

# *Phragmites Australis* Invasion and Herbicide Treatment Changes Freshwater Wetland Carbon Dynamics

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## Research Article

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## Abstract

Wetland carbon budgets largely depend on the wetland communities' relative rate of carbon assimilation and carbon emission. Invasive plants with growth or decomposition patterns that differ from reference plant communities may shift wetland carbon budgets, as may invasive plant suppression efforts. For example, *Phragmites australis* (European Common Reed), which replaces meadow and cattail marsh in the Laurentian Great Lakes area, has high biomass production and foliar nitrogen, can modify the environment conditions that effect decomposition rates, creates thick stands of slowly decomposing standing dead stems, and is often controlled using broad-spectrum herbicides. Our objectives were to determine if *P. australis* control efforts in freshwater coastal marshes were sufficient to return net primary productivity, decomposition rates, and environmental conditions to within their pre-invasion range. We find that *P. australis* invasion had the greatest effect on carbon sequestration when replacing meadow marsh, as opposed to cattail marsh. We conclude that control efforts, one-year post-treatment, dramatically reduce total biomass and carbon assimilation compared to meadow and cattail marsh. However, floating and submersed aquatic vegetation rapidly colonized treated areas, suggesting that continuing plant community recovery may restore the carbon budget in subsequent years.

## Introduction

Wetlands are global sinks for carbon (Mitsch et al. 2013), with vegetation playing a critical role in carbon assimilation (Rothman and Bouchard 2007; Schultz et al. 2011). However, invasive wetland plants can affect the carbon budget through several pathways. Invasive plants can directly influence carbon cycling, for example, if they are more productive than the species they displace (e.g., Lei et al. 2019), or if they produce more nutrient-rich litter (e.g., Yuckin and Rooney 2019). They can also affect carbon cycling indirectly, by altering key environmental factors in the regulation of decomposition rates, such as light penetration, oxygen availability, or water levels (e.g., Robichaud and Rooney 2021). Invasive plants tend to increase the size of the carbon pool and the rate of carbon cycling in wetlands (Liao et al. 2008; Vilà et al. 2011), but the impact of any invasive plant on a wetland's carbon budget will depend on the relative properties of the invader and the vegetation community being displaced (Ehrenfeld 2003, 2010; Liao et al. 2008). Thus, the consequences of invasion are system specific.

Invasive *Phragmites australis* ssp. *australis* (hereafter *P. australis*), has relatively high above- and belowground biomass production (Windham 2001; Rothman and Bouchard 2007; Duke et al. 2015; Lei et al. 2019) and high rates of carbon assimilation (Farnsworth and Meyerson 2003; Tho et al. 2016). Additionally, stands of *P. australis* tend to accumulate dead stems over time, which may remain upright for > 3 y (Rooney lab, unpublished data). The productivity and recalcitrant nature of *P. australis* stem litter suggests that *P. australis* invasion may provide an ecosystem service in the form of increased carbon sequestration and storage. However, this may be offset by the reported high methane emissions from invasive *P. australis* (Mozdzer et al. 2013) coupled with a capacity to root more deeply than native plants and thereby access previously untapped soil-carbon stores (Bernal et al. 2016; but see Lei et al. 2019). *Phragmites australis* also has relatively high nitrogen in its foliar tissue (Findlay et al. 2002; Hirtreiter and Potts 2012; Yuckin and Rooney 2019), which could expedite decomposition. Thus, the direct influence of *P. australis* invasion on the carbon budget is unclear. *Phragmites australis* invasion is also likely to influence carbon cycling indirectly. In some wetland habitats *P. australis* can reduce the depths of standing water (Windham and Lathrop 1999) and intercept more light than native plant communities (Hirtreiter and Potts 2012). Such alterations to environmental conditions can drive changes in primary production and decomposition rates. Deeper standing water can increase macrophyte biomass and decomposition rates (van der Valk et al. 1991; Christensen et al. 2009; Duke et al. 2015), while higher light interception creates shading that can reduce water temperatures, which mediate the rate of decomposition (Hirtreiter and Potts 2012).

Due to the documented negative effects of invasion in wetlands, there have been extensive efforts to control *P. australis* in North America (Hazelton et al. 2014; Martin and Blossey 2013). Most of these control projects apply a herbicide, such as glyphosate or imazapyr, to kill living tissue and then follow this approach with a secondary treatment such as rolling or cutting to remove standing dead biomass (e.g., Hazelton et al. 2014). Controlling an established invasive species is challenging, and treatment often requires the evaluation of potential trade-offs between habitat conservation and other ecosystem services (e.g., Alldred et al. 2016). Reducing *P. australis* populations in a marsh is likely to improve habitat quality for wildlife (Schummer et al. 2012; Markle and Chow-Fraser 2018), but this may be at the cost of reduced carbon sequestration – an increasingly necessary ecosystem service.

Working alongside an on-going *P. australis* suppression project, we measured changes in primary production and decomposition to provide insight into the effects that invasion and herbicide treatment have on short-term carbon sequestration in freshwater marshes. Our objectives were to 1) quantify the effect of invasive *P. australis* on freshwater coastal marsh carbon dynamics and relevant environmental conditions and, 2) evaluate if, in the short-term, herbicide-based *P. australis* suppression restores primary production and decomposition to rates observed in equivalent uninvaded 'reference' marsh. We predict that primary production will decrease, and decomposition will increase in herbicide-treated sites compared to both invaded and reference plant communities as a result of changes to the plant community, litter composition, and environmental conditions.

## Methods

### Study location

Our study took place in Long Point (42° 34' N, 80° 24' W), a peninsula located on the north shore of Lake Erie, Ontario, Canada (Fig. 1). Invasive *Phragmites australis* populations have been expanding since the late 1990s, and most frequently replaced meadow marsh and cattail marsh communities in Long Point (Wilcox et al. 2003). In 2016, the Ontario Ministry of Natural Resources and Forestry (OMNRF) obtained an Emergency Registration (no. 32356) under the Pest Control Products Act from Health Canada's Pest Management Regulation Authority and a provincial Permit to Perform an Aquatic Extermination of invasive *P. australis* to apply a glyphosate-based herbicide (Roundup® Custom for Aquatic & Terrestrial Use Liquid Herbicide (Bayer CropScience, Whippany, New Jersey, USA)) combined with a nonionic alcohol ethoxylate surfactant (Aquasurf®, registration no. 32152, Brandt Consolidated, Springfield, IL, USA), to control *P.*

*australis* (OMNRF 2016). Herbicide was applied via helicopter (Eurocopter A-Star equipped with GPS guidance and Accu-flo boom nozzles) in September 2016 and via ground application (Marsh Master™) in September 2017. In the winter, treated areas were rolled with a drum pulled by an Argo™ track vehicle or mowed using the Marsh Master™ to reduce the number of standing dead stems and enhance light penetration. Herbicide was applied across the much of the study area, but certain portions of the invaded marsh were reserved as experimental controls (Figure 1).

### Field methods

#### Site establishment

To assess primary production, decomposition rates, and environmental conditions we established 10 sites in *P. australis*-invaded habitat, 10 in recently herbicide-treated habitat, and 10 in uninvaded, reference habitat. Reference vegetation differs along the naturally occurring water depth gradient, resulting in distinct vegetation communities of meadow marsh (n = 5) and emergent cattail marsh (n = 5). Meadow marsh is in areas of shallow standing water and saturated soil, where *Calamagrostis canadensis* (Canada Bluejoint grass) is dominant, while cattail marsh is in areas with deeper standing water and is dominated by a cattail species complex (*Typha* spp.). Sites within each of the three vegetation types (invaded, reference, herbicide-treated) were distributed along a water depth gradient which ranged from 14 to 56 cm (Table 1). At each of these thirty sites, we measured above and belowground biomass as an index of primary production. From these thirty sites, we selected a site at a shallow (mean = 16.5 cm ±10.8 SD), intermediate (mean = 26.7 cm ±10.8 SD) and deep (mean = 34.1 cm ±11.1 SD) water depth in each habitat type (3 habitat type x 3 water depths = 9). We deployed litter bags at these nine sites in a transplant experiment to measure the direct and indirect effects of invasion and herbicide treatment on decomposition rates.

Table 1. Site characteristics of the reference meadow, reference cattail, *P. australis*-invaded and herbicide-treated sites in July 2017 (n = 30). 'Reference average' provides the average of meadow and cattail values. Standard deviations are reported in brackets.

	Meadow (reference)	Cattail (reference)	Reference average	<i>P. australis</i> invaded	Herbicide-treated
Marsh Community					
Sample size	5	5	10	10	10
July water depth (cm)	18 (± 7.0)	41 (± 8.5)	29 (± 14.0)	36 (± 10.5)	40 (± 10.0)
Canopy height (cm)	102 (± 26)	266 (± 14)	184 (± 86)	350 (± 48)	15 (± 14)
Litter depth (cm)	8.5 (± 3.7)	7.1 (± 3.0)	7.8 (± 3.3)	17.8 (± 9.9)	9.3 (± 5.7)
Living (stems/m <sup>2</sup> )	776 (± 160)	83 (± 66)	429 (± 383)	91 (± 48)	16 (± 21)
Living (% cover)	59 (± 5)	62 (± 9)	61 (± 15)	79 (± 11)	41 (± 8)
Standing dead (% cover)	17 (± 10)	25 (± 12)	21 (± 12)	11 (± 6)	0.6 (± 0.4)

#### Primary production

To measure aboveground biomass, we collected live ramets, standing dead stems, and leaf litter of all species present from every vegetation community within three randomly established 0.25 m<sup>2</sup> quadrats at each of the 30 sites (Fig. 1). We collected this material July 22 – 25<sup>th</sup> 2017, during peak aboveground biomass (Yuckin and Rooney 2019) and then dried the plant material for 48 hr at 100°C before weighing it to determine the mass of fallen litter, live aboveground biomass, and standing dead litter.

To measure belowground biomass, we used a modified soil ingrowth method (Neill 1992) at each site to measure the amount of biomass produced over the growing season (60 - 65 days). From May 20 – 25<sup>th</sup> 2017 we removed seven soil cores (4.8 cm diameter x 11.3 cm depth) at each site and replaced the sediment with a vermiculite mixture, which was then retrieved during peak biomass (22 – 25<sup>th</sup> July). The root and rhizome matter from each vermiculite core was then separated and weighed.

#### Decomposition rates

We carried out a litter transplant experiment to separate the direct and indirect effects of *P. australis* invasion and herbicide-based control on decomposition rates. Litterbags were made from 2 mm fiberglass mesh and contained five grams of either *P. australis* leaves, *Typha* spp. leaves, or *C. canadensis* leaves and stems. *Calamagrostis canadensis* stems were included in the litterbags because the growth form of *C. canadensis* did not allow for effective separation of the leaves from stems. The C:N ratio of all plant tissue was determined prior to deployment (Yuckin and Rooney 2019). From May 12-14<sup>th</sup>, 2017, we deployed litterbags containing each type of litter at the nine shallow, medium, and deep-water sites, anchoring them to the substrate in clusters of three (one of each litter type). To mimic standing dead plant material, we tied replicates to poles above the water at the three intermediate water depth sites. We refer to these sites as “dry” throughout to indicate that they were not submerged or exposed to substrate. We collected three replicates of each litterbag type from each site after two weeks and then monthly until May 15, 2018. Upon retrieval, we dried the litter at 100°C for 48 hours before weighing it.

#### Environmental variables

To relate primary productivity and decomposition to the environmental conditions, we measured water depth, water temperature, and photosynthetically active radiation at each site. To measure daily fluctuations in water depth and temperature, we installed data loggers (HOBO U20-001-02-Ti data logger, Onset, MA, USA) at each litterbag site (n = 9). Data loggers were installed in June 2017 and recorded from June 14<sup>th</sup> to October 16<sup>th</sup>, 2017. In July 2017, we measured

incident photosynthetically active radiation (PAR) (400-700 nm) and PAR extinction profiles at each site. Extinction profiles captured the % of incident PAR in 50 cm increments from the top of the canopy to the water or sediment surface. All PAR measurements were taken between 9:00 and 14:45 hrs on cloudless days in June, using a pair of LI-190SA Quantum Sensors to simultaneously capture PAR above the canopy and within the canopy. Extinction profiles were not measured at herbicide-treated sites due to the low emergent vegetation cover and lack of canopy interception.

### Data analysis

#### Primary production

We considered six primary production response variables: 1) aboveground biomass, 2) belowground biomass, 3) total live biomass, 4) root:shoot ratio, 5) standing dead biomass, and 6) litter biomass. To test for differences in these variables among the habitat types and the water depth gradient, we ran general linear models (ANCOVA) with habitat type (reference, invaded, herbicide-treated) and water depth as predictor variables, and included an interaction term. All variables were square-root transformed to meet the assumption of normally distributed residuals. When an interaction was not significant, we interpreted the fixed factors independently and conducted a Tukey's post hoc test among the habitat types. As water depth was measured at the beginning of the field season in May and again at each site in July, we ran each model twice using the two different depth measurements. We then compared the model fit between water depth measurements using Akaike's Information Criterion (AICc) and present the results of the best fitting model. AICc model comparisons were run using the *MuMIn* package in R (Barton 2018).

#### Decomposition rates

To calculate the decay rate of litter types in different water depths, we calculated the mass loss as: [(original mass loss - average travel loss for that plant species) - remaining mass]. We fit the percent mass lost over time using two models: the single exponential model ( $k$ ) (Olson, 1963) and the decaying coefficient model ( $k_1$ ) (Godshalk et al. 1978), as described by Ágoston-Szabó and Dinka (2008). Decay rates were determined by using a nonlinear least-squares algorithm to fit the percent of dry-weight litter mass remaining over time using the Levenberg-Marquardt method in R. The decaying coefficient model ( $k_1$ ) is the most appropriate decay model for comparisons among different litter types and vegetation communities, and for when the decay rate is expected to fluctuate. However, the single exponential model ( $k$ ) is more common in the literature and allows for an easier comparison to published studies (Dinka et al. 2004). In addition, because the relative decay coefficient ( $k_2$ ) is dependent on the initial decay coefficient ( $k_1$ ) there cannot be a direct comparison of relative decay coefficients. We report decay coefficients from both model types and conducted statistical analyses on the single exponential decay rate ( $k$ ) and the initial decay rate in the decaying coefficient model ( $k_1$ ).

After calculating  $k$  and  $k_1$  over the deployment period, we averaged the values over time to generate one value per site. This value was our response variable and was used in a GLM to test if the single exponential decay rate ( $k$ ) or the initial ( $k_1$ ) decay coefficient was predicted by species of litter (*P. australis*, *Typha* spp., and *C. canadensis*), site type (reference, *P. australis* invaded, and herbicide-treated), water depth (dry, shallow, intermediate, deep) and their interactions. We selected the general linear model with the lowest AICc value as the optimal model for each decay rate. The single exponential decay coefficient ( $k$ ) was log transformed and the initial decay coefficient ( $k_1$ ) was square-root transformed to meet the assumption of normally distributed residuals. Decay rate function fitting was done using the *minpack.lm* (Elzhov et al. 2016) package in R (R Core Team 2016).

#### Environmental conditions

To characterize hydrologic conditions, we calculated the daily water depth range, water depth coefficient of variance, frequency intensity and fluctuation intensity (sensu Trebitz 2006) for each site. We converted PAR to percent insolation for analysis of light interception, with 100% indicating that all the incident PAR radiation penetrated the canopy to reach the water surface or sediment and 0% indicating that it was fully intercepted by the canopy. To determine if water depth range, water temperature and PAR interception differed among the vegetation communities, we ran three general linear models with water depth, water temperature and percent PAR as response variables and site type the predictor variable. Daily water depth fluctuations and daily water temperature fluctuations were square-root transformed. Analyses were conducted using R Studio (R Core Team 2016).

## Results

#### Primary production

Comparing model fits using May vs. July water depths showed that the more predictive water depth measurement depended on the response variable (Appendix 1). Aboveground biomass, total biomass, litter biomass, and standing dead litter were best predicted by July water depths in the model while root:shoot ratio and belowground biomass were better predicted using May water depths in the model. The alternative models can be found in Appendix 2.

Aboveground biomass, total biomass, and litter biomass did not have a significant interaction between habitat type and water depth, but did differ significantly among *P. australis*-invaded, reference, and herbicide-treated sites and along the water depth gradient separately (Table 2, Fig. 2). Aboveground biomass was highest in *P. australis* invaded sites ( $34.77 \text{ g/m}^2 \pm 7.08 \text{ SD}$ ) and lowest in herbicide-treated sites ( $9.83 \text{ g/m}^2 \pm 5.29 \text{ SD}$ ), and had a significant positive relationship with water depth (slope estimate  $0.439 \pm 0.164 \text{ SE}$ ) (Fig. 2A).

Total biomass followed a similar pattern, with the highest values in *P. australis* sites ( $36.51 \text{ g/m}^2 \pm 7.17 \text{ SD}$ ) and the lowest values in herbicide-treated sites ( $14.74 \text{ g/m}^2 \pm 4.57$ ) and a significant positive relationship between total biomass and water depth (slope estimate  $0.452 \pm 0.154 \text{ SE}$ ) (Fig. 2B). In contrast, litter biomass was significantly higher in herbicide-treated sites ( $31.31 \text{ g/m}^2 \pm 10.77 \text{ SD}$ ) compared to *P. australis* ( $22.23 \text{ g/m}^2 \pm 4.42 \text{ SD}$ ) or reference sites ( $18.25 \text{ g/m}^2 \pm 8.45 \text{ SD}$ ) and had a significant negative relationship with water depth (slope estimate  $-0.062 \pm 0.214 \text{ SE}$ ) (Fig. 2C).

Standing dead biomass had a significant interaction between site type and water depth, indicating that the relationship to water depth differed among site types (Fig. 2D). Herbicide-treated sites had very little standing dead, as it had been removed via secondary treatments such as cutting and rolling, while *P. australis* sites had a high mass of standing dead along the entire water depth gradient. The standing dead present in reference sites increased along the water depth gradient, with more standing dead in the deeper cattail marsh sites compared to shallower meadow marsh sites. There was more dead aboveground biomass than live biomass (dead:live biomass) per meter-squared of wetland in *P. australis*-invaded ( $2.00 \pm 1.04$  SD), cattail marsh ( $1.90 \pm 0.59$  SD), and meadow marsh ( $0.60 \pm 0.29$  SD) while herbicide-treated sites had very little aboveground biomass and > 47 times more dead plant material ( $47.39 \pm 89.12$  SD) than the other sites.

The root:shoot ratio differed significantly among the sites, with the highest ratio in reference conditions and the lowest ratio in herbicide-treated sites, and root:shoot had a significant negative relationship with water depth (slope estimate  $-0.052 \pm 0.039$  SE; Fig. 2E). Finally, belowground biomass did not differ among the sites but did exhibit a significant positive relationship with water depth (slope estimate  $0.111 \pm 0.077$  SE; Fig. 2F).

Table 2. Summary of general linear model results for variables related to primary productivity as a function of site type (reference (n = 10), invaded (n = 10) and herbicide-controlled (n = 10)) and water depth. The July water depth was used for all variables except belowground biomass and root:shoot ratio, which used the May water depth measurements based on AICc model comparisons.

	Aboveground biomass			Belowground biomass			Total Biomass			Root:Shoot			Standing Dead			Litter		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Type	2	65.52	<0.001	2	1.08	0.359	2	57.80	<0.001	2	15.21	<0.001	2	60.38	<0.001	2	4.73	0.01
Depth	1	10.11	0.004	1	22.46	<0.001	1	16.66	<0.001	1	9.94	0.004	1	9.39	0.005	1	9.65	0.01
Interaction	2	1.73	0.198	2	2.53	0.101	2	1.62	0.220	2	1.52	0.238	2	4.83	0.017	2	2.97	0.01
Residuals	24			24			24			24			24			24		

#### Decomposition rates

The decaying coefficient model had a consistently better fit ( $R^2 = 0.970 \pm 0.002$  SE) than the single exponential model ( $R^2 = 0.819 \pm 0.009$  SE; Appendix 3). The same model best predicted both the single exponential coefficient ( $k$ ) (Appendix 4) and the initial decay coefficient ( $k_1$ ) (Appendix 5): decay rate coefficient = intercept + litter type + site type + water depth + site type \* water depth. By the end of the experiment, litter loss ranged from 5.75 to 74.65%, depending on the litter type and water depth (Fig. 3; Appendix 4). In general, submerged *P. australis* leaf litter decomposed the fastest, while the standing litter ("dry" water depth treatment) of all plant species decomposed the slowest. Decay rates ( $k$ ,  $k_1$ ) differed significantly among litter types, as *P. australis* leaf litter decomposed significantly faster than *C. canadensis* and *Typha* spp. (Figure 3; Table 3 & 4). Water depth had a significant effect on the single exponential coefficient ( $k$ ) and initial decaying coefficient ( $k_1$ ), and litter placed in deeper sites decayed faster (Table 3 & 4). However, there was only a statistically significant difference between litter that was fully submerged (shallow, intermediate, deep) and litter that was dry (standing treatment). The rate of decay also differed among site types depending on water depth ( $k$ ,  $k_1$ ; Table 3 & 4). In reference sites and *P. australis*-invaded sites submerged litter decomposed fastest in deep water, while submerged litter decayed fastest at intermediate water depths in herbicide-treated sites. The initial decaying coefficient ( $k_1$ ) did not significantly differ among site type (Table 4). The single exponential coefficient ( $k$ ) differed significantly among site type and appeared to initially decay slightly faster in submerged *P. australis*-invaded locations and slower in dry *P. australis*-invaded locations than in reference plant communities and herbicide-treated sites (Table 3).

Table 3. Summary of general linear model for single exponential model coefficient ( $k$ ) as a function of litter species (*C. canadensis*, *P. australis*, *Typha* spp.), site type (reference plant communities, invaded, herbicide-treated) and water depth treatment (dry, shallow, intermediate, deep). "Invaded" sites were withheld as a reference for litter and site type, and the "deep" treatment was withheld as a reference for water depth variable. Residual standard error for the model = 0.083,  $F_{13,22} = 39.39$ ,  $p$ -value = <0.001,  $R^2 = 0.959$ .

Term	Coefficient	Standard error	t-value	p-value
Intercept	-2.020	0.052	-39.148	<0.001
<i>Calamagrostis canadensis</i>	-0.282	0.034	-8.358	<0.001
<i>Typha</i> spp.	-0.317	0.034	-9.379	<0.001
Herbicide-treated	-0.113	0.676	-1.667	0.110
Reference sites	0.141	0.676	2.081	0.049
Dry	-0.590	0.676	-8.737	<0.001
Shallow water depth	-0.211	0.676	-3.126	0.005
Intermediate water depth	-0.091	0.676	-1.342	0.193
Herbicide-treated * dry	-0.014	0.096	-0.145	0.886
Reference sites * dry	-0.213	0.096	-2.227	0.036
Herbicide-treated * shallow	0.160	0.096	1.676	0.108
Reference plant * shallow	-0.039	0.096	-0.405	0.690
Herbicide-treated * intermediate	0.327	0.096	3.427	0.002
Reference sites * intermediate	-0.352	0.096	-3.682	0.001

Table 4. Summary of general linear model for initial decay coefficient ( $k_1$ ) from the decaying coefficient model as a function of species litter (*C. canadensis*, *P. australis*, *Typha* spp.), site type (reference plant communities, invaded, herbicide-treated) and water depth (dry, shallow, intermediate, deep). "Invaded" sites were withheld as a reference for litter and site type, and the "deep" treatment was withheld as a reference for water depth variable. Residual standard error for the model = 0.083,  $F_{13,22} = 39.39$ ,  $p$ -value = <0.001,  $R^2 = 0.959$ .

Term	Coefficient	Standard error	t-value	p-value
Intercept	-1.772	0.041	-43.033	<0.001
<i>Calamagrostis canadensis</i>	-0.284	0.027	-10.555	<0.001
<i>Typha</i> spp.	-0.272	0.027	-10.094	<0.001
Herbicide-treated	0.098	0.054	1.821	0.082
Reference sites	0.078	0.054	1.449	0.162
Dry	-0.526	0.054	-9.750	<0.001
Shallow water depth	-0.070	0.054	-1.302	0.206
Intermediate water depth	-0.000	0.054	-0.007	0.994
Herbicide-treated * dry	-0.260	0.076	-3.409	0.003
Reference * dry	-0.163	0.076	-2.144	0.043
Herbicide-treated * shallow	0.151	0.076	1.985	0.060
Reference plant * shallow	0.132	0.076	1.737	0.096
Herbicide-treated * intermediate	0.124	0.076	1.632	0.117
Reference plant * intermediate	-0.187	0.076	-2.455	0.022

#### Environmental covariates

*Phragmites australis* sites were, on average, deeper and had a greater daily range in water depth and the greatest variation over the study period compared to reference vegetation communities and herbicide-treated sites (Appendix 6). Daily water depths differed significantly among herbicide-treated, invaded, and reference sites between June 14<sup>th</sup> and October 16<sup>th</sup> (GLM  $F_{2,1122} = 61.600$ ,  $p$ -value = <0.001, RSE = 0.132,  $R^2 = 0.099$ ; Appendix 7), and each site type was significantly different from one another ( $p$  value < 0.001). *P. australis* invaded sites were significantly deeper than reference or herbicide-treated sites. Water depth and site type had a significant interaction such that the degree of daily fluctuation in water depth among *P. australis* invaded, reference, and herbicide-treated sites depended on the relative water depth ( $F_{8,1116} = 62.760$ ,  $p$ -value = <0.001,  $R^2 = 0.310$ ; Appendix 8). At shallow and intermediate water depths *P. australis* invaded sites had a significantly greater daily fluctuation in water depth than herbicide-treated sites; at the deepest water depth, reference plant communities had significantly greater daily fluctuations in water depth compared to other site types (Appendix 9).

The model predicting average daily water temperature based on site type, water depth, and their interaction provided a reasonable fit ( $F_{8,1116} = 61.710$ ,  $p$ -value = <0.001,  $R^2 = 0.307$ ; Appendix 10). Water depth category and site type had a significant interaction such that the average daily water temperature among

reference, *P. australis*-invaded, and herbicide-treated sites depended on the relative water depth (Appendix 10). Water temperature was positively correlated with water depth for the *P. australis*-invaded sites and reference vegetation communities, while herbicide-treated sites were warmer in shallower water.

The model predicting daily fluctuations in water temperature based on site type, the water depth and their interaction provided a reasonable fit ( $F_{8,1116} = 369.000$ ,  $p$ -value = <0.001,  $R^2 = 0.659$ ; Appendix 11). Water depth category and site type had a significant interaction such that the average daily fluctuations in water temperature among reference, *P. australis*-invaded, and herbicide-treated sites depended on the relative water depth. Herbicide-treated sites also had the greatest variation in daily water temperature fluctuations, likely because they have a higher amount of open water, while *P. australis*-invaded sites had the smallest temperature fluctuations (Appendix 12). Relatively less PAR reached the bottom of the canopy in *P. australis*-invaded sites compared to uninvaded meadow and cattail sites, but this difference was not significant ( $F_{2,16} = 1.195$ ,  $p$ -value = 0.328,  $R^2 = 0.130$ ; Appendix 13).

## Discussion

Invasive *P. australis* is altering North American wetlands by displacing native vegetation communities with dense, tall monocultures. The establishment of *P. australis* has the potential to alter carbon budgets directly by increasing the production of above or belowground biomass and indirectly by altering environmental conditions that control rates of decomposition. Best management practices to suppress *P. australis* include applying a glyphosate-based herbicide and conducting a secondary treatment, such as rolling, to knock over standing dead stems. Despite the negative impacts of invasion on biodiversity, it is possible that *P. australis* effectively stores more carbon than the species it outcompetes.

We quantified the effect of *P. australis* invasion and herbicide-based *P. australis* suppression efforts on carbon dynamics in a coastal marsh. Uniquely, we compare *P. australis* to the reference cattail and meadow marsh communities it primarily displaced, and importantly, our results emphasize that the effect of *P. australis* invasion on net primary production, decomposition rates and environmental conditions depends on which plant community was invaded. Our work also documents, for the first time, the immediate effects of herbicide-based treatment of *P. australis* on carbon dynamics. This topic has been an important knowledge gap, as thousands of hectares of *P. australis* invaded marsh are treated with herbicide annually in North America (Hazelton et al. 2014).

### *Invasion changes standing crop biomass*

In reference vegetation communities, the aboveground and total plant biomass are heterogenous. That is, cattail and meadow marsh vegetation communities differ from one another, and as such the effect of *P. australis* invasion on primary production depends on which reference community is being invaded. This limits generalizations regarding the effect of *P. australis* invasion in coastal marshes. Cattail marsh and *P. australis*-invaded marsh in the Great Lakes are much more productive than meadow marsh and are usually reported to have similar total and aboveground biomass (Rothman and Bouchard 2007; Duke et al. 2015; Yuckin and Rooney 2019). As such, when *P. australis* replaces meadow marsh, there is a dramatic increase in total biomass and a net increase in carbon sequestration. The conversion of meadow marsh to a community dominated by *P. australis* also results in the extirpation of an assembly of native species with distinct plant traits and a change in community composition. In contrast, cattail marsh in our study region is composed of a species complex that is dominated by invasive *Typha x. glauca*, a hybrid of invasive *T. angustifolia* and native *T. latifolia*. This invasive species also has high productivity (Farnsworth and Meyerson 2003; Tho et al. 2016) and creates tall, dense monocultures (e.g., Bansal et al. 2019) like *P. australis*, and as such there are no significant changes in standing crop biomass when cattail marsh is converted to *P. australis*. We conclude that *P. australis* only increases marsh carbon sequestration when it displaces meadow marsh, and any benefits from increased carbon sequestration are likely outweighed by the loss of this important vegetation community which contains unique and rare plant species and provides habitat for many wetland species, including endangered turtles (Markle and Chow-Fraser 2018).

### *Invasion causes changes to decomposition*

The net effects of *P. australis* invasion on wetland decomposition rates are difficult to quantify because of conflicting direct and indirect effects of invasion. Similar research with *P. australis* has not determined whether direct or indirect effects are more important: in some studies, environmental conditions were most important for decomposition (e.g., Duke et al. 2015), while in others the litter composition was important (e.g., Windham 2001). In our study, environmental conditions exerted the largest influence on decomposition rates - specifically whether litter was submersed or dry. Suspended litter, regardless of litter species or vegetation community in which it was deployed, decomposed considerably more slowly than submersed litter. The positive influence of submergence on decomposition has been documented in numerous marshes: litter that is continually submerged decomposes faster than litter occasionally inundated (van der Valk et al. 1991; Dolinar et al. 2015; Vymazal and Březinová 2016), and occasionally inundated litter decomposes faster than litter in consistently dry sites (Bedford 2005; Dolinar et al. 2015; Vymazal and Březinová 2016). These results highlight the importance of secondary treatment that will break *P. australis* stems and submerge them, increasing the pace of decomposition after herbicide-treatment.

When considering only the submerged litter, differences between species were more apparent. As nutrient quality has a strong relationship with decomposition rate when litter is submerged (Enriquez et al. 1993), the high foliar nitrogen concentration in *P. australis* leaf litter (Farnsworth and Meyerson 2003; Hirtreiter and Potts, 2012; Yuckin and Rooney 2019) suggests it would decompose significantly faster than *C. canadensis* or *Typha* litter. In fact, *P. australis* leaf litter did decompose fastest, while *Typha* spp. and *C. canadensis* tissues had similar nitrogen concentrations (Yuckin and Rooney 2019) and decomposed at equivalent rates. Considering both primary production and decomposition, when *P. australis* replaces cattail marsh there is no significant change in total biomass or carbon assimilation, but the decomposition rate of submerged *P. australis* litter is faster than *Typha* spp. litter. It is possible then, that *P. australis* invasion leads to a potential reduction in overall carbon storage when it displaced *Typha* spp. marsh, even though we did not observe a difference in aboveground or total standing crop biomass.

### *Unique environmental conditions in P. australis-invaded sites, but no net effect on decomposition*

Despite sites being selected based on common water depths in May, *Phragmites australis*-invaded sites retained deeper standing water than reference communities (particularly meadow marsh) later in the growing season. This contradicts studies that noted *P. australis* invasion reduces standing water depth due to increased losses from evapotranspiration, or to infilling from increased belowground biomass or litter accumulation (Windham and Lathrop 1999; Rooth et al. 2003; Duke et al. 2015). In our study, we expect water depths were deeper because *P. australis* sites have lower light penetration and lower water temperatures, thus reducing evaporation. However, these environmental conditions had a negligible effect on the decomposition of submersed litter. We suspect this was because changes that should increase decomposition rates (i.e., prolonged immersion in invaded sites) were offset by simultaneous changes that reduced decomposition rates (i.e., cooler more stable water temperature and reduced light exposure in invaded sites). This combination of environmental changes caused by *P. australis* invasion offset one another, such that the consequent changes in litter quality dominated the net effect of invasion on decomposition rates in our study.

### *Response to herbicide treatment*

The year after treatment, herbicide-treated sites had lower primary production than uninvaded reference vegetation. However, this difference may be short-lived. By July, approximately ten months after herbicide treatment, live plant cover within treated marsh averaged 41% ( $\pm$  8.0 SD). Most of the vegetation community was composed of floating or submersed aquatic vegetation, with few emergent plant species. Submerged and floating vegetation tissues may decompose faster than emergent macrophytes (Chimney and Pietro 2006; Ping et al. 2017), and it is likely that this community change will alter decomposition and carbon sequestration rates in herbicide-treated marsh. Yet, it is difficult to assess the future trajectory of the vegetation community after only a single year. Passive recovery after *P. australis* suppression, i.e., allowing the native seedbank to re-establish unassisted, has been successful in some areas (Ailstock et al. 2001; Carlson et al. 2009; Baldwin et al. 2010) but there remains the possibility that *P. australis* or other undesirable species will establish (Hazelton et al. 2018; Robichaud and Rooney 2021).

Environmental conditions play an important role in vegetation community establishment. Secondary treatment increased light penetration to nearly 100% of incident PAR in some sites, and increased the water temperature, which can benefit the general recovery of plant communities (Bonnewell et al. 1983; Leck 1996; Kettenring et al. 2006). Despite these advantages, the above-average water depths in 2017 and 2018 (The Canadian Hydrographic Service 2016), promoted the establishment of floating or submerged aquatic plant species rather than native species with emergent growth forms (Euliss et al. 2004). In addition to high water levels, the litter layer present in herbicide-treated sites is sufficient to affect vegetation recovery. Rolling led to a thick mat of dead *P. australis* stems that will decompose faster than if they had been left standing but might impede seedling germination by changing environmental conditions, such as soil temperature or light availability, or by physically preventing new shoots from being able to push through the litter layer (Holdredge and Bertness 2011). Studies have demonstrated that removing *P. australis* litter results in increased species richness and native plant biomass recovery in the first year post-treatment (Ailstock et al. 2001; Carlson et al. 2009; Holdredge and Bertness 2011). Rolling or mowing standing dead litter to submerge it post-treatment will increase the pace of its decomposition, but burning or other practices that remove *P. australis* litter entirely may expedite recovery.

## Conclusion

Land managers face trade-offs when considering whether to treat established *P. australis* populations. While biodiversity may increase (e.g., Markle and Chow-Fraser 2018; Polowyk 2020) following treatment, it is likely that carbon sequestration will be reduced in the short term. We found that control efforts dramatically reduced total biomass and carbon assimilation, at least in the first year post-treatment. Despite increased water depth, water-level stability, and temperature in herbicide-treated sites, no increase in decomposition rates was observed in treated-sites relative to reference uninvaded or *P. australis*-invaded sites, suggesting that carbon stores might be unaffected despite reductions in sequestration rate. Plant community recovery is crucial to restore carbon sequestration in herbicide-treated marsh, and rapid recovery of floating and submerged aquatic vegetation provides evidence that this gap in carbon sequestration services may be temporary. Provided the recovering plant community shifts to an emergent marsh over time, there should be recovery of the carbon sequestration function within the herbicide-treated marsh. However, this will depend on lake water levels (van der Valk et al. 1994; Euliss et al. 2004) and the health of the seedbank (Ailstock et al. 2001; Carlson et al. 2009; Baldwin et al. 2010). Understanding these net effects on ecosystem functions provides necessary context for decision-makers who must consider societal values, economic feasibility, and other uncertainties (Liu et al. 2011; Martin and Blossey 2013), when deciding whether to treat established *P. australis*.

## Declarations

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**Ethics approval:** not applicable

**Consent to participate:** not applicable

Consent to publish: all authors consent to publication of the manuscript

Availability of data and materials: The datasets used for analyses during the current study are available in a Figshare repository: primary productivity (<https://doi.org/10.6084/m9.figshare.15067341.v1>), decomposition data (<https://doi.org/10.6084/m9.figshare.15067374.v1>), photosynthetically active radiation (<https://doi.org/10.6084/m9.figshare.15067686.v1>) and site characteristics (<https://doi.org/10.6084/m9.figshare.15067383.v1>).

Code availability: Available upon request

Author's contributions: SJY and RCR conceptualized the study, RCR acquired funding, supplied resources, supervision and administered the project, provided validation and curates the data, SJY, CDR and GH conducted field work, SJY and CDR conducted formal analysis and visualized the data, SJY wrote the original draft, and CDR, GH and RCR revised and edited the text.

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## Figures

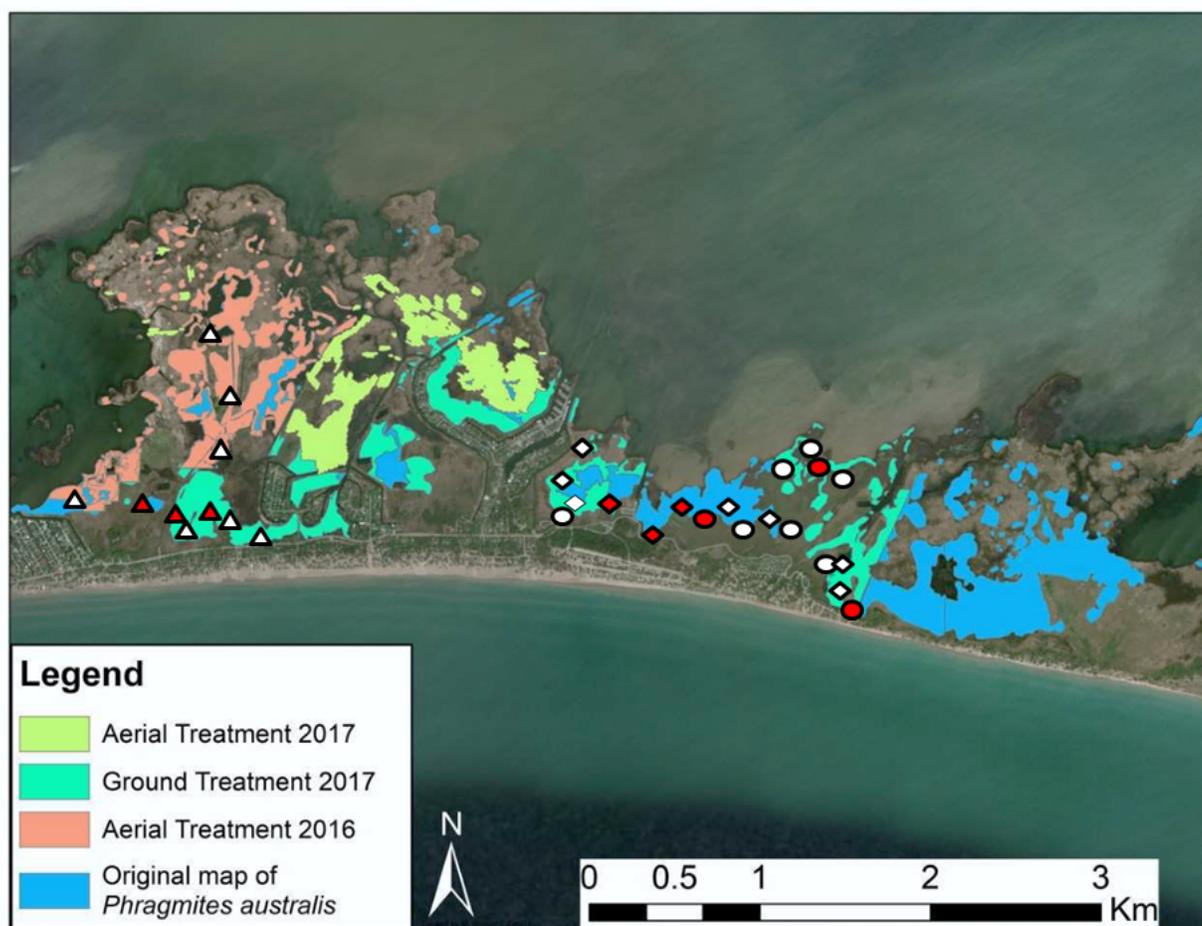
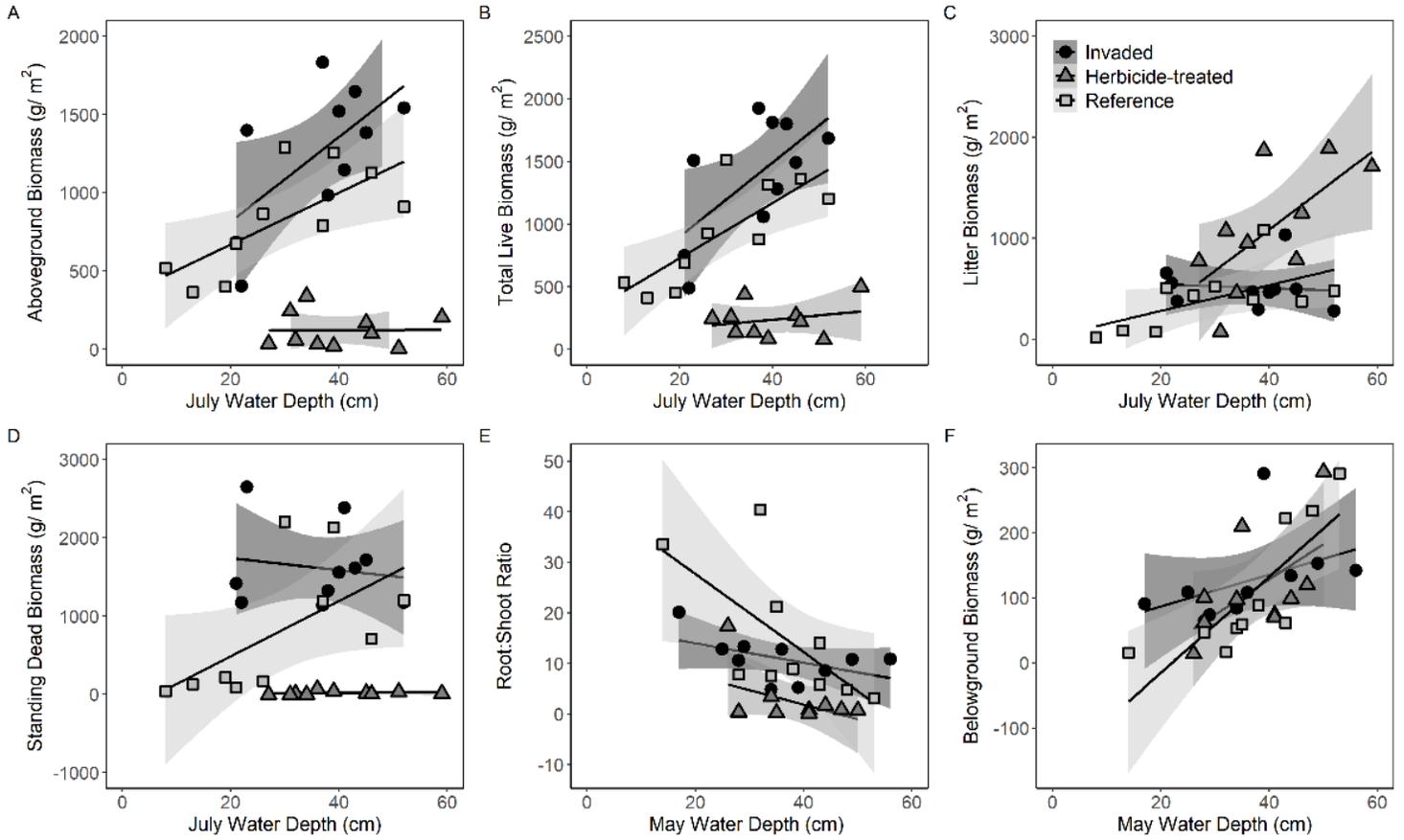
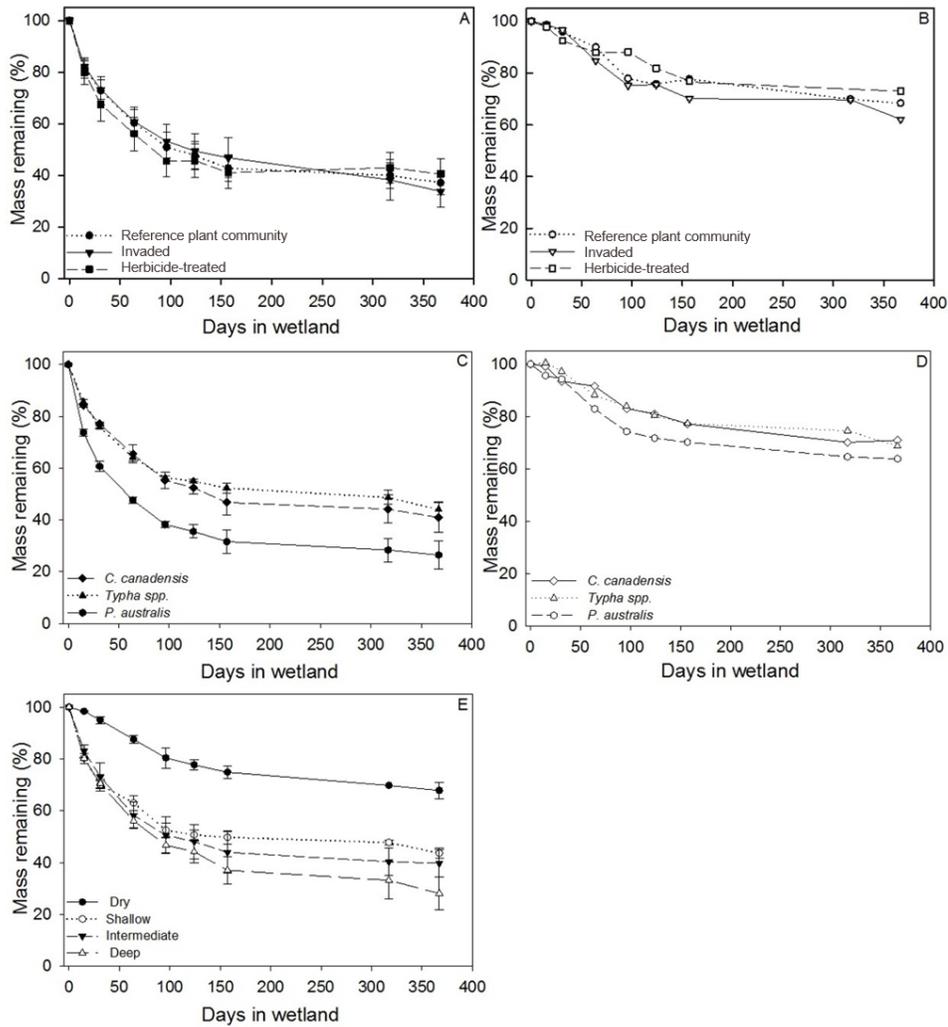


Figure 1

Long Point Peninsula (42° 34' N, 80° 24' W) is located on the north side of Lake Erie in Ontario. Net primary production measurements were taken at all sites, red symbols represent a subset of sites where decomposition measurements were taken. Triangles are herbicide-treated sites, circles are reference sites, and diamonds are *P. australis*-invaded sites. Image credit Matthew Bolding.



**Figure 2**  
 Relationships between primary productivity variables among habitat types and a water depth gradient. Aboveground biomass (A), total biomass (B), and litter (C) exhibited a significant relationship with habitat type and July water depth separately. Standing dead biomass differed among habitat types depending on the water depth (D). The root:shoot ratio was different among habitat types and along the May water depth (E) and belowground biomass had a significant positive relationship with May water depths (F). Shaded areas around the line of best fit represent 95% confidence intervals.



**Figure 3**  
 Change in percent mass remaining of submerged litter (average mass loss of all plant species litter in shallow, intermediate and deep-water depths) (A), change in percent mass remaining of standing “dry” litter (average mass loss of all plant species litter) (B), change in % mass remaining of *C. canadensis*, *Typha* spp. and *P. australis* litter in submerged sites (C), change in % mass remaining of *C. canadensis*, *Typha* spp. and *P. australis* standing litter (D), and change in mass remaining of standing and submerged litter (average mass loss across all plant species and site types) (E) over 367 days (day 0: May 12-14, 2017).

## Supplementary Files

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