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Drought-induced carbon loss in peatlands

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Peatlands store vast amounts of organic carbon, amounting to approximately 455 Pg. Carbon builds up in these water-saturated environments owing to the presence of phenolic compounds—which inhibit microbial activity and therefore prevent the breakdown of organic matter. Anoxic conditions limit the activity of phenol oxidase, the enzyme responsible for the breakdown of phenolic compounds. Droughts introduce oxygen into these systems, and the frequency of these events is rising. Here, we combine *in vitro* manipulations, mesocosm experiments and field observations to examine the impact of drought on peatland carbon loss. We show that drought stimulates bacterial growth and phenol oxidase activity, resulting in a reduction in the concentration of phenolic compounds in peat. This further stimulates microbial growth, causing the breakdown of organic matter and the release of carbon dioxide in a biogeochemical cascade. We further show that re-wetting the peat accelerates carbon losses to the atmosphere and receiving waters, owing to drought-induced increases in nutrient and labile carbon levels, which raise pH and stimulate anaerobic decomposition. We suggest that severe drought, and subsequent re-wetting, could destabilize peatland carbon stocks; understanding this process could aid understanding of interactions between peatlands and other environmental trends, and lead to the development of strategies for increasing carbon stocks.

Peatlands are unbalanced systems where production rates exceed decomposition rates, leading to the accretion of around 455 Pg of carbon[1,2]. Traditionally, this impaired decay is attributed to anoxia[1,3], low nutrients, low temperatures and low pH (refs 1,4), but recently it has been suggested that O_2 constraints on phenol oxidases could be all that prevents this vast carbon stock being re-released as CO_2 (ref. 5). Phenol oxidases are among the few enzymes able to fully degrade phenolic compounds, but they require O_2 (ref. 3). The predominantly anoxic conditions in peat enable the build-up of inhibitory phenolic compounds, which, in turn, prevent the main agents of carbon and nutrient cycling, hydrolase enzymes, from carrying out normal decay processes[5,6]. However, if O_2 is introduced, for example through drought, phenol oxidase can remove phenolic inhibitors, enabling hydrolases to resume normal mineralization of organic matter—hence, the phrase 'an enzymic "latch" on a global carbon store'[5] was coined to describe this carbon preservation mechanism.

At high latitudes, where much of the world's peat resides, drought frequency and severity is predicted to increase[7]. There is evidence that this is already occurring, with attendant losses as CO_2 and dissolved organic carbon (DOC; ref. 8) from peatlands. Here, we test the hypothesis that drought will increase phenol oxidase activity, leading to enhanced hydrolase enzyme activities and microbial growth rates, and therefore CO_2 production. We identify the sequence of events and mechanisms responsible for each process in this regulatory pathway (below), using selective inhibition, manipulation of precursors, drought simulations and field evaluation.

Enzyme activity

Increased extracellular phenol oxidase activities reported under raised O_2 levels[3,5,9] (process 1) may be due to a recovery of edaphic activity (because enzymes can form stable complexes in soils), or microbial *de novo* synthesis[5,10,11]. By removing microbial intracellular metabolism, leaving only edaphic enzyme activity, we found that, contrary to our hypothesis, only the soil capable of *de novo* synthesis responded positively to increased O_2 (2,941%, $P < 0.05$; Supplementary Fig. S1). Consequently, it is the microbial community that initiates the response, in line with findings in *Sphagnum* tissues[12].

Hydrolases could be stimulated (process 2) by the removal of phenolics, because phenolics represent either (1) hydrolase or (2) microbial metabolic inhibitors. To differentiate between the two, we selectively lowered phenolic abundance[13], while preventing *de novo* hydrolase synthesis. If higher activities were directly due to the elimination of phenolics as hydrolase inhibitors, then both treated and control systems should respond to increased O_2. If however, the response requires *de novo* synthesis, then only the control should respond. Hydrolase activities in both systems were similar ($P > 0.05$), implying that higher activities (mean β-glucosidase 85%, xylosidase 119%, cellobiosidase 241%; Supplementary Fig. S2) are due to the elimination of phenolics as hydrolase inhibitors and that, once phenolics have been depleted sufficiently (by phenol oxidase and physicochemical processes such as precipitation), it is the edaphic hydrolases that will first accelerate decomposition and nutrient cycling.

Microbial growth and drought simulation

Sensitive assays of microbial abundance and growth rates were used to determine the timing of any rise in microbial metabolism during simulated drought, in relation to the three potential precursors of that rise: increased O_2 availability, decreased phenolics, or increased carbon and nutrient abundance (process 3a). Bacterial, rather than fungal, parameters were the first to respond ($P < 0.05$) to lowered water tables (although fungi responded later), consistent with bacterial dominance in waterlogged habitats[14,15] and the increased diversity of a bacterial phenol oxidase, catechol 2,3-dioxygenase, reported at our primary field sites after simulated drought[9].

Contrary to our hypothesis, bacterial growth rates were stimulated (day 4, $P < 0.01$) before extracellular phenol oxidase and this was attributed to increased O_2 abundance, because it was the only precursor to change within this time (2 days, $P < 0.01$; Supplementary Table S1). Overall though, a negative correlation was found between growth rates and phenolics ($R^2 = -0.84$, $P < 0.05$), confirming that phenolics are potent inhibitors of

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microbial metabolism, and that both O_2 and lowered phenolics are precursors of higher metabolic activities.

Extracellular phenol oxidase activities increased within 16 days ($P < 0.05$), concurrent with a decrease in phenolics ($P < 0.05$). This is consistent with *de novo* synthesis (process 1), because (1) no increase in *de novo* synthesis would be expected without a change in bacterial growth rates, and (2) phenol oxidase activities do not increase until after growth rates, suggesting a lag period before synthesis occurs. Previous work[5] had found a rapid phenol oxidase response to O_2, within 18 h, and therefore attributed it to edaphic activity, but *de novo* synthesis can occur within 5–24 h (ref. 16). Activities were correlated with pore-water O_2 saturation ($R^2 = 0.98$, $P < 0.001$), and thus both biological and physicochemical phenolic removal processes will accelerate decomposition as drought proceeds.

Bacterial abundance also increased within 16 days of drought. Cocci in particular were correlated with dissolved O_2 ($R^2 = 0.85$, $P < 0.05$), whereas total abundance was more variable ($R^2 = 0.79$, $P = 0.064$), probably owing to decreases in obligate anaerobes. Total abundance, however, was negatively correlated with phenolic compounds ($R^2 = -0.84$, $P < 0.05$). Phenolics, therefore, act as microbial inhibitors (secondary in chronological terms, though not magnitude, to insufficient O_2), but the inhibitory effect of phenolics on edaphic hydrolases is relieved at higher concentrations, that is, microbial populations are more sensitive to inhibition by a given concentration of phenolics than edaphic hydrolases. This has important implications for a latch-type mechanism, because the hydrolases that are deployed by microbes will be less sensitive to phenolic inhibition, that is, decomposition can continue, even when intracellular metabolism is compromised with the return of waterlogging.

Of the potential precursors to a rise in microbial metabolism, dissolved carbon and nutrients were the last to respond, with DOC (accumulated under anaerobic conditions) falling after 32 days of drought ($P < 0.05$), along with ammonium ($P < 0.01$), after which concentrations increased, concurrent with enhanced aerobic decomposition of the peat matrix. Sulphate was released as the drought proceeded (day 32, $P < 0.01$), as was nitrate (day 48, $P < 0.05$), driving acidification (Supplementary Table S1), whereas potassium and phosphorus were depleted in this period ($P < 0.05$). Such changes reflect both biological turnover (plants and microbes) and physicochemical processes. Acidification during drought, which has been widely reported (for example ref. 4 and references therein), increased with nutrient status (Supplementary Tables S1, S2) and acts to limit any stimulation of decomposition due to regeneration of electron acceptors[2,17] and nutrient release. These latter two stimulants are inextricably linked, but it is only after phenol oxidase has depleted the inhibitor pool that enzymic decomposition is fully initiated.

Aerobic conditions induced by drought favour efficient CO_2 production[18] as the ultimate product of decomposition, and a marked increase occurred here, but only after changes in the above determinands (64 days 1,490%, $P < 0.05$), showing that a succession of processes is required to achieve maximum mineralization.

Microbial growth and selective manipulation

The second approach involved a stimulation of each precursor (O_2, phenolics, carbon substrates and nutrients) to a rise in microbial growth rates (process 3b). The relative stimulation produced was then evaluated, with the drought simulation plus the selective manipulation, enabling us to determine whether each step can occur independently, or whether preceding steps, in sequence, are necessary for maximum stimulation.

Both oxygenation (98%, $P < 0.001$) and lowered phenolics increased bacterial growth rates (97%, $P < 0.01$), again indicating that both precursors stimulate growth and that rates will increase as drought proceeds. When carbon and nutrients were introduced in the presence of phenolics, growth rates remained suppressed (−20%, $P < 0.01$), illustrating the potency of these inhibitors. Such materials must be removed before microbial growth rates can reach their optimum as a result of increased substrate and nutrient release through hydrolases. Moreover, this sequence of events substantiates the drought simulation.

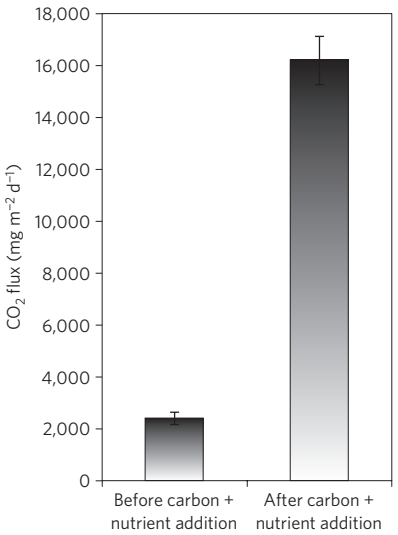

Figure 1 | Effect of carbon and nutrient addition on oligotrophic peat CO_2 flux (gross) in the absence of phenolic inhibitors *in vitro*. Only when inhibitory phenolics are first removed can the increased carbon and nutrient levels stimulate maximum CO_2 release, showing that each preceding step in the biogeochemical cascade is necessary for maximum stimulation. Final concentrations of carbon and nutrients were matched to those in the field following severe drought. Error bars denote s.e.m. ($n = 6$, 10 cm depth).

When the effects of these same manipulations on extracellular phenol oxidase were investigated, oxygenation of anoxic peat produced significant stimulation and the highest absolute activities (32%, $P < 0.05$; Supplementary Fig. S3). Surprisingly, however, nutrient and carbon additions produced a larger percentage increase (63%, $P < 0.05$), indicating that carbon and nutrients are severely limiting phenol oxidase activities in peatlands: a finding consistent with the theory that low nutrients limit carbon loss[4] and with work in *Sphagnum* tissues, whereby fresh carbon was found to determine microbial phenol oxidase activity[12]. Similarly, decomposition of ancient organic carbon is primed in soils by the addition of new carbon[19]. Moreover, this suggests that increased labile carbon inputs due to elevated atmospheric CO_2 (ref. 20) could weaken the enzymic latch, promoting positive feedback to climate change. Carbon-cycling hydrolases (β-glucosidase 76%) and cellobiosidase (85%) were also stimulated by carbon and nutrients ($P < 0.05$), but this was despite the presence of phenolics (unlike growth rates, which remained suppressed) and lower pH. However, the largest increase in phenol oxidase activities was seen when pH was allowed to rise to re-wetted levels (75%, $P < 0.05$), again suggesting limited decomposition during the drought phase, an important issue in disentangling conflicting reports (below). Indeed, activities are known to increase exponentially with rising pH (refs 21,22).

CO_2 production

The final stage in the pathway, CO_2 production (process 4), could arise through (1) stimulation of edaphic enzymes (only), (2) stimulation of microbial metabolism by lower levels of phenolics or (3) supply of O_2 to aerobic microorganisms (Supplementary Information). Because there was no stimulation of CO_2 emissions

from irradiated soils on phenolic depletion, enzyme-only CO_2 production (1) is not of major importance during drought (contributing up to 37%). Lowering phenolics (2) was insufficient to stimulate microbial CO_2 production directly, but addition of carbon and nutrients caused a substantial stimulation (66%, $P < 0.05$). Moreover, when carbon and nutrients were allowed to increase following phenolic extraction, a huge increase in CO_2 efflux was seen (575%, $P < 0.001$, Fig. 1). Thus, each preceding step in the pathway is necessary for maximum stimulation, and release of further resources for the microbes by hydrolases supports increased CO_2 emissions. When the direct impact of O_2 was evaluated (3), CO_2 contributions from the microbes increased (43%, $P < 0.01$) to a similar magnitude as phenol oxidase activities (process 3b). This again supports the theory that a microbial response is rapidly initiated (processes 1, 3a), but processes during drought further stimulate CO_2 production, as was true for phenol oxidase activity (process 3b).

From these *in vitro* measurements, the enzymic latch sits within a regulatory pathway of process-specific limitations, which are sequentially removed as drought proceeds, constituting a biogeochemical cascade with potent positive feedbacks to carbon loss. However, our proposed pathway requires rearrangement (Fig. 2). Ingress of O_2 enables increased microbial growth rates (A) with an associated modest increase in CO_2 release, and increased synthesis of phenol oxidase (B), leading to a decline in inhibitory phenolics, reinforcing redox effects (C). Lower inhibitor abundance enables further stimulation of microbial metabolism and also edaphic hydrolases (D). Stimulated hydrolases release carbon and nutrients from the peat matrix (E), all of which support enhanced microbial activity and abundance (F), and hence increased synthesis of hydrolases, phenol oxidases and subsequently maximum CO_2 emissions (G), but also a direct stimulation of edaphic enzyme activities (H). Further evidence for the same pathway was also found in the field (below, Tables 1 and 2).

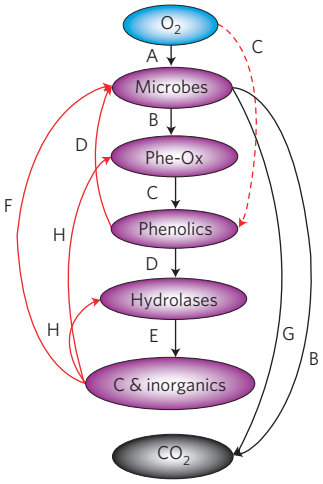

Figure 2 | The biogeochemical 'cascade', whereby constraints on decomposition are removed by severe drought in oligotrophic peatlands. Oxygen stimulates bacterial growth rates (A), modest CO_2 release and *de novo* synthesis of phenol oxidase (B), leading to a decline in inhibitory phenolics (C). Lower inhibitor abundances enable further stimulation of microbial metabolism and edaphic hydrolases (D). Increased cleavage of carbon and nutrients through stimulated hydrolases (E) provides resources and more favourable pH (when waterlogging returns) for enhanced microbial activity and abundance (F), and hence *de novo* production of hydrolases, phenol oxidases and maximum CO_2 emissions (G), but also a direct nutrient-driven stimulation of enzyme activities (H). Positive feedbacks accelerating carbon losses are shown (red) including physicochemical phenolic removal (dotted line).

Re-wetting phase

Applying the same techniques to the re-wetting phase showed that edaphic phenol oxidases initially predominate ($P < 0.05$), representing a legacy of the previous aerobic community, while anaerobic metabolism becomes prevalent, shifting end products towards DOC, CH_4 and CO_2 (rather than primarily CO_2). Moreover, once the system re-wetted, markedly higher carbon losses were observed than in the drought phase, as even more limitations are removed (pH and moisture stress). This two-phase regulation, where decay is triggered by drought, but accelerated during re-wetting (Table 2, Fig. 3), further unravels the complexities of peatland response.

First, a huge CO_2 efflux was found when carbon and nutrients were allowed to rise following phenolic extraction, under anaerobic conditions, at field pH (601%, $P < 0.001$), suggesting dramatic short- and medium-term effects (weeks–months), after a severe drought event, lasting until phenolics re-accumulate. However, in the longer term (months), and arguably of more concern, is the stimulation ($P < 0.05$) of phenol oxidase (75%), β-glucosidase (80%) and cellobiosidase (89%), with consequent increased CO_2 effluxes (78%), as a result of nutrient additions alone, particularly at field pH, indicating a dual nutrient/pH driver initiated by drought. Moreover, eutrophication[23] and recovery from acidification[24] alone, or in conjunction with increased drought frequency and elevated CO_2 (ref. 20), are likely to have marked effects on carbon stocks through this mechanism, because key carbon-cycling enzymes are severely carbon, nutrient and pH limited. Enzymes already present or newly released will be considerably more active, driving decomposition of the peat matrix long after re-wetting (months–years), even with re-accumulated inhibitors. Indeed, under anaerobic conditions, the lower sensitivity of extracellular enzymes compared with microbial metabolism would disproportionately favour DOC release (partial decomposition products), rather than complete mineralization through intracellular pathways, with implications for declining drinking water quality[9,20]. Thus, a severe drought could contribute to rising DOC trends[8,20,24] by stimulating carbon solubilization (through extracellular cleavage) from the peat matrix, at a time when microbial consumption (through intracellular mineralization) is inhibited by phenolics, that is, decoupling DOC production and consumption.

Severe natural droughts and peatland carbon

Our focus was on the most common Northern latitude peatland types, namely nutrient-poor, acidic systems (ombrotrophic and oligotrophic) likely to be most vulnerable to climate change[7]. In these systems, accelerated carbon losses in the re-wetted phase were pronounced, even where nutrients or pH were so severely limiting that decomposition was actually decreased during drought (Table 2, Supplementary Table S2) owing to acidification (Supplementary Information) or other counteracting drivers (for example moisture stress, particularly in ombrotrophic systems)[4,21,25]. However, mesotrophic and eutrophic systems are also subject to the cascade (Table 2, Supplementary Tables S2, S3 and Fig. S4), as is peat from different climatic regions (Supplementary Table S3), and this again modifies their dominant drivers of carbon loss (inhibitor abundance, nutrients, pH) and will, on a longer timescale (decadal), affect the dominant vegetation, which, in turn, affects biogeochemical conditions[4].

When we studied this cascade *in situ*, at our primary field sites, during the severe natural drought of 2006, we found further evidence for the regulatory pathway (Tables 1 and 2). Moreover, intracellular phenol oxidase measurements suggested increased capacity for complete phenolic mineralization, rather than partial decomposition only (Table 1). The positive feedback

Table 1 | Timing of changes ($P < 0.05$) in processes of the biogeochemical cascade and their precursors, induced by the 2006 severe natural drought (water table 30 cm below surface) in replicate oligotrophic peatlands (A, B Cerrig-yr-Wyn).

Process/precursor	Wetland A	Day	Wetland B	Day
Water table (−)	−1.1 cm	0	−5.9 cm	0
Intracellular phenol oxidase (+)	99%	2	106%	2
Bacterial growth rates (+)	24%	4	75%	4
Extracellular phenol oxidase (+)	455%	4	310%	4
Phenolics (−)	25%	4	38%	4
C-cycling hydrolases (+)	1,564%	4	389%	4
CO_2 (+)	80%	4	45%	4
Phosphatase (+)	407%	8	971%	8
Sulphatase (+)	635%	16	616%*	16
Bacterial abundance (cocci) (+)	56%	39	37%	32
DOC (−)	12%	39	17%	39
Maximum CO_2 (+)	119%	59*	181%	59

Means from five sampling stations per wetland at 10 cm depth are shown. Water tables were typically at the surface (0 cm) before the drought event and had significantly dropped in both wetlands by 5 June 2006, assigned day 0. *$P = 0.064$.

Table 2 | Percentage CO_2 losses (net) during and after drought in mesocosm or short-term field sites (open) and long-term field sites in relation to the predrought mean (2 months, 6 months and 5 years for mesocosms plus Cors Goch field site, Migneint and Cerrig-yr-Wyn field sites respectively).

Country	Site	Description	Treatment	% CO_2 loss drought	% CO_2 loss re-wetting
UK	Migneint	Ombrotrophic bog (hummock)	Simulated	0	354
Finland	Lakkasuo	Ombrotrophic bog (forested)	Simulated	0	325
UK	Cors Goch	Calcareous poor fen	Natural	10	62
Malaysia	Bukit Kemuning	Tropical swamp (forested)	Simulated*	13	60
Finland	Lakkasuo	Minerotrophic fen (forested)	Simulated	23	101
High water tables					
UK	Migneint	Oligotrophic bog	Natural	102	253
UK	Cerrig-yr-Wyn A	Oligotrophic bog	Natural	119	255
UK	Cerrig-yr-Wyn B	Oligotrophic bog (artificial moderate summer droughts)	Natural	181	551
Low water tables					
UK	Cerrig-yr-Wyn C	Oligotrophic bog (naturally drained & artificially re-wetted)	Natural	48	255
UK	Cerrig-yr-Wyn D	Oligotrophic bog (naturally drained)	Natural	89	330

Mesocosm systems ($n = 6$, at 10 cm depth) were exposed to a moderate, simulated drought (water table 15 cm below the surface for 1 month). Field sites experienced the 2006 natural severe drought (water table −30 cm) and means from five sampling stations per wetland are shown at 10 cm depth. **In vitro* material exposed to moderate, simulated drought.

loops to decomposition posited (Fig. 2) can account for the increasing CO_2 losses as drought proceeds, but also the step changes in carbon lost as CO_2 (Fig. 3, replicate wetlands A and B: $P < 0.01$), DOC (A, 261%, $P < 0.001$; B, 188%, $P < 0.001$) and CH_4 (A and B increasing from <1 to >40 mg m^{-2} d^{-1}, $P < 0.001$) after drought, which again dominated the response, as with our other sites (Table 2). Indeed, our results provide a mechanism for step changes in DOC flux with anaerobic characteristics following severe droughts[26]; anaerobic metabolism was accelerated by the release of nutrients and consequent raised pH (Supplementary Fig. S5). DOC-solubilizing extracellular enzymes were more stimulated than intracellular mineralization ($P < 0.05$), despite re-accumulated phenolics, consistent with *in vitro* work. pH correlated strongly with CH_4 emissions in both wetlands (A, $R^2 = 0.754$, $P < 0.01$; B, $R^2 = 0.794$, $P < 0.01$) and CH_4 correlated with CO_2 flux (A, $R^2 = 0.705$, $P < 0.01$; B, $R^2 = 0.813$, $P < 0.001$), indicating that (anaerobic) community decomposition[27] was stimulated. This finding again predicts enhanced carbon loss with eutrophication[23] and recovery from acidification[24], but also provides new insight into interactions between these atmospheric-chemistry-driven and climatic (CO_2 and drought)-driven DOC trends. Whereas it is not known how long a cascade effect would persist following a severe drought, because 2006 was the first truly severe drought recorded at our sites, a moderate natural drought (1995) produced a 3–4 year increase in CO_2 effluxes (Supplementary Fig. S6). This period is exactly that modelled in ref. 8 from a UK peatland. It predicts an 11-year half-life for severe drought effects and warns that return periods are getting ever closer to this (15.5 years), after which peatlands may never recover[8].

Many studies have found increased carbon loss in response to severe summer drought[4,8,28,29] and to a lesser extent in moderate droughts[8,9,29] or even relatively dry summers[29,30]. From our results, drought of certain duration and severity is necessary before the majority of limitations on carbon loss are removed and the cascade reaches a climax. The particular duration required to elicit a response in a given peatland will depend on the balance between nutrient release and counteracting processes, such as acidification and moisture stress, which, in turn, depends on the original water table. In particularly acidic systems (ombrotrophic bogs and systems with low water tables originally), decomposition is limited, even during drought, and therefore carbon loss is low or prevented

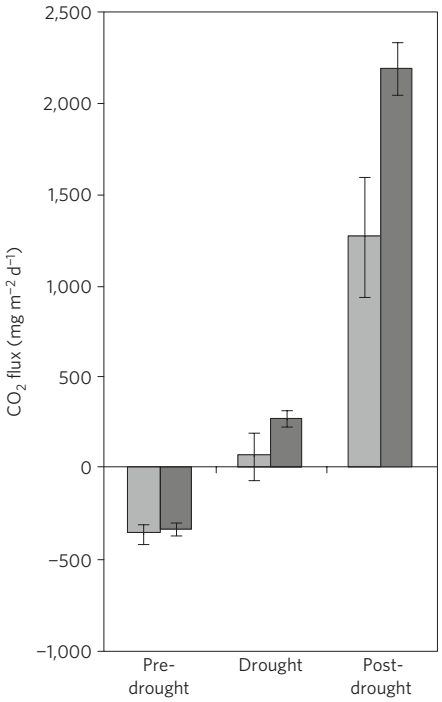

Figure 3 | Effects of the 2006 severe natural drought (water table 30 cm below surface) on oligotrophic peatland net CO_2 flux. CO_2 losses increase during the drought but are further accelerated during the re-wet phase. Light and dark shading denote replicate wetlands A and B respectively. The mean of five sampling stations averaged over distinct four-month periods (before, during and 1 year after the event, at 10 cm depth) is shown. Error bars denote s.e.m.

altogether (Table 2; ref. 31). In the former case this is accompanied by extremely low nutrient availability, and in the latter by moisture stress[4,25]. However, during re-wetting and beyond (years), these limitations can be overcome, and the two-phase response resolves some of the apparent conflict in the literature (Supplementary Information; refs 21,25,31).

Taken together, our results imply that severe drought could destabilize peatland carbon stocks for periods approaching drought return periods[8], triggering a sequential removal of limitations on decomposition, which is, counterintuitively, accelerated with re-wetting. Furthermore, this could apply to 60% of all peatlands, because these are classed as oligotrophic[32]. Moreover, mesotrophic and eutrophic systems showed similar drought-triggered cascades, suggesting a regulatory pathway of fundamental importance to our understanding of global carbon stocks. Indeed, elucidating the sequential, process-specific limitations on carbon losses that constitute the cascade (1) resolves conflicting evidence on drought response, (2) indicates that, although controversial, harnessing preservation mechanisms in peatlands to increase carbon storage could now be possible (Supplementary Information), (3) provides a new mechanism that contributes to rising DOC trends, with implications for drinking water quality[9,20] and moreover (4) highlights the potential for accelerated carbon loss by way of the cascade through interactions with other global drivers, such as elevated CO_2 (refs 7,20), eutrophication[23] and recovery from acidification[24].

Methods

Peat collection. Regulatory pathways (processes 1–4) were determined using selective inhibition, drought simulation (artificial drought) and selective stimulation (below), across a nutrient and organic-matter gradient represented by (1) an ombrotrophic and oligotrophic *Sphagnum* peatland (Migneint region, UK national grid reference, NGR, SH816440), receiving nutrients mainly from rainfall, (2) a lowland, mesotrophic, calcareous fen (Cors Goch, UK NGR SH497826), which receives intermediate levels of nutrients from surrounding land, and (3) a minerotrophic, riparian wetland (Nant Ffrancon Valley, UK NGR SH643625), which receives the most nutrients by intercepting nutrient-laden (eutrophic) waters from terrestrial systems[20] (Supplementary Information). We also determined whether processes (1–4) occurred in a forested pristine bog and fen from Finland (Lakkasuo mire complex 61°47 N, 24°18 E) and a tropical forested swamp from Malaysia (2°56′ N, 101°37′ E). In the latter case, small peat cores were used (100 cm^3 in 2008) rather than standard volumes (below). (See Supplementary Information.)

For *in vitro* work, that is, 'knockouts' and selective stimulation (processes 1, 2, 3b, 4), replicate peat blocks were collected from the field in Spring 2004–2006 and housed in amber glass vessels ($n = 6$). Green vegetation was removed and the remaining peat homogenized using a stomacher (Seward Colworth model 400, UK), to avoid cell disruption. Treatments were carried out in a laminar flow cabinet using aseptic techniques. For drought simulation work (process 3a), intact plant-peat mesocosms (collected from the field in Spring 2004–2006) were subjected to a moderate drought (water table −15 cm). Sampling frequency was every 2 days in mesocosms ($n = 6$). (See Supplementary Information.)

Field evaluation. The sequence of processes 1–4 was evaluated *in situ* at the primary field sites (four peatlands at Cerrig-yr-Wyn) and the Migneint and Cors Goch sites (Tables 1 and 2). Cerrig-yr-Wyn is an upland, oligotrophic, flush system on the Wye catchment (Plynlimon, UK NGR SN820866) characterized by *Sphagnum* and *Juncus* communities with a pH range of 4.0–4.8 (refs 9,20) and was chosen as the primary field site. (See Supplementary Information.)

Enzyme, hydrochemical and trace gas measurements. Peat extracellular phenol oxidase activities[22], hydrolase activities[13] and pore-water phenolics[13] were measured using routine methods. Pore-water DOC concentrations were determined using a Total Organic Carbon Analyser (Shimadzu 5000, Tokyo, Japan). Inorganic nutrients (pore-water anions and cations) were measured using a DX 120 ion chromatograph (Dionex Corporation, USA). Microbial abundance was measured on peat extractions using epifluorescent microscopy and microbial growth rates (^{3}H thymidine incorporation into DNA for bacteria and ^{14}C acetate incorporation into ergosterol for fungi) on the same extractions. Intracellular phenol oxidase activity (catechol 2,3-dioxygenase) was measured spectrophotometrically. Gas concentrations (CO_2, CH_4, N_2O) were measured using a gas chromatograph (Ai Cambridge, model 92, Analytical Measuring Systems, Cambridge, UK). (See Supplementary Information.)

Knockout procedures. Treated samples were irradiated to kill microbes while retaining edaphic enzyme activity. *De novo* hydrolase synthesis was prevented by using streptomycin sulphate (bacteria) and cycloheximide (fungi), to block protein synthesis. (See Supplementary Information.)

Selective stimulation. Oxygen enrichment was achieved using sterilized, compressed-air manifold units with flow regulation valves. Depletion of phenolics (>63%) was achieved using N-vinyl-2-pyrrolidone extraction[13], and Bristol's medium supplemented by peat leachate (without phenolics) provided excess labile carbon and inorganic nutrients (final concentrations informed by appropriate field data). Non-manipulated variables were maintained constant by either purging with nitrogen (constant low O_2, monitored by an O_2 sensor), inhibition of phenol oxidase (constant high phenolics, that is, no activity; monitored using the phenol oxidase assay and phenolics assay), or supply with ultrapure water (constant low carbon and nutrients monitored by total organic carbon analyser and ion chromatography). (See Supplementary Information.)

Statistical analyses are detailed in Supplementary Information.

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Author contributions

N.F. wrote the paper and carried out the experiments. C.F. co-wrote the paper and conceived the experiments.

Additional information

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