

Patterns of global peat chemistry suggest a novel temperature-dependent carbon cycling mechanism

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SUMMARY

Peatlands contain a disproportionate share of global carbon stocks, such that their biogeochemistry plays an outsized role in carbon balance and climate regulation. The precise mechanisms underpinning peat formation and stabilisation are not yet clear, with several hypotheses co-existing. Further opacity stems from a strong historical bias in research efforts towards boreal and temperate peatlands in the Northern Hemisphere, leaving the tropical case relatively under-studied. On the basis of the economics of oxidative decomposition and juxtaposition of chemical compositional data from tropical peatlands and northern peatlands, we make the case that a rapid, globally-consequential but as yet unidentified endergonic oxidation process must be occurring in tropical but not cold-climate peatlands. We suggest that low temperature limits this process in northern peatlands and, therefore, that a significant quantity of carbon in these systems is more vulnerable to warming than previously thought. We conclude that the existence of tropical peatlands - and their role in regulating global climate - may be partially underwritten by a mechanism largely unmapped by our current knowledge of soil carbon turnover.

KEY WORDS: enzymology, greenhouse gas emissions, microbial ecology, oxidative decomposition, soil organic matter, tropical peat swamp forest

INTRODUCTION

In proportion to their land area, peatlands store an outsized fraction of the global terrestrial carbon (C) stock, estimated to be in the same order as the current atmospheric C stock (Hoyos-Santillan *et al.* 2015) on less than 5 million km² (Page *et al.* 2011) or 3 % of Earth's land surface (Minasny *et al.* 2019). Tropical peatlands - much less well studied than their northern, cold-climate counterparts - account for 10–30 % of this stock (Hodgkins *et al.* 2018), although estimates tend to be revised upwards with further study (Dargie *et al.* 2017, Gumbrecht *et al.* 2017). Carbon cycling is considerably more rapid in tropical peatlands compared to northern peatlands (Hoyos-Santillan *et al.* 2015), such that a comparison of the energetic economics of decomposition in tropical and northern peatlands is a particularly useful window through which to develop a mechanistic view of peat formation and degradation.

Peatlands occur under waterlogged conditions and degrade or even disappear following drainage. It is thus commonly perceived that waterlogging and the consequent displacement of oxygen (anoxia) cause peat to form. This account is phenomenologically incontestable. A seemingly obvious causative thread can be drawn from displacement of oxygen to

suppression of oxidation, but oxygen is not the only compound that can take up electrons from another (i.e. oxidise it). Examples of other potential oxidisers in peat include NO₃, Fe(III), Mn (III, IV), SO₄ and humic substances (Keller *et al.* 2009). In fact, we do not yet know exactly why waterlogging suppresses the decomposition of plant residues sufficiently to form peat (Yarwood 2018), particularly in the tropical case (Hodgkins *et al.* 2018). A number of Fe-redox associated hypotheses have been proposed to account for protection (and loss) of organic matter during periodic water table drawdown (Dubinsky *et al.* 2010, Bhattacharyya *et al.* 2018), including the Iron Gate (Wen *et al.* 2019), but the most prominent hypotheses specifically addressing waterlogging are: i) lack of terminal electron acceptors (TEAs) (Hall *et al.* 2014); ii) inhibition of hydrolytic enzymes by phenols (the 'Enzymatic Latch' hypothesis) (Freeman *et al.* 2004); and iii) reduction of the ATP yield of microbial metabolism (Hall *et al.* 2014). All of these share a common logic that inundation displaces oxygen, which begets reduced oxidation, which in turn reduces decomposition, and finally allows peat formation. The linkage between oxidation and decomposition is nuanced, however, and warrants a more granular evaluation, as follows below.



OXIDATION AND DECOMPOSITION

Plant residues comprise a wide variety of compounds, which require a wide variety of strategies for soil microorganisms to decompose. The bulk of plant residue decomposition is catalysed by microbial enzymes, which are hugely diverse but can be broadly classified into two types: hydrolytic and oxidative enzymes. Hydrolytic enzymes catalyse *hydrolysis*, a reaction that consumes water molecules to break chemical bonds. Because hydrolytic enzymes are compound-specific, they are vast in number, but all rely on water to cleave substrates. Oxidative enzymes catalyse *oxidation* reactions, in which electrons are removed from a target substrate. In principle, they do not rely on any specific compound, but the currently known oxidative enzymes with significant potential to decompose plant residues (often termed oxidases and peroxidases) rely on either O₂ or H₂O₂. Finally, microbes can also drive oxidation reactions non-enzymatically, using low molecular weight reactive oxygen species (free radicals) such as the hydroxyl radical (Bonner *et al.* 2019).

An organic compound may be ‘completely’ decomposed by a microbe transforming the substrate into energy and CO₂ - known as *mineralisation* - or ‘incompletely’ decomposed which involves breaking down a larger organic molecule into smaller organic molecules. In this context we may define three classes of compound that compose plant residues:

- **Class I** compounds, that can be completely mineralised hydrolytically (e.g. starches, sugars, most peptides, etc.);
- **Class II** compounds, that can be mineralised hydrolytically, but only after initial oxidation to overcome physical or chemical barriers to hydrolysis (e.g. cellulose and hemicellulose within lignocellulose); and
- **Class III** compounds, that can only be mineralised oxidatively (e.g. lignin, waxes, polyphenols, etc.).

The constituent compounds of plant residues viewed in isolation, as ‘model compounds’ in pure form, will largely appear to belong to Classes I and III. However, plant residues do not begin the process of decomposition as pure, separate compounds; some are bound up within or behind others. In particular, the most abundant biopolymer on earth, cellulose, is typically bound with and protected by the second most abundant biopolymer, lignin (Talbot & Treseder 2012). In addition, hydrolytic access to cellulose in its typical crystalline form seems to require oxidation to overcome protection from stacking interactions between cellulose chains

(Vaaaje-Kolstad *et al.* 2010, Westereng *et al.* 2011, Frommhagen *et al.* 2016, Li *et al.* 2021). Also, in industrial processing applications, lignocellulose requires substantial pre-treatment to allow hydrolytic enzymes to act (Johansen 2016). Thus, a dominant fraction of plant residues appears to comprise Class II compounds, for which hydrolytic mineralisation depends on prior oxidation.

THE CHEMICAL STORY

Examining the chemical composition of peat with particular focus on the proportions of Class I, II and III compounds has strong potential to elucidate the relationship between oxidation and decomposition in peatland systems. Integrating a global dataset spanning the Arctic to the tropics, Hodgkins *et al.* (2018) found a significant decrease in the ratio of carbohydrates (mostly cellulose, Class II) to aromatics (mostly lignin-derived) in peat soils with decreasing latitude. Aliphatics (mostly Class III compounds) remained high throughout the latitudinal gradient. The pattern was observable after accounting for differences in the chemistry of parent material (greater lignin content in tropical peatland litter) and was robust into the catotelm. Normand *et al.* (2021) analysed nuclear magnetic resonance (NMR) spectra from a global collection of peat soils, ranging from arctic to tropical, and found that aromatic and methoxyl C (lignin and derivatives) increased and O-alkyl (carbohydrates) decreased with mean annual temperature. Their results suggest a possible inflection point in the dominance of O-alkyl C in peat soils somewhere between 11 °C and 21 °C mean annual temperature. Comparing additional NMR spectra from the published literature (Preston *et al.* 1987, Béasse *et al.* 2015, Sjögersten *et al.* 2016, Sangok *et al.* 2017, 2020; Normand *et al.* 2021) reveals a very similar pattern, with large O-alkyl peaks (corresponding to carbohydrates) in boreal but not in tropical peats, large methoxyl peaks (corresponding to lignin) in tropical but not in boreal peats, and aromatic (lignin) and alkyl (aliphatics) peaks high in all samples (Figure 1).

The much more well-studied northern peatlands show preservation of both Class II and Class III compounds. This supports a classic, straightforward reasoning that anoxia suppresses oxidation, which in turn suppresses decomposition. Expanding the field of view to include the tropical case and comparing the chemistry of parent material and peat (Hodgkins *et al.* 2018), we see that Class II compounds appear to decompose rapidly enough to avoid accumulation, even with very high rates of input, in tropical

systems. Only Class III compounds - those that can only be mineralised oxidatively - appear to be consistently preserved.

These observations justify two related inferences. First, inundation alone is insufficient to explain the suppression of oxidation in northern peatlands and, secondly, very substantial and rapid oxidation is occurring in tropical peatlands.

THE ROLE OF PLANTS

Plants play two roles in carbon cycling in peat. The first and most well studied is that of providing the parent material or input of organic matter for peat accumulation. The dominant peat-forming residues derive from a range of vegetation types, from mosses through sedges and reeds to trees, but all comprise large quantities of Class II compounds. In tropical peats it has been suggested that the majority of litterfall is 'pre-recycled' or aerobically decomposed on the forest floor, such that organic matter input from small tree roots into the catotelm (the deeper, continually saturated peat layer) is the most important source material for peat accumulation (Brady 1997). The second role that plants play in carbon cycling in peat, which has received less

research attention, is the potential to facilitate gas transport between above and below ground. Thus, vascular plants may play a role in oxygenation of acrotelm and even catotelm peat, which is likely to be more significant in tropical peatlands than in northern peatlands (Bjorn Robroek, personal communication). Nonetheless, any subsoil aeration is evidently insufficient to enable oxidative mineralisation in bulk soil (because peat accumulates), and oxygenation of live roots is unlikely to support their own oxidative decomposition once they have senesced (because they are no longer metabolically active plant tissue).

THE ROLE OF THE WATER TABLE

It is possible that intermittent rapid oxidation is enabled by the high-amplitude water table variation in tropical peats. If so, catotelms in northern and tropical peatlands ought to be chemically similar after accounting for litter chemistry - but this is not what has been observed (Hodgkins *et al.* 2018). In addition, periodically oxic surface layers in tropical peats experience similar conditions to non-peat soils in tropical humid forests, including frequent but intermittent anoxia (Hall *et al.* 2014). Decomposition in tropical humid forests is typically complete, fully

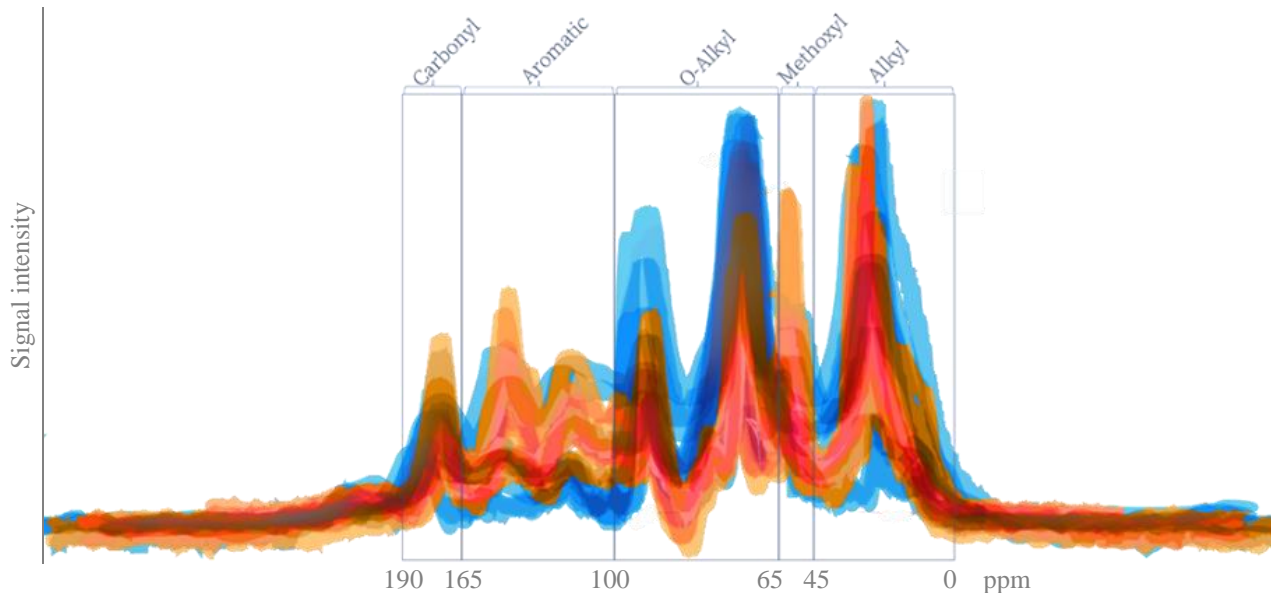


Figure 1. Stacked NMR spectra from published literature (Preston *et al.* 1987, Béasse *et al.* 2015, Sjögersten *et al.* 2016, Sangok *et al.* 2017, 2020; Normand *et al.* 2021) across a range of sampling depths, including four studies of boreal peatlands (blue) and four of tropical peatlands (orange). Colour intensity reflects number of overlapping spectra, and red depicts overlap between blue and orange spectra. O-Alkyl C largely corresponds to carbohydrates, alkyl C to aliphatics, and both methoxyl and aromatic C tend to correspond to lignin and derivatives. The most noteworthy differences can be found in the O-alkyl region (carbohydrates), where high peaks are disproportionately blue (boreal peat) and low peaks disproportionately orange (tropical peat); and in the methoxyl and aromatic regions (lignin), where tropical peats have higher peaks.

mineralising the overwhelming majority of Class I, II and III compounds, evidenced by several tonnes of lignin and aliphatics per hectare reaching the soil annually (Parsons *et al.* 2014) but largely failing to accumulate in the long term (Trumbore 1993, Rillig *et al.* 2001, Don *et al.* 2011). Therefore, we argue that considerable oxidative mineralisation occurs in surface horizons of tropical peats, both enzymatically and through Fe redox cycling (as observed in humid tropical forests; Dubinsky *et al.* 2010), such that peat formation occurs primarily in deeper, more saturated zones (Belyea & Clymo 2001). Thus, it is likely that tropical and northern peats form under similarly anoxic conditions, leaving temperature difference as the most plausible physical driver of differences in oxidation.

THE ROLE OF TEMPERATURE: ENDERGONIC OXIDATION

The microbial economics of decomposition could explain a temperature effect on oxidation. It is game-theoretically axiomatic that a microbe will only decompose a substrate when it receives a positive return on its investment. Thus, Class I compounds ought to be decomposed when hydrolysis yields positive returns, and Class III compounds ought to be decomposed when oxidation is energetically gainful (LaRowe & Van Cappellen 2011). Class II compounds, on the other hand, may be decomposed even when oxidation occurs at a net loss of energy, provided that the subsequent hydrolysis yields a large

enough energy return. Under conditions where oxidation is endergonic (i.e. requiring an input of energy) but hydrolysis is highly exergonic (i.e. resulting in a release of energy), we would predict both Class I and II compounds to be mineralised, leaving only Class III compounds; which is precisely what we see in tropical peat. If the ATP yield of hydrolysis is limited both by a lack of O₂ (Hall *et al.* 2014) and low temperatures, such that it becomes insufficiently exergonic to overcome endergonic oxidation costs, we would predict both Class II and Class III compounds to accumulate - as seen in northern peatlands. On this basis we hypothesise that oxidation in northern peatlands is limited in part by a temperature effect on hydrolysis (Figure 2). This proposal contrasts with the Enzymatic Latch hypothesis, which posits that hydrolysis is limited by a lack of oxidation; although the two processes could occur simultaneously.

AN UNDESCRIBED PROCESS

Substantial oxidation appears to be taking place in tropical peatlands. Enzymatic oxidation is largely dependent on O₂ directly (in the case of phenol oxidases and laccases), or indirectly via enzymatic reduction of O₂ to H₂O₂ (in the case of peroxidases). Therefore, it is likely that the large-scale oxidation in tropical peatlands is non-enzymatic, functionally approximating to the 'brown rot' decomposition of wood (Bonner *et al.* 2019). However, the brown rot process requires H₂O₂ together with redox cycling of

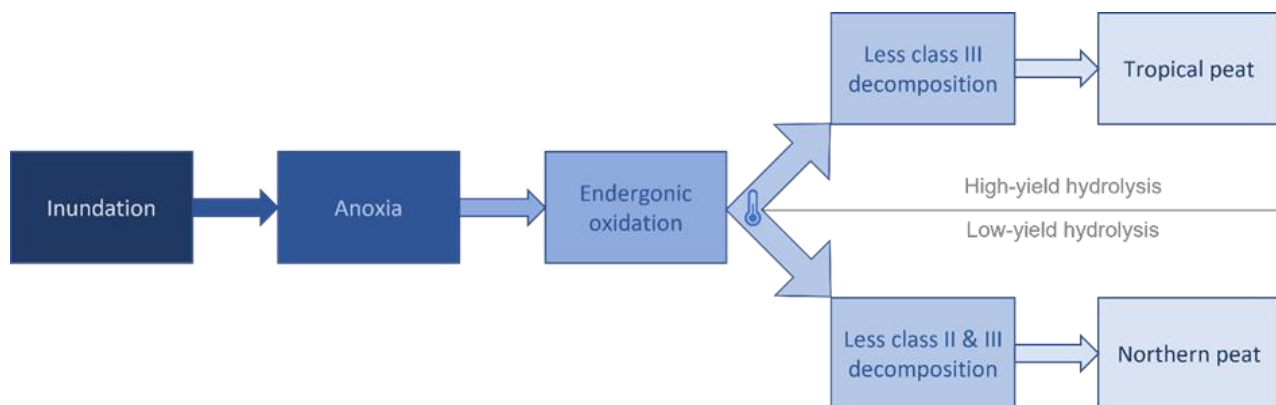


Figure 2. Hypothesised causal cascade from soil inundation to peat formation, depicting the branch point around hydrolysis energy yield that results in differential effects of suppressed oxidation on overall decomposition. If $Y_{\text{hyd}}(t)$ is the energy yield of hydrolysis (which is a function of temperature, t) and C_{ox} is the cost of oxidation, then Class II carbon is protected if and only if $Y_{\text{hyd}}(t) - C_{\text{ox}} < 0$. The depicted branch point represents the capacity of temperature to flip this inequality, by virtue of increasing the energy yield of hydrolysis beyond the cost of prerequisite oxidation (so that $Y_{\text{hyd}}(t) - C_{\text{ox}} > 0$), and enable the decomposition of Class II carbon

iron, the former of which depends on O₂ and the latter of which ought to be limited in organic wetland soils (McLatchey & Reddy 1998). Anaerobic bacterial lignocellulose decomposition, as currently understood, is unlikely to keep pace with the scale and rapidity of lignocellulose inputs to tropical peatlands, especially with the persistent anoxia and limited iron supply (Brown & Chang 2014, Merino *et al.* 2021). Thus, we contend that the evidence points to an as yet undescribed process regulating tropical peatland C cycling.

VULNERABLE CARBON

The arctic and boreal zones, in which a disproportionate share of peatlands is located, are experiencing disproportionately fast warming relative to the global average (Hansen *et al.* 2010, Goddard Institute for Space Studies 2022). Precipitation may also be increasing in this area, albeit minimally (Chen *et al.* 2021). If Class II carbon in northern peatlands is protected by virtue of low temperatures situating them below the branch point in Figure 2, then rising temperatures are liable to trigger a release of large quantities of C from northern peatlands quite suddenly, even if water tables remain high. As temperatures increase, the energy yield of hydrolysis $Y_{hyd}(t)$ increases (Figure 2), but Class II carbon remains protected until the yield exceeds the cost of prerequisite oxidation (the inequality in Figure 2 flips), after which this globally significant store of carbon may be rapidly released to the atmosphere.

CONCLUDING REMARKS

In this article we have outlined a plausible explanation for why Class II compounds are present in higher quantities in boreal peats compared to tropical peats from analysis of the literature, leading us to posit a new but unidentified endergonic mechanism that limits the net energy balance for oxidation-hydrolysis linkages for Class II compounds. A mechanism largely unmapped by our current knowledge of soil carbon turnover seems to be enabling rapid, large-scale oxidation in tropical peatlands. Crucially, the mechanism is likely to be temperature-dependent, suggesting that northern peatlands have potential to release huge quantities of Class II C if a warming climate exceeds a tipping point. Given the global implications of change in C stocks and fluxes in and through peatland ecosystems, it seems a mechanism that urgently

warrants further detailed investigation, including a meta-analysis of existing studies as well as a globally co-ordinated series of field and laboratory experiments.

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AUTHOR CONTRIBUTIONS

MB: conceptualisation, investigation, writing (original draft); SG: acquisition of funding, writing (review and editing), supervision, project administration.

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