant differences found in the mean soil temperature between the treatments of natural, restored or unrestored (GLM: $F_{2,9}$ = 0.30, p = 0.74). The mean soil temperature was significantly higher at BDB and SJ than PR and SB ($F_{3,8}$ = 4.24, p = 0.04; Table 1). There was no significant difference in mean soil temperature between bog and fen sites ($F_{1,11}$ = 0.01, p = 0.89), and no significant relationship found between the mean k_{TBI} and the mean soil temperature ($F_{1,10}$ = 0.07, p = 0.79). However, there was a significant negative relationship between *S* and the mean soil temperature (r = –0.59, p = 0.02; Fig. 3).

There were no significant differences in the mean water table depth between the natural, restored or unrestored treatments across all sites ($F_{2,9}$ = 0.39, p = 0.68; Table 1 and Fig. 3). The mean water table depth was significantly different between sites ($F_{3,8}$ = 4.11, p = 0.048), with the dry area at SB2012 experiencing the lowest water levels and SB1991 frequently experiencing flooding over much of the study area. The mean water table depth was significantly closer to the surface at the fen sites than the bogs ($F_{1,11}$ = 12.66, p = 0.004). The restored sites tended to have a highly fluctuating water table during the study period with ranges of around 70 cm, and reaching up to 111 cm at SB2012, compared to ranges of 38 to 79 cm at unrestored and 25 to 75 cm at natural sites. There was no significant relationship between mean k_{TBI} and the mean water table depth ($F_{1,10}$ = 2.93, p = 0.11), as well as the water table range ($F_{1,10}$ = 2.01, p = 0.18). However, there were significant negative relationships between the mean *S* and the mean water table depth (r = –0.68, p = 0.007; Fig. 3) and with the mean water table range (r = –0.58, p = 0.02). Linear mixed effects models indicated a significant effect of variation in water table (p = 0.035), soil temperature (p = 0.004), restoration state (p = 0.0016), and the interactions between water table and temperature (p = 0.0041) and temperature and restoration treatment (p < 0.001) for *S* but no significant relationships for k_{TBI} and any tested parameter.

In addition to differences in mean water table, treatments at each site experienced mostly

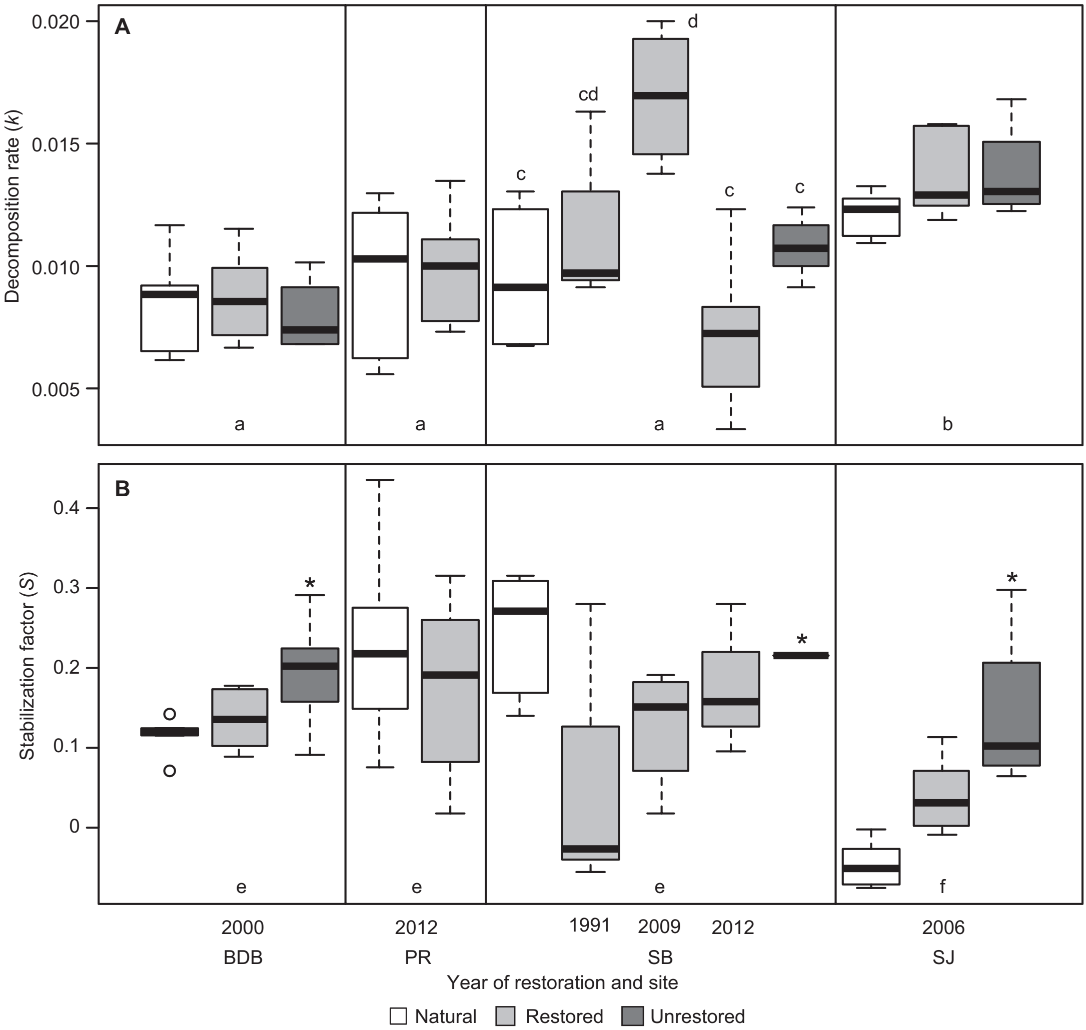

Fig. 2. (**A**) Distributions of the decomposition rate (k_{TBI}) and (**B**) stabilization factor (*S*) in treatments at four sites. Boxplots show median (dark line), 1st and 3rd quartiles (boxes), and range (error bars) for each parameter. Year of restoration for restored treatments is indicated below each restored treatment box. Sites (letters below) and treatments (letters above) are significantly different if they share no lowercase letters; asterisk (*) indicates differences in *S* between unrestored and other treatments.

consistent differences in water table depth, with unrestored sites almost always having deeper water tables than either restored or natural sites within a given site such as at SJ. Some of the restored treatments at SB, such as the dry part of SB2012, often had water tables at similar depths as the SB unrestored site, and others such as SB2012 wet and SB1991 had higher water tables than the natural site for most or all of the study period (Fig. 4). SB1991 had the highest water table depth at Seba Beach, with tea bags there almost always below the water table, yet SB1991 did not show an exceptionally high nor low k_{TBI} (Fig. 2). Peat pH ranged from 4.13 at BDBN to 6.74 at SJN (Table 1), and variation between treatments within a site itself varied across our four study sites. A linear regression found no significant effect ($p > 0.05$) of pH on either k_{TBI} or *S* when all sites were considered together.

Litter bags

The mass lost from the litter bags ranged from

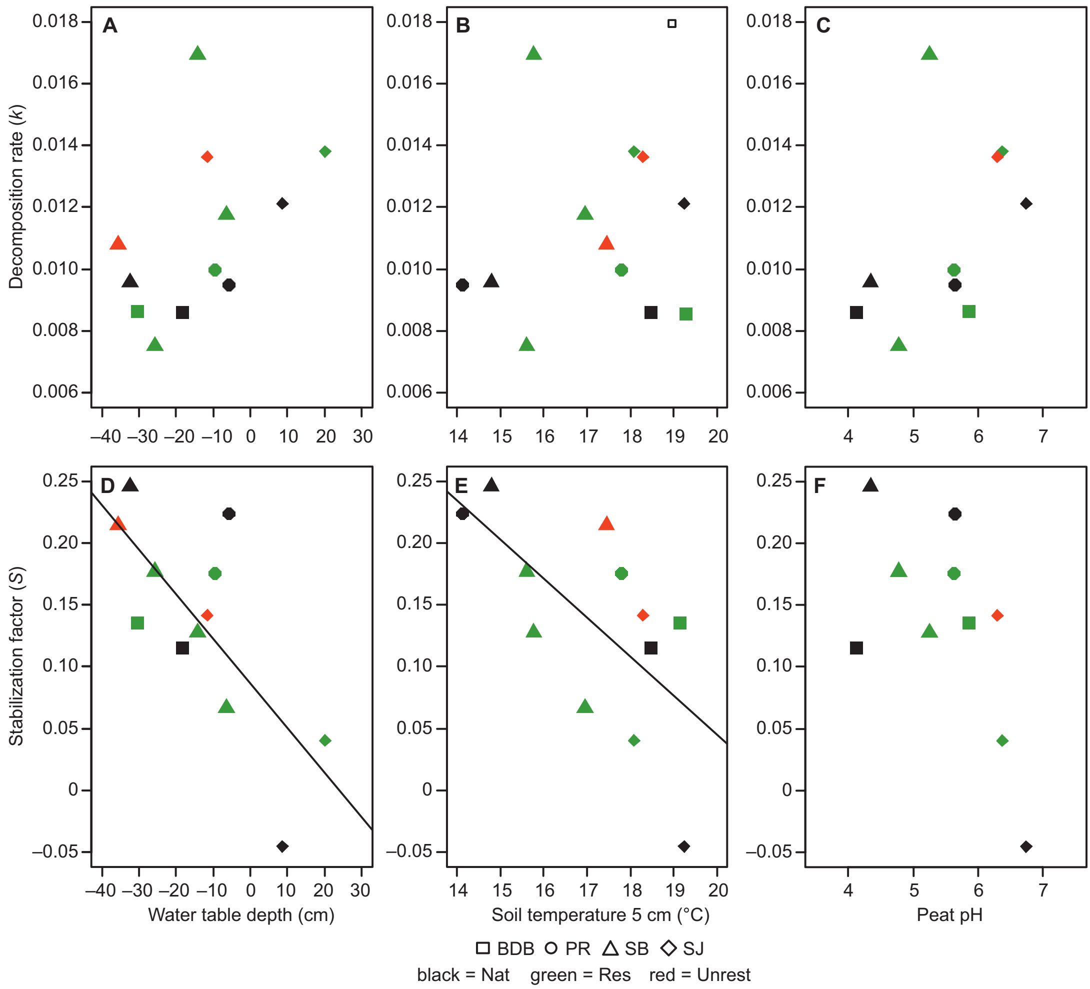

Fig. 3. The mean k_{TBI} and S against water table depth (**A**, **D**), soil temperature (**B**, **E**), and pH (**C**, **F**) across the sites and treatments. The linear regression line represents a slope significantly different from zero ($p < 0.05$). S = –0.0036(water table) + 0.0847 (r^2 = 0.47, p = 0.007). S = –0.0302(soil temperature) + 0.6514 (r^2 = 0.35, p = 0.02).

27.5% to 65.1%, with a mean (SE) of 48.5% (1.9%) during one year. The litter bag annual decomposition rate constant (k) ranged from 0.32 to 1.05 yr^{-1}, with the mean (SE) of 0.67 (0.03) yr^{-1}, depending on species. The annual rate was converted to a daily rate for comparison to the k_{TBI} and ranged from 0.0008 to 0.002 d^{-1}, with a mean of 0.0018 (0.0001) d^{-1} (Table 2). There were no significant differences between k for the different plant species ($F_{3,20}$ = 2.48, p = 0.09). The litter bags were buried in a wet area and a dry area, with mean summer water table depths of –18 and –33 cm, respectively. A Welch two-sample t-test confirmed a significant difference in the water table depths between the two areas ($t_{26.2}$ = 2.53, p = 0.01), but there was not a significant difference in k between wet and dry areas ($F_{1,22}$ = 1.95, p = 0.17). However, there was a significant interaction between the litter bag plant species and water table depth ($F_{9,3}$ = 4.26, p = 0.043). Only *Carex canescens* had significantly higher k in the wet area.

The tea bags buried near the litter bags had mass loss ranging from 58.0% to 69.3%, with the mean (SE) of 63.1% (1.8%) in green tea, and 15.8% to 25.0% with the mean of 21.5% (1.6%) in rooibos tea. The k_{TBI} ranged from 0.003 to 0.008 d^{-1} with a mean of 0.006 (0.0008) d^{-1}, and

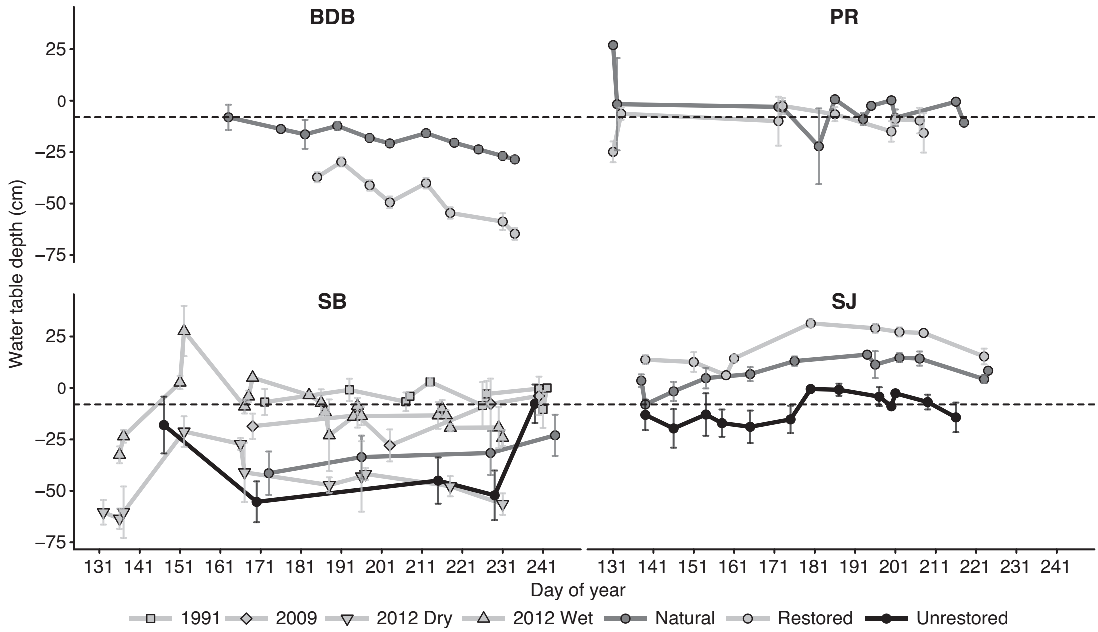

Fig. 4. Water table depth relative to the peat surface as measured by water table wells. Negative values indicate below ground readings. Points are means on the dates of measurement, error bars are ±1SE. The dashed line represents –8 cm, the depth at which tea bags were buried.

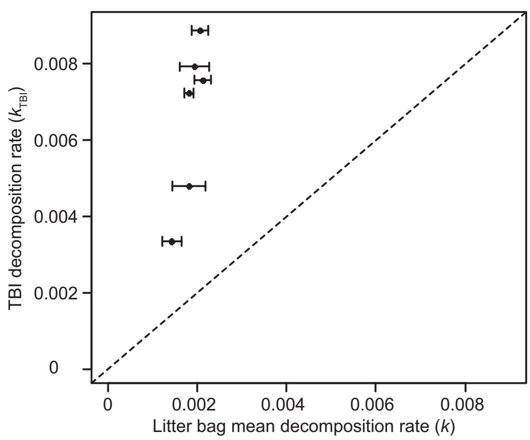

Fig. 5. Relationship between k from litter bags with kTBI at the site SB2012 k_{TBI} = 7.45 ($k_{Litter\ bag}$) – 0.0072 (r^2 = 0.69, p = 0.02). Data points represent mean of 12 litter bags (three replicates of four species) with standard error and one tea bag. Dashed line indicates 1:1 relationship.

was significantly different from the litter bag estimated k ($F_{1,28}$ = 110, p < 0.001). Similar to the litter bags, k_{TBI} did not have a significant relationship with the mean water table depth ($F_{1,10}$ = 2.93, p = 0.12). The mean litter bag k including all plant species was significantly related to the k_{TBI} (r = 0.83, p = 0.02,) but litter bag k was always lower than k_{TBI} (Fig. 5).

Discussion

Effect of restoration on k_{TBI} and S

The mass lost from the green tea bags was greater than from the rooibos tea bags, consistent with the expected results due to the more labile material in the green tea (Keuskamp *et al.* 2013). Our results were similar to previously published peatland TBI values from Ireland and the Netherlands (Keuskamp *et al.* 2013), providing confidence for the TBI results in the present study.

Decomposition is a key process for the release of CO_2 from soils (Davidson and Janssens 2006). Peat drainage and extraction can convert peatlands to CO_2 sources, largely due to mineralization of the peat deposit under dry conditions (e.g. Waddington *et al.* 2002, Straková *et al.* 2012). We hypothetized that k_{TBI}

would be lower in natural than disturbed sites and that rewetting would result in decreased k_{TBI} in restored sites relative to the disturbed sites. While the general trend for the mean k_{TBI} was lower for natural and higher for unrestored sites, overall we observed no significant differences between treatments.

One possible reason why differences between restoration treatments were not statistically significant is because the peatlands studied span a broad geographical range and have considerable variation in environmental conditions, resulting in microorganisms present in each site with different requirements (Preston *et al.* 2012). The k_{TBI} and *S* were significantly different between sites, where SJ exhibited some of the highest decomposition rates and was different from all other sites (Fig. 2). It is possible that the differences in the environment of each site overwhelmed any differences in decomposition rates due to the treatment (natural, restored, unrestored) alone. The k_{TBI} between treatments were not significantly different within each site except at SB, where the treatments restored at different dates showed differences in k_{TBI}. In addition, there was no clear direction in k_{TBI} value differences associated with time since restoration at SB (Fig. 2).

Tea bags and other litter bags may lose mass through both biotic processes, primarily decomposition, and abiotic processes such as leaching. When inundated, soluble material may be transported away from buried litter bags or tea bags, resulting in mass loss that may be erroneously attributed to biologically-mediated decomposition within the bag (Cotrufo *et al.* 2010). This may be a contributing factor for the lack of apparent pattern among treatments at sites, particularly at SB where some temporally discrete treatments had similar k_{TBI} values (Fig. 2) but experienced different conditions, particularly water table (Fig. 4). High water tables that inundated tea bags at SB1991 may have led to considerable mass loss to leaching, increasing the estimated k_{TBI} and concealing lower decomposition rates due to greater periods of limited oxygen availability.

Alternatively, differences between restoration treatments may not have been detected due to little effect of restoration on decomposition rates, or because the response to restoration varies between sites. Watts *et al.* (2007) measured decomposition rates using traditional litter bags in restored peatlands post-extraction and found that the decomposition rates were lower in restored peatlands compared to the natural sites. The reduced rates were attributed to the removal of active microbial communities during the extraction of peat, which were unable to rebound to natural rates one year after restoration (Watts *et al.* 2007). Graf and Rochefort (2009) used litter bags to measure decomposition rate in extracted, spontaneously revegetated and undisturbed fens and also observed slightly higher values at the undisturbed sites.

Perhaps the most surprising finding for us was the lack of large differences in measured decomposition rates (k_{TBI}) between natural and unrestored sites. The three unrestored sites, at BDB, SB, and SJ are broadly similar to each other, with large areas of bare peat and sparse colonisation by plants such as *Eriophorum vaginatum* and *Betula papyrifera*, but these apparent visual features conceal considerable variation. Water table, for example, has a mean depth below the surface of 35.6 cm at the unrestored treatment at SB but is shallower, with a mean of 11.6 cm deep, at SJ. The three sites with unrestored sites, BDB in Quebec, SJ in Manitoba, and SB in Alberta, span most of the full longitudinal width of Canada and are separated by thousands of kilometres. We propose that differences in local climate are the primary drivers of the observed variation in decomposition rates as measured by the TBI.

In contrast, we did observe significantly higher *S* at unrestored areas compared to both restored and natural. *S* represents the inhibiting effects from the environment that may cause a deviation from the actual decomposition rate due to labile compounds being stabilized into recalcitrant material (Keuskamp et al. 2013). We would have expected *S* to increase with restoration as anoxic conditions were reinstated, but instead observed a reduction. It is likely that enhanced decomposition of labile compounds at unrestored sites results in their conversion to more recalcitrant material leading to higher S. The similarity in *S* between restored and natural sites suggests that this may be a good parameter for evaluating the effectiveness of restoration in relation to litter decomposition.

Environmental controls on TBI

The mean soil temperature and mean water table depth were not significantly different between treatments, but were different between sites, consistent with the pattern observed for k_{TBI}. SJ had the highest mean summer water table depth that was, on average, inundated, i.e. water table was above peat surface at two of three SJ treatments (Table 1), and a high mean summer soil temperature and high k_{TBI} rates. However, across all sites there was no significant relationship between the mean soil temperature or water table depth with the k_{TBI}. Laiho (2006) found that when the water table is at least as deep as –20 cm for most of the summer, such as in SB and BDB, further lowering the water table may not measurably affect the decomposition rate. The quality of the peat may be a more important factor than soil temperature for controlling decomposition rates (Preston *et al.* 2012), and dry conditions or anoxia may reduce the influence of soil temperature on the rate of decomposition (Laiho 2006).

In contrast, there were significant negative relationships found for mean soil temperature, water table depth, and water table range with *S*. We expected that rewetting of the peat deposit during restoration activities would increase *S* and decrease k_{TBI} as anoxic conditions result in slower decomposition and stabilization of organic matter in recalcitrant forms. We observed the opposite trend for *S*. Greater water content may have removed inhibitory effects on decomposing organisms associated with dry conditions, but low *S* was observed for fen sites that were more often wet, complicating the ability to tease apart these two effects on *S*.

The k_{TBI} and *S* were higher and significantly lower, respectively, at the fen sites compared to the bog sites. Preston *et al.* (2012) observed greater microbial activity in fens compared to bogs, related to higher nutrient concentrations that can enhance decomposition. Peat pH, which is typically lower for bogs than for fens (Thormann *et al.* 1999, Locky *et al.* 2005), did not vary in a consistent fashion across the study areas, though the two bogs BDB and SB had lower pH in the natural areas than in their respective restored areas. Furthermore, the restored and unrestored areas at all sites had higher, near-neutral pH (Table 1). The parameters calculated from the tea bags, k_{TBI} and *S*, did not significantly vary with pH, though we had expected pH to influence decomposition in these soils. Low pH, associated with bogs due to the organic acids released by living and dead *Sphagnum* spp. (Szumigalski and Bayley 1996, Halsey *et al.* 1997), is associated with reduced decomposition rates that drive the accumulation of organic matter in these wetlands (Thormann *et al.* 1999). That we did not detect such a difference suggests a mismatch between the locally-adapted decomposer community and the organic matter available for decomposition in the tea bags, with peatland decomposer organisms metabolizing the tea at similar rates across the pH range of our study sites.

Litter bags

The mass loss and annual decomposition rate constant (*k*) from the litter bags were comparable to peatland values in the literature (Moore *et al.* 2005, Moore *et al.* 2007). The k_{TBI} was significantly greater than the litter bag *k*, suggesting that the TBI is not an easily comparable method to traditional litter bags for estimating decomposition rates in restored peatlands. Differences are likely associated with strong control of litter type on rate, as observed across the various graminoid species used in the litter bags (Table 2). However, k_{TBI} and the mean litter bag *k* (including all four plant species) were both higher in the wet area than the dry, suggesting that the TBI reflects spatial patterns in decomposition trends. Didion *et al.* (2016) also compared TBI to litter bags and found a significant difference in decomposition rates but observed similar responses and trends between the two methods, which aligns with our results.

Potential consequences of decomposition on CO_2 fluxes post-restoration

Ecosystem CO_2 balance can be considered as one measure of restoration success. While decomposition rates do not directly translate to CO_2 flux, organic matter decomposition is an important contributor to ecosystem respiration. Just as we observed several patterns of k_{TBI} variation between treatments at each site, Basiliko *et al.* (2007) found contrasting patterns of CO_2 production from restored peatlands: one site had reduced CO_2 production, while another site had increased CO_2 production in the restored areas compared to the natural areas. Strack *et al.* (2016) measured CO_2 flux from BDB, SB, and PR peatlands that were used in this study, and found a significant difference in photosynthesis and ecosystem respiration between treatment sites. Those results found that on average, the restored sites were acting as net CO_2 sinks, while the natural sites acted as CO_2 sources (Strack *et al.* 2016), but that these differences were largely driven by increased CO_2 uptake by plant productivity following restoration. In fact, this increase in vascular plant production may enhance decomposition initially following restoration due to priming (Walker *et al.* 2016), linked to the release of root exudates into the remnant peat deposition (e.g. Trinder *et al.* 2008). Peatland restoration aims to return carbon accumulation function to peatlands that should reduce litter decomposition rates, but the effect varies between sites and with time since restoration. This is further hampered by additional factors such as the development of a post-restoration community, dominated by either vascular plants or bryophytes, which continue to shape the environmental characteristics that drive local decomposition rates.

Limitations and recommendations

Peatlands are formed by the accumulation of partially decomposed material that is achieved by a lower rate of decomposition than production, suggesting that a low rate of decomposition relative to production is an intrinsic and integral component of a functioning peatland. The success of ecological restoration is evaluated by comparing aspects of ecosystem function to reference ecosystems (McDonald *et al.* 2016). Measuring the decomposition rate as the primary proxy to infer restoration success depends on on the maximum rate of decomposition that supports accumulation of material and thus, a functioning peatland. While quantifying decomposition rate has a reliable theoretical basis, we sought to determine whether this proxy could be applied using a simple method such as the Tea Bag Index to gauge restoration success.

There are limitations to the use of litter bags, whether it is the traditional construction or a tea bag substitute, to estimate decomposition rates of an ecosystem. Some of the main concerns that have been highlighted are the creation of a micro-climate within the litter bag that could alter decomposition rates, and either the inclusion or exclusion of particles within the enclosed area (Moore 1984). The tea bags in this study were buried at an approximate depth of 8 cm that is thought to be a suitable depth within the soil (Keuskamp *et al.* 2013), but decomposition rates may change throughout the soil profile (Rezanezhad *et al.* 2016). The most appropriate depth for evaluating the effect of restoration on decomposition is unknown, and requires further investigation in a range of soil types and terrestrial ecosystems.

A goal of this study was to evaluate effectiveness of the TBI for potential application by land managers to monitor restoration outcome, it is worth noting some limitations that were encountered to provide advice for future projects. Extra care should be taken when retrieving the tea bags so as not to remove the tea label and additional tags or markers should be used to ensure proper identification, as vegetation growth during the summer had completely obscured some surface tags. The TBI was developed to measure decomposition rates across a wide range of ecosystem types, but burial period and depth may not be optimized for peatland ecosystems. Differences in decomposition rates between restoration treatments appear too minor to detect and experimentation with more replicates, longer burial periods and both shallower and deeper depths should be evaluated. Based on our results, S appears to be more sensitive to restoration than k_{TBI}, while large differences between peatlands illustrates the importance for comparison of restored sites with local unrestored and natural reference sites. We also recommend that the TBI be used in conjunction with other parameters such as soil temperature, water table depth, precipitation, pH, nutrient analysis, or carbon flux. Researchers and other workers involved in ecological restoration may not have access to all of the techniques and equipment necessary for such a comprehensive research program, but we do urge other researchers interested in evaluating the TBI in their studies to include additional parameters such as these when possible to assist in interpretation of unexpected patterns and other observations.

Conclusions

No significant differences in decomposition rates between unrestored, restored and natural peatland treatments were identified using the Tea Bag Index (TBI) except within one site where some areas had been restored decades earlier. There were significant differences in S and significant negative relationships for this parameter with both depth to water table and peat temperature at all study sites. The k_{TBI} and the litter bag k were different but varied in a consistent manner across wet and dry areas. These results suggest that the TBI is not easily comparable to traditional litter bags and may not be sufficient as an individual method to identify restoration success in peatlands. The TBI does reduce effort and time, and may still be effective to estimate broad decomposition patterns, but should be used in conjunction with other measurements before firm conclusions can be drawn.

Acknowledgments: We thank Sun Gro Horticulture and Shell Canada Ltd. for site access, and Sari Juutinen and two anonymous reviewers who provided critical advice to improve the manuscript. Research was funded by an NSERC Canada Research Chair to MS.

References

Basiliko N., Blodau C., Roehm C., Bengtson P. & Moore T.R. 2007. Regulation of decomposition and methane dynamics across natural, commercially mined, and restored northern peatlands. *Ecosystems* 10: 1148–1165.

Belyea L.R. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos* 77: 529–539.

Bourbonniere R.A. 2009. Review of water chemistry research in natural and disturbed peatlands. *Canadian Water Resources Journal* 34: 393–413.

Bridgham S.D., Cadillo-Quiroz H., Keller J.K. & Zhuang Q. 2013. Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. *Global Change Biology* 19: 1325–1346.

Brummell M.E., Lazcano C. & Strack M. 2017. The effects of *Eriophorum vaginatum* on N_2O fluxes at a restored, extracted peatland. *Ecological Engineering* 106: 287–295.

Chimner R.A., Cooper D.J., Wurster F.C. & Rochefort L. 2017. An overview of peatland restoration in North America: where are we after 25 years? *Restoration Ecology* 25: 283–292.

Clewell A. & Aronson J. 2007. *Ecological restoration: principles, values and structure of an emerging profession*. Island Press, Washington DC.

Cotrufo M.F., Ngao J., Marzaioli F. & Piermatteo D. 2010. Inter-comparison of methods for quantifying above-ground leaf litter decomposition rates. *Plant and Soil* 334: 365–376.

Davidson E.A. & Janssens I.A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440: 165–173.

Didion M., Repo A., Liski J., Forsius M., Bierbaumer M. & Djukic I. 2016. Towards harmonizing leaf litter decomposition studies using standard tea aags — a field study and model application. *Forests* 7(8), 167, doi:10.3390/f7080167.

Freeman C., Liska G., Ostle N.J., Lock M.A., Reynolds B. & Hudson J. 1996. Microbial activity and enzymatic decomposition processes following peatland water table drawdown. *Plant and Soil* 180: 121–127.

Graf M. & Rochefort L. 2009. Examining the peat-accumulating potential of fen vegetation in the context of fen restoration of harvested peatlands. *Ecoscience* 16: 158–166.

Graf M.D., Bérubé V. & Rochefort L. 2012. *Restoration of peatlands after peat extraction*. In: Vitt D. & Bhatti J. (eds.), *Restoration and reclamation of boreal ecoysystems*, Cambridge University Press, New York, pp. 259–280.

Hagemann U. & Moroni M.T. 2015. Moss and lichen decomposition in old-growth and harvested high-boreal forests estimated using the litterbag and minicontainer methods. *Soil Biology and Biochemistry* 87: 10–24.

Halsey L.A., Vitt D.H. & Trew D.O. 1997. Influence of peatlands on the acidity of lakes in northeastern Alberta, Canada. *Water, Air, & Soil Pollution* 96: 17–38.

Keuskamp J.A., Dingemans B.J.J., Lehtinen T., Sarneel J.M., Hefting M.M. & Muller-Landau H. 2013. Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods in Ecology and Evolution* 4: 1070–1075.

Laiho R. 2006. Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. *Soil Biology and Biochemistry* 38: 2011–2024.

Locky D.A., Bayley S.E. & Vitt D.H. 2005. The vegetational ecology of black spruce swamps, fens, and bogs in southern boreal Manitoba, Canada. *Wetlands* 25: 564–582.

Lucchese M., Waddington J.M., Poulin M., Pouliot R., Rochefort L. & Strack M. 2010. Organic matter accumulation in a restored peatland: evaluating restoration success. *Ecological Engineering* 36: 482–488.

McDonald T., Gann G.D., Jonson J. & Dixon K.W. 2016. *International standards for the practice of ecological restoration — including principles and key concepts*. Society for Ecological Restoration, Washington, DC.

Moore T.R. 1984. Litter decomposition in a subarctic spruce-lichen woodland, eastern Canada. *Ecology* 65: 299–308.

Moore T.R. & Basiliko N. 2006. *Decomposition in boreal peatlands*. In: Wieder R.K. & Vitt D.H. (eds.), *Ecologial studies*, Springer-Verlag, Berlin, pp. 125–143.

Moore T.R., Bubier J.L. & Bledzki L. 2007. Litter decomposition in temperate peatland ecosystems: the effect of substrate and site. *Ecosystems* 10: 949–963.

Moore T.R., Trofymow J.A., Siltanen M., Prescott C. & Group C.W. 2005. Patterns of decomposition and carbon, nitrogen, and phosphorus dynamics of litter in upland forest and peatland sites in central Canada. *Canadian Journal of Forest Research* 35: 133–142.

Murray K.R., Barlow N. & Strack M. 2017. Methane emissions dynamics from a constructed fen and reference sites in the Athabasca Oil Sands Region, Alberta. *Science of The Total Environment* 583: 369–381.

Nwaishi F., Petrone R.M., Price J.S., Ketcheson S.J., Slawson R. & Andersen R. 2015. Impacts of donor-peat management practices on the functional characteristics of a constructed fen. *Ecological Engineering* 81: 471–480.

Olson J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322–331.

Page S.E. & Baird A.J. 2016. Peatlands and global change: response and resilience. *Annual Review of Environment and Resources* 41: 35–57.

Péli E.R., Nagy J. & Cserhalmi D. 2016. Decomposition rate, and carbon and nitrogen dynamics of *Sphagnum* litter: lessons from a peat bog. *Polish Journal of Ecology* 64: 231–240.

Prescott C.E. 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101: 133–149.

Preston M.D., Smemo K.A., McLaughlin J.W. & Basiliko N. 2012. Peatland microbial communities and decomposition processes in the James Bay lowlands, Canada. *Frontiers in microbiology* 3: 70.

R Development Core Team. 2013. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rezanezhad F., Price J.S., Quinton W.L., Lennartz B., Milojevic T. & Van Cappellen P. 2016. Structure of peat soils and implications for water storage, flow and solute transport: A review update for geochemists. *Chemical Geology* 429: 75–84.

Rochefort L., Quinty F., Campeau S., Johnson K. & Malterer T. 2003. North American approach to the restoration of *Sphagnum* dominated peatlands. *Wetlands Ecology and Management* 11: 3–20.

Strack M., Cagampan J., Fard G.H., Keith A.M., Nugent K., Rankin T., Robinson C., Strachan I.B., Waddington J.M. & Xu B. 2016. Controls on plot-scale growing season CO_2 and CH_4 fluxes in restored peatlands: do they differ from unrestored and natural sites? *Mires and Peat* 17: 1–18.

Strack M., Zuback Y., McCarter C. & Price J. 2015. Changes in dissolved organic carbon quality in soils and discharge 10 years after peatland restoration. *Journal of Hydrology* 527: 345–354.

Straková P., Penttilä T., Laine J. & Laiho R. 2012. Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. *Global Change Biology* 18: 322–335.

Szumigalski A.R. & Bayley S.E. 1996. Decomposition along a bog to rich fen gradient in central Alberta, Canada. *Canadian Journal of Botany* 74: 573–581.

Thormann M.N., Szumigalski A.R. & Bayley S.E. 1999. Aboveground peat and carbon accumulation potentials along a bog-fen-marsh wetland gradient in southern boreal Alberta, Canada. *Wetlands* 19: 305–317.

Trinder C.J., Artz R.R.E. & Johnson D. 2008. Contribution of plant photosynthate to soil respiration and dissolved organic carbon in a naturally recolonising cutover peatland. *Soil Biology and Biochemistry* 40: 1622–1628.

Waddington J.M., Warner K.D. & Kennedy G.W. 2002. Cutover peatlands: a persistent source of atmospheric CO_2. *Global Biogeochemical Cycles* 16: 1–7.

Walker T.N., Garnett M.H., Ward S.E., Oakley S., Bardgett R.D. & Ostle N.J. 2016. Vascular plants promote ancient peatland carbon loss with climate warming. *Global Change Biology* 22: 1880–1889.

Watts C.H., Vojvodic-Vukovic M., Arnold G.C. & Didham R.K. 2007. A comparison of restoration techniques to accelerate recovery of litter decomposition and microbial activity in an experimental peat bog restoration trial. *Wetlands Ecology and Management* 16: 199–217.

Wiedermann M.M., Kane E.S., Potvin L.R. & Lilleskov E.A. 2017. Interactive plant functional group and water table effects on decomposition and extracellular enzyme activity in Sphagnum peatlands. *Soil Biology and Biochemistry* 108: 1–8.