

PHENOL OXIDASE ACTIVITY IN PEATLANDS IN NEW YORK STATE: RESPONSE TO SUMMER DROUGHT AND PEAT TYPE

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Abstract: We studied phenol oxidase (PO) activity in two *Sphagnum*-dominated peatlands and a *Carex*-dominated freshwater marsh during a strong summer drought in Central New York, USA to determine whether PO activity might respond to expected climatic changes. Peat was sampled at different depths and within distinct vegetation types within the marsh. *Carex*-derived peat supported substantially higher PO activity (average = 0.030, range = 0.011–0.051 $\mu\text{MOL diqc min}^{-1} \text{ mg dry peat}^{-1}$, at soil pH 5.5) than *Sphagnum* peat (average = 0.006, range = 0.001–0.015 $\mu\text{MOL diqc min}^{-1} \text{ mg dry peat}^{-1}$, at soil pH 3.8). In both peat types, PO activity showed a strong exponential increase with increased solution pH. Phenol oxidase activity in *Sphagnum* peat did not vary significantly during the drought, suggesting that PO activity may be constrained by low pH and enzyme inhibitors. Conversely, PO activity in the marsh peat varied with peat type and sample date but not as a consistent function of water-table depth. As a result, PO activity in *Sphagnum* peat appears to be regulated less by aeration and more by pH and possibly enzyme inhibitors. When pH is favorable, PO activity depends more on wetland vegetation type and botanical composition of the peat than climatic factors.

Key Words: *Carex*, L-dopa, peat soil, soil enzyme, *Sphagnum*

INTRODUCTION

Sphagnum-dominated, northern peatlands contain about 455 Pg of carbon in the form of partially decomposed organic matter (i.e., peat) (Gorham 1991). Even a small portion of this stored carbon released back into the atmosphere could have a tremendous impact on the atmospheric budget of CO₂ and, in turn, climate (Mitchell et al. 1996) if conditions become more favorable for its decomposition. Whether this occurs depends on the extent that climate controls the decomposition of *Sphagnum*-derived peat. However, this is not easy to predict because *Sphagnum* has a unique biochemical nature (no lignin, but rather a polyphenolic network) that strongly resists microbial activity (see van Breeman 1995).

Decomposition of *Sphagnum* peat is notoriously slow, and many studies have focused on addressing environmental factors that may be responsible (see Johnson and Damman 1993). Recently, the role of *Sphagnum* chemical composition in controlling decomposition rates was reviewed by Verhoeven and Li-

efveld (1997), who demonstrated that a suite of chemical compounds may interact to inhibit organic matter decomposition in *Sphagnum*-dominated peatlands. Water-soluble phenolic compounds released by living *Sphagnum* (Rasmussen et al. 1995) may have an immediate impact on decomposition rates by generating acidity and inhibiting microbial activity (Verhoeven and Toth 1995). Furthermore, decaying peat releases a substantial amount of relatively recalcitrant phenolic compounds (van Breeman 1995) in addition to end product CO₂ and CH₄. These phenolic compounds also slow decomposition and may play a role in the formation of aquatic humic acids. Thus, turnover of phenolic acids may play a key role in carbon dynamics in *Sphagnum*-dominated peatlands.

One component of carbon cycling in peatlands involves the breakdown of phenolic compounds. The degradation of phenolic compounds occurs enzymatically through phenol oxidases (EC 1.10.3.1 and 1.14.18.1). This has been addressed only recently in peat (Pind et al. 1994, Freeman et al. 1996). Circumstantial evidence suggests that controlling factors in-

clude aeration, temperature, pH (Ladd 1978), and notably, plant species composition of the wetland (Kuprevich and Shcherbakova 1971, Duxbury and Tate 1981). Climatic and hydrologic changes could enhance phenol oxidase (PO) activity. Specifically, warmer, drier conditions would increase aeration (Gorham 1991), which may enhance PO activity (Pind *et al.* 1994). On the other hand, PO activity may be insensitive to changes in water table in some situations (Freeman *et al.* 1996). Secondly, it seems that peatlands are sub-optimal for this enzyme because pH is too low (Pind *et al.* 1994). An additional factor is that vascular plants may be a source of PO (Ladd 1978); hence, changes in plant species composition may indirectly influence the turnover of phenolic compounds.

We took advantage of a strong summer drought that lowered ground-water levels in local wetlands to collect basic information about how PO activity varies with changes in water level and aeration. We expected PO activity to increase during the drought then decrease when rain ended the drought. We also studied a *Carex*-dominated wetland with higher native pH than *Sphagnum*-derived peat to address pH limitation of PO activity.

METHODS

Three study sites included two *Sphagnum*-dominated peatlands and a freshwater *Carex*-dominated marsh. Rome Bog is a 20-ha peatland within the 10,000-ha Rome Sand Plains (75°26'W, 43°15'N) near Utica, New York, USA. Samples were collected in a *Sphagnum rubellum* Wils. lawn. McLean Bog is a 1-ha ombrotrophic peatland located in McLean Preserve in McLean, NY (76°10'W, 42°33'N). Samples were collected in an open area of the wetland dominated by *Sphagnum magellanicum* Brid.. Michigan Hollow is a 20-ha freshwater marsh located 10 km south of Ithaca, NY (76°30'W, 42°15'N). The marsh vegetation is dominated by *Carex lucustris* Willd. with patches of *Typha latifolia* L. and *Juncus effusus* L. in the central portion of the wetland. Samples were collected from each distinctive vegetation type.

The summer of 1995 (June–August) in New York State was characterized by below normal rainfall and above normal temperatures. Local summer rainfall averaged just 54% of normal for the summer, and the Central Lakes Region was categorized as being in a “Severe Drought” on the Palmer Drought Severity Index. Local temperatures averaged 1.8° C above normal. Rainfall was below normal until October 1995, and by the end of November 1995, ground-water levels at monitoring stations were at or above normal.

Table 1. Soil pH and water-table depth from four peat types during an 81 day sampling period.

Sample Site	Soil pH	Average Depth to Water Table (cm)	Range of Water Table Depth (cm)
<i>Carex lucustris</i>	5.5	21	0–47
<i>Typha latifolia</i>	5.0	19	0–47
<i>Juncus effusus</i>	5.5	13	0–30
<i>Sphagnum magellanicum</i>	3.8	10	0–29

Depth Distribution

We collected peat cores using an open PVC cylinder (10-cm diameter × 24-cm length) by first making a cylindrical incision through the peat surface with a knife, then driving the cylinder through the surface vegetation into the underlying peat. The intact core was then lifted from the site and capped at both ends with a rubber cap held in place with a hose clamp. The headspace of the cores was purged with nitrogen and kept at 4° C until analysis.

Temporal Patterns

Bulk peat samples were collected periodically between August 25, 1995 and November 29, 1995 at McLean Bog and Michigan Hollow for PO activity measurements. Samples were collected by excavating a trench in the peat and then collecting about 500 cc of peat from the exposed vertical face of the trench at 2, 15, and 30 cm depths. Samples were stored in sealed plastic bags under a nitrogen headspace until analysis, usually within 24 h of collection. The depth to water table was also recorded at the time of sampling (Table 1).

pH Response

The effect of soil solution pH on PO activity was determined by manipulating the solution pH of enzyme assays of the *Carex* and *Sphagnum* peat. Soil solutions were buffered at pH 2.5, 4.0, 6.8, and 7.6 using Sørensen's phosphate and Sørensen's Citrate I buffers (Fasman 1975).

Analytical Methods

PO enzyme activity was determined using the method described in Pind *et al.* (1994) with slight modifications. Fresh peat (2 g wet mass) and 10 mL distilled water were combined and gently mixed on a platform shaker for 10 minutes. Aliquots of 3 mL containing about 0.1 grams peat (dry weight) were transferred to

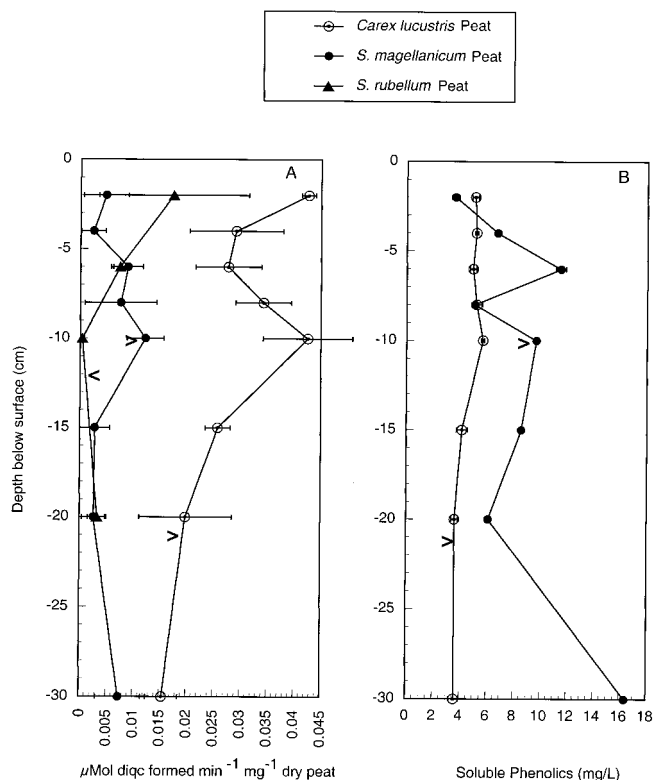


Figure 1. (a) Depth distribution of phenol oxidase activity and (b) soluble phenolic compounds within *Carex lucustris*, *Sphagnum magellanicum*, and *Sphagnum rubellum* peat cores. Values are means \pm standard errors, $n = 2$. Symbol (>) denotes water-table depth.

replicate 10-mL centrifuge tubes. Samples were dried at 45°C to constant weight for dry weight determination. To each tube, 2 mL of 10mM L-dihydroxy phenylalanine (L-DOPA, Sigma Chemical, St Louis, MO, USA) solution or 2 mL distilled water (control) were added, and samples were incubated for 5 minutes at 18°C. In earlier trials, we determined that the rate of L-DOPA oxidation remained approximately linear during the course of the incubation. The reaction was terminated by immediate centrifugation. The supernatant was filtered through a Whatman GF/B filter, and the absorbance was measured at 460 nm on a Spectronic Spec 21. Phenol oxidase activity was expressed as μMOL 2,3-dihydroindole-5,6-quinone-2-carboxylate (diqc) formed per minute per mg dry peat. Soluble phenolic compounds were measured by the method of Box (1983) using Folin-Ciocalteu phenol reagent.

Statistical Analyses

We used analysis of variance (ANOVA) to test the null hypothesis of no difference in PO activity among peatland sites and depth per site. We used regression analysis to describe seasonal patterns in PO activity.

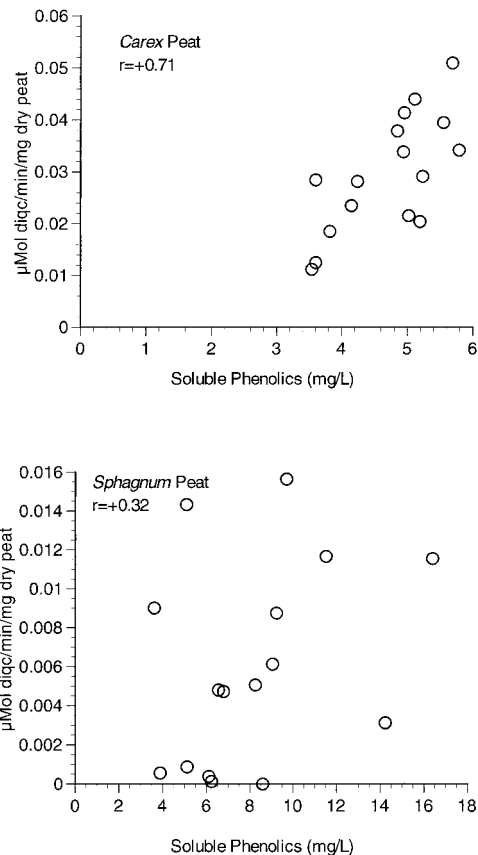


Figure 2. Relationship between phenol oxidase activity and soluble phenolic compounds within *Carex lucustris* and *Sphagnum magellanicum* derived peat cores.

Differences in soluble phenolic compound concentrations were analyzed with a two sample t-test.

RESULTS

There was a significant difference ($F_{2,36} = 34.90$, $p < 0.0001$) in PO activity among the three study sites. Phenol oxidase activity was higher in *Carex*-derived peat (average = 0.030, range = 0.011–0.051 μMOL diqc min⁻¹ mg dry peat⁻¹) than in the two *Sphagnum*-derived peats (average = 0.006, range = 0.001–0.015 μMOL diqc min⁻¹ mg dry peat⁻¹). Phenol oxidase activity did not differ as a function of depth in *Sphagnum*-derived peat. Conversely, in *Carex*-derived peat, PO activity was significantly higher in the top 10 cm of the profile than in deeper peat (Figure 1a). There were significantly higher concentrations of soluble phenolic compounds ($p = 0.0031$, t-test) in *Sphagnum*-derived peat than in *Carex*-derived peat (Figure 1b). On the other hand, PO activity was positively correlated ($P < 0.01$) with soluble phenolic concentrations in *Carex*-derived peat but not in *Sphagnum*-derived peat (Figure 2).

Depth to water table was greatest in all sites at the

Table 2. Regression analysis of phenol oxidase activity on wetland water-table depth and julian date for three depths from four peat types.

Peat Type Sample Depth	Average PO Activity*	Water Table Depth		Julian Date	
		r ²	p	r ²	p
<i>Carex lucustris</i> ; n = 6					
2 cm	30	0.06	0.6393	0.04	0.6887
15 cm	36	0.21	0.2692	0.57	0.2326
30 cm	22	0.18	0.4024	0.23	0.3358
<i>Typha latifolia</i> ; n = 5					
2 cm	19	0.05	0.7280	0.20	0.4540
15 cm	25	0.01	0.8825	0.04	0.7439
30 cm	22	0.01	0.9315	0.02	0.8341
<i>Juncus effusus</i> ; n = 5					
2 cm	26	0.25	0.3900	0.39	0.2611
15 cm	52	0.39	0.2577	0.32	0.2759
30 cm	26	0.20	0.4500	0.10	0.5984
<i>Sphagnum magellanicum</i> ; n = 5					
2 cm	8	0.38	0.3821	0.77	0.1200
15 cm	5	0.22	0.8527	0.28	0.4692
30 cm	2	0.06	0.7580	0.01	0.9014

* nMOL diqc min⁻¹ mg⁻¹ dry peat.

start of the sampling period and gradually reached the soil surface by the end of the sampling period. On average, the depth to water table at each sample site followed the order: *Carex* > *Typha* > *Juncus* > *Sphagnum* (Table 1). Phenol oxidase activity did not differ significantly among sampling dates for *Sphagnum*-derived peat or with water-table depth (Table 2). For *Carex*-derived peat, maximum activity at the 15-cm depth (0.057 $\mu\text{MOL diqc min}^{-1} \text{mg dry peat}^{-1}$) occurred in November; however, peat from the other

depths showed no clear seasonal patterns. Notably, peat from *T. latifolia* and *J. effusus* sites had slightly lower average PO activity (0.022 and 0.026 $\mu\text{MOL diqc min}^{-1} \text{mg dry peat}^{-1}$, respectively), with smaller temporal variations than the *Carex*-derived peat, except for *Juncus*-derived peat from the 15-cm depth.

There was a strong exponential increase in PO activity with increasing adjusted pH for both *Sphagnum* and *Carex*-derived peat (Figure 3). Maximum PO activity in *Carex* peat (0.097 $\mu\text{MOL diqc min}^{-1} \text{mg dry peat}^{-1}$) occurred at pH 7.6 and was 3-fold greater than the average PO activity for *Carex* peat at its native pH (5.5). Similarly, maximum PO activity in *Sphagnum* peat (0.036 $\mu\text{MOL diqc min}^{-1} \text{mg dry peat}^{-1}$) occurred at pH 7.6, with PO activity 6-fold higher than for *Sphagnum* peat at native pH (3.8). Notably, the native pH of the *Sphagnum*-derived peat was much lower pH (3.8) than *Carex*-derived peat (5.5) and *Juncus*-derived peat (5.5). The pH of *Typha*-derived peat varied from 4.4 at the 2-cm depth to 5.2 at the 30-cm depth.

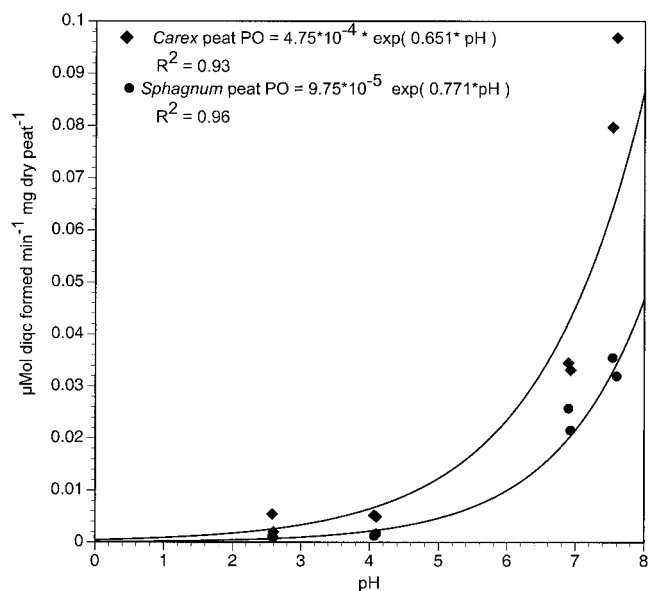


Figure 3. Effect of suspension pH on phenol oxidase activity in *Sphagnum magellanicum* and *Carex lucustris* peat.

DISCUSSION

Our result of higher PO activity in *Carex*-derived peat than in *Sphagnum*-derived peat versus lower concentrations of soluble phenolic compounds (Figure 1) suggests faster phenolic turnover in *Carex*-derived peat. There are a number of possible explanations for the higher activity. The most obvious difference is botanical composition of the peat. For example, *Carex* lack condensed tannins, which have been shown to reduce PO activity (Nichols-Orians 1991). Conversely,

Sphagnum-dominated peatlands are known for their high tannin concentrations present in both *Eriophorum* spp. (Jonassen et al. 1986) and possibly *Sphagnum* (Wilson et al. 1989). Polyuronic acids found in the cell walls of *Sphagnum* also act as enzyme inhibitors (Painter 1991). Therefore, low PO activity in the *Sphagnum*-derived peat suggests an enzyme inhibitory effect by compounds derived from the vegetation. Further, Banerjee and Sen (1979) demonstrated that Gram-positive bacteria can be inhibited by extracts from *Sphagnum*. Borga et al. (1994) showed that *Sphagnum*-derived peat tends to support a Gram-positive microbial community versus a Gram-negative community in a *Carex*-derived peat. Interestingly, Gram-positive bacteria tend to excrete more extracellular enzymes than Gram-negative bacteria (Wetzel 1991), suggesting that despite the presence of an active microbial community capable of secreting large amounts of extracellular enzymes, the enzymes seem to be inhibited. In sum, differences in peat botanical composition may result in differences in peat microbial community structure (cf. Borga et al. 1994) and subsequent differences in PO activity.

Our data also are consistent with the hypothesis that vascular plant roots are a potential source of PO enzymes. This has been shown for ericoid mycorrhizas associated with wetland plants such as *Culluma*, *Vaccinium*, *Erica*, and *Gaultheria* spp. that have a wide range of enzymatic capabilities (Read 1992) and are able to use a phenol oxidase to degrade phenolic compounds (Leake 1987). Furthermore, it is accepted that free enzymes in soils originate from plant as well as microbial sources (Ladd 1978). Although we are not aware of any studies of the presence of PO in the tissues of wetland vascular plants, it is possible that plant detrital inputs may act as an additional source of the PO enzyme to wetland systems. Notably, there is evidence that *Sphagnum* do not contain PO enzymes (Sherman et al. 1991). The stability of these free-enzymes is not well known, although complexation with humic acids may protect the PO enzyme from protolytic attack and preserve it in the soil solution, albeit with reduced activity (Wetzel 1991).

The most obvious chemical difference between the *Sphagnum*- and *Carex*-derived peat is pH. While there is a paucity of information on the *in situ* pH optimum of the PO enzyme, there are general observations that the acidic pH of wetlands may be sub-optimal for the activity of the PO enzyme (Lähdesmäki and Piispanen 1988, Pind et al. 1994). Our assay of PO activity at various solutions pH indicates a pH optimum for PO that is higher than the pH of these peatlands. This observation is contrary to the generality that most organisms and their enzymatic systems in natural habitats are adapted to the pH of their environments (Münster

1991). However, the peat assayed from the marsh site had higher activity than peat from the bog site when assayed at the same pH. This suggests that, in addition to a pH control over PO activity, a second factor such as inhibition may be regulating PO activity.

The slight increase in activity at 10 cm below the surface in *Carex*-derived peat may be related to the location of a zone of fluctuating water level. Peats experiencing alternating periods of anaerobic and aerobic conditions have higher organic matter oxidation rates than peats with constant moisture levels (Tate 1980). Higher PO activities in this region may reflect an established and active microbial community at this depth. There seems to be a general tendency for the activities of most enzymes to decrease with increasing depth in peat profiles (Freeman et al. 1995). This has been observed for PO (Pind et al. 1994), although there is a great deal of variability in the literature on PO activity changes with depth. For example, Lähdesmäki and Piispanen (1988) found PO activity to increase with depth in a *Sphagnum* peat deposit. Conversely, Duxbury and Tate (1981) showed that PO activity did not vary with depth in peat under a sugar cane crop but did decrease in a fallow Pahokee muck. The wide variation in reported PO activity is probably a function of the variety of peat types and the individual environmental differences in each peatland and the resulting microbial community.

No strong seasonal trend in PO activity in *Sphagnum*-derived peat despite the strong local drought suggests that PO activity is constrained and unresponsive to changes in water level. This is consistent with the hypothesis that sub-optimal pH and the presence of enzyme inhibitors are the "master" variables controlling PO activity for *Sphagnum* peat; hence, the change in degree of aeration has no effect on the PO activity. Despite a relatively higher oxygen content at the surface, deeper peat seems to have been oxygen-limited. It is possible that a persistent drought may be required to bring about the required changes in aeration and pH before PO activity can increase. Although radical changes in hydrologic regime seem to stimulate PO activity (Kuprevich and Shcherbakova 1971), presumably by increasing aeration, we found no evidence of seasonal fluctuations promoting PO activity in the *Sphagnum* peat.

The *Carex*-derived peat also experienced water levels low enough to increase aeration, yet we found no strong seasonal trend. Nevertheless, there were discrete differences in the patterns of PO activity among vegetation sites within the marsh. While we can only speculate as to the causes of these changes, they may in part be related to differences in substrate availability as the plants senesced and died, releasing phenolic compounds into solution. PO activity and phenol me-

tabolism have been shown to respond positively to seasonal inputs of organic matter (Peters and Colwell 1989, Sinsabaugh and Linkens 1990). For example, the strong positive correlation between the soluble phenolic content and PO activity in the *Carex*-derived peat suggests a linkage between substrate availability and enzyme activity. However, despite this temporal variability, we found no strong pattern in PO activity as the water table rebounded to pre-drought levels. It is notable that this rebound occurred at the end of the growing season, which may have reduced any plant-mediated PO activity.

Our results indicate that despite a considerable difference in PO activity between *Sphagnum*-derived peat and *Carex* peat, PO activity did not respond predictably to changes in local water level during prolonged drought. Even though the 10-cm decrease in water level was similar to that expected to take place in northern peatlands if climate warming occurs (Gorham 1991), PO activity was unresponsive. Notwithstanding, summer droughts are ephemeral, and long-term drought might be necessary to overcome pH limitations and the presence of enzyme inhibitors. Plant species composition and peat botanical origin seem to influence PO activity to a greater extent than short-term changes in wetland hydrology. The unresponsive behavior of PO to changes in wetland hydrologic regime suggests that more detailed study of decomposition related enzymes in peatlands may be necessary to fully understand the relationship between decomposition and climate in peatlands.

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