Detecting the effects of biological invasion and subsequent control efforts on wetland ecological processes

by

Sarah Yuckin

A thesis

presented to the University of Waterloo

in fulfillment

of thesis requirements for the degree of

Master of Science

in

Biology

Waterloo, Ontario, Canada, 2018

Author's declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Meadow and emergent cattail wetland communities in eastern North America are being replaced by an invasive lineage of *Phragmites australis*. This invasion has consequences for wetland ecosystem functions; including macronutrient storage due to invasion-driven changes in net primary productivity, decomposition rates and altered environmental site conditions. Because *P. australis* invasion degrades wetland ecological integrity, extensive efforts to control *P. australis*, mainly through herbicide application, have been undertaken. While the effects of *P. australis* control efforts on recovering plant communities has been studied, the success of these efforts at restoring ecosystem functions to pre-invasion ranges is unknown. My objectives were to 1) quantify the effect of *P. australis* invasion on macronutrient storage in the annual vegetative standing stock compared to uninvaded meadow and cattail marshes, and 2) to evaluate the success of large-scale, herbicide-based *P. australis* control efforts at re-establishing rates of net primary productivity, decomposition and environmental conditions to levels comparable to those in uninvaded marsh. I conclude that the effect of invasion on macronutrient storage was dependent on the plant community being replaced. Significant increases in annual macronutrient vegetative standing stock were observed when *P. australis*-dominated marsh was compared to meadow marsh, but few differences were observed between *P. australis* and cattail marsh. My analysis also revealed a reduction in carbon sequestration services one-year post-herbicide application. Emergent plant community recovery will likely be critical to increasing carbon sequestration in herbicide-treated marsh. My work indicates that *P. australis* invasion and subsequent control efforts represent trade-offs in ecosystem services. *Phragmites australis* invasion can increase macronutrient storage in the marsh but decrease biodiversity, and *P. australis* control efforts aiming to increasing biodiversity reduce carbon sequestration, at least temporarily. Understanding these net effects of *P. australis* invasion and control efforts on wetland functions informs decision makers considering whether to attempt *P. australis* eradication.

Acknowledgements

This work was supported by NSERC Discovery, Mitacs Accelerate, Ontario Ministry of Natural Resources and Forestry, Ontario Parks, and the Nature Conservancy of Canada. I would like to thank my supervisor, Dr. Rebecca Rooney, for being an outstanding mentor and creating a collaborative lab that I was privileged to be a part of. I must also thank my committee member, Dr. Janice Gilbert, for her constant encouragement and for being a wonderful example of an ecologist. I would also like to thank my committee members Dr. Merrin Macrae, Dr. Roland Hall and Dr. Marcel Pinheiro for their advice and for agreeing to sit on my committee. This work could not have been completed without help from many volunteers and lab technicians; thank you Jacob Basso, Bailey Dhanani, Megan Jordan, Madison Brook, Taylor Blackwell, Lauren Koiter, and Calvin Lei.

Thank you Graham Howell, for taking me under your wing when I first arrived, showing me the best parts of Long Point, and the way the Rooney Lab gets things done. Thank you Courtney Robichaud, Heather Polowyk, and Jessie Pearson for the wonderful field summer full of field adventures, bread Fridays, and RuPaul. And to everyone in the Rooney Lab, those mentioned above and also Daina Anderson, Jenny Gleason, Mathew Bolding, Adam Kraft, Jody Daniels, and Cari Ficken thank you for all your help on this project and for the wonderful fun breaks. You were all so welcoming, and made this time in Ontario very memorable.

I would also to thank my Mom and Dad and extended family for their support, encouragement and interest in what I was doing so far from home. And to all my close friends who are far, especially Katie Low, Grace Box and Taylor Cameron, thank you cheering me onwards when I tripped, keeping me grounded, and always making me laugh.

Table of Contents

List of Figures

List of Tables

1 Literature review and thesis scope

Wetland plant communities in eastern North America, such as cattail and meadow marsh, are being replaced by an invasive lineage of *Phragmites australis*, which has invaded fresh and brackish wetlands throughout Canada and the United States (Catling and Mitrow 2011, Saltonstall and Meyerson 2016). This invasion likely has repercussions for wetland ecosystem functions, including macronutrient pools and fluxes, due to invasion-driven changes to the size and nutrient composition of the annual vegetation standing stock, decomposition rates, and environmental conditions in invaded wetlands (Meyerson et al. 2000, Windham 2001, Rothman and Bouchard 2007, Engloner 2009, Duke et al. 2015). Furthermore, site specific conditions, including nutrient availability and standing water depth, can alter how invasion influences macronutrient storage (Currie et al. 2014, Duke et al. 2015). However, how *P. australis* invasion will change macronutrient storage across a natural water depth gradient and in high vs. low nutrient environments in the Great Lakes region is not well understood. Because of the changes *P. australis* invasion causes to wetland flora, fauna, and ecosystem processes, an immense effort has been made to control *P. australis*, mainly through herbicide application (Martin and Blossey 2013). While we understand the difficulties of eradicating *P. australis* (Lombard et al. 2012, Quirion et al. 2018), and have some knowledge of the effects of control efforts on the composition of plant communities (Ailstock et al. 2001, Breen et al. 2014), the ability of control efforts to restore wetland functions to rates characteristic of uninvaded habitat is still unresolved.

The recovery of ecosystem processes to their pre-invasion rates and scales is required to restore the ecological integrity of *P. australis* invaded wetlands (Karr 1993). In some management units

in Long Point (Lake Erie), Canada, *P. australis* replaced up to 70% of wetland resident plant communities (helicopter mapping; data provided by Erling Armson, Invasive Species Specialist, Ducks Unlimited Canada). In 2016, the first aerial application of herbicide over standing water in Canada treated 400 ha of invaded wetland in Long Point, and an additional >100 ha was treated in 2017 (Ministry of Natural Resources and Forestry et al. 2016, 2017). In chapter 2 of my thesis, I examine how invasion changes nutrient storage compared to resident plant communities in Long Point across a range of water depths and in a low versus high nutrient environment. In chapter 3 of my thesis, I evaluate the effect of *P. australis* invasion and subsequent control efforts on carbon sequestration in the Long Point wetlands. In chapter 4, I discuss the implications of my research for invasive species management and the potential to recover ecological processes. The following literature review provides background information in support of my thesis objectives. I review the current literature on wetland ecosystem functions, invasion by *P. australis* and its effects on carbon and other macronutrient pools and fluxes, and our current knowledge about *P. australis* control efforts.

1.1 Wetland ecosystem functions and invasion

Wetlands provide ecological services such as support for biodiversity, habitat for wildlife, improved water quality and carbon storage, all of which are of high value to people (Zedler and Kercher 2005, Maltby and Barker 2009, Engle 2011). On a global scale, wetlands store carbon at higher rates than upland ecosystems, which, in the context of climate change, is of increasing importance (Bernal and Mitsch 2012). Nutrient loading from agricultural pollution is also of increasing concern, and wetlands are usually nutrient sinks that remove nutrients from surface water to improve downstream water quality (Bernal and Mitsch 2012). In particular, phosphorus pollution in Lake Erie has led to its re-eutrophication (Watson et al. 2016), resulting in harmful

algae blooms, contamination of drinking water (e.g. CBS News 2018), and hypoxia in the central basin. This led to the negotiation of interim phosphorus load and concentration objectives as part of the 2012 Great Lakes Water Quality Agreement (United States - Canada 2013). Wetlands intercept and retain phosphorus, helping us meet these objectives, but their value in this regard may be affected by *P. australis* invasion or by control efforts to manage *P. australis*.

Macronutrient storage in wetlands is influenced by the net primary production and decomposition of wetland macrophytes, and related environmental characteristics (Maltby and Barker 2009, Currie et al. 2014). The macronutrient carbon is of particular interest because of its role in regulating the earth's climate (e.g., Mitsch et al. 2013), and because vegetation can fix it directly from the atmosphere through photosynthesis. Whether a wetland is ultimately a carbon sink or source depends on the relative net primary production and decomposition rates of the wetland macrophyte community (Maltby and Barker 2009). Carbon assimilation in wetlands occurs primarily through photosynthesis, which can be measured directly or estimated by measuring net primary production (Maltby and Barker 2009). Typically, most of the carbon incorporated in vegetation returns to the atmosphere through the decomposition of dead plant tissue in aerobic conditions (Maltby and Barker 2009). The remaining portion of the plant decomposes in anaerobic conditions due to soil saturation and standing water, which is less efficient and often results in incomplete decomposition (Maltby and Barker 2009). The carbon remaining in the incompletely decomposed litter is sequestered in the wetland. Therefore, the amount of carbon sequestered in a wetland depends upon the difference between the amount of carbon assimilated from the atmosphere during the photosynthesis of wetland vegetation and the amount of carbon returned to atmosphere during decomposition (Maltby and Barker 2009).

Generally, wetlands composed of plant communities with higher net primary productivity and slower decomposition rates should have greater rates of carbon sequestration.

A wetland's capacity to sequester and store other macronutrients is generally a water quality improvement service that can reduce nutrient loading in downstream aquatic environments and prevent eutrophication (e.g., Smith et al. 2006). I consider the macronutrients phosphorus, nitrogen, calcium, magnesium, and potassium jointly, as any one of these could limit primary productivity. Notably, the size of macronutrient pools and the rate of nutrient removal in wetlands is, like carbon, influenced by the net primary production and decomposition of the wetland plant community, as well as the nutrient concentration in the tissues of the plant species forming the wetland community (Maltby and Barker 2009; Windham and Ehrenfeld 2013; Currie et al. 2014). Yet the relationship between nutrient uptake and plant tissue nutrient concentrations is complicated by recursive feedbacks. For example, the rate of primary production is partially dependent on the availability of limiting nutrients, which in turn is partially dependent on the concentration of nutrients in plant tissues and the rate of decomposition and remineralization of the nutrients from plant litter (Maltby and Barker 2009, Schlesinger and Bernhardt 2013). Wetland vegetation takes up inorganic nutrients, such as nitrate (NO_3), nitrite (NO_2) and ammonia (NH_3), and converts them into organic forms as the plant creates its own tissues (e.g. amino acids; Maltby and Barker 2009). Higher net primary production increases the amount of nutrients stored in the vegetation standing stock, however nutrient storage is generally short-term, especially in wetland plants with annual tissues where the nutrients re-enter the nutrient cycle during decomposition of plant litter (Maltby and Barker 2009). Decreasing the decomposition rates of plant litter, or storing nutrients in perennial tissues like rhizomes increases the storage of nutrients assimilated by the vegetation.

Wetland vegetation can also alter important environmental covariates that influence the net primary production and decomposition rate. For example, oxygen transport into belowground plant tissues creates aerobic rhizospheres in the anaerobic soil zone (Fig. 1.1). This can increase the decomposition rate and allow nitrification to occur in an otherwise anaerobic environment; essentially coupling nitrification with denitrification and releasing more nitrogen into the atmosphere (Fig. 1.1; Maltby and Barker 2009; Schlesinger and Bernhardt 2013). Densely growing macrophytes can also affect macronutrient cycles indirectly by creating conditions that favour denitrification and could slow decomposition rates. For example, dense vegetation stands can decrease dissolved oxygen levels by shading out algae and submersed or floating vegetation or by decreasing temperature and intercepting insolation (Maltby and Barker 2009).

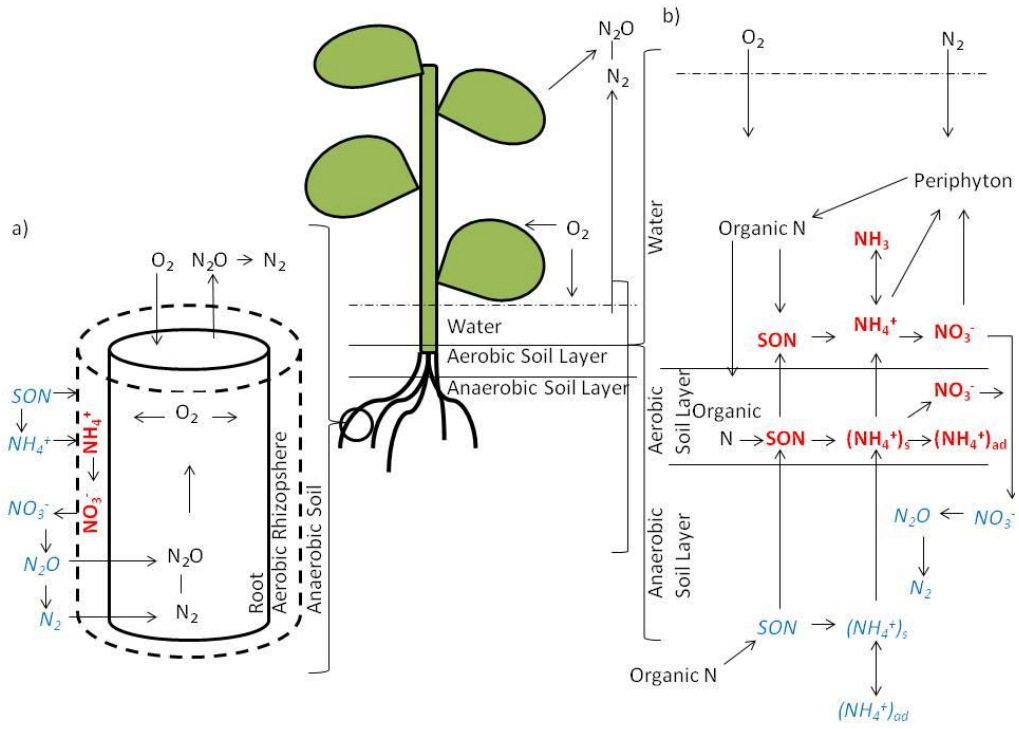

Figure 1.1 Nitrogen cycle portraying the N transformations within the aerobic and anaerobic areas of the wetlands soils a) at the root-soil and b) the water-soil interface. Red, bolded text indicates nitrification processes, blue, italicized text indicates denitrification processes. Adapted from Maltby and Barker (2009).

Invasive plant species are able to directly impact macronutrient accretion because they often have higher production of aboveground and belowground biomass, higher rates of carbon assimilation, high leaf area indices and slower decomposition rates than resident plant species (Ehrenfeld 2003, 2010, Rothman and Bouchard 2007, Duke et al. 2015). Invasions can also change site conditions that affect carbon and nutrient cycling rates, such as the depth of standing water, shading of sediment, and changed redox potential of the sediment, which in turn can affect net primary production (including biomass and root: shoot ratios) and decomposition rates (van der Valk et al. 1991, Holdredge and Bertness 2011, Dolinar et al. 2015). Two reviews on the influence of invasive species on the carbon cycle reported that invasive species generally increase the carbon pool and the rate of carbon cycling in wetlands (Liao et al. 2008, Vilà et al. 2011). The effect of each invasive species, however, was site specific (Ehrenfeld 2003, 2010, Liao et al. 2008).

1.2 Background on Phragmites australis *invasion*

Phragmites australis is a perennial grass that may have the broadest distribution of any grass in the world (Saltonstall 2002, Saltonstall and Meyerson 2016). Within North America, it can be found throughout the continental United States of America (Saltonstall 2002) as well as the provinces and Northwest Territories of Canada (Mal and Narine 2004). Despite the taxonomic uncertainties surrounding *Phragmites australis*, three lineages have been generally recognized within North America (Saltonstall et al. 2004). One native lineage, which had a historical range across the provinces of Canada and the continental USA, was formerly known as *Phragmites australis* subsp. *americanus* (Saltonstall et al. 2004). The second native lineage, which had a historic distribution restricted to the southern portion of North America, is known as *Phragmites australis* subsp. *berlandieri* (Saltonstall et al. 2004). The third lineage is the invasive lineage of

Phragmites australis (hereafter *P. australis*), which has been rapidly increasing its distribution and abundance throughout the eastern side of North America for the last two hundred years (Saltonstall 2002, Saltonstall et al. 2004).

Invasive *P. australis* likely arrived in North America in the 19th century when ship ballast from Europe was used to fill marshes in (Saltonstall 2002). Next, it spread up the St. Lawrence River (Lelong et al. 2007) and then used drainage ditches along roads and railways to expand into nearby natural wetlands (Catling and Carbyn 2006, Jodoin et al. 2008, Brisson 2010). Invasive *P. australis* was not recognized, however, until the 1970's (after its rapid invasion in the eastern Canadian provinces) because it is morphologically similar to the native lineage (Saltonstall 2002). In approximately 20 years, invasive *P. australis* replaced most native *P. australis* stands in Ontario and Quebec and continued to expand past the historic distribution and abundance of the native lineage (Catling and Carbyn 2006, Lelong et al. 2007, Albert et al. 2015).

Invasive *P. australis* is able to rapidly establish and replace resident plant communities because of its morphological traits, tolerance to a wide range of environmental conditions, and various reproductive strategies. Because it grows tall aboveground stems (maximum height 4 - 6 m) and creates a thick litter layer, *P. australis* limits light and space for shorter plants (Mal and Narine 2004, League et al. 2006). In addition, an extensive and deep root and rhizome system allows *P. australis* to access nutrients deeper in soil than most native plants, at least in brackish environments (League et al. 2006, Moore et al. 2012). *Phragmites australis* is also able to reproduce sexually, creating hundred of wind dispersed seeds, and vegetatively through laterally growing rhizomes, aboveground stolons, and by creating new shoots from broken plant parts, which allows it to rapidly colonize and establish in disturbed areas (Saltonstall 2002, Mal and Narine 2004, Albert et al. 2015). Because *P. australis* is tolerant of varied environmental

conditions, it can spread in high salinity and nutrient conditions (for example in ditches along highways) and in wetlands that have been disturbed (Saltonstall 2002, Catling and Carbyn 2006). The success of invasive *P. australis* compared to the native Atlantic coast lineage may be due to trait differences; in a literature review invasive *P. australis* had taller and denser aboveground biomass, a higher root:shoot ratio, a greater specific leaf area, and an increased growing season compared to the native lineage (Mozdzer et al. 2013).

In Canada, invasive *P. australis* continues to invade new areas and is of particular concern in the Great Lakes region (Ministry of Natural Resources and Forestry et al. 2016, Braun et al. 2016). The spread of *P. australis* in Long Point (a coastal marsh area on Lake Erie, Ontario), which includes the management areas of Big Creek National Wildlife Area (Big Creek NWA), Crown Marsh Waterfowl Management Unit and Long Point Provincial Park (Fig. 1.2), has also been closely examined (Wilcox et al. 2003, Maraccio and Chow-Fraser 2016). Throughout the >40,000 ha of Long Point, *P. australis* was uncommon until the mid 1990s, when it expanded from 18 ha to 137 ha between 1995 and 1999 (Wilcox et al. 2003). Across the Great Lakes region, low water levels and disturbance to coastal marshes may have facilitated the invasion of *P. australis* (Wilcox et al. 2003, Croft and Chow-Fraser 2007, Tulbure et al. 2007). By 1999, *P. australis* stands covered 3.7 ha (0.3%) in Big Creek NWA and 13.1 ha (2.3%) in Crown Marsh (Wilcox et al. 2003). By 2015 - 2016 *P. australis* spread to cover 74 ha (6.2%) of the eastern portion of Big Creek NWA (UAV method; Maraccio and Chow-Fraser 2016; Fig. 1.3) and approximately 70% of Crown Marsh (helicopter mapping; data provided by Erling Armson, Invasive Species Specialist, Ducks Unlimited Canada; Fig. 1.4). Models developed by Jung et al. (2017) suggest that invasive *P. australis* would continue to spread at a similarly rapid rate within the Big Creek and Long Point National Wildlife Areas until 2022.

Figure 1.2 Coastal wetlands within study area at Long Point Peninsula, Ontario on the north shore of Lake Erie. Image credit: Matt Bolding.

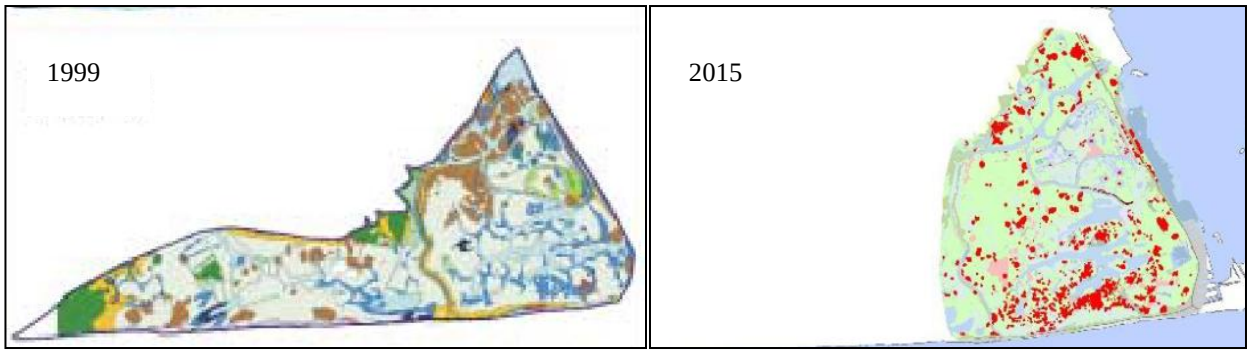

Figure 1.3 Extent of invasive *P. australis* in 1999 (3.7 ha) and in 2015 (74 ha) at Big Creek NWA, Long Point ON; *P. australis* in red. 1999 figure credit: Wilcox et al. (2003) p. 669; 2015 figure credit: Maraccio and Chow-Fraser (2016) p. 79.

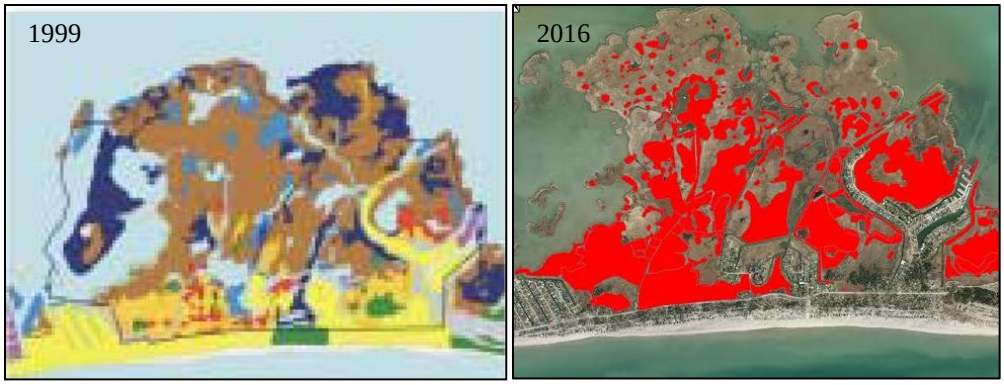

Figure 1.4 Extent of invasive *P. australis* in 1999 (13.1 ha) and in 2016 (70%) at Crown Marsh, Long Point ON; *P. australis* in red. 1999 figure credit: Wilcox et al. (2003) p. 670; 2016 figure credit Matthew Bolding using unpublished data supplied by Erling Armson, Invasive Species Specialist, Ducks Unlimited Canada.

The wetland plant communities most often replaced by invasive *P. australis* in Big Creek NWA and Crown Marsh was "Graminoid Coastal Meadow Marsh Type" (Imperiled [S2]; Ministry of Natural Resources and Forestry 2018), as well as more common cattail marsh (Wilcox et al. 2003). Generally, meadow marsh has a higher species richness than cattail marsh or *P. australis* invaded marsh in Long Point (Table 1.1). Meadow marsh found at the base of Long Point Peninsula is characterized by the dominance of Canadian bluejoint grass (*Calamagrostis canadensis*) and Ohio goldenrod (*Solidago ohioensis*), as well as the presence of twigrush (*Cladium mariscoides*) and dogwood (*Cornus* spp.) (Reznicek and Catling 1989). Cattail marsh in Long Point is more of a monoculture (Table 1.1) and is usually dominated by the non-native hybrid *Typha* x. *glauca* (Reznicek and Catling 1989). While canopy height and leaf width can separate F1 *Typha* x *glauca* from the parental species (*Typha angustifolia* and *Typha latifolia*) (Zapfe and Freeland 2015), backcrossing between the hybrids and parental cattails can increase the difficulty in identifying individual cattail plants to species (Kirk et al. 2011). Therefore I

refer to cattail in Long Point as *Typha* spp. to indicate that more than one species or hybrid may be present within the cattail marsh.

Several studies located in Long Point investigated the effect of *P. australis* invasion on birds (Meyer et al. 2010, Robichaud and Rooney 2017), amphibians (Greenberg and Green 2013), and turtles (Bolton and Brooks 2010). Most of these studies reported that *P. australis* had a negative effect on wildlife (Bolton and Brooks 2010, Greenberg and Green 2013, Robichaud and Rooney 2017) but at low stem densities some studies report that *P. australis* does provide habitat values for wetland species (Meyer et al. 2010, Kiviat 2013).

Table 1.1 Plant cover and species richness in different marsh types in Long Point in 2016 and 2017, n = 5 for each row except invaded and herbicide-treated marsh in 2017 (n = 10). Standard deviation in brackets.

Wetland	Marsh	Year	Total living cover (%)	Species Richness
Big Creek NWA	Meadow	2016	81 (8)	3.2 (5.7)
	Cattail		74 (10)	3.0 (2.1)
	Invaded		81(6)	2.6 (2.2)
Long Point Provincial Park	Meadow	2016	65 (3)	14.4 (1.1)
	Cattail		70 (7)	3.4 (1.0)
	Invaded		78 (7)	5.8 (1.8)
	Meadow	2017	59(14)	11.4 (4.4)
	Cattail		63(16)	3.0 (1.9)
	Invaded		80 (9)	3.7 (2.5)
	Herbicide-treated		41 (36)	2.9 (1.1)

1.3 Carbon and nutrient standing stock of P. australis *and other wetland macrophytes*

Generally, when invasive plants replace resident plant communities, there is an increase in tissue nutrient composition, net primary productivity, aboveground and belowground biomass, and root: shoot ratio (Liao et al. 2008, Ehrenfeld 2010). For example, *P. australis* is a highly

productive wetland plant; it can produce over 100 stems m^{-2} and attain heights of 6 m (Meyerson et al. 2000, Mal and Narine 2004), dwarfing most native species. Such invasion-driven changes can impact the amount of carbon and other macronutrients stored within the wetland, either by changing the amounts stored within the vegetation pool, creating environments that favour faster cycling (for example tighter coupling of nitrification and denitrification), or by affecting the decomposition rate of plant litter (Maltby and Barker 2009). *Phragmites australis*, in its native range, is used in constructed wetlands to remove nutrient pollution (Gumbricht 1993, Bhatia and Goyal 2014), which suggests *P. australis* may provide an important water quality improvement function in North America where it has invaded.

The nutrient concentration in plant tissues can vary by plant species and tissue type. *Phragmites australis* has relatively high nitrogen and phosphorus concentrations, with the highest concentration of nutrients during the growing season located in the foliar tissue, median amounts in the belowground tissues and the lowest concentration in the stems (Li et al. 2016, Tho et al. 2016). At the marsh-level, *P. australis* retained almost two times more nitrogen than *Typha angustifolia* in living aboveground biomass (Findlay et al. 2002). In this study, *P. australis* had both a higher nitrogen tissue concentration and 50 % more biomass production than *T. angustifolia* (Findlay et al. 2002). Nutrient concentrations of *C. canadensis* tissues were not found in the current literature, however work by Kao et al. (2003) reported that compared to other wetland macrophytes *C. canadensis* did not assimilate as much nitrogen and phosphorus pollutants in a planted riparian wetland.

Globally, foliar nitrogen concentrations, on a mass basis, have been positively correlated with carbon assimilation rates (Reich et al. 2009). Carbon assimilation rates and foliar nitrogen concentrations are both high for *P. australis* (Farnsworth and Meyerson 2003). However,

maximum carbon assimilation rates (measured between >1000 - 2000 µmol m^{-2} s^{-1} of photosynthetically active radiation) were similar between *Typha* spp. (~20 - 25 µmol CO_2 $m^{-2}s^{-1}$) and *P. australis* (~15 - 28.21 µmol CO_2 $m^{-2}s^{-1}$) in freshwater and brackish marshes in the USA (Farnsworth and Meyerson, 2003; Tho et al., 2016), despite lower foliar nitrogen concentrations in *Typha* spp. (Findlay et al. 2002). Carbon assimilation rates of *C. canadensis* appear to be lower than *Typha* spp. and *P. australis,* although these measurements were taken at lower levels of photosynthetically active radiation (7.4 - 22.7 µmol CO^2 m^{-2} s^{-1} at 650 µmol m^{-2} s^{-1} photosynthetic active radiation; Hogg and Lieffers 1991).

Light levels throughout the canopy also affect carbon assimilation rates. Hirtreiter and Potts (2012) reported that *P. australis* dominated stands captured more light at the top of the canopy than *Typha* spp. dominated stands. Surprisingly, *P. australis* carbon assimilation rates remained high throughout the canopy despite the lower light levels reaching lower in the canopy (Hirtreiter and Potts 2012). *Typha* spp., however, had decreased carbon assimilation rates lower in the canopy despite greater light penetration (Hirtreiter and Potts 2012). Hirtreiter and Potts (2012) suggest that by having more foliar nitrogen in low canopy leaves, *P. australis* is better able to take advantage of low light penetration than *Typha* spp. In contrast, *Typha* spp. is more efficient in its allocation of nitrogen throughout the canopy (Hirtreiter and Potts 2012).

Plant-level carbon assimilation rates and total biomass production have been strongly correlated in a review of the current literature (Sutton-Grier and Megonigal 2011). The annual aboveground standing crop produced by *P. australis* has been reported in numerous studies conducted in Europe and North America; and can be as low as 506 g m^{-2} and as high as 3378 g m^{-2} (147% difference; Table 1.2). *Phragmites australis* belowground biomass production may be even more variable than aboveground biomass (Table 1.2). In a tidal brackish marsh (New Jersey, USA), *P.*

australis root biomass was recorded as 120 - 1080 g m^{-2} and rhizome biomass ranged between 250 to 5830 g m^{-2} (Windham 2001). Individual replicates of roots and rhizomes in a greenhouse experiment could vary by approximately a third of the average (946 g m^{-2} ± 356 SD; Ouellet-Plamondon et al., 2004). Despite the variation reported, belowground biomass is mostly rhizomes (up to 72%; Windham 2001, Ouellet-Plamondon et al. 2004, Rothman and Bouchard 2007).

Differences between the standing crop of *P. australis* and the resident plant communities it replaces determines the magnitude of effect that *P. australis* invasion will have on carbon and other macronutrient cycles in an invaded wetland (Rothman and Bouchard 2007). Invasive *P. australis* and *Typha* spp. stands both produce significantly more total (above and belowground) biomass than smaller emergent species such as *Spartina* spp., *Leersia oryzoides* and *Sagittarius latifolia* (Table 1.2). *Phragmites australis* also had deeper roots and rhizomes than *S. patens*, but the peak amount of belowground biomass for both species was present within 10 cm of the surface of the soil (Rothman and Bouchard 2007). In a greenhouse experiment, *C. canadensis* produced more aboveground biomass than *Typha angustifolia* but less aboveground biomass than *P. australis* (Ouellet-Plamondon et al., 2004). In addition, *C. canadensis* produced the lowest and shallowest belowground biomass of the three plant species (Ouellet-Plamondon et al., 2004). Most relevant to my study, however, is work focussed on belowground biomass in Long Point. Rooting depths in Long Point among *C. canadensis*-dominated meadow marsh, cattail marsh and *P. australis* invaded marsh did not differ, but belowground biomass was greatest in *P. australis* invaded marsh and intermediate in cattail marsh (Lei 2018). Lei (2018) suggests that rooting depths may not differ among plant communities in Long Point because the sandy

substrate or high fluctuations in daily water depth could restrict root growth or because deeper roots are less advantageous in freshwater.

Notably, *P. australis* tends to produce more aboveground biomass than *Typha* spp. in dry years, though perhaps not in wet years (Duke et al. 2015), suggesting it may be driven by climate and hydrology. Some of the variation in standing crop biomass of *P. australis* among published studies is likely due to the range of climate and latitude that the data was collected from; however, there was still a large range of aboveground biomass (1522 to 3378 g m^{-2}) captured in two proximate studies (approximately 50 km apart) on Lake Erie (Rothman and Bouchard 2007, Duke et al. 2015; Table 1.2). Thus, other environmental factors such as water depth, soil nutrient levels, salinity, or light exposure may play a role.

In brackish water there seems little difference in total (above and belowground) biomass between *P. australis* and *Typha* spp. (Farnsworth and Meyerson 2003). In freshwater, however, *P. australis* stands typically have a larger total biomass in the field (Farnsworth and Meyerson 2003, Rothman and Bouchard 2007, Duke et al. 2015), although not in greenhouse experiments (Ouellet-Plamondon et al 2004).

Biomass production by a single species may also vary under different nutrient environments (Engloner 2009) or water depths (Wetzel and van der Valk 2005, Dolinar et al. 2015). For example, nitrogen loading is correlated with increased biomass, increased foliar nitrogen and phosphorus concentrations, and altered root: shoot ratios in various studies (e.g., Caplan et al., 2015; Graham and Mendelssohn, 2016; Kvet et al., 2008; Li et al., 2016; Powelson and Lieffers, 1992; Rong et al., 2014). In addition, models indicate that increased nitrogen loading could increase the biomass of *P. australis* more than the biomass of resident plant species (Caplan et al.

2015). Simulations run by Caplan et al. (2015) suggest that higher nitrogen loading results in earlier and protracted canopy growth and a longer period of high photosynthetic rates for *P. australis*. Thus, the difference in *P. australis* biomass and above versus belowground resource allocation reported from proximate experiments by Rothman and Bouchard (2007) and Duke et al. (2015) may be a result of different nutrient loading from the tributaries located near their respective study areas.

The effect of water depth on biomass production is reported to vary. Engloner (2009) reviewed the effect of water depth on *P. australis* biomass and reported different results depending on the location and system-specific settings, such as different water depth treatments, brackish versus freshwater wetlands and different continents. Dolinar et al. (2015) measured *P. australis* aboveground biomass from 1986 - 2014 within the same littoral site on Lake Cerknica and reported it was significantly and negatively correlated with deeper water and positively correlated with July air temperature. On Lake Erie, *P. australis* may be sensitive to water depth as more biomass was reported in a study that had higher levels of standing water (Rothman and Bouchard 2007) than in a shallower water study (Duke et al. 2015). *Typha* spp. and *C. canadensis* may also increase biomass production in deeper standing water. Duke et al. (2015) reported increased aboveground biomass production by *Typha* spp. in wetter years. Similarly, *C. canadensis* aboveground biomass was greater in continuously flooded versus alternating wet and dry conditions in a greenhouse study (Wetzel and van der Valk 2005). Measuring invaded and resident plant species across a water depth gradient and in different nutrient environments within a single study would clarify how the production of different plant species responds to changes in environmental conditions.

Table 1.2 Above- and belowground biomass of *P. australis* and other wetland macrophytes, negative or zero water depths represent dry sites. Standard deviation in brackets.

Location		Species	Aboveground ($g\ m^{-2}$)	Belowground ($g\ m^{-2}$)	Water Depth (cm)	Citation
Brackish tidal marsh Great Bay, New Jersey, USA		*P. australis*	1855 (70)	1368	0 - 120, floods 20% of annual high tide	Windham 2001
		Spartina patens	694 (46)	757		
Connecticut River, Connecticut, USA	Fresh tidal marsh	*P. australis*	~1719		Tidal amplitude 0.75 m	Farnsworth and Meyerson 2003
		T. angustifolia	~816			
		Leersia oryzoides	~45			
	Brackish tidal marsh	*P. australis*	~2208		Tidal amplitude 1 m	
		T. angustifolia	~2025			
		Spartina alterniflora	600-800			
Horizontal subsurface flow constructed wetland (greenhouse experiment)		*P. australis*	1115 (36)	946 (356)	- 4	Ouellet-Plamondon et al. 2004
		T. angustifolia	988 (51)	2461 (817)		
		C. canadensis	1057 (12)	256 (147)		
Lake Erie, Ohio, USA		*P. australis*	1522 (464)	886 (167)	7.5 - 8.5	Rothman and Bouchard 2007
		Mixed T. latifolia and *T. angustifolia.*	1177 (164)	742 (238)		
		Sagittaria latifolia	500 (80)	345 (121)		
Lake Erie, Michigan, USA		*P. australis*	2870 (702) - 3378 (1075)	-	12.5 - 16.7	Duke et al. 2015
		Typha spp.	1611 (312) - 2930 (884)	-		
-Lake Cerknica, Slovenia		*P. australis*	506 - 848	-	0 - 200	Dolinar et al. 2015
Long Point, Lake Erie, ON, Canada		*P. australis*	-	3137 (1908)	16.8 - 55.7	Lei 2018
		Typha spp.	-	2372 (1264)	35.0 - 53.3	
		meadow marsh	-	1146 (702)	13.7 - 43.0	

1.4 Storage and release of macronutrients from P. australis *and other wetland macrophytes*

As described previously, macronutrient cycling in wetlands is affected by decomposition rates of plant litter. Plant litter can be divided into two categories, the first is the litter that falls from the plants and lays in the water or on the soil that is typically though of when describing litter. The second is standing dead litter which does not bend or lay in the water of the wetland but remains

erect and emergent in the air. This standing dead litter is thus rarely inundated and has been noted to accumulate at high densities in *P. australis* invaded habitat, reaching stem densities of up to 360 stems m^{-2} and individual standing dead stems remaining upright for two or more years (Rooney lab, unpublished data).

Litter from plant species may decompose at faster or slower rates because of differences in litter quality (Enriquez et al. 1993, Windham 2001) and unique environmental conditions present in the sites where the litter decomposes (van der Valk et al. 1991, Vymazal and Březinová 2016). The relative importance of litter quality versus environmental conditions remains unclear; understanding how each factor influences decomposition rates will help inform management decisions and explain how nutrient cycling changes in invaded wetlands.

A widely employed method to measure decomposition rates is the use of litterbags that are positioned in the wetland and collected periodically over the course of a year or more. Litterbag experiments may underestimate decomposition rates due to the exclusion of invertebrates and/ or the protection of the litter within the mesh, but litterbag experiments allows standardization across experimental treatments and for comparisons across the literature (Bedford 2004, Christensen et al. 2009). Decay rates are calculated using mass loss and several models have been used in the literature. The single exponential model, as described by Olson (1963) is the most commonly used (Dinka et al. 2004). The single exponential model is: $W_t = W_0 \exp(-kt)$, where W_t describes the mass of litter (%) remaining a time t, W_0 is the initial mass of litter (%) and k is the exponential decomposition rate (Olson, 1963). This model assumes that decomposing litter has a constant rate of decay over time. The decaying coefficient model as described by Godshalk et al. (1978), however, is more appropriate to describe decomposition when rates may fluctuate or where different litter types are being compared (Dinka et al. 2004).

The decaying coefficient model is: $W_t = W_0 \exp((k_1/k_2)*(\exp(k_2 t) - 1))$, where k_1 equals the initial decay coefficient and k_2 equals the relative decrease of the decay coefficient (Godshalk et al. 1978). This model is based on the assumption that litter is composed of two parts, a quickly decaying (labile) portion that decays initially, followed by the slower decay of the remaining (refractory) litter (Dinka et al. 2004).

Several studies have focussed on the rate of decomposition for *P. australis* and other wetland macrophytes (Table 1.3). In most litterbag studies, *P. australis* generally has a slow daily decomposition rate which ranges from 0.0005 to 0.385 depending on the tissue used in the study and on environmental conditions, including the microbial community (Table 1.3). Generally, *Typha* spp. stem and leaf litter decomposes slightly faster than *P. australis* leaf and stem litter, despite both species being tall, clonal wetland macrophytes (Table 1.3). Two Lake Erie studies examined the decomposition of *Typha* spp. and *P. australis* (Rothman and Bouchard 2007, Duke et al. 2015), but only one study found a significant difference in decomposition rates (Duke et al. 2015), which is possibly because different *Typha* species might have been used in the two studies. *Phragmites australis* also decomposed more slowly than smaller macrophytes (*Scolochloa festucacea*, *Scirpus lacustris*, *Spartina patens* and *Sagittaria latifolia*) in studies conducted in freshwater and brackish marshes (van der Valk et al. 1991, Windham 2001, Rothman and Bouchard 2007; Table 1.3).

The decomposition rate of different litter may depend upon the lignin content (Berg et al. 1984, Dinka et al. 2004) or the nutrient content of the tissues (Enriquez et al. 1993). In a review of 256 decomposition rate studies of everything from algae to tree species, 89% of the variation in decay rates of litter was dependent on the ratio of carbon, nitrogen and phosphorus in the tissue (Enriquez et al. 1993). Furthermore, the nutrient ratio of litter was more predictive than the lignin

content (Enriquez et al. 1993). Leaves of *P. australis* have a higher nitrogen and phosphorus concentration than stems of *P. australis*, and the stems decompose over two times more slowly than leaves (Table 1.3; Dinka et al. 2004; Vymazal and Březinová 2016). *Phragmites australis* leaves and stems however, have an overall lower nitrogen content than *S. patens* and decomposed more slowly in a brackish marsh (Windham 2001). Thus, differences in nutrient concentrations (litter quality) can affect the decomposition rates of different tissue types within the same plant and the decomposition rate between plant species.

As living plants senesce and decompose the nutrient concentration of the tissue changes; nutrient retention in senescing vegetation depends on the plant species and nutrient type. In a review of the ability of natural wetlands to retain nitrogen and phosphorus, Nichols (1983) reported that only ~25 - 65% of nitrogen and phosphorus assimilated by the living plants remained in senesced vegetation. *Phragmites australis* shed litter and standing dead litter lost more nitrogen (~40 - 60%) and phosphorus (~75 - 85%) compared to *T. angustifolia*, which increased in nitrogen and decreased slightly in phosphorus (~0 - 25%) (Findlay et al. 2002). *Calamagrostis canadensis* has an intermediate ability to retain nutrients, in a riparian wetland *C. canadensis* litter lost ~ 30% of the nitrogen assimilated and ~ 49% of its phosphorus (Kao et al. 2003).

Decomposition rates can also be affected by environmental conditions including temperature, light levels and water depth, which in turn is partially dependent on the height, stem density and litter layer thickness of the prevalent plant species (Windham and Lathrop 1999, Bedford 2005, Dolinar et al. 2015, Duke et al. 2015). Therefore *P. australis* invasion could also alter decomposition rates by changing the environmental conditions that affect microbes and fungal activity, even if litter quality does not change. For example, temperature was positively correlated with decomposition rates of *P. australis*, though this effect was small overall (Bedford

2005). Water depth also influences decomposition rates in numerous studies in North America and Europe (Table 1.3), and prior research has observed that *P. australis* invasion can decrease standing water depth (Weinstein and Balletro 1999, Windham and Lathrop 1999). Litterbags placed in standing water or partially submerged decomposed faster than those in dry sites in freshwater and brackish wetlands (van der Valk et al. 1991, Bedford 2005, Dolinar et al. 2015, Vymazal and Březinová 2016). *Phragmites australis* litter decomposed twice as fast in flooded sites compared to dry sites (van der Valk et al. 1991) and decomposed 20 - 45% faster in standing water (Vymazal and Březinová 2016). Bedford (2005) noted that in periodically inundated sites, decay rates of *P. australis* litter slowed while litter was under water and increased when the litter was above water, but attributed this observation to time lags in the change in decomposer communities (Bedford 2005). Litter in this study still decomposed significantly faster in periodically flooded sites than continually dry sites (Bedford 2005), and other research reported *P. australis* litter in continually submerged sites decomposed significantly faster than sites that were periodically dry (Dolinar et al. 2015, Vymazal and Březinová 2016).

Litterbag transplant experiments involve the placement of litter of one plant species into another plant community and then subsequent monitoring of mass loss to quantify decomposition rates. This experimental approach can separate the influence of changes in litter quality due to invasion from the influence of environmental changes created by an invading plant species on decomposition rates (Windham 2001, Duke et al. 2015). In North America, two litterbag transplant experiments using *P. australis* were carried out. Windham (2001) placed *P. australis* litter in invaded brackish marsh and placed *P. australis* litter and *S. patens* litter in an *S. patens* dominated brackish marsh and reported that *S. patens* decomposed faster than *P. australis*,

indicating that litter quality had a greater effect than environmental site characteristics. Duke et al. (2015), however, concluded that environmental conditions (decreased standing water in an invaded marsh) had greater effect than litter quality in a *Typha* spp. and *P. australis* litter transplant experiment on Lake Erie. More dramatic changes in nutrient concentrations between *S. patens* and *P. australis* litter versus *Typha* spp. and *P. australis* litter may explain these conflicting conclusions. Site conditions would also differ between the resident plant communities examined in the studies: *S. patens* dominant communities would be shorter than *P. australis* invaded or cattail communities. Moreover, one study was conducted in a brackish tidal marsh (Windham 2001) and the other was conducted in a freshwater coastal marsh (Duke et al. 2015). Thus, ion concentrations and electrical conductivity may also moderate the effects of invading *P. australis* on decomposition rates.

Decomposition rates can also be affected by interactions between litter quality and environmental conditions. In a review of decomposition studies, Enriquez et al. (1993) reported that nutrient quality had a stronger correlation to decomposition rates when the litter was submerged than when it was in dry sites, although all wetland litter decomposed faster in wet than dry sites. Correspondingly, decomposition rates for *P. australis* leaves (high quality) and stems (lower quality) both increased in submerged sites, but the increase in decomposition rate was slightly higher for the higher quality leaf litter (Table 1.3; Dolinar et al., 2015; Vymazal and Březinová, 2016).

Table 1.3 Summary of decomposition rates of *P. australis* and other wetland macrophytes. Reported decomposition rates (*k*) from the single exponential decay model. Studies ranged in length from 208 - 1004 days. North American native lineage of *P. australis* denoted with an *.

Location	Species	Plant tissue	Water treatment	Duration of study	Decomposition rate (*k*)	Citation
Delta Marsh on Lake Manitoba, Manitoba, CND	*P. australis**	Stem & leaf	Dry/ standing water	356 -505 days	0.00029	Van der Valk et al. 1991
			Standing water		0.00072	
	T. glauca	Stem & leaf	Mostly standing water		0.00115	
			Standing water		0.00147	
	Scolochloa festucacea	Stem & leaf	Dry/ standing water		0.00125	
			Standing water		0.00217	
	Scirpus lacustris	Stem & leaf	Mostly standing water		0.00131	
			Standing water		0.00120	
Brackish tidal marsh, New Jersey, USA	*P. australis*	Stem & leaf	Dry/ standing water	390 days	0.25	Windham 2001
	Spartina patens	Stem & leaf	Dry/ standing water		0.57	
Lake Ferto, Hungary	*P. australis*	Stem	Standing water	~1004 days	0.0005	Dinka et al. 2004
		Leaf	Standing water		0.0026	
Leighton Moss wetland, England	*P. australis*	Stem	Dry	891 days	0.0007	Bedford 2005
			Dry/ standing water		0.0016	
		Leaf	Dry	559 days	0.0012	
			Dry/ standing water		0.0025	
Lake Erie, Ohio, USA	*P. australis*	Stem & leaf	Standing water	208 days	50% loss at 327 days	Rothman and Bouchard 2007
	T. latifolia & *T. angustifolia.*	Stem & leaf	Standing water		50% loss (273 days)	
	Sagittaria latifolia	Stem & leaf	Standing water		50% loss at 9 days	
Lake Feher, Hungary	*P. australis*	Stem & leaf	Standing Water	630 days	0.0022	Agoston-Szabo and Dinka 2008
	T. angustifolia	Stem & leaf	Standing Water		0.0025	
Lake Cerknica, Slovenia	*P. australis*	Stem	Dry	335 days	0.024	Dolinar et al. 2015
			Dry/ standing water		0.025	
			Standing water		0.049	
		Leaf	Dry		0.050	
			Dry/ standing water		0.088	
			Standing water		0.385	
Lake Erie, Michigan, USA	*P. australis*	Stem & leaf	Standing water	344 days	49.1% loss at 344 days	Duke et al. 2015
	Typha spp.	Stem & leaf	Standing water		39.4% loss 344 days	
Fish ponds, Prague, Czech Republic	*P. australis*	Lower Stem	Dry	365 days	0.0009	Vymazal and Brezinova 2016
			Dry/ standing water		0.0010	
			Standing water		0.0011	
		Upper Stem	Dry		0.0013	
			Dry/ standing water		0.0020	
			Standing water		0.0024	
		Leaf	Dry		0.0022	
			Dry/ standing water		0.0035	
			Standing water		0.0047	

Examining decomposition rates provides valuable information about how *P. australis* invasion changes macronutrient storage in vegetation stocks. However, additional information on carbon cycling specifically is provided by examining how *P. australis* invasion impacts soil carbon dioxide efflux and soil methane efflux rates. Changes in soil carbon efflux may be dependent on the traits of the vegetation; plant productivity and the amount of oxidized iron on roots impacts the rate of carbon dioxide to methane soil respiration (Sutton-Grier and Megonigal 2011). In a greenhouse experiment, Mozdzer and Megonigal (2013) reported that invasive *P. australis* had a greater release of soil methane than native *P. australis*. Bernal et al. (2016) reported that invaded brackish marsh could release more carbon to the atmosphere because *P. australis* had deeper roots than the resident vegetation found in the marsh system, and therefore *P. australis* could access deeper carbon pools in the wetland soil. However, recent work at Long Point, Lake Erie reported no difference in rooting depth between *P. australis* dominated and uninvaded marsh habitats (Lei 2018). Duke et al. (2015) compared *P. australis* to *Typha* spp. at a different site on Lake Erie and did not report a significant increase in soil carbon dioxide efflux in invaded sites. *Typha* x. *glauca*, however, may also increase soil methane release. For example, Lawrence et al. (2017) reported that *Typha* x. *glauca* dominated mesocosms released more methane than native meadow vegetation in wet conditions. Overall, there is still a high amount of uncertainty regarding the effect of *P. australis* on carbon dynamics with some research suggesting that wetlands dominated by *P. australis* are carbon sinks over long time periods (>100 years) (Brix et al. 2001, Kvet et al. 2008), and other research suggesting that *P. australis* invasion changes wetlands to carbon sources (Mozdzer and Megonigal 2013, Bernal et al. 2016).

1.5 Phragmites australis *control efforts*

In North America, *P. australis* control efforts have a 40 year history (Breen et al. 2014). In a five year timeframe, combined control efforts in the USA cost an estimated $16 million USD (Martin and Blossey 2013). In Ontario, a recent survey of municipalities concluded that about $2 million CDN is spent annually on *P. australis* control (*Economic impacts of invasive species to Ontario municipalities and Conservation Authorities* 2018). This is likely an underestimation for the province, as the Ministry of Natural Resources and Forestry reported spending $2 million CDN on controlling 500 ha of *P. australis* in Long Point and Rondeau Provincial Parks in 2016 alone (Ministry of Natural Resources and Forestry et al. 2016).

Most control efforts (79 - 94%) in the USA utilize either glyphosate or imazapyr based herbicides (Martin and Blossey 2013, Hazelton et al. 2014) instead of mechanical control (burning, cutting, mowing) because mechanical control alone is not effective at eradicating *P. australis* (Breen et al. 2014, Hazelton et al. 2014). Glyphosate and imazapyr are broad spectrum herbicides and can affect resident plant species growing alongside *P. australis*. Glyphosate was most often used to control *P. australis* in the USA because it was the first approved by the USA Environmental Protection Agency for use in sites with standing water (Hazelton et al. 2014). Imazapyr and glyphosate are both effective at controlling *P. australis*. Imazapyr may be more effective (Mozdzer et al. 2008, Hazelton et al. 2014) but could potentially have a greater negative effect on resident plant re-growth (Mozdzer et al. 2008). As with any application of herbicide, there are concerns about resistance evolving in *P. australis* (Powles 2008), and so a mixed-control method approach is considered the best management practice.

In Canada, herbicides used to control *P. australis* cannot be legally used over standing water. However, in 2016 the Ontario Ministry of Natural Resources and Forestry successfully obtained an Emergency Use Registration from the federal Pest Management Regulatory Authority to enable a pilot project involving glyphosate application to control *P. australis* in areas with standing water in the Long Point region and Rondeau Provincial Park (Ministry of Natural Resources and Forestry et al. 2016). In 2016, about 500 ha were treated with glyphosate as an isopropylamine salt via aerial application at a rate of 4210 g ae/ha. This pilot project was continued in 2017 to expand the treatment area using a combination of aerial and ground-based application. Ground-based application was achieved by a mix of boat and track vehicle access to regions either too close to drinking water intake sites or too contorted in shape to be safely treated by helicopter and involved a lower glyphosate loading rate: 1200-3600 g ae/ha.

Determining the effectiveness of eradicating *P. australis* from an area requires long term monitoring. In well established *P. australis* stands, one application of herbicide will significantly reduce the abundance of *P. australis* the next year, but does not completely eliminate *P. australis* (Ailstock et al. 2001, Lombard et al. 2012). In a brackish marsh in the USA, *P. australis* began to increase in abundance three years after herbicide treatment, and the authors recommended follow-up herbicide application (Ailstock et al. 2001). In swale wetlands in Cape Cod, USA an initial herbicide application was followed up with spot treatments (Lombard et al. 2012). Even after five to seven years, *P. australis* was not completely eliminated, though the abundance and distribution of *P. australis* decreased (Lombard et al. 2012). Seed regeneration of *P. australis* may contribute to its reinvasion of treated areas (Galatowitsch et al. 2016). In a park in the state of New York, there was a 0.02 probability of eradicating *P. australis* (defined by the authors as no living *P. australis* present for 3 consecutive years) using annually applied glyphosate-based

herbicide treatment in the largest patch size (> 3000 m²), though small (0.36 m²) and medium patches (45 m²) had higher probabilities of eradication (0.82 and 0.26 , respectively) (Quirion et al. 2018). In wetlands with large *P. australis* patches, long term eradication of *P. australis* might not be achievable because of re-invasion of the area, monetary limitations and site inaccessibility (Lombard et al. 2012, Martin and Blossey 2013, Hazelton et al. 2014). Instead, authors suggest that uncertain long-term control, ecological effects, and financial costs mean that small areas or areas with low abundance of *P. australis* should be prioritized for control efforts over heavily invaded areas.

Even if *P. australis* is successfully eradicated, control of *P. australis* is not the only objective of land managers. Another objective of surveyed land managers involved in the control of *P. australis* in the USA was the restoration of native vegetation (Martin and Blossey 2013). Monitoring the plant community that establishes after herbicide treatment of *P. australis* suggests that native plant communities can re-establish from the native seed bank without any further restoration efforts (Ailstock et al. 2001, Carlson et al. 2009, Baldwin et al. 2010). Recent work by Hazelton et al. (2018) however, indicates that while the seedbank present after herbicide treatment of *P. australis* is sufficient to establish resilient wetland communities, wetlands may benefit from active revegetation through seeding or planting native species. Furthermore, in a review by Martin and Blossey (2013) and a study by Alldred et al. (2016), differences between the plant community that re-established after treatment of *P. australis* and adjacent uninvaded communities were reported. This suggests that controlling *P. australis* alone does not always bring back the desired plant community. Furthermore, the re-established plant communities may have novel traits compared to the uninvaded plant communities (Alldred et al. 2016). For example, Alldred et al. (2016) reported that two years after herbicide-treatment the plant

community that re-established had less biomass and lower nitrogen assimilation than the near-by, native *T. angustifolia* dominated communities.

Despite the reported differences between the re-established and uninvaded plant communities (Martin and Blossey 2013, Alldred et al. 2016), long-term monitoring of ecological processes that depend on the plant community, including primary production and decomposition, is seldom undertaken. A few studies have looked at how controlled sites and invaded sites differ. Kennedy et al. (2012) examined how the application of glyphosate effected the decomposition rate and decomposer community of *P. australis* litter. While there were some differences in the microbial community, overall there were few differences in macro invertebrates, decomposition rates, or litter chemistry (Kennedy et al. 2012). Martin and Moseman-Valtierra (2017) studied how carbon dioxide and methane soil efflux changed between *P. australis* stands and mechanically removed *P. australis*. They reported increased carbon dioxide and methane emissions in mechanically controlled sites (Martin and Moseman-Valtierra 2017), likely due to the removal of all living *P. australis.* Monitoring that encompasses how control efforts change net primary production, decomposition rates and environmental conditions would further our understanding of whether control efforts are capable of restoring ecological processes to desirable rates and scales.

1.6 Thesis structure

In chapter 2, I examined the effect of *P. australis* invasion on macronutrient standing stocks in Long Point, specifically carbon, nitrogen, phosphorus, potassium, calcium and magnesium. The first objective of this chapter was to compare the composition of the tissue of *P. australis, Typha* spp., and *C. canadensis*, which dominate invaded, cattail marsh and meadow marsh habitats

respectively. Then, at the marsh level, I compared biomass and the annual vegetative nutrient stocks in invaded, cattail and meadow marsh communities. I hypothesized that invaded areas will have greater annual nutrient stocks in vegetation, especially in terms of tissue concentrations (Findlay et al. 2002, Hirtreiter and Potts 2012) because *P. australis* has high net primary production, foliar chlorophyll and foliar nitrogen compared to other plant species (Windham 2001, Farnsworth and Meyerson 2003). Because total production can be influenced by water depth, I evaluated sites along a gradient in water depth. I hypothesized that, in deeper water, standing crop biomass will increase as wetland plants are sensitive to water depth and its fluctuations (Wetzel and van der Valk 2005, Rothman and Bouchard 2007, Duke et al. 2015). My second objective for the chapter focused on how the effect of invasion may be moderated by nutrient levels in the environment. I achieved this by comparing relatively high and low nutrient regions within Long Point. I hypothesized that areas with higher soil nutrient content would contain plant communities with increased standing crop biomass and higher tissue nutrient content because macrophytes in high nutrient environments would have luxury consumption of nutrients (Gumbricht 1993 and references therein), whereas plants growing in lower nutrient environments could face nutrient limitation.

In chapter 3, I investigated how *P. australis* control efforts employed in Long Point influenced vegetative carbon pools and fluxes, comparing glyphosate-treated areas to untreated controls and uninvaded reference (resident plant community) sites. I examined the net primary productivity, decomposition rates, water depth and fluctuations, water temperature, and light penetration in resident plant communities, *P. australis* invaded marsh and herbicide-treated sites. To factor out the influence of water depth on overall productivity and decomposition rates, I arranged my study so that sites in resident plant communities, invaded marsh and herbicide-treated areas were

paired along a water depth gradient. To separate the effects of invasion and herbicide treatment on environmental covariates from the effects of changes in dominant plant tissue composition and primary production, I also completed a litter transplant experiment. My first objective was to quantify the impact of *P. australis* invasion on carbon dynamics and related environmental covariates. I predicted that *P. australis* invaded sites would have greater primary production, as measured through standing crop biomass and carbon assimilation rates, than resident plant community sites because *P. australis* has high concentrations of foliar nitrogen and is highly productive (Farnsworth and Meyerson 2003, Engloner 2009). I also predicted that decomposition rates of *P. australis* leaf litter would be greater than *C. canadensis* or *Typha* spp. litter because *P. australis* litter has higher nitrogen content (Findlay et al. 2002), and that all wetland litter types would decompose faster when submerged (Enriquez et al. 1993). The second objective of my third chapter was to evaluate the immediate (within 1 year of treatment) ability of herbicide-based control efforts to recover net primary production and decomposition rates to within the range typical of resident plant community marsh habitat. I hypothesized that net primary production will decrease and decomposition rates will increase in herbicide-treated sites compared to resident plant communities and invaded sites because the recovery of plant communities should take several years.

In chapter 4, I synthesized my results on the impacts of *P. australis* invasion and control efforts on macronutrient cycling in Long Point, and discussed the significance of the research in terms of invasive species management in wetlands.

2 Phragmites australis *invasion of coastal marsh causes significant change in nutrient standing stocks*

2.1 Introduction

Invasive species are considered a major threat to biodiversity and a driver of ecological degradation (Zedler and Kercher 2005, Simberloff 2011). Recent research, however, has found evidence that invasive species can provide ecological functions equal to or greater than those provided by native species (Norkko et al. 2012, Bertness and Coverdale 2013, Grutters et al. 2015) and may lead to increased local and regional biodiversity (Sax and Gaines 2003). Recognition of the potential of invasive species to provide ecological functions has led to debate about whether conservation objectives should include the eradication of all invasive species (Schlaepfer et al. 2011, 2012, Vitule et al. 2012). It has been proposed that the decision to control invasive species should be made on a case-by-case basis through evaluation of the impact of a given invasive species on ecological function (Hershner and Havens 2008, Hobbs et al. 2009, Davis et al. 2011).

Throughout North America the invasive lineage of *Phragmites australis* (hereafter *P. australis*) is increasing in abundance and distribution (Catling and Mitrow 2011). *Phragmites australis* is a tall wetland macrophyte whose impact on ecological functions in inland coastal marshes is not fully understood, though its effects on wetland flora and fauna are well documented. *Phragmites australis* forms dense monocultures that replace resident plant communities (Keller 2000, Mal and Narine 2004, Tulbure et al. 2007) and can negatively affect wetland birds (Robichaud and Rooney 2017), amphibians (Greenberg and Green 2013) and turtles (Bolton and Brooks 2010, Markle et al. 2018).

In the Great Lakes region, *P. australis* took advantage of historically low lake levels (Wilcox et al. 2003, Tulbure et al. 2007, Tulbure and Johnston 2010) and increased nutrient loading in the watershed (Croft and Chow-Fraser 2007) to rapidly expand into coastal marsh habitat on Lake Erie. The Long Point peninsula constitutes more than 70% of the remaining coastal marsh on the north shore of Lake Erie (Ball et al. 2003) and is designated as a Ramsar wetland and an UNESCO World Biosphere Reserve. *Phragmites australis* expanded exponentially in this valuable habitat between 1995 and 1999 (Wilcox et al. 2003). As of 2016, *P. australis* covered up to 70% of some coastal marsh management units in the Long Point Peninsula (helicopter mapping; data provided by Erling Armson, Invasive Species Specialist, Ducks Unlimited Canada) and is continuing to increase (Jung et al. 2017). In Long Point, *P. australis* is primarily replacing rare "Graminoid Coastal Meadow Marsh" (Imperiled [S2]; Ministry of Natural Resources and Forestry 2018), as well as cattail marsh (Wilcox et al. 2003). These plant communities are naturally stratified by water depth with cattail marsh in deeper water (11 - 52 cm) and meadow marsh in shallower water (0 - 27 cm; Appendix 1).

Stands of *P. australis* vary in density, typically due to age (Rooth et al. 2003), and while a reduction in wildlife habitat quality is evident at high stem densities (e.g., 100 live stems m^{-2}), at lower densities some research has determined that *P. australis* does provide habitat value (Meyer et al. 2010, Kiviat 2013). There is also evidence that invasion may affect nutrient and carbon cycling (Rothman and Bouchard 2007, Windham and Ehrenfeld 2013) as a result of high net primary production (Windham 2001, Rothman and Bouchard 2007, Duke et al. 2015), high rates of carbon assimilation (Farnsworth and Meyerson 2003, Tho et al. 2016) and high nitrogen content in its foliar tissues (Findlay et al. 2002, Hirtreiter and Potts 2012). In its native range, *P. australis* is often used in constructed wetlands to remove nutrient pollution (Gumbricht 1993,

Bhatia and Goyal 2014), suggesting it could provide an important water quality improvement function where it has invaded.

Research on invasion and nutrient cycling in the Great Lakes region has primarily focused on the difference in nitrogen between *P. australis* and cattail (*Typha* spp.) (Findlay et al. 2002, Farnsworth and Meyerson 2003, Hirtreiter and Potts 2012). Despite the acknowledgment of the importance of macronutrients like phosphorus, potassium, calcium, and magnesium (Ehrenfeld 2010), there has been little work on these nutrient pools and fluxes within invaded and uninvaded wetlands (but see Findlay et al. 2002 and Ouellet-Plamondon et al. 2004). In addition, there are no published comparisons between the nutrient content of *P. australis* and species typical of meadow marsh communities (i.e., sedges and grasses), which differ in diversity and physical structure from stands of cattail.

Given that climate change and eutrophication are two immense environmental threat facing Lake Erie (Watson et al. 2016, Jarvie et al. 2017, Environment and Climate Change Canada and the U.S. Environmental Protection Agency 2017) the capacity of a marsh plant, regardless of its origin, to take up and store nutrients represents a critically important ecosystem function. With the limited success (Lombard et al. 2012, Quirion et al. 2018) and high costs (Martin and Blossey 2013) of *P. australis* control in North America, quantifying the ecosystem functions provided by *P. australis* to the Great Lakes ecosystem will inform decision makers considering whether to attempt its eradication.

My objective is to evaluate the influence of *P. australis* invasion on nutrient standing stocks. I will compare standing crop above- and belowground biomass, nutrient tissue concentrations, and annual standing stocks in marsh invaded by *P. australis* with marsh dominated by *Typha* spp.

and *C. canadensis* (Canadian bluejoint grass) in Long Point. I hypothesize that due to the high net primary production, foliar chlorophyll and nitrogen content of *P. australis* (Windham 2001, Rothman and Bouchard 2007, Duke et al. 2015) invaded areas will support higher nutrient stocks in vegetation, at least in terms of tissue concentrations (Findlay et al. 2002, Hirtreiter and Potts 2012). I also hypothesize that tissue concentrations and standing crop biomass will be greater in areas with more plentiful soil nutrients because emergent wetland plants can carry out luxury consumption of nutrients (Gumbricht 1993 and references therein). I further hypothesize that standing crop biomass will increase in deeper water because these emergent macrophytes may allocate more resources to aboveground biomass in deeper water (Wetzel and van der Valk 2005, Duke et al. 2015).

2.2 Methods

2.2.1 Experimental design

I conducted the study in freshwater coastal marshes within Long Point Peninsula (42° 34' N, 80° 24' W), in the management units Big Creek National Wildlife Area (Big Creek NWA) and Long Point Provincial Park located on the north shore of Lake Erie, Ontario, Canada (Fig. 2.1). I compared the carbon, nitrogen, phosphorus, potassium, calcium and magnesium concentrations in leaf, stem, and belowground tissues of *P. australis, C. canadensis,* and *Typha* spp. (picture of species in Appendix 2). To estimate the annual nutrient stock on a wetland-area basis I scaled up from nutrient concentrations in plant tissues, using measures of above and belowground biomass and leaf:stem ratios. Thus, I could test for differences in annual nutrient vegetative stock between *P. australis* invaded and uninvaded emergent cattail and meadow marsh.

Sampling was designed to capture the variation in water depth and soil nutrient environments in the Long Point peninsula. In 2016, I measured nutrient concentrations in plant tissues and peak biomass from two wetland complexes that contrast a high and low nutrient environment. Fifteen sites in Big Creek NWA (high nutrient environment) and 15 sites in Long Point Provincial Park (low nutrient environment) were equally divided between meadow marsh, emergent cattail and invasive *P. australis* stands. In 2017, I measured peak biomass in Long Point Provincial Park along a water depth gradient to account for variation in plant communities as a response to water depth. The 2017 sites were equally divided between resident plant community sites (meadow marsh; n = 5 and emergent cattail; n = 5) and *P. australis* invaded sites (n = 10).

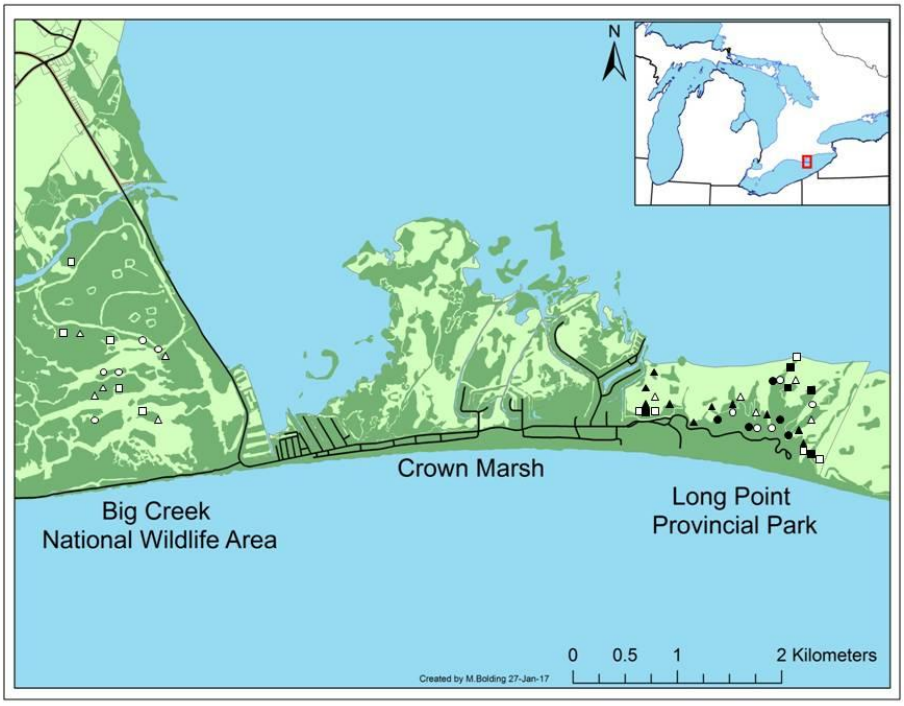

Figure 2.1 Big Creek National Wildlife Area (42° 35' N, 80° 27' W) and Long Point Provincial Park (42° 34' N, 80° 22' W), two wetland complexes within the Long Point peninsula, are located on the north shore of Lake Erie in Ontario. Circles were meadow marsh sites, squares are cattail marsh sites, and triangles are *P. australis* invaded sites. Black symbols were sampled in 2017, white symbols were sampled in 2016. Image credit to Matthew Bolding.

2.2.2 Study area

I recorded site characteristics, including plant cover, stem density, water depth, and canopy height at each sampling location (Fig. 2.1) in July (Table 2.1). In general, sites in Big Creek NWA consisted of taller, lower diversity plant communities growing in deeper water than sites in Long Point Provincial Park (Table 2.1).

Table 2.1 Average site characteristics of meadow, cattail, and *P. australis* invaded marsh sampled in coastal wetlands of the Long Point peninsula in July 2016 and 2017. Sample sites in 2016 contrasted a higher and lower nutrient environment. Sample sites in 2017 captured a water depth gradient in the lower nutrient environment. Standard deviation in brackets.

Site characteristic	Plant community	n	July water depth (cm)	Canopy height cm)	Living (stems/ m²)	Living (% cover)	Species richness
2016 Big Creek National Wildlife Area	Meadow	5	20.5 (±6.0)	178 (±13)	837 (±165)	81 (±8)	3.2 (±5.7)
	Cattail	5	15.5 (±3.0)	276 (±30)	47 (±6)	74 (±10)	3.0 (±2.1)
	Invaded	5	20.5 (±2.0)	409 (±29)	59 (±18)	81 (±6)	2.6 (±2.2)
2016 Long Point Provincial Park	Meadow	5	2.5 (±3.5)	101 (±16)	802 (±284)	65 (±3)	14.4 (±1.1)
	Cattail	5	14.5 (±3.5)	265 (±7)	71 (±45)	70 (±7)	3.4 (±1.0)
	Invaded	5	15.5 (±9.0)	319 (±27)	125 (±53)	78 (±7)	5.8 (±1.8)
2017 Long Point Provincial Park	Meadow	5	17.5 (±7.0)	102 (±26)	776 (±160)	59 (±14)	11.4 (±4.4)
	Cattail	5	41.0 (±8.5)	266 (±14)	83 (±66)	63 (±9)	3.0 (±1.9)
	Invaded	10	36.0 (±10.5)	350 (±48)	91 (±48)	80 (±9)	3.7 (±2.5)

Meadow marshes in Long Point Provincial Park and Big Creek NWA differed in plant species composition more than cattail or *P. australis* invaded marshes (Table 2.1). I chose *C. canadensis* as the focus species for meadow marsh in my study because it was the dominant or co-dominant species that characterized the meadow community (Reznicek and Catling 1989). In Long Point Provincial Park, meadow marshes consisted of more diverse communities of graminoids, sedges, and forbs; other plant species were often co-dominant with *C. canadensis* (Fig. 2.2). In Big Creek NWA, *C. canadensis* more strongly dominated the meadow marsh plant community (Fig. 2.2).

While cattail marsh in both wetland complexes consisted of monocultures composed of *Typha* spp., more than one species of *Typha* may be present within a single site. Cattail marshes in the Great Lakes region are predominately formed by the hybrid species *Typha* x. *glauca* (Freeland et al. 2013); however, back crossing between the hybrid and parental species of *Typha latifolia* and *Typha angustifolia* make it difficult to positively identify cattail to the species level without genetic testing (Kirk et al. 2011). As a result, I refer to cattail as *Typha* spp. to indicate that the species is uncertain and that multiple cattail species may be present within cattail stands.

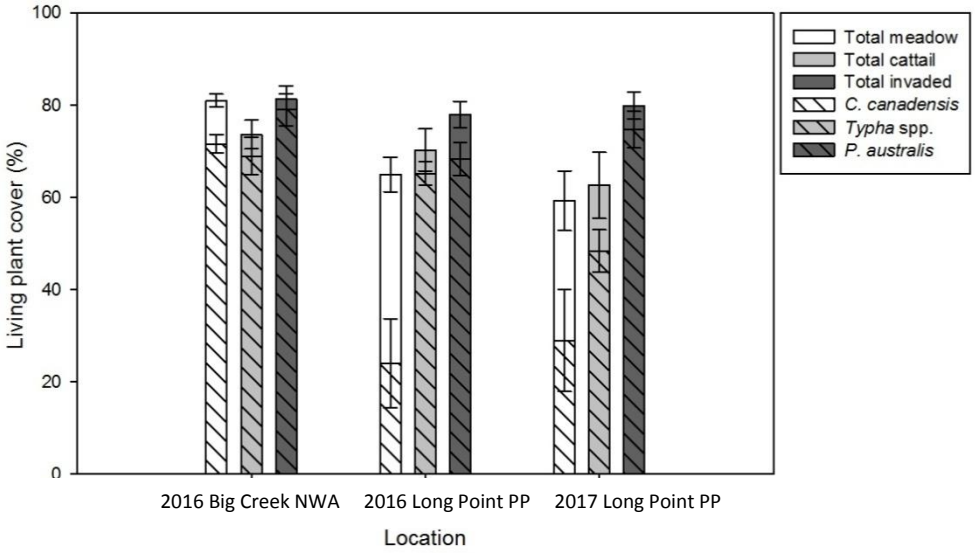

Figure 2.2 Percent cover of all living plant species (total cover) in meadow, cattail and invaded plant communities and the dominant species (*C. canadensis*, *Typha* spp., and *P. australis*, respectively). Location of study plots contrast a high nutrient (Big Creek NWA) and lower nutrient (Long Point Provincial Park) environment sampled in July 2016: meadow (n = 5/ environment), cattail (n = 5/ environment), and *P. australis* invaded (n = 5/ environment). Note that in high nutrient Big Creek NWA, all three communities are dominated by a single species, whereas in the lower nutrient Long Point Provincial Park meadow marsh is more diverse. A similar trend is evident in 2017 data from Long Point Provincial Park covering a gradient in water depth: meadow (n = 5), cattail (n = 5) and *P. australis* invaded (n = 10). Standard error bars shown.

2.2.3 Biomass

To determine the timing of peak aboveground biomass I clipped all live rametes from three replicate 0.25 m² quadrats every ten days during the growing season from one meadow, one cattail and one *P. australis* site. Clipped tissues were air dried for 48 hours and then weighed. Biomass plateaued in August 2016 and July 2017 (Appendix 2), which triggered more extensive sampling of aboveground and belowground standing crop during August 16 - 19, 2016 and July 22 - 25, 2017.

Because all three study species are rhizomatous perennials, belowground biomass was measured using a modified soil ingrowth method (Neill 1992) to restrict belowground biomass collection to the current growing season. In 2016, I inserted five replicate cores (11.3 cm deep by 4.8 cm diameter) consisting of an equal mixture of sand and peat at each sampling location (Fig. 2.1) during early May and harvested during peak aboveground biomass (Aug 16-19) for a total of 91 - 99 days in the wetland. Then I rinsed the cores over stacked sieves with 1.4 mm and 500 um mesh screening and removed all roots, rhizomes, and shoots (dead and alive). Belowground biomass measurements thus reflect the annual contribution to belowground biomass within the upper 11.3 cm, which includes the peak rooting depth in each of my study communities, but not all roots or rhizomes (Lei 2018).

In 2017, I replicated the 2016 belowground biomass protocol, but increased the number of replicate cores from five cores to seven cores because I observed highly variable root mass in the ingrowth soil cores in 2016. I also changed the ingrowth soil core mixture from a mixture of sand and peat to vermiculite in 2017 to increase the efficiency of root removal during processing. The seven replicate cores consisting of vermiculite were inserted at each site during mid May 2017

and harvested during peak aboveground biomass (22-25 July) for a total of 60 – 65 days in the wetland. The decreased time the cores spent in the wetland in 2017 is from an extended deployment period and an earlier harvest date due to earlier peak biomass in 2017. This did not result in a significant change in belowground biomass between samples collected in Long Point Provincial Park when compared between 2016 and 2017 (Appendix 3).

During the same period that I harvested ingrowth soil cores, I also collected aboveground biomass samples from each sampling location (Fig. 2.1). The aboveground living tissues of all species were collected by clipping just above the sediment from three replicate 0.25 m² quadrats deployed randomly at each sampling location.

I then dried all harvested above and belowground samples at 80°C (2017) or 100°C (2016) for 48 hours before measuring their dry-weight to the nearest 0.01 g (Advanced Balance PB602-S, Mettler Toledo, ON, Canada). Due to drying oven availability, I dried samples at a lower temperature in 2017. This did not result in a significant change in aboveground or belowground biomass between samples collected in Long Point Provincial Park when compared between 2016 and 2017 (Appendix 3).

2.2.4 Plant morphology

At each site in 2017, leaf:stem ratio was determined for the dominant species (*P. australis*, *Typha* spp., or *C. canadensis* in invaded, cattail, and meadow marsh, respectively). I collected *C. canadensis*, *Typha* spp. and *P. australis* rametes from one 0.25 m² quadrat per site in June 2017. Then I separated the collected rametes into leaves and stems, oven-dried the leaves and stems for 48 hours at 80°C, and weighed them to the nearest 0.01 g (Advanced Balance PB602-S, Mettler Toledo, ON, Canada). I then determined the leaf to stem mass ratio for each sample.

2.2.5 Plant and soil nutrients

In August 2017, I revisited the 2016 sites and collected soil samples from each site using a 11.3 cm deep corer. I dried the samples at 35°C for one week, and then sieved samples through a 2 mm screen to remove large root particles. I sent samples from the sites with the highest, median and lowest total biomass from each plant community in each wetland complex (n = 18) to an external laboratory (Agriculture and Food Laboratory, University of Guelph) to determine the amount of total nitrogen, total carbon, and plant available phosphorus, potassium, magnesium and calcium present in the soil. Total nitrogen and carbon were measured using thermal conductivity detection, plant available phosphorus was extracted using sodium bicarbonate (Reid 1998), and the other nutrients were extracted using ammonium acetate (Simard 1993, Agriculture and Food Laboratory University of Guelph 2017).

In July 2016, during peak aboveground biomass, I collected leaf, stem, and root and rhizome plant tissues in ten sites per meadow, cattail and *P. australis* invaded marsh in Big Creek NWA and Long Point Provincial Park. I took subsamples of leaf, stem, and belowground tissues from *C. canadensis*, *Typha* spp. and *P. australis* and oven-dried the subsamples at 100°C for 48 hours and then mechanically ground them until the samples reach a homogenous particle size. I sent the samples of each tissue type from each target plant species to an external laboratory (Agriculture and Food Laboratory, University of Guelph). They determined total concentration (% dry weight) of nitrogen and carbon using thermal conductivity detection (Reid 1998) and the total concentration (% dry weight) of phosphorus, potassium, magnesium and calcium using mass spectrometry (Agriculture and Food Laboratory University of Guelph 2017).

Using the tissue nutrient concentrations, I then estimated annual nutrient standing stocks characteristic of each habitat type: *P. australis* invaded, cattail, and meadow. To achieve this, I multiplied tissue nutrient concentrations by the above and belowground biomass weights of the total community and the ratio of leaf:stem and root:shoot tissue weights for meadow, cattail, and invaded marsh habitats. For example, to calculate nitrogen standing stock I used the following formula: [(% leaf *aboveground biomass of all living species in the plant community)*leaf nitrogen] + [(% stem*aboveground biomass of all living species in the plant community)*stem nitrogen] + (belowground biomass of all living species in the plant community * belowground nitrogen), where nitrogen concentrations were in % dry weight and biomass measurements were in grams of dry weight per meter-squared. This was completed for each nutrient and plant community. For additional comparison, I also estimated nutrient standing stocks per meter-squared of wetland using the estimated biomass (determined using percent cover of dominant species) of only the dominant species (*P. australis*, *Typha* spp. and *C. canadensis*) in their respective communities.

2.2.6 Statistical analysis

To test differences in aboveground biomass, belowground biomass, total biomass, and root:shoot among *P. australis* invaded, emergent cattail and meadow marsh habitats, I used general linear models. Samples collected in 2016 enabled these treatments to be crossed with soil nutrient levels to compare between a high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) environment. Samples collected in 2017 enabled the effect of plant community type (*P. australis* invaded, emergent cattail and meadow marsh) to be tested with water depth as a covariate (measured in both May and July 2017). I determined whether to use May or July 2017 water depths in the general linear models by comparing the Akaike's Information Criterion

(corrected for small sample size) for each 2017 response variable. I selected the general linear model which produced the lower AICc value as my final model.

Next, I examined differences in nutrients. I first used a general linear model to test if soil nutrients differed between the two wetland complexes (high soil nutrients in Big Creek NWA and lower soil nutrients in Long Point Provincial Park), crossed with the three plant communities (meadow, cattail and *P. australis* invaded).

Then I tested for a significant difference in tissue nutrient concentrations (% dry weight of plant tissue) and nutrient standing stocks estimated using total biomass (g m^{-2} of wetland) between *P. australis* invaded and resident plant community habitats. I also used general linear models to evaluate the difference in nutrient concentrations between plant species (*P. australis*, *Typha* spp. and *C. canadensis*) and plant part (leaf, stem, and belowground tissue) and their interaction. Nutrient standing stocks were compared among plant communities (meadow, cattail and *P. australis* invaded). To meet normality assumptions in my general linear models, I square-root transformed belowground biomass (g m^{-2}) and root: shoot ratio and I log-transformed magnesium (g m^{-2}) and calcium (g m^{-2}).

All general linear models were calculated using the "lm" function from the "stats" package (R Core Team 2016). Even if interaction terms were non-significant, I retained them in my final models if the model itself had a good fit. To determine the best fit for the 2017 biomass response variable, I used the "AICc" function in the "MuMIn" package (Barton 2018). Significant differences in response variable among treatments were determined at $p < 0.05$, and I performed all statistical tests using R Studio (R Core Team 2016).

2.3 Results

2.3.1 Biomass

The models predicting biomass measurements based on plant community (meadow, cattail and *P. australis* invaded), the nutrient environment (low and high) and their interaction provided a reasonable fit (Table 2.2). There was no significant interaction between the impact of nutrient environment and plant community on biomass (Appendix 3). Overall, there was a significant increase in aboveground biomass and total biomass for all plant communities in the high nutrient environment, but no significance difference in belowground biomass or root:shoot ratio between nutrient environments (Appendix 3). While not significant, in the high nutrient wetland there was lower belowground biomass and lower root:shoot ratio in all plant communities (Fig. 2.3, Appendix 3).

Regardless of the nutrient environment, *P. australis* invaded communities produced greater aboveground and total biomass than resident plant communities. Averaged across the high nutrient and low nutrient wetlands, *P. australis* invaded communities produced significantly more aboveground and total biomass than emergent cattail, and meadow marsh produced significantly less than either (Fig. 2.3). While there was no significant difference in belowground biomass or root:shoot ratios between plant communities, emergent cattail communities produced the highest amount of belowground biomass (Fig. 2.3).

Table 2.2. Results of general linear model fit test for biomass and nutrient environment variables, where plant community refers to meadow marsh (n = 10), emergent cattail (n = 10) and invaded (n = 10), and nutrient environment refers to Big Creek NWA (high nutrient) and Long Point Provincial Park (low nutrient) in 2016. The general model form is predicted biomass variable = $\beta_0 + \beta_1$ plant community + β_2 nutrient environment + β_3 (plant community * nutrient environment). Belowground biomass and root: shoot were square root transformed to meet the assumptions of normality. See Appendix 3 for full models.

Biomass variable	*F*-test (d.f.)	*p*-value	R^2
Aboveground	23.340 (5, 24)	<0.001	0.829
SQRT (Belowground)	4.252 (5, 24)	0.007	0.470
Total live	15.200 (5, 24)	<0.001	0.760
SQRT (Root:shoot)	6.017 (5, 24)	0.001	0.556

The average water depth in *P. australis* invaded and resident plant community sites in May 2017 were similar (36 cm ± 12 SD in *P. australis* invaded versus 37 cm ± 11 SD in resident plant communities; Appendix 1). By July 2017, the average water depth of resident plant community sites had decreased (29 cm ± 14 SD) and there was no change in the average invaded water depth (36 cm ± 11 SD in July; Appendix 1). The models predicting biomass measurements based on plant community (meadow, cattail and *P. australis* invaded), the water depth gradient and their interaction provided a reasonable fit (Table 2.3). While there was no significant difference in aboveground and total biomass among plant communities (Fig. 2.3, Appendix 3), aboveground biomass and total biomass increased significantly with increasing water depth (Appendix 3). For aboveground biomass and total biomass, models using July water depth yielded a better fit than models using May water depth (aboveground biomass: May water depth AICc = 311.184, d.f. = 7; July water depth AICc = 301.871, d.f. = 7; total biomass: May water depth AICc = 313.552, d.f. = 7; July water depth AICc = 304.464, d.f. = 7; Appendix 3).

There was a significant interaction between May water depth and plant community type for belowground biomass and root:shoot ratio (Appendix 3). In water depths above 40 cm, cattail had significantly greater belowground biomass than *P. australis* invaded sites (Appendix 4),

while meadow sites had the lowest belowground biomass at all water depths. Similarly, the root:shoot ratio of cattail sites was greater than *P. australis* invaded sites at water depths greater than 40 cm. Models predicting belowground biomass and root:shoot ratio using May water depth were a better fit than models using July water depth (belowground biomass: May water depth AICc = 101.628, d.f. = 7; July water depth AICc = 114.388, d.f. = 7; root:shoot: May water depth AICc = -30.205, d.f. = 7; July water depth AICc = -20.581, d.f. = 7; Appendix 3).

Table 2.3 Results of general linear model fit tests for peak biomass in 2017 across a water depth gradient, where plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded marsh (n = 10). Belowground biomass and root:shoot were square-root transformed to meet the assumptions of normality. Water measurement (May versus July) determined by choosing lowest AICc value (Appendix 3). The general model form is predicted biomass variable = $\beta_0 + \beta_1$ plant community + β_2 water depth gradient + β_3 (plant community * water depth gradient). Belowground biomass and root: shoot were square root transformed to meet the assumptions of normality. See Appendix 3 for full models and AICc values.

Biomass variable	Water measurement	*F*-test (d.f.)	*p*-value	R^2
Aboveground	July	5.250 (5, 14)	0.006	0.652
SQRT (Belowground)	May	10.080 (5, 14)	<0.001	0.783
Total live	July	5.770 (5, 14)	0.004	0.673
SQRT (Root:shoot)	May	4.190 (5, 14)	0.015	0.599

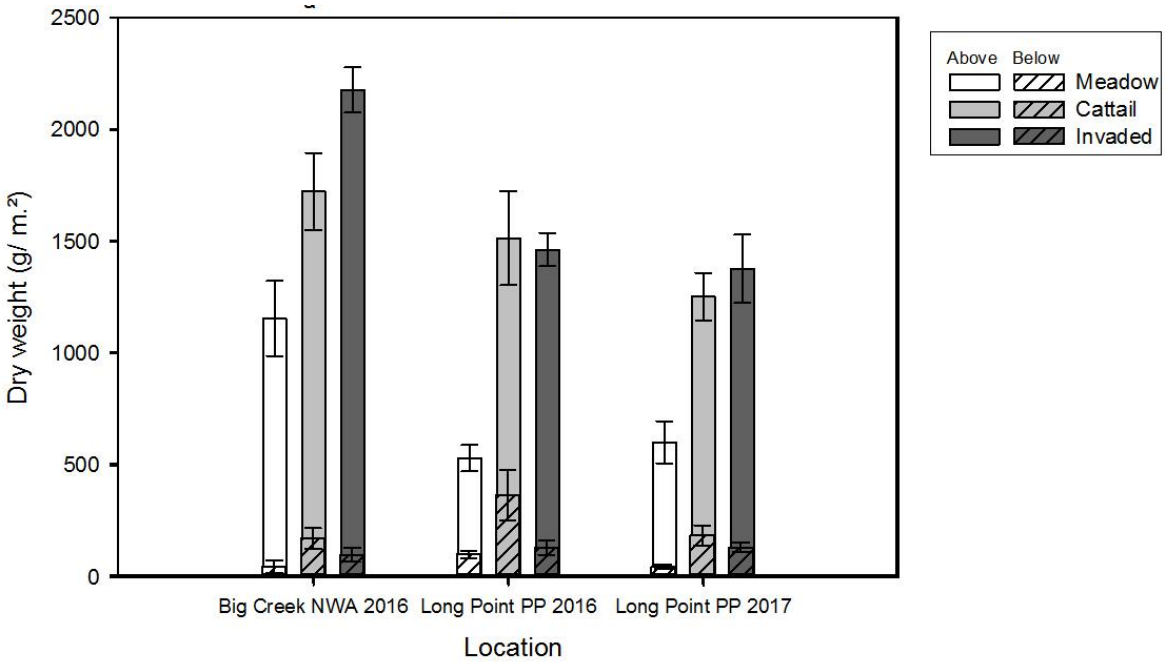

Figure 2.3 Stacked bar graph indicating peak annual total biomass, including belowground biomass to a depth of 11.3 cm, broken down by aboveground (solid bars) and belowground components (stripped bars). Contrasting standing crop biomass of all species in meadow marsh, emergent cattail and *P. australis* invaded plant communities in high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) environments in 2016 and averaging across a water depth gradient in Long Point Provincial Park in 2017. Standard error bars shown. See text and Appendix 3 for statistical significance of differences.

2.3.2 Plant morphology

Overall, there was little difference in leaf:stem ratio between *P. australis* (0.36 ± 0.10 SD) and *C. canadensis* (0.33 ± 0.08 SD). *Typha* spp., however, had a leaf: stem ratio almost three times greater than either *P. australis* or *C. canadensis* (0.90 ± 0.33 SD).

2.3.3 Plant and soil nutrients

The models predicting soil nutrients based on plant community (meadow, cattail and *P. australis* invaded), the nutrient environment (low and high) and their interaction provided a reasonable fit (Table 2.4). There was no significant interaction between the influence of wetland and plant community on soil nutrients (Appendix 3). Soil concentrations of total nitrogen, total carbon,

plant available phosphorus, plant available magnesium, and plant available calcium are significantly higher in Big Creek NWA than Long Point Provincial Park (Appendix 3). There was no significant influence of plant community on soil nutrient content (Appendix 3) but generally meadow in Long Point Provincial Park had the lowest amount of nutrients (Appendix 5). Overall, nutrient concentrations (% dry weight) were higher in the plant tissues growing in the higher nutrient environment. Nutrient content in leaves, stems and belowground tissues of *P. australis*, *Typha* spp. and *C. canadensis* varied by macronutrient (Fig. 2.4).

Table 2.4 Results of general linear model fit tests for soil nutrient content in 2017 in Big Creek NWA and Long Point Provincial Park wetlands. The general model form is predicted soil nutrient = $\beta_0 + \beta_1$ plant community + β_2 nutrient environment + β_3 (plant community * nutrient environment). Plant community refers to meadow marsh (n = 6), emergent cattail (n = 6) and *P. australis* invaded (n = 6) and nutrient environment refers to low nutrient (Long Point Provincial Park) and high nutrient (Big Creek NWA). See Appendix 3for full models.

Soil nutrient		*F*-test (d.f.)	*p*-value	R^2
Total	Nitrogen	11.370 (5, 12)	<0.001	0.826
	Carbon	9.490 (5, 12)	<0.001	0.798
Plant available	Phosphorus	7.943 (5, 12)	0.002	0.768
	Potassium	5.866 (5, 12)	0.006	0.710
	Magnesium	11.920 (5, 12)	<0.001	0.832
	Calcium	10.090 (5, 12)	<0.001	0.808

The model predicting plant tissue nutrient concentrations based on plant species (*C. canadensis*, *Typha* spp. and *P. australis*), tissue type (leave, stem, roots and rhizomes) and their interaction provided a reasonable fit (Table 2.5). Carbon:nitrogen, phosphorus, potassium, and magnesium differed significantly among tissue types (Appendix 3). Generally nutrient concentrations tended to be lowest in the stem tissue of the plants and higher in the leaf and belowground tissues (Fig. 2.4). Specifically, leaf tissue contained the highest concentrations of phosphorus and potassium, while root tissue had the highest concentration of magnesium. The highest carbon:nitrogen ratio, however, was in the stem tissues.

In addition, phosphorus and potassium concentrations differed among plant species, and *P. australis* had the highest concentration, significantly more phosphorus and potassium than *C. canadensis* and significantly more potassium than *Typha* spp. (Fig. 2.4, Appendix 3). *Typha* spp. had intermediate concentrations of phosphorus and did not significantly differ from *P. australis* or *C. canadensis* (Fig. 2.4). There was no significant differences in nitrogen:phosphorus ratio among plant species or tissues (Fig. 2.4).

Trends with carbon, nitrogen and calcium were more complex as they exhibited significant interactions between plant species and tissue type (Appendix 3). For example, *Typha* spp. contained significantly more carbon in its roots than leaves, whereas the other species did not exhibit differences in carbon content among tissues (Fig. 2.4). Nitrogen was much higher in *P. australis* leaf tissue than in *C. canadensis* or *Typha* spp. leaves, but there were no differences in the nitrogen concentration of stems and belowground tissue among species (Fig. 2.4). Calcium concentrations in *Typha* spp. stem tissue was much higher than in *C. canadensis* or *P. australis*, but similar calcium concentrations were present in *P. australis* and *Typha* spp. foliar tissue and *C. canadensis* and *Typha* spp. belowground tissue (Fig. 2.4).

The model predicting annual nutrient standing stock on an area basis (using biomass of all plant species within the site) based on plant community (meadow marsh, cattail and *P. australis* invaded) provided a reasonable fit (Table 2.5). Overall, the nutrient stocks of nitrogen, carbon, phosphorus and potassium were lower in meadow marsh, but equivalent in *P. australis* invaded and emergent cattail (Fig. 2.5, Appendix 3). Nutrient stocks of calcium and magnesium were similarly lowest in meadow marsh, but were also lower in P. *australis* invaded marsh than in cattail marsh (Fig. 2.5). Furthermore, the same trend in annual nutrient standing stock was observed regardless of whether the total biomass present in each plant community or only the

percent of biomass composed of the target species was used to calculate annual nutrient standing stock: there was no difference in macronutrient stocks for carbon, nitrogen, phosphorus and potassium between cattail and *P. australis* invaded marsh, but all nutrient standing stocks were lowest in meadow marsh (Appendix 6). In addition, calcium and magnesium were highest in cattail marsh (Appendix 6).

Table 2.5 General linear model fit test results for nutrients in plant tissue (% dry weight) and nutrient standing stock (g m^{-2}). The general model form for predicted plant tissue nutrient concentration = $\beta_0 + \beta_1$ plant community + β_2 tissue type + β_3 (plant species * tissue type). Plant community refers to meadow marsh dominated by *C. canadensis* (n = 15), emergent cattail dominated by *Typha* spp. (n = 15) and *P. australis* invaded (n = 20). To calculate tissue content samples were amalgamated from ten meadow, ten cattail and ten *P. australis* invaded sites equally divided between Big Creek NWA and Long Point Provincial Park. Tissue refers to leaf, stem and belowground tissue. Nutrient standing stock was calculated for ten sites per plant community in Big Creek NWA and Long Point Provincial Park using biomass from 2016 and ten sites from *P. australis* invaded and ten sites from resident plant communities in Long Point Provincial Park across a water depth gradient using biomass in 2017. The general model form for predicted nutrient standing stock = $\beta_0 + \beta_1$ plant community. Magnesium (g m^{-2}), calcium (g m^{-2}) were log-transformed to meet normality assumptions. See Appendix 3 for full models.

Nutrient	Units	*F*-test (d.f.)	*p*-value	R^2
Nitrogen	% dry weight	51.480 (8, 21)	<0.001	0.952
Carbon		2.288 (8, 21)	0.062	0.466
Carbon: Nitrogen		32.020 (8, 21)	<0.001	0.924
Phosphorus		10.380 (8, 21)	<0.001	0.798
Nitrogen: Phosphorus		1.381 (8, 21)	0.261	0.345
Potassium		16.240 (8, 21)	<0.001	0.861
Magnesium		13.490 (8, 21)	<0.001	0.837
Calcium		112.500 (8, 21)	<0.001	0.977
Nitrogen	g m^{-2} wetland	14.840 (2, 47)	<0.001	0.387
Carbon		16.450 (2, 47)	<0.001	0.412
Phosphorus		14.330 (2, 47)	<0.001	0.379
Potassium		29.760 (2, 47)	<0.001	0.559
LOG (Magnesium)		35.760 (2, 47)	<0.001	0.604
LOG (Calcium)		150.000 (2, 47)	<0.001	0.865

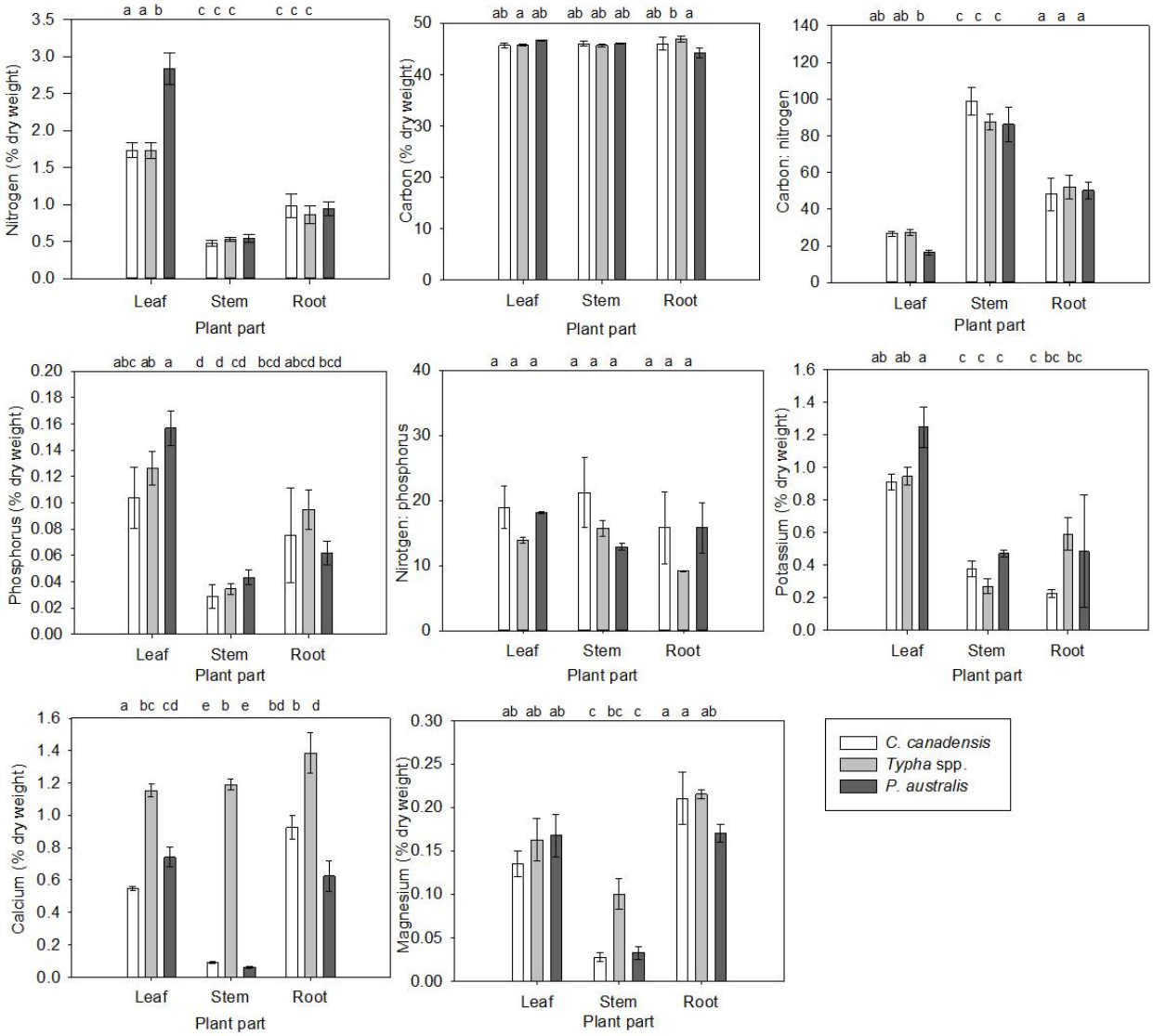

Figure 2.4 Percent dry weight of nutrients in *C. canadensis*, *Typha* spp., and *P. australis* leaves, stems, and roots and rhizomes. Samples collected from meadow (n = 5/ wetland), cattail (n = 5/ wetland) and *P. australis* invaded (n = 5/ wetland) in Big Creek National Wildlife Area (n = 15) and Long Point Provincial Park (n = 15) in July 2016. Note that this averages tissues from a relatively high nutrient environment (Big Creek) with tissues from a relatively low nutrient environment (Long Point Provincial Park). Error bars represent standard error. Letters above bars indicate significant differences in nutrient content between plant species and tissue type at $p < 0.05$ (Appendix 3).

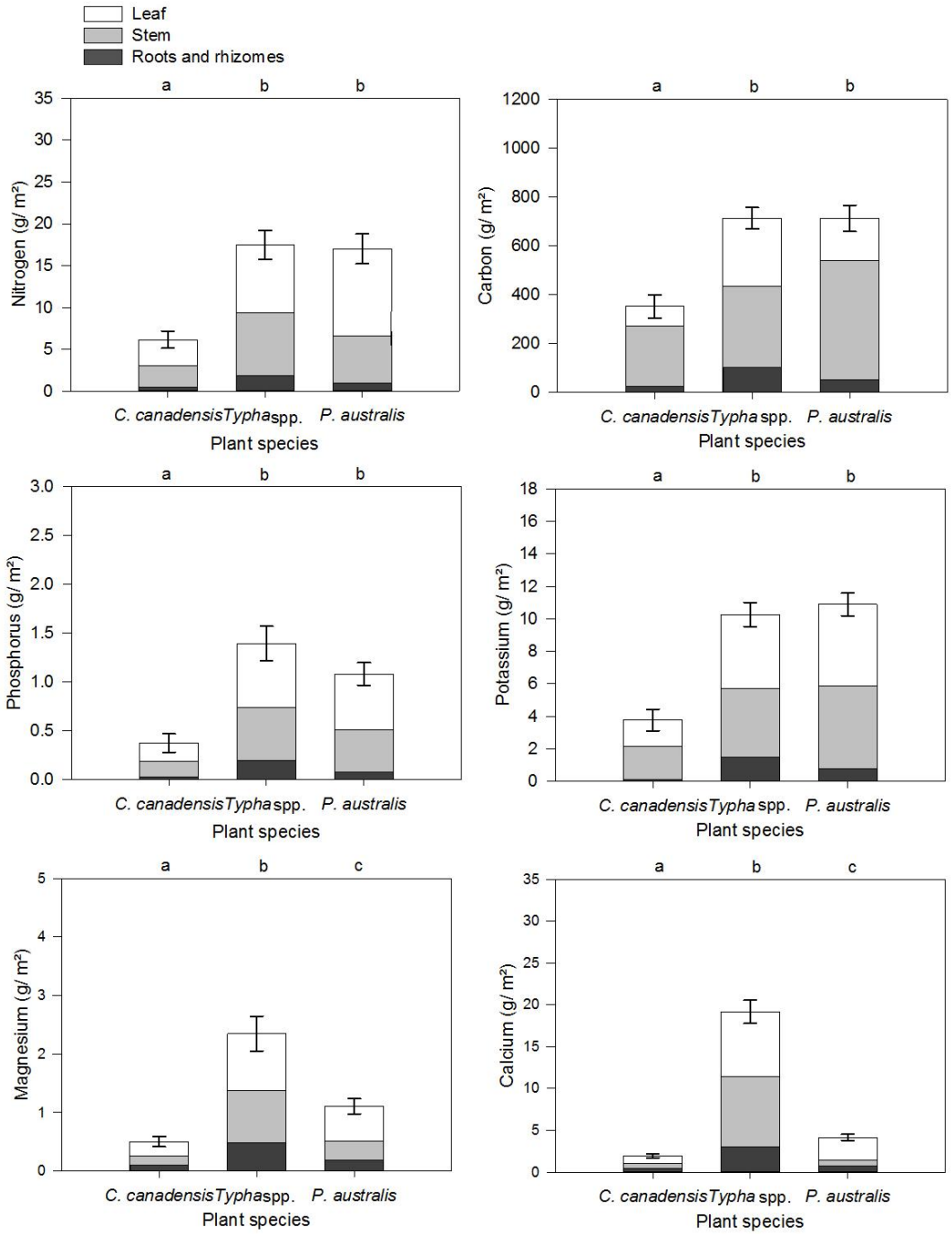

Figure 2.5 Estimated annual nutrient standing crop, considering belowground tissues to a depth of 11.3 cm in *C. canadensis*, *Typha* spp., and *P. australis* from meadow (n = 5/ wetland), cattail (n = 5/ wetland) and invaded (n = 5/ wetland) in Big Creek National Wildlife Area and Long Point Provincial Park in 2016 and five meadow, five cattail and ten invaded sites along a water depth gradient in Long Point Provincial Park in 2017. Total annual biomass (g m^{-2}) of all living plant species within each site was used to estimate annual nutrient standing stock. Standard error bars shown represent total nutrient standing stock, summed from all tissues. Letters above bars indicate significant differences between species at $p < 0.05$ (Appendix 3).

2.4 Discussion

Well-established invasive species may provide unexpected ecological functions within invaded systems (Kopf et al. 2017). In the Great Lakes region, there is a lack of research comparing nutrient pools and fluxes in invaded *P. australis* habitat compared to resident plant community habitat, such as resident cattail or rare meadow marsh. This creates a knowledge gap in wetland management, as the decision of whether to proceed with *P. australis* control methods hinges on a thorough understanding of the ecological effects of invasion (Hershner and Havens 2008, Hobbs et al. 2009, Davis et al. 2011). The results of my research suggest that the effects of *P. australis* invasion on wetland nutrient cycling are contingent on the vegetation community that is being replaced.

The hypotheses that *P. australis* invasion would increase above and belowground biomass as well as nutrient stocks in vegetation were overly simplistic. Abiotic conditions influence nutrient stocks generally, as the higher nutrient environment produced greater standing crop biomass (Fig. 2.3), and higher tissue nutrient concentrations. Similarly, standing crop biomass in all communities increased with water depth (Appendix 4). Most importantly, however, the effect of invasion depends upon what vegetation community is being replaced. When considering invasion of rare meadow marsh habitat by *P. australis*, I observed a major increase in biomass (Fig. 2.3) and nutrient standing stock per unit of wetland area (Fig. 2.5). Yet, when *P. australis* invades cattail marsh, little change in biomass or nutrient standing stocks is evident. This indicates that the impact of *P. australis* invasion on ecological nutrient cycling, while influenced by abiotic conditions, ultimately depends on what plant community is being replaced. Invasive *P. australis* provides nutrient retention functions and productivity levels similar to those of emergent cattail marsh in Long Point, but assimilates more nutrients than meadow marsh.

Invaded plant communities in my study had higher nutrient standing stock than meadow marsh communities, but not higher than cattail marsh. Notably, the cattail marsh in my study area was composed mostly of *Typha* x. *glauca* (Freeland et al. 2013). *Typha* x. *glauca*, like *P. australis,* is a large, non-native monocot that forms monocultures and can have a negative impact on native species (Larkin et al. 2012). Thus, *P. australis* and *Typha* spp. are larger and more dominant in their respective communities than *C. canadensis,* which is found in more diverse meadow marsh (Table 2.1). Other studies have linked the differences in size and density of non-native plant species to increased nutrient assimilation (Ehrenfeld 2003, Kao et al. 2003, Duke et al. 2015). However, it is important to note that *C. canadensis* is only a component of its community and scaling up from the tissue level to marsh-level standing stocks likely does not accurately estimate the true nutrient standing stocks in diverse meadow marsh communities. Nutrient standing stock was estimated as if the entirety of the biomass collected from meadow marsh was *C. canadensis,* and thus did not account for the potential for species (e.g. *Carex* spp., see Appendix 6) to possess different nutrient concentrations in their tissues or different ratios between tissue types. Because the tissue concentrations and morphology of other common meadow species were not quantified in my study, the nutrient stock of other meadow species may be over- or under-estimated. However, based on relative canopy heights and total biomass, I expect my conclusion that nutrient standing stocks are lower in meadow marsh than in cattail and *P. australis* invaded marsh is accurate.

The marsh complexes in my study had different levels of nutrients which can likely be attributed to location and proximity to agriculture and development (Fig. 2.1). All measured soil nutrients, except potassium, were significantly higher in Big Creek NWA than in Long Point Provincial Park. Big Creek NWA is located near a drainage basin that is 71.1 % agricultural (Essex Region Conservation Authority 2013) and therefore receives substantial amounts of phosphorus and nitrate; phosphorus levels within the marsh were above the Provincial Water Quality Objectives (> 0.03 mg/ L) although nitrate levels were below the Canadian Environmental Quality Guidelines (< 2.93 mg/ L; Essex Region Conservation Authority 2013). In contrast, Long Point Provincial Park, which is approximately four kilometres away from Big Creek NWA, is located on nutrient poor sand substrate. Interestingly, there was no difference in soil nutrients among marsh types in Big Creek NWA, where soil nutrients were abundant. However, the soil nutrient concentrations in Long Point Provincial Park were universally lower in meadow marsh habitats than in cattail and *P. australis*-invaded habitats, though the difference was generally not statistically significant.

This difference in nutrient availability between the Big Creek and Long Point Provincial Park marshes is important because invasive *P. australis* has been noted to allocate more resources to aboveground biomass in high nutrient environments, which is believed to facilitate its spread in disturbed environments (Minchinton and Bertness 2003). Thus, contrasting a high and low nutrient environment allowed me to examine the effects of invasion on nutrient pools and fluxes in different nutrient conditions.

The high soil nutrients in Big Creek NWA likely account for the increased biomass, lower root: shoot ratio, and higher nutrient tissue concentrations in all plant communities at Big Creek NWA compared to Long Point Provincial Park. Widespread studies have demonstrated that increasing

nutrient loads leads to increased total biomass of vegetation, foliar nitrogen, and phosphorus concentration, and may decrease the root: shoot ratio (Powelson and Lieffers 1992, Kvet et al. 2008, Rong et al. 2014, Caplan et al. 2015, Graham and Mendelssohn 2016, Li et al. 2016). Luxury consumption of nutrients by plants in high nutrient environments (Gumbricht 1993 and references therein) is likely responsible for the increased tissue nutrient concentrations in Big Creek NWA relative to Long Point Provincial Park.

In 2016, I estimated net primary production by looking at above and belowground standing crop biomass, excluding perennial belowground tissues produced in prior years in high and low nutrient environments. Averaged across the nutrient environments, aboveground and total biomass were significantly greater in *P. australis* invaded communities, intermediate in cattail, and significantly lower in meadow marsh (Fig. 2.3). Previous work indicates that nitrogen loading may increase *P. australis* biomass more than native species, and *P. australis* allocates more biomass to plant structures that facilitate its spread (Minchinton and Bertness 2003, Caplan et al. 2015). While there was no significant interaction between nutrient environment and plant community on biomass (Appendix 3), in the high nutrient environment there was a greater increase in biomass observed in *P. australis* invaded marsh compared to cattail marsh (Fig. 2.3) indicating that *P. australis* may be slightly more responsive to increased nutrients than *Typha* spp.

Studies on the influence of water depth on net primary production report varied results; depending on the plant species, biomass may increase, decrease or not change with water increasing depth (Fraser and Karnezis 2005, Miller and Zedler 2013, Middleton et al. 2015). Within my study, the total biomass of *P. australis, Typha* spp. and *C. canadensis* increased in deeper water depths, but the mechanism driving this correlation is uncertain. When other studies

conclude that water depth influences plant biomass, changes in biomass allocation may occur because of increased oxygen demands in rooting systems, greater availability of some nutrients in saturated soil, or higher nutrient uptake within the roots due to increased root length: root mass ratio (Rubio et al. 1995, Rubio and Lavado 1999). It is also possible that plants may grow taller in deeper water to meet needs for structural support or access to incoming light. Study specifics, such a site location (e.g. brackish versus freshwater) or study design (e.g. water depth treatments) can also affect the response of macrophyte biomass to water depth. For example, the response of *P. australis* biomass to water depth has been reviewed by Engloner (2009) and contrasting results were reported, which I attribute to varied location and water depth treatments. Within the Great Lakes region, Duke et al. (2015) reported that *Typha* spp. increased aboveground biomass when water depths increased and ascribed this to the ability of *Typha* spp. to produce more aboveground biomass in deeper water. The response of *C. canadensis* to water depth has not been assessed within the Great Lakes region, but a greenhouse experiment observed higher *C. canadensis* aboveground biomass in flooded conditions compared to well-watered and dry conditions (Wetzel and van der Valk 2005), which indicates that in at least some situations *C. canadensis* biomass increases in standing water. These findings agree with my observations.

When I sampled Long Point Provincial Park in 2017, I intentionally sampled across a water depth gradient, which significantly influenced aboveground biomass in my plant communities. Thus, it is likely the incorporation of water depth and the restriction to the lower nutrient environment that masked statistical differences in standing crop biomass among plant communities in 2017. However, other recent field studies in the Great Lakes region also reported no significant differences between aboveground biomass in *P. australis* invaded and

cattail marsh (Duke et al., 2015; Rothman and Bouchard, 2007). These studies reported wide ranges in aboveground biomass values that were similar to my own observations (cattail: 1661 - 2930 g/ m² and *P. australis* invaded: 1522 - 3378 g/ m²; Duke et al., 2015; Rothman and Bouchard, 2007). This variation may be due to differences in water or nutrient regimes that were not accounted for in these studies. Conversely, studies examining native sedge, grass, and forb dominated wetlands report that these wetlands all produced less biomass than *P. australis* invaded marsh or cattail marsh (Windham and Lathrop 1999, Windham 2001, Rothman and Bouchard 2007). While no field studies comparing *C. canadensis*-dominated meadows to *P. australis* invaded or cattail marsh have been conducted, the aboveground biomass in meadow marsh reported in my study (Fig. 3) is similar to that reported in a greenhouse experiment (1057 ±12 g/ m²; Ouellet-Plamondon et al., 2004). As this is lower than the low end of the range reported for cattail marsh and *P. australis* invaded marsh, it is surprising that no significant difference between meadow marsh and cattail or *P. australis* invaded marsh was observed in 2017. Instead, since water depth did have a significant effect on total biomass, I would suggest that in my study water depth had a greater effect on aboveground and total biomass than plant community.

Unlike aboveground biomass, belowground biomass to a depth of 11.3 cm and root:shoot ratio in my study was significantly higher in cattail marsh in 2017 at water depths greater than 40 cm. This result differs from previous reports of no difference between belowground biomass in cattail and *P. australis* invaded communities (Ouellet-Plamondon et al. 2004, Rothman and Bouchard 2007), which may also be a result of sampling across a water depth. My belowground biomass values, and subsequent root: shoot ratios, were also low compared to the published literature. This is likely a combination of two things. First, I employed a modified ingrowth soil

core method to ensure that only one season's growth was included in my measurements, as this excludes long-lived rhizomes and can provide similar estimates of net primary production as traditional soil cores (Neill 1992). Other field studies (Farnsworth and Meyerson 2003, Rothman and Bouchard 2007) included all belowground tissues using traditional soil core methods. Second, because I used this ingrowth core technique, my soil cores were restricted to 11.3 cm in depth and did not include roots and rhizomes that may have grown deeper in the soil, whereas Ouellet-Plamondon et al. (2004) included belowground biomass at every depth. Rhizomes of *Phragmites* can account for an average of 55 - 60 % of its total biomass (reviewed by Mason and Bryant 1975) and *T. latifolia* and *T. angustifolia* have similar or more belowground biomass than *P. australis* (Ouellet-Plamondon et al. 2004; Rothman and Bouchard 2007). When belowground biomass was collected to a depth of 30 cm, root: shoot ratios of *T. angustifolia* and *P. australis* in a freshwater tidal wetland were recorded as 2.5 ± 0.1 SE and 0.7 ± 0.04 SE, respectively (Farnsworth and Meyerson 2003). In Alberta, *C. canadensis* root: shoot ratios ranged from 0.29 to 0.62 under different nutrient and light regimes (Powelson and Lieffers 1992). A depth of 40 cm would have yielded a more accurate assessment of total belowground biomass produced in a single growing season, as research in my study area determined that >90% of all root and rhizome biomass is accounted for within 40 cm of the soil surface in all three of my study communities (Lei 2018). Yet, I believe my ingrowth soil cores yielded a reasonable estimate of belowground production, as approximately 38% ± 21% SD of belowground production was accounted for in the top 10 cm, regardless of plant community (Lei 2018).

Macronutrients (nitrogen, phosphorus, carbon, calcium, magnesium, and potassium) were examined in terms of tissue concentration and, by using annual plant biomass production, scaled-up to estimate annual vegetative nutrient standing stock. On an annual vegetative nutrient

standing stock basis, my results disagree with previous work that suggested that *P. australis* assimilates more nitrogen or phosphorus than *Typha angustifolia* (Findlay et al. 2002). At the marsh-level, *P. australis* retained almost two times more nitrogen than *Typha angustifolia* in living aboveground biomass (Findlay et al. 2002). In this study, *P. australis* had both a higher nitrogen tissue concentration and 50 % more biomass production than *T. angustifolia* (Findlay et al. 2002). In my study, annual vegetative nutrient standing stocks appear equivalent between *P. australis* and *Typha* spp., and so I conclude that the invasion provides no increase in nutrient retention services. This discrepancy between Findlay et al. (2002)'s results and my own is likely due to cattail in my study likely comprising *Typha* x *glauca* instead of *T. angustifolia*. However, if meadow marsh is invaded by *P. australis,* then a significant increase in nutrient standing stocks can be anticipated, and invasion of *C. canadensis*-dominated marsh by *P. australis* does increase the nutrient retention service provided by the wetland. Of course, a net assessment of the effects of *P. australis* invasion on ecosystem services must account for the resulting loss of plant biodiversity (Keller 2000, Tulbure et al. 2007) and associated degradation of bird (Robichaud and Rooney 2017) and turtle habitat (Markle and Chow-Fraser 2018). As recently suggested by Alldred et al. (2016), invasion by *P. australis* triggers a variety of opposing changes in wetland ecosystem services that really reflect trade-offs among service types.

Interestingly, nutrient standing stocks for carbon, nitrogen, phosphorus or potassium were not higher in *P. australis* invaded marsh than in cattail marsh (Fig. 2.5), despite higher leaf-tissue concentrations in *P. australis* (Fig. 2.4). This is a consequence of off-setting differences in plant morphology as *Typha* spp. has a much higher leaf:stem ratio than *P. australis* or *C. canadensis*. Such differences in morphology must be accounted for if researchers intend to infer marsh-level processes from tissue concentration data. My tissue concentration results reflect an average

between a relatively higher and lower nutrient environment (Fig. 2.4), and agree with those reported in the literature: overall *P. australis* generally has high nitrogen and phosphorus tissue concentrations compared to *Typha* spp. (*P. australis* = 0.81% N; 0.12% P; *Typha* spp. = 0.43 % N, 0.04% P; Findlay et al. 2002), with the highest concentration of nutrients present in the leaf tissue of *P. australis* (3.1 - 3.9% N; 0.13% P; Li et al. 2016, Tho et al. 2016), medium levels in the belowground tissue (1.6 - 2.3% N; 0.10% P; Li et al. 2016, Tho et al. 2016), and lowest levels in the stem (0.6 - 1.7% N; 0.06 % P; Li et al. 2016, Tho et al. 2016).

Calcium, and magnesium, despite their potential importance in nutrient cycling, receive much less attention than carbon, nitrogen and phosphorus in the literature (Ehrenfeld 2010). *Typha* spp. had the highest concentration of calcium in all tissues and magnesium in its stems (Fig. 2.4). Consequently, the annual cattail nutrient standing stock of calcium and magnesium was significantly greater than in *P. australis* invaded or meadow marsh (Fig. 2.5). Though the difference in terms of magnesium was only one to two grams per meter squared, the difference in calcium standing stock was more pronounced; nearly 10 fold higher in cattail marsh than meadow marsh, for example. One possible explanation is that *Typha latifolia* produces calcium oxalate raphide crystal bundles (Borrelli et al. 2011), which may be used for structural support, defense against herbivores, or produced as a metabolic end product (Franceschi and Horner 1980). The presence of these crystals may account for the high levels of calcium in *Typha* spp. documented in my study. In general, it appears that *Typha* spp. often accumulated high levels of calcium and magnesium (Olivares et al. 2002, Parzych et al. 2015) and *P. australis* had lower concentrations (Parzych et al. 2015). However, based on the similarity in soil nutrient calcium and magnesium concentrations, the activity of *Typha* spp. is not sufficient to deplete soil levels of calcium or magnesium to a detectable degree. Nor is the distribution of *Typha* spp. restricted

to areas with higher calcium or magnesium levels in the soil. This is somewhat surprising for calcium, as 19.2 g m^{-2} ± 4.5 SD calcium in standing stock in cattail marsh is not an insignificant concentration, given the soil concentration of 6.1 g kg^{-1} ± 2.0 SD (Appendix 5).

To my knowledge, no other field studies have compared *C. canadensis* nutrient assimilation to *P. australis* or *Typha* spp. Overall, nitrogen, carbon, phosphorus, and potassium in the tissues of *C. canadensis* did not differ significantly from *Typha* spp., and only differed from *P. australis* in terms of foliar nitrogen (Fig. 2.4). There were not, however, any significant differences in my study among *P. australis, Typha* spp. or *C. canadensis* in terms of the carbon: nitrogen or nitrogen: phosphorus ratios in any tissues, although the carbon: nitrogen ratio was lowest in *P. australis* leaves (Fig. 2.4). This is important because carbon: nitrogen ratios and nitrogen: phosphorus ratios are often indicative of how easily degraded tissues will be (Enriquez et al. 1993), and so could have an important influence on nutrient cycling. Once scaled up to the annual vegetative nutrient standing stock, however, meadow had significantly less nutrients than invaded and cattail marsh (Fig. 2.5), which makes sense if you simply consider the differences in canopy height and total biomass among the three plant communities. While no studies in the Great Lakes region have examined the nutrient standing stock of *C. canadensis* dominated communities, other work has established that *C. canadensis* had a low ability to assimilate nitrogen and phosphorus pollutants compared to other wetland macrophytes (~7 g m^{-2} N, ~1 g m^{-2} P; Kao et al. 2003). Based on equivalent tissue concentrations of the six macronutrients studied, this is likely because of differences in the total biomass of tissues produced in meadow marsh.

The difference in carbon, nitrogen and phosphorus assimilation between meadow marsh and invaded marsh is not negligible. Scaled up to metric tonnes per hectare, *P. australis* invaded marsh has an annual standing stock of carbon that is 3.87 T ha^{-1} greater than meadow marsh.

Canada is implementing a carbon pricing system beginning in 2019 that would price one tonne of CO_2 or equivalent at $16 USD, and by 2022 plan to increase that price to $39 USD/ T CO_2 (Goyal et al. 2018). After converting tons of carbon to CO_2, every conversion of one hectare of meadow marsh to *P. australis* invaded marsh would be worth $227.32 in 2019 and $554.10 in 2022. Furthermore, large portions of Lake Erie are invaded with *P. australis*, with invasion estimates ranging from 2 553 ha within Lake Erie coastal wetlands (Carson et al. 2018) to 8 233 ha invaded within 10 km of the American side of Lake Erie (Bourgeau-Chavez et al. 2013). If we assume all of this area was previously meadow marsh, invasion by *P. australis* would assimilate an additional $580 354 - $4 561 898 USD worth of carbon dioxide. Of course, this is likely a large overestimate, as *P. australis* invaded habitat was not all rare meadow marsh prior to invasion, and the difference in carbon stock between cattail marsh and *P. australis* is negligible.

While the overall amount of phosphorus in the annual vegetative standing stock of *P. australis* invaded marshes is much smaller than the annual carbon standing stock, it still represents an almost three-fold increase compared to meadow marsh (a difference of 0.01 T ha^{-1}). Scaled up to the Lake Erie basin using estimates from Carson et al. (2018) and Bourgeau-Chavez et al. (2013), the standing stock of phosphorus in *P. australis* invaded marshes is between 29 - 95 T of phosphorus in total; 20 - 64 T more phosphorus than if meadow marsh occupied the same area. The current Great Lakes Water Quality Agreement between Canada and the United States of America has a interim target load for phosphorus of 11 000 T $year^{-1}$ for Lake Erie (United States - Canada 2013). Annual phosphorus standing stock in *P. australis* invaded marsh in Lake Erie then represents approximately 1 % of this target load. This is slightly more than the phosphorus output from smaller tributaries; for example, phosphorus output from Big Creek is about 19 T phosphorus $year^{-1}$ (OMECC 2017).

Phragmites australis invaded marshes also incorporate three times more nitrogen into the annual vegetative standing stock than meadow marsh (increase of 0.12 T ha^{-1} N). Scaled up to the Lake Erie basin using the same estimates for the area of invasion, the standing stock of nitrogen in *P. australis* invaded marshes is between 464 - 1495 T in total, or 307 - 990T greater than meadow marsh if meadow marsh dominated the same area. Nitrogen loading in Lake Erie was estimated at 136 000 T in 2002 (Robertson and Saad 2013). On an annual basis, *P. australis* invaded marsh in the Lake Erie basin would incorporate a maximum of 1 % of the 2002 nitrogen input into the vegetative standing stock. Overall, annual standing stock of nitrogen and phosphorus in *P. australis* invaded marshes in Lake Erie represent small portions of the overall nitrogen and phosphorus loading, but substantial increases from meadow marsh.

These economic benefits should be balanced against the potential economic costs of *P. australis* invasion. Invasive species were identified as the most severe threat to 22% of the 488 species at risk identified in Canada in 2006 (Venter et al. 2006). In 2018, Canada allocated $1.3 billion CND over a five year time period towards conservation activities, including increased protection of species at risk (Department of Finance Canada 2018). Conservation actions for a single species at risk in the Great Lakes region may therefore cost more than annual economic benefits provided by *P. australis* through carbon sequestration. For example, the Ontario Ministry of Natural Resources and Forestry, through the Species at Risk Stewardship Program, spent $120,218 CND alone on eastern hog-nosed snake (*Heterodon platirhinos*) conservation, with an additional $4,428,435 spent on projects that benefited multiple species at risk (Ministry of Natural Resources and Forestry 2017). In addition, an estimated value of $7,101,289 CND was contributed through volunteer hours and additional funding (Ministry of Natural Resources and Forestry 2017). In this light, the potential savings through increased carbon, nitrogen, and

phosphorus sequestration where *P. australis* replaces biodiverse meadow marsh seem less impressive.

Benefits provided by nutrient assimilation by *P. australis* also requires the consideration of how long these nutrients are retained. This study focuses on the assimilation of nutrients into the vegetative standing stock of different plant communities but does not examine their long-term storage. In wetlands, nutrients taken up by macrophytes are quickly cycled by decomposition (Maltby and Barker 2009). Long term retention of nutrients in plant tissue varies by species and nutrient; during vegetative senescence approximately 35 - 75 % of phosphorus and nitrogen assimilated by the living plant is released (Nichols 1983). *Phragmites australis* litter and standing dead can decrease in nitrogen by approximately 40 - 60 % and in phosphorus by 75 - 85 % compared to the living tissue (Findlay et al. 2002). In contrast, *T. angustifolia* litter nitrogen increased and there was 0 - 25 % decrease in phosphorus (Findlay et al. 2002), indicating that although the standing stocks of nitrogen and phosphorus may not differ significantly between cattail and *P. australis* invaded marsh, the long term consequences for nutrient retention may differ significantly. As with *T. angustifolia*, during decomposition *C. canadensis* litter can retain 70 % of the nitrogen and 51 % of the phosphorus it assimilates (Kao et al. 2003). The ability of different litter to retain nutrients and the relative decomposition rates of the litter determine the long-term storage of assimilated nutrients. For example, the nutrient concentrations in the living tissue of *P. australis* are greatest in the leave tissue, but these tissues are annual and decompose quicker than stem tissues (Dinka et al. 2004, Dolinar et al. 2015, Vymazal and Brezinova 2016) and therefore quickly release nutrients. If nutrient storage is not long term, the nutrients in *P. australis* invaded marshes may be released back into the watershed during senescence and decomposition, unless more radical action, such as harvesting biomass (Carson et al. 2018), is

undertaken. My research into the decomposition of *P. australis*, *Typha* spp. and *C. canadensis* tissues are presented in Chapter 3 and help clarify how invasion changes long term nutrient storage in freshwater coastal marshes.

My study clearly demonstrates that *P. australis* has the capacity to assimilate nutrients at an amount and rate equal to or greater than meadow marsh communities though not more than cattail marsh. It may therefore provide an important ecosystem service in some contexts. Furthermore, *P. australis* responded under predicted climate change scenarios and increased nitrogen loading by increasing carbon assimilation and storage (Caplan et al. 2015). In addition, *P. australis* appeared to be more responsive than other wetland plants to these scenarios and increased its carbon assimilation more than native species (Caplan et al. 2015). However, the cost of managing species at risk, and the negative effects of invasive species on these species at risk is likely greater than any benefit of increased nutrient retention, especially as the nutrient retention is mainly temporary, with most nutrients released back into the environment on seasonal senescence. The value of increased nutrient assimilation in *P. australis* invaded marshes under increasing stresses (provided this translates to long-term storage) should be weighed against the negative impacts on biodiversity, especially when considered in the framework of the financial costs and feasibility of managing *P. australis*.

3 Phragmites australis *invasion and subsequent control efforts change carbon dynamics in freshwater wetlands*

3.1 Introduction

On the whole, wetlands are global sinks for carbon (Mitsch et al. 2013), though the behavior of individual wetlands can be quite variable. Freshwater mineral wetlands in particular may vary in their carbon balance, depending on wetland type (e.g., Bernal and Mitsch 2012), climate (Mitsch et al. 2013, Chu et al. 2015), hydrology (Bernal and Mitsch 2013, Lou et al. 2016), disturbance (Finocchiaro et al. 2014, Furlanetto et al. 2018) or other factors (e.g., Kayranli et al. 2010). Because the carbon balance of wetlands depends largely on the relative rate of carbon assimilation through primary production and carbon emission through decomposition of plant biomass, vegetation plays a critical role in the wetland carbon budget (Rothman and Bouchard 2007, Schultz et al. 2011). Consequently, invasive plants with traits relating to primary production and decomposition that differ from resident plant communities have the potential to shift the wetland carbon balance (Ehrenfeld 2003, Currie et al. 2014). Generally, invasive species 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 species on the carbon budget will depend on the properties of the vegetation community being displaced and is thus system specific (Ehrenfeld 2003, 2010, Liao et al. 2008).

Plant invasions may increase the rate of carbon sequestration directly by increasing aboveground and belowground biomass, altering nutrient concentrations in tissues, increasing photosynthetic rates, having higher leaf area indices, or by reducing litter decomposition rates. For example, invasive *Phragmites australis* (hereafter *P. australis*), which has been termed Canada's worst

invasive plant (Catling and Mitrow 2011), is a highly productive wetland grass spreading through Canada and the Great Lakes region (Wilcox et al. 2003, Catling and Mitrow 2011, Braun et al. 2016). *Phragmites australis* is reported to have relatively high biomass production (Windham 2001, Rothman and Bouchard 2007, Duke et al. 2015) and high rates of carbon assimilation (Farnsworth and Meyerson 2003, Tho et al. 2016). Also, stands of *P. australis* tend to accumulate dense standing litter (e.g. in our study the typical ratio of live to dead standing stems is 91: 167 per m^2), and dead stems may remain upright for at least two years (Rooney lab, unpublished data) . This suggests that *P. australis* invasion may provide an ecosystem service in the form of increased carbon sequestration in wetlands. However, other research has concluded that *P. australis* has relatively high nitrogen in its foliar tissue (Findlay et al., 2002; Hirtreiter and Potts, 2012, Chapter 2), which could make it more easily decomposed. Still other research has examined soil carbon efflux in *P. australis* dominated wetlands and determined that in *P. australis*' native range these wetlands are carbon sinks over long time periods (Brix et al. 2001). Yet in North America, invasive *P. australis* releases more methane than native lineages of *P. australis* (Mozdzer and Megonigal 2013) and has greater deep soil carbon release than native vegetation in brackish coastal marshes (Bernal et al. 2016). Thus, the direct influence of *P. australis* invasion on the carbon budget is uncertain. Any change in carbon balance will depend on the nature of the resident plant community that is displaced by invading *P. australis*.

Invasion may also modify environmental conditions that influence the carbon budget indirectly. Environmental conditions relevant to the carbon budget that can be affected by invasion include water depth, light penetration and sediment characteristics, which may affect net primary production (including total biomass, and root: shoot allocation) and decomposition rates (van der Valk et al. 1991, Holdredge and Bertness 2011, Dolinar et al. 2015). Using the example of *P.*

australis invasion again, it may reduce insolation and sediment temperatures (Rooth et al. 2003, Holdredge and Bertness 2011, Hirtreiter and Potts 2012), decrease water depths (Lathrop et al. 2003, Hunter et al. 2006), and reduce sheet flow of water through the marsh (Weinstein and Balletro 1999). These would combine to reduce decomposition and export rates.

The combination of uncertain direct and indirect mechanisms complicates our understanding of how an invading plant species like *P. australis* may alter the carbon budget in a wetland (Ehrenfeld 2010, Vilà et al. 2011). Distinguishing between direct and indirect mechanisms is particularly challenging because changes in net primary production and decomposition rates may interact with changed environmental conditions. For example, increased macrophyte biomass and increased decomposition rates have been correlated with deeper water depths (van der Valk et al. 1991, Christensen et al. 2009, Duke et al. 2015), and *P. australis* has been demonstrated to reduce water depths in some wetland habitats (Windham and Lathrop 1999). Determining the relative importance of direct changes (net primary production and decomposition traits) and indirect changes (water levels, temperature and insolation) caused by *P. australis* invasion will further our understanding of how invasive species may alter wetland carbon budgets and improve our ability to model interactions between biological invasions and climate change. However, clearly parsing of direct and indirect effects of invasion on the wetland carbon budget will require controlled experiments.

Understanding the net effects of wetland plant invasions on wetland functions and ecosystem services is critical to inform decisions about invasive species control efforts (e.g., Gaertner et al. 2016). Extensive efforts to control *P. australis* have been undertaken in North America (Hazelton et al., 2014; Martin and Blossey, 2013) but eradication may be impossible (e.g. Quirion et al. 2018). If complete eradication is not an option, then managers face potential trade-

offs between biodiversity conservation and other ecosystem services (e.g. Alldred et al. 2016). Removing *P. australis* may improve habitat quality for wildlife (Schummer et al. 2012, Markle and Chow-Fraser 2018), but is this at the cost of lost carbon sequestration? Limited work has examined the effect of *P. australis* control efforts on litter decomposition rates (Kennedy et al. 2012), and soil carbon dioxide and methane efflux rates between invaded and controlled marshes (Martin and Moseman-Valtierra 2017). A comprehensive study examining whether control efforts are sufficient to return net primary productivity, decomposition rates, and environment conditions to within their pre-invasion range has not yet been undertaken.

My objectives are 1) to quantify the effect of invasive *P. australis* on freshwater coastal marsh carbon dynamics and relevant environmental covariates, such as water depth variability, water temperature, and light penetration and, 2) to evaluate the immediate efficacy of herbicide-based *P. australis* control efforts at restoring primary production and decomposition rates, as well as important environmental covariates, to their natural levels. I will test my prediction that primary production (biomass and carbon assimilation) will decrease and decomposition will increase in herbicide-treated sites compared to both invaded and resident plant communities along a water depth gradient. I also predict that there will be an increase in soil carbon dioxide efflux in herbicide-treated sites. I predict these changes are a result of changes to the plant community and abiotic factors (changes in water depth, water temperature, and light penetration).

3.2 Methods

3.2.1 Study area

This study was located on northern Lake Erie, Ontario, Canada (Fig. 3.1) within Long Point Peninsula (42° 34' N, 80° 24' W). On Lake Erie, more than 70% of the remaining coastal marsh

in Canada is located on the Long Point Peninsula (Ball et al. 2003); a recognized Ramsar wetland and UNESCO World Biosphere Reserve. By 2016, *P. australis* had invaded up to 70% of portions of the marsh (helicopter mapping; data provided by Erling Armson, Invasive Species Specialist, Ducks Unlimited Canada) and most commonly replaced rare "Graminoid Coastal Meadow Marsh Type" (Imperiled [S2]; Ministry of Natural Resources and Forestry 2018) and cattail marsh (Wilcox et al. 2003). Meadow and cattail marsh are naturally stratified by water depth in the Great Lakes region (Chapter 2; Grabas and Rokitnicki-Wojcik, 2015). Meadow marsh is composed of graminoids, forbs and sedges, however Canadian bluejoint grass (*Calamagrostis canadensis*) was identified as a dominant or co-dominant species characteristic of Long Point meadow marsh (Reznicek and Catling 1989). As such, I chose *C. canadensis* as the study's target species for the meadow community. Conversely, cattail marshes are monocultures of *Typha* spp. and in the Great Lakes region are predominately composed of hybrid cattail (*Typha* x. *glauca*) (Freeland et al. 2013). I refer to cattail as *Typha* spp. because in the field it is difficult to identify cattail to species due to back-crossing between *Typha* x. *glauca* and the parental species *Typha latifolia* and *Typha angustifolia* (Kirk et al. 2011). Like cattail, *P. australis* invaded stands were also monocultures but composed of invasive *P. australis*.

In Canada, no herbicides are legally registered to use on *P. australis* over standing water. In 2016, however, the Ontario Ministry of Natural Resources and Forestry obtained an emergency use registration to apply glyphosate to control *P. australis* in wet areas (Ministry of Natural Resources and Forestry et al. 2016). Aerial application of glyphosate to 400 ha of invaded wetland in Long Point was completed September 2016 (Veenhof 2017). In September 2017, an additional ~107 ha were treated in Long Point (Ministry of Natural Resources and Forestry et al. 2017). During the winter months, herbicide-treated areas were rolled or mowed to push down

standing dead stems. Herbicide-treated areas were at an early recovery stage and did not have distinct emergent plant communities, however, there was often high cover of submersed aquatic vegetation (Table 3.1, Appendix 7).

3.2.2 Experimental design

I compared the primary production and decomposition rates in the resident plant communities of meadow and cattail marsh to *P. australis* invaded marsh and herbicide-treated sites. The ten resident plant community sites were equally split between five meadow and five cattail marsh sites. I estimated annual net primary production by measuring peak above and belowground biomass, plus standing dead and submerged litter mass at 30 sites, equally divided between resident plant communities, invasive *P. australis* stands and herbicide-treated sites (Fig. 3.1, Table 3.1). To capture variation in primary production as a response to water depth, I placed sites along a water depth gradient ranging from 14 - 56 cm in May 2017. Carbon assimilation rates and plant morphology were measured at the resident plant community sites and *P. australis* invaded sites in June 2017 (Table 3.1).

My study also measured how decomposition rates, estimated using a mass loss approach, differed as result of litter type, site type, and water depth using a litterbag transplant experiment. In addition, I measured how soil carbon dioxide efflux differed between resident plant communities, invaded marsh and herbicide-treated sites throughout the growing season. I estimated decomposition rates and soil carbon dioxide efflux in nine of the primary production sites (Fig. 3.1, Table 3.1), equally divided between resident plant communities, *P. australis* invaded and herbicide-treated sites and located in 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 depths. I

also measured soil carbon dioxide efflux once in April 2018 in one *P. australis* invaded, one cattail, and one site treated with herbicide in fall 2017 to measure soil carbon dioxide release during spring thaw.

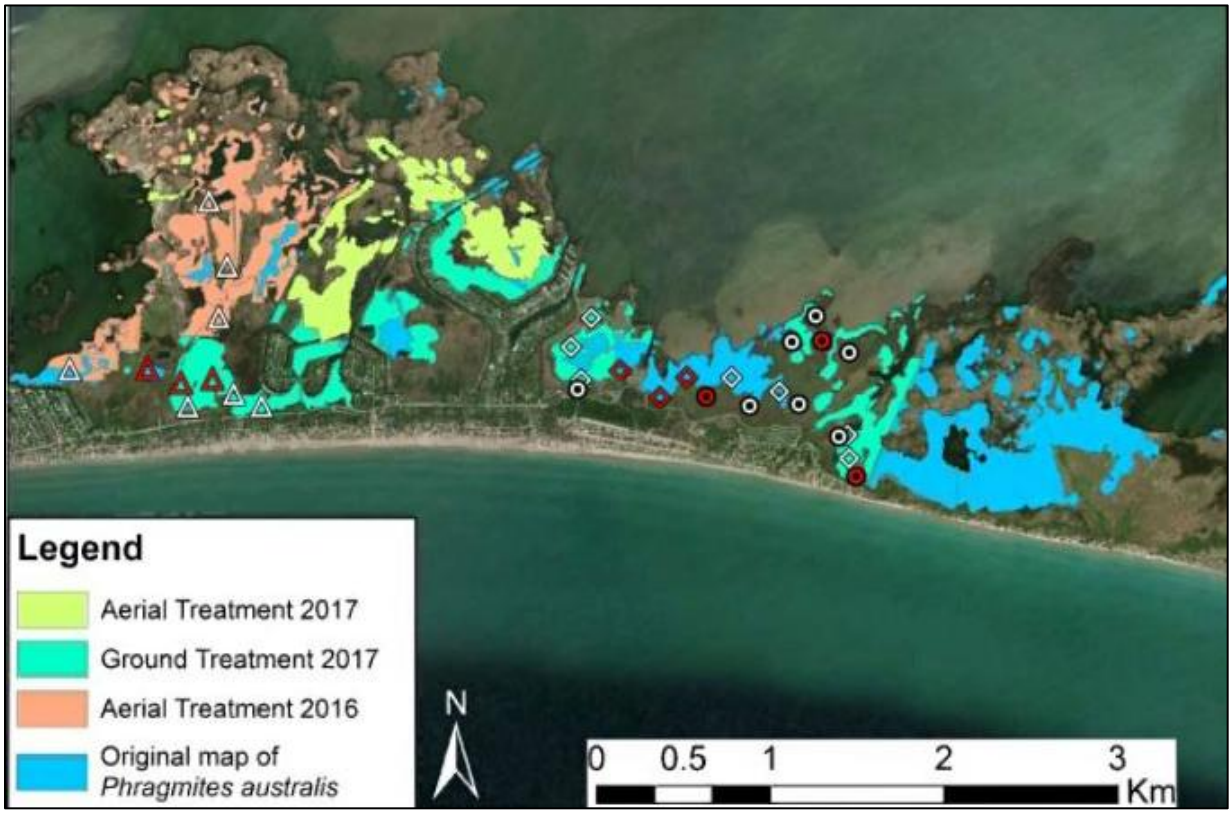

Figure 3.1 Long Point Peninsula (42° 34' N, 80° 24' W), is located on the north side of Lake Erie in Ontario; image credit Matthew Bolding. Net primary production measurements were taken at all sites, red symbols represent a subset of sites where decomposition measurements were taken. Triangles were herbicide-treated sites, circles were resident plant community sites, diamonds were untreated *P. australis* invaded sites.

Table 3.1 Location of field methods in 30 sites in Long Point divided equally between resident plant communities, *P. australis* invaded marsh and herbicide-treated sites.

Site name	Plant community	Total # of sites	Net primary production (# of sites measured)		Decomposition (# of sites measured)		
			Biomass	Carbon assimilation	Litterbag	HOBOs	Soil CO_2 efflux
Resident	Meadow and cattail marsh	10	10	10	3	3	3
Invaded	*P. australis*	10	10	10	3	3	3
Herbicide -treated	Submerged/ floating	10	10	-	3	3	3

3.2.3 Field methods

I measured plant community characteristics, including canopy height, litter depth and plant species composition (percent cover and stems counts) at the 30 sites in July 2017 (Table 3.2). Resident plant communities, *P. australis* invaded and herbicide-treated sites had distinct plant communities associated with them (Appendix 7).

Canopy structure, aboveground and belowground biomass, and other plant community traits can influence abiotic characteristics in wetlands. In May 2017 I measured water depth at each site. In July 2017, I re-measured water depth and also measured other abiotic site characteristics that may influence primary production and decomposition rates at each site. I measured soil temperature using a moisture probe (HHR Moisture Meter, Delta-T Devices, Cambridge, UK), dissolved oxygen using a multi-meter (HQ30d Multi Meter, Hach, Loveland, CO), and water depth (Table 3.2).

Table 3.2 Site characteristics of meadow, cattail, invaded and herbicide-treated sites in July 2017; standard deviation in brackets. Uninvaded average provides the average of meadow and cattail values. Standing dead stems were not counted in meadow marsh.

Marsh Community	Meadow	Cattail	Uninvaded average	*P. australis* invaded	Herbicide-treated
Sample size	5	5	10	10	10
May water depth (cm)	30 (±10.5)	44 (±7.5)	37 (±11.0)	36 (±11.5)	37 (±8.5)
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)
Soil temperature (°C)	22.8 (± 0.3)	21.1 (± 0.1)	22.0 (± 0.2)	21.3 (± 0.3)	24.6 (± 0.2)
Dissolved oxygen (mg/L)	4.43 (± 0.82)	3.21 (± 0.46)	3.82 (± 0.64)	4.27 (± 0.65)	3.27 (± 0.33)
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/ m²)	776 (± 160)	83 (± 66)	429 (± 383)	91 (± 48)	16 (± 21)
Living (% cover)	59 (± 5)	62 (± 9)	61 (± 15)	79 (± 11)	41 (± 8)
Standing dead (stems/ m²)	NC	122 (± 42)	NC	167 (± 60)	5 (± 2)
Standing dead (% cover)	17 (± 10)	25 (± 12)	21 (± 12)	11 (± 6)	0.6 (± 0.4)

1. Abiotic characteristics

a) Water depth and temperature

Previously, I noted large fluctuations in water depth at sites in Long Point (personal observation) that could not be captured by bi-monthly water depth measurements. Furthermore, Lake Erie is reported to have the highest level of daily water fluctuations of all the Great Lakes (Trebitz 2006). To measure variability in water depth and temperature at my sites I installed nine data loggers (HOBO U20-001-02-Ti data logger, Onset, MA, USA); one at each site used for the decomposition experiment (Fig. 3.1, Table 3.1). Loggers were installed in stilling wells, positioned below the wetland substrate to prevent exposure of the data logger if water levels dropped below the sediment surface. Water depth and temperature were recorded hourly from June 14 to October 16, 2017, with pressure readings corrected using a single barometric logger placed on land nearby.

I employed a number of strategies to analyze the difference in variation in water depth between sites (resident plant communities, *P. australis* invaded and herbicide-treated communities crossed with shallow, intermediate and deep water depths). I calculated coefficient of variance for each site to allow for relative comparison of water depth variation between sites. Frequency intensity (sensu Trebitz 2006), a measure of magnitude and frequency of water fluctuation, was calculated using the one half sum of daily water level increments every hour. Average daily water depth range (maximum - minimum) and fluctuation intensity are reported using the back-transformed logarithmic means and standard deviation, as recommended by Trebitz (2006).

b) Incident light

I created photosynthetically active radiation (PAR) profiles from canopy top to water surface using a pair of radiation sensors that are uniformly sensitive to light from 400-700 nm (LI-190SA Quantum Sensor, LI-COR, Inc., NE, USA). PAR profiles were created between 9:00 am and 2:45 pm in June 2017 in sunny conditions. One sensor remained above the canopy for reference, while the other was used to measure PAR extinction vertically in 50 cm increments from the top of the canopy to the water or substrate. I converted the raw PAR to percent insolation for analysis.

2. Primary production

a) Biomass

To determine aboveground living and dead biomass, I collected living rametes, standing dead plants and litter from every plant species within three randomly established 0.25 m^2 quadrats at each of the 30 sites (Fig. 3.1) at the time of peak aboveground biomass, which occurred between July 22 – 25 in 2017 (Appendix 2).

I collected aboveground living and standing dead biomass from just above the soil surface, and litter down to the root mat or soil. The three study species (*P. australis, Typha* spp., and *C. canadensis*) are rhizomatous perennials, so I measured belowground biomass produced over a 60 - 65 day growing season using a modified soil ingrowth method (Neill 1992) to restrict belowground biomass to annual growth. At each site I inserted seven cores (4.8 cm diameter) composed of vermiculite to a depth of 11.3 cm. Cores were inserted between May 21 and 26 and collected between July 22 and 25 in 2017. All roots and rhizomes were removed from the cores by rinsing the cores over stacked sieves (1.4 mm and 500 um mesh size). Root:shoot ratio was calculated using the annual belowground biomass captured in the ingrowth soil cores.

I dried all tissues at 80°C for 48 hours and then measured their dry-weight. I weighed aboveground biomass and litter to the nearest 0.01 g (Advanced Balance PB602-S, Mettler Toledo, ON, Canada) and belowground biomass to the nearest 0.0001 g (MS Precision Balance, Mettler Toledo, ON, Canada).

b) Plant morphology

In June 2017, at each resident plant community and invaded site (Fig. 3.1, Table 3.1), I determined specific leaf area for the dominant species (*C. canadensis, Typha* spp., or *P. australis* in meadow, cattail, and invaded marsh, respectively). Using a scanner (CanoScan 9000F Mark II, Canon, ON, Canada) I determined leaf area to 0.01 cm and then leaf dry-weight to 0.0001 g (MS Precision Balance, Mettler Toledo, ON, Canada).

At the same time, I calculated leaf to stem mass ratio for *C. canadensis*, *Typha* spp. and *P. australis*. I collected all the *C. canadensis*, *Typha* spp. and *P. australis* rametes from one 0.25 m^2 quadrat per respective site. Then I separated the collected rametes into leaves and stems, oven-

dried the leaves and stems for 48 hours at 80°C, and weighed them to the nearest 0.01 g (Advanced Balance PB602-S, Mettler Toledo, ON, Canada). I used these masses to determine the leaf:stem ratio.

c) Carbon assimilation

At each of the ten resident plant communities and ten invaded sampling locations (Fig. 3.1), I measured *in situ* instantaneous photosynthetic rates on a new, unblemished leaf of one ramete near the top of the canopy; for a total of five *C. canadensis,* five *Typha* spp. and ten *P. australis* rametes. Carbon assimilation rates were not measured in herbicide-treated sites because emergent vegetation was sparse and did not form distinct communities (Table 3.2, Appendix 7). I measured photosynthetic rates using a portable true differential infrared gas analyzer system (CIRAS-3, PP Systems, MA, USA) between 9:00 am and 2:45 pm in June 2017. I used light saturation levels of 0, 50, 100, 200, 500, 1000, and 1500 µmol m^{-2} s^{-1} to create carbon assimilation curves.

I also scaled up the carbon assimilation rate to the marsh-level for each resident plant community and invaded marsh site. To do so, I calculated the standing leaf surface area of *C. canadensis* in meadow, *Typha* spp. in cattail and *P. australis* in invaded marsh on a wetland area basis (m^{-2}). I calculated the standing leaf surface area by multiplying the average specific leaf area of each species by the dry leaf weight as measured in June 2016 (see plant morphology above). I then scaled up the carbon assimilation rate (as measured at 1500 µmol CO_2 m^{-2}s) from the area used in the CIRAS-III (2.4 cm^2) to the standing leaf surface area estimated for *C. canadensis* in meadow, *Typha* spp. in cattail and *P. australis* in invaded marsh. I chose to use carbon assimilation rate measured at 1500 µmol m^{-2} $s^{-1}$for the basis of calculating the maximum carbon

assimilation rate at the marsh-level because average ambient PAR reaching the top of the canopy during measurement collection was similar (1575.6 µmol m^{-2} s^{-1}±102.4 SE).

3. Decomposition rates

a) Litterbag transplant experiment

Decomposition rates of plant litter were calculated using a mass loss approach in a litterbag transplant experiment. I used either *P. australis* leaves, *Typha* spp. leaves, or *C. canadensis* leaves and stems in the litterbags. *Calamagrostis canadensis* leaves and stems were used because I was unable to isolate an appropriate mass of leaves due to their small size. Litterbags were made from 2 mm fibreglass mesh and contained five grams of plant tissue. Plant material used in the litterbags was collected August 2016 and oven dried at 100°C to a constant weight. The carbon:nitrogen ratio of each plant species and tissue was determined prior to deployment (Chapter 2). Extra litterbags of each type were created and brought from the field without being deployed to calculate travel loss (Robertson 1999).

I deployed litterbags between May 12 and 14, 2017 and anchored them to the substrate randomly in clusters of three (one of each litter type) in shallow, intermediate and deep water depths in resident plant communities, *P. australis* invaded and herbicide-treated sites (Appendix 8). In addition, I tied replicates to poles above the water at the intermediate water depth each community type to mimic standing dead plant material and create a "dry" water depth treatment.

I collected three replicates of each litterbag type from each site periodically until May 15, 2018 (Table 3.3). In March and May 2018, some replicates of submerged litter from the intermediate depth *P. australis* invaded site and standing litter in herbicide-treated sites and could not be retrieved.

Table 3.3 Average number of days litter spent in the wetland from deployment May 12 - 14, 2017 to retrieval date.

Retrieval date	2017 28-May	13-Jun	16-Jul	18-Aug	14-Sep	17-Oct	2018 26-Mar	15-May
Days in wetland	15	31	64	96	124	157	317	367

On retrieval, I removed the remaining litter from the collected litterbags, separating it from soil, living plants, and invertebrates. Then I dried the litter at 100°C for 48 hours to calculate mass loss. I determined litter weight to 0.0001 g (MS Precision Balance, Mettler Toledo, ON, Canada).

To calculate decay rate of litter types and marsh communities in different water depths I used mass loss [(original mass loss - average travel loss for that plant species) - remaining mass]. I fit the percent mass lost over time using two models: the single exponential model (Olson, 1963) and the decaying coefficient model (Godshalk et al. 1978), as described by Ágoston-Szabó and Dinka (2008). The single exponential model is: $W_t = W_0 \exp(-kt)$, where W_t describes the amount of litter (%) remaining a time t, W_0 is the initial mass of litter (%) and k is the exponential decomposition rate (Olson, 1963). The decaying coefficient model is: $W_t = W_0 \exp((k_1/k_2)*(\exp(k_2 t) - 1))$, where k_1 equals the initial decay coefficient and k_2 equals the relative decrease of the decay coefficient (Godshalk et al. 1978). Decay rates (single coefficient and decay coefficients) 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 Studio.

The decaying coefficient model is the most appropriate decay model for comparisons between different litter types and vegetation communities and for when the decay rate is expected to fluctuate, however the single exponential model is more common in the literature and allows for

more 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. I 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).

b) Soil carbon dioxide efflux

I measured soil carbon dioxide efflux every month from June to October 2017 at the nine sites containing litterbags (Fig. 3.1, Table 3.1). I supplemented these data with measurements collected on April 20, 2018 to capture CO_2 release during spring thaw. During soil efflux measurements, I also measured water depth and water temperature. For the April 2018 measurements, I selected five sites in each treatment type: resident plant community (cattail marsh), *P. australis* invaded, and herbicide-treated marsh. Whereas the June to October 2017 measurements of herbicide-treated habitat were conducted in sites that had been treated in September 2016, the April 2018 measurements were collected from herbicide-treated habitat that had been treated in September 2017. These spring sites were located within 150 m of each other.

I measured soil carbon dioxide efflux for 300 seconds per measurement using a portable open gas exchange system and opaque chamber (SRC-1 Soil Respiration Chamber and a CIRAS-3, PP Systems, MA, USA). I calculated soil carbon dioxide efflux rate (CO_2 µmol/mol/min) using the change in CO_2 concentration from the 90 to 270 second interval. The chamber volume was 1171 cm^3 with an opening 78.5 cm^2 in area, however the collar volume varied depending on the depth of the water. The area of the base of the collar was 75.4 cm^2. The volume and area of the chamber and collar were used to calculate the CO_2 $m^{-2}d^{-1}$ for each site.

3.2.4 Statistical analysis

I used R studio to execute all statistical analyses (R Core Team 2016). General linear models were calculated using the "lm" function from the "stats" package (R Core Team 2016). Model selection was carried out using an AICc framework to identify the optimal model for each response variable. The "AICc" function in the "MuMIn" package was used (Barton 2018). Significant differences were determined at $p < 0.05$.

To examine if invasion and subsequent control efforts influence the mean or variance of water depth and temperature or affect the percent of incident PAR radiation that reaches the water surface, I used general linear models. I analysed the mean and variance of water depth and temperature using the measurements taken from the HOBOs. I tested for a difference in water depth among site types, averaging measurements from June 14 to October 16, 2017 within the three wetland types: resident plant communities, invaded marsh and herbicide-treated sites. In addition, to compare daily water depth range, daily average water temperature, and daily water temperature range I used a general linear model that included the predictors site type (resident plant communities, *P. australis* invaded marsh and herbicide-treated sites), water depth category (shallow, intermediate, deep), and their interaction. I also tested for a difference in mean percent incident PAR radiation that reaches the water surface among plant communities (meadow marsh, cattail marsh and invaded marsh). Daily water depth fluctuations and daily water temperature fluctuations were square root transformed to meet normality assumptions.

Using general linear models, I tested for differences in primary production among resident plant communities, *P. australis* invaded and herbicide-treated site types, with water depth (measured once in May or July) as a continuous, fixed factor, and included an interaction term between

water depth and site type. Note that this included measurements from all 30 study sites. For each response variable I ran each model twice, first with the May water depth and then with the July water depth, where the response variable = $\beta_0 + x_1 \beta_1 + x_2 \beta_2 + x_3 \beta_1 * \beta_2$, and β_0 = intercept, $x_1 \beta_1$ = site type, $x_2 \beta_2$ = water depth, and $x_3 \beta_1 * \beta_2$ = interaction. For each response variable I decided whether to use the general linear model with the May or July 2017 water depth by comparing the Akaike's Information Criterion (corrected for small sample size). I selected the model with the lowest AICc value as the optimal model. If the interaction term was not significant, I removed the it and ran the model with only the two main predictor variables: site type and water depth. I followed this modeling approach to test for differences in six response variables indicative of primary productivity: 1) aboveground biomass, 2) belowground biomass, 3) total biomass, 4) root:shoot ratio, 5) mass of standing dead material, and 6) litter mass. Aboveground biomass, belowground biomass, total biomass, standing dead, litter, and root:shoot ratio were square root transformed to meet normality assumptions.

I also used general linear models to test for differences in plant morphology and carbon assimilation rate among plant species (*P. australis*, *Typha* spp. and *C. canadensis*), with water depth (measured once in May or July) as a continuous, fixed factor, and included an interaction term between water depth and site type. Note that this included measurements from all of the five meadow marsh, five cattail and ten *P. australis* invaded study sites. For each response variable I ran each model twice, first with the May water depth and then with the July water depth, where the response variable = $\beta_0 + x_1 \beta_1 + x_2 \beta_2 + x_3 \beta_1 * \beta_2$, and β_0 = intercept, $x_1 \beta_1$ = site type, $x_2 \beta_2$ = water depth, and $x_3 \beta_1 * \beta_2$ = interaction. For each response variable I decided whether to use the general linear model with the May or July 2017 water depth by comparing the Akaike's Information Criterion (corrected for small sample size). I selected the model with the

lowest AICc value as the optimal model. If the interaction term was not significant, I removed it and ran the model with only the two predictor variables: site type and water depth. I followed this modeling approach to test for differences in four different response variables: 1) maximum carbon assimilation rate, 2) specific leaf area, 3) leaf surface area, and 4) maximum carbon assimilation per meter-squared of wetland. Leaf surface area and maximum carbon assimilation per meter-squared of wetland were square root transformed to meet normality assumptions.

I also used general linear models to test for differences in either the single exponential decay rate (k) or the initial (k_1) decay coefficient among litter types (*P. australis, Typha* spp. and *C. canadensis*), site types (resident plant communities, *P. australis* invaded, and herbicide-treated) and water treatment (dry, shallow, intermediate, deep) and their interaction. Water treatment was considered a categorical variable; where the "dry" treatment refers to suspended litter that mimics moisture conditions for standing litter. For each response variable, I compared the full model including all three predictors (litter type, site type, and water depth) against models with each possible pairing of two predictors, and against a model containing only a single predictor (litter type, site type, or water depth) in an Akaike's Information Criterion (corrected for small sample size) model competition framework. I selected the 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 normality assumptions. Decay rate function fitting was done using the "minpack.lm" package (Elzhov et al. 2016).

A general linear model was also used to compare the rate of soil carbon dioxide efflux (CO_2 $m^{-2}d^{-1}$) among sites (resident plant communities, *P. australis* invaded, and herbicide-treated) crossed with the water depth (cm) that was measured within the soil chamber during each

measurement for measurements collected from June to October 2017. An additional linear model was constructed to compare the rate of soil carbon dioxide efflux (CO_2 $m^{-2}d^{-1}$) among invaded, cattail and areas treated with herbicide in fall 2017 to capture the spring soil carbon efflux in April 2018. The June to October measurements of soil carbon dioxide efflux was log transformed to meet normality assumptions.

3.3 Results

3.3.1 Abiotic site characteristics

a) Water depth

Abiotic characteristics varied among plant communities. The water depth gradient in *P. australis* invaded (17-56 cm) and resident plant community (14-53 cm) sites spanned a similar range in May 2017, but herbicide-treated areas were not as shallow (26 - 50 cm). Despite this, the mean water depths in May 2017 were similar among site types (Table 3.2). By July, the average water depth of resident plant communities had decreased, whereas the average water depth of herbicide-treated sites increased slightly and there was little change in the average water depth in *P. australis* invaded sites (Table 3.2).

At the nine decomposition sites where water depth and temperature was measured hourly (Fig. 3.1, Table 3.1), water depths were lowest in September when some sites had no standing water (Appendix 9). The model predicting average water depth based on the site type provided a reasonable fit ($F_{2,1122} = 61.600$, p-value = <0.001, $R^2 = 0.099$). The average daily water depth from June 14 -October 16, 2017 significantly differed among site types with *P. australis* invaded sites significantly deeper than resident plant communities or herbicide-treated sites (Appendix 9).

The model predicting daily fluctuations in water depth (daily maximum - daily minimum) based on the site type (resident plant communities, *P. australis* invaded and herbicide-treated), the water depth treatment (shallow, intermediate, deep) and their interaction provided a reasonable fit ($F_{8,1116}$ = 62.760, *p*-value = <0.001, R^2 = 0.310). Water depth treatment and site type had a significant interaction (Appendix 9) such that the degree of daily fluctuation in water depth among *P. australis* invaded, resident plant communities, and herbicide-treated sites depended on the relative water depth. 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, resident plant communities had significantly greater daily fluctuations in water depth compared to other site types (Appendix 9).

In addition to being deeper and having a greater daily range in water depth, *P. australis* invaded sites generally had the largest frequency intensity and coefficient of variation across the water depth gradient compared to uninvaded and herbicide-treated sites (Table 3.4). The site with the largest frequency intensity, however, was the deep uninvaded cattail site (Table 3.4). The coefficient of variation also showed a strong trend along the water depth gradient; sites with a higher mean water depth had a higher coefficient of variation (Table 3.4).

Table 3.4 Daily water level range and frequency intensity (one half sum of daily water level increments) expressed as the back-transformed logarithmic mean and standard deviation (SD). Coefficient of variation compares variability of groups with different means. Site refers to invaded, uninvaded and herbicide-treated sites. Water depth refers to the relatively shallow, intermediate and deep water sites where water depth and temperature loggers were installed.

Site	Water depth	Daily range (cm)		1/2 Σ Daily increments (cm)		Coefficient of variance
		Log. mean	± 1 SD	Log. mean	± 1 SD	average daily depth/ SD
Invaded	Shallow	13.7	8.0 - 23.6	25.3	14.6 - 43.8	2.00
	Intermediate	12.0	6.6 - 21.9	20.0	10.7 - 37.3	2.99
	Deep	14.2	8.1 - 25.1	25.5	14.3 - 45.3	3.51
Resident plant communities	Shallow	6.1	2.3 - 15.9	8.7	3.2 - 23.6	1.14
	Intermediate	4.5	1.9 - 10.9	6.4	3.0 - 13.6	2.09
	Deep	14.2	8.3 - 24.2	25.8	15.5 - 42.8	3.07
Herbicide-treated	Shallow	4.0	1.6 - 9.9	5.5	2.4 - 12.6	1.38
	Intermediate	6.4	2.2 - 18.7	10.0	3.5 - 28.5	2.31
	Deep	4.2	1.8 - 10.1	5.8	2.6 - 13.0	2.60

b) Water temperature

Daily water temperatures also differed among the nine sites where loggers were installed (Table 3.1, Appendix 9). The model predicting average daily water temperature from June 14-October 16, 2017 based on site type (resident plant communities, *P. australis* invaded and herbicide-treated), the water depth treatment (shallow, intermediate, deep) and their interaction provided a reasonable fit ($F_{8,1116} = 61.710$, p-value = <0.001, $R^2 = 0.307$). Water depth category and site type had a significant interaction (Appendix 9) such that the average daily water temperature among resident plant communities, *P. australis* invaded, and herbicide-treated sites depended on the relative water depth. Resident plant communities and *P. australis* invaded sites were warmest in the deep water depth category, while herbicide-treated sites were warmest in the shallow water category (Table 3.5, Appendix 9).

The model predicting daily fluctuations in water temperature from June 14-October 16, 2017 based on site type (resident plant communities, *P. australis* invaded and herbicide-treated), the water depth treatment (shallow, intermediate, deep) and their interaction provided a reasonable

fit ($F_{8,1116}$ = 369.000, *p*-value = <0.001, R^2 = 0.659). Water depth category and site type had a significant interaction (Appendix 9), such that the average daily fluctuations in water temperature among resident plant communities, *P. australis* invaded, and herbicide-treated sites depended on the relative water depth. Different site types had the greatest daily fluctuations in water temperature at different water depth categories (Appendix 9). Daily fluctuations were greatest in herbicide-treated sites compared to resident plant communities or *P. australis* invaded sites and the greatest fluctuations in water temperature occurred in the intermediate water depth category (Table 3.5, Appendix 9). Resident plant communities had intermediate daily fluctuations in water temperature, but the greatest fluctuations occurred in the shallow water depth category (Table 3.5). Invaded sites had the smallest daily fluctuations in water temperature and shallow, intermediate, and deep water depth categories all had similar daily water temperature fluctuations (Table 3.5).

Table 3.5 Average daily water temperature and average daily fluctuation in water temperature from June 14 to October 16, 2017. Site refers to resident plant communities, invaded sites and herbicide-treated sites. Water depth refers to the categorical shallow, intermediate and deep water depth sites where water depth and temperature loggers were installed. Standard deviation in brackets.

Site	Water depth treatment	Mean daily water temperature (°C)	Mean daily fluctuation of water temperature (°C)
Invaded	Shallow	17.75 (±1.48)	0.33 (±0.31)
	Intermediate	18.06 (±1.79)	0.44 (±0.50)
	Deep	18.96 (±1.72)	0.42 (±0.36)
Resident plant communities	Shallow	19.67 (±2.58)	1.53 (±0.71)
	Intermediate	17.93 (±2.14)	1.03 (±0.82)
	Deep	20.10 (±2.44)	0.84 (±0.61)
Herbicide-treated	Shallow	20.97 (±2.34)	1.58 (±1.05)
	Intermediate	22.23 (±2.91)	3.09 (±1.06)
	Deep	21.50 (±3.12)	2.92 (±0.96)

c) Incident light

Canopy height was the tallest in the *P. australis* invaded marsh, intermediate in cattail, and shortest in meadow (Table 3.2). Relative photosynthetically active radiation (PAR; 400-700 nm) capture was greater in the upper canopy of *P. australis* invaded marshes compared to the upper canopy of cattail or meadow marsh (Fig. 3.2). In addition, relatively less PAR reached the bottom of the canopy in *P. australis* invaded marshes compared to uninvaded meadow and cattail marshes (Fig. 3.2), but this difference was not significant ($F_{2,16}$ = 1.195, *p*-value = 0.328, R^2 = 0.130). Ambient light levels are summarized in Appendix 9.

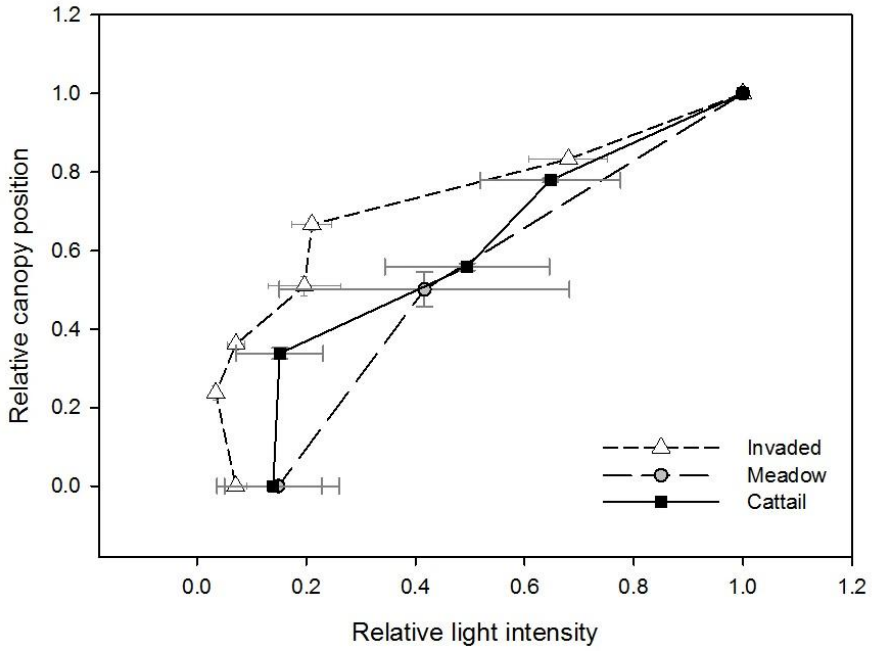

Figure 3.2 Relative light intensity in relation to relative canopy position of meadow (n = 5), cattail (n = 5) and *P. australis* invaded (n = 10) marsh sites in June 2017 in Long Point Provincial Park. Error bars show standard error. Light is measured as PAR (400-700 nm) in units of µmol m^{-2} s^{-1}.

3.3.2 Primary production

a) Biomass

There was no significant interaction between site type and water depth (measured in either May or July) for aboveground biomass, belowground biomass, total live biomass, root: shoot ratio or litter mass (Table 3.6). Aboveground biomass, total live biomass, root:shoot ratio and litter significantly differed among *P. australis* invaded, resident plant communities and herbicide-treated sites once the non-significant interaction term was removed from the general linear models (Appendix 10). Significant differences in biomass measurements among resident plant communities, *P. australis* invaded and herbicide-treated sites are indicated by lowercase alphabetic symbols in Figure 3.3.

Water depth had a significant effect on aboveground biomass, belowground biomass, and total live biomass (Appendix 10). In addition, once the non-significant interaction term was removed, litter was also significantly affected by water depth (Table 3.6, Appendix 10). With the exception of belowground biomass, models using the water depth in July had lower AICc values, higher adjusted R^2 values and lower *p*-values than models using water depth measured in May, but models with either water depth generally yielded a good fit to response variables (Appendix 10). Generally total living biomass increased with increasing water depths in May and July (Appendix 10).

There was a significant interaction between site type and water depth on the mass of standing litter present at a site (Table 3.6, Appendix 10). The statistical model using the water depth measured in July had a lower AICc value, higher adjusted R^2 value and similar *p*-values compared to the model using water depth measured in May (Appendix 10). At depths of less

than approximately 40 cm (as measured in July 2017) *P. australis* invaded sites had more standing litter than resident plant communities, but at depths greater than approximately 40 cm (as measured in July 2017) resident plant communities had more standing litter (Appendix 10). Herbicide-treated sites had very little to no standing litter present, regardless of water depth (Appendix 10).

There was more dead plant biomass (standing litter mass and mass of litter in the litter layer) present than live aboveground biomass per meter of wetland in both *P. australis* invaded and uninvaded cattail marsh. Invaded and cattail marsh had double (or close to) the amount of dead plant biomass compared to living (invaded: 2.00 ± 1.04 SD; cattail: 1.90 ± 0.59 SD, respectively). Herbicide-treated sites, which had very little aboveground biomass, had over 47 times more dead plant material present (47.39 ± 89.12 SD). Dead biomass in meadow marsh, however, weighed slightly more than half the biomass of live aboveground plants (0.60 ± 0.29 SD).

Table 3.6 General linear model fits for peak biomass across a water depth gradient, where site type refers to invaded, resident plant communities and herbicide-treated sites. Aboveground biomass, annual belowground biomass to a depth of 11.3 cm, total biomass, root: shoot, standing dead and litter were square root transformed to meet the assumptions of normality. Which water depth measurement was included in the model (May or July measurements) was that which yielded the lower AICc value. This tended to be the same model that yielded the highest adjusted R^2 and lowest *p*-value (Appendix 10). Bolded models are discussed in text and used in figures. Full models are in Appendix 10.

Response variable	Date water measured	Interaction?	*F*-test (df)	*p*-value	R^2
Aboveground (SQRT)	July	Yes	26.970 (5, 24)	<0.001	0.849
Aboveground (SQRT)	**July**	**No**	**41.460 (3, 26)**	**<0.001**	**0.827**
Belowground (SQRT)	May	Yes	5.799 (5, 24)	0.001	0.547
Belowground (SQRT)	**May**	**No**	**7.143 (3, 26)**	**0.001**	**0.452**
Total live (SQRT)	July	Yes	24.380 (5, 24)	<0.001	0.836
Total live (SQRT)	**July**	**No**	**37.770 (3, 26)**	**<0.001**	**0.813**
Root: shoot (SQRT)	July	Yes	5.318 (5, 24)	0.002	0.526
Root: shoot (SQRT)	**July**	**No**	**9.211 (3, 26)**	**<0.001**	**0.515**
Standing dead	**July**	**Yes**	**26.350 (5, 24)**	**<0.001**	**0.846**
Litter (SQRT)	July	Yes	6.922 (5, 24)	<0.001	0.591
Litter (SQRT)	**July**	**No**	**8.299 (3, 26)**	**<0.001**	**0.489**

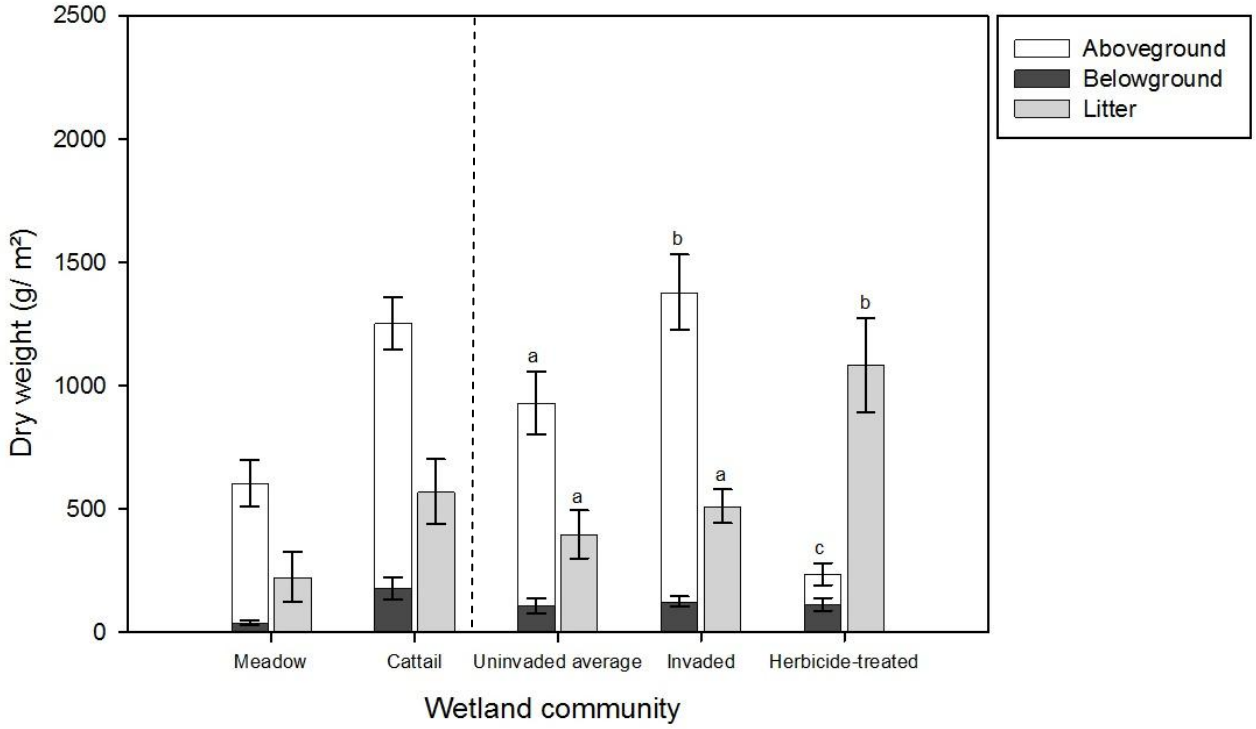

Figure 3.3 Average dry weight (g m^{-2}) of annual total biomass (divided into aboveground and belowground components and the mass of litter in the litter layer in uninvaded (meadow: n = 5, cattail: n = 5), *P. australis* invaded (n = 10) and herbicide-treated (n = 10) sites. The bars labelled "uninvaded average" reflect the mean of values from meadow and cattail sites (n = 10). Error bars show standard error for aboveground biomass, belowground biomass, and litter mass from the litter layer. The dashed line separates the cattail and meadow marsh site types from the other bars. Cattail and meadow marsh are averaged to yield the uninvaded average data. Lowercase letters indicate significant differences in total biomass and litter among the site types left of the dashed line: uninvaded, *P. australis* invaded and herbicide-treated sites at $p < 0.05$.

b) Plant morphology

There was no significant interaction between plant species (*C. canadensis*, *Typha* spp., *P. australis*) and water depth for specific leaf area (Appendix 10). The model predicting specific leaf area based on plant species (*C. canadensis*, *Typha* spp., *P. australis*) and water depth as measured in July provided the best model fit (Table 3.7; Appendix 10). Specific leaf area did significantly differ among plant species (Appendix 10); *C. canadensis* had significantly higher

specific leaf area than *P. australis* and *Typha* spp. and *P. australis* had significantly higher specific leaf area than *Typha* spp. Water depth (as measured in either May or July) had no significant effect on specific leaf area (Appendix 10).

The mean leaf:stem ratio was lowest for *C. canadensis* (0.34 ± 0.08 SD) and *P. australis* (0.36 ± 0.10 SD) and higher for *Typha* spp. (0.90 ± 0.33 SD).

Table 3.7 Results of linear model fit tests for plant morphology and carbon assimilation across a water depth gradient, where plant refers to *C. canadensis*, *Typha* spp. and *P. australis*. Leaf area per meter of wetland and carbon assimilation rates at a marsh-level were square root transformed to meet the assumptions of normality. I decided which water depth measurement to include (May versus July) by comparing AICc values and selecting the water depth yielding the lower AICc. This typically also yielded a higher adjusted R^2 and lower *p*-value (Appendix 10). Bolded models are discussed in text and used in figures. Full models are in Appendix 10.

Biomass variable	Date water measured	Interaction?	*F*-test (df)	*p*-value	R^2
Maximum carbon assimilation rate	May	Yes	4.504 (5, 14)	0.012	0.617
Maximum carbon assimilation rate	**May**	**No**	**6.501 (3, 16)**	**0.006**	**0.535**
Specific leaf area	May	Yes	8.667 (5, 14)	0.001	0.756
Specific leaf area	**July**	**No**	**15.510 (3, 16)**	**<0.001**	**0.744**
Leaf area per meter of wetland (SQRT)	July	Yes	5.711 (5, 14)	0.004	0.671
Leaf area per meter of wetland (SQRT)	**May**	**No**	**8.582 (3, 16)**	**0.001**	**0.617**
Carbon assimilation rate at the marsh-level (SQRT)	July	Yes	10.040 (5, 14)	<0.001	0.782
Carbon assimilation rate at the marsh-level (SQRT)	**July**	**No**	**15.020 (3, 16)**	**<0.001**	**0.738**

c) Carbon assimilation

Mean carbon assimilation was high for all species measured, ranging from 10.92 to 25.72 µmol CO_2 $m^{-2}s^{-1}$ of carbon assimilation at PAR levels of 1500 µmol $m^{-2}s^{-1}$ (Fig. 3.4), which approximated average ambient insolation during the period of measurement. At low levels of PAR (~ 200 µmol $m^{-2}s^{-1}$), carbon assimilation rates appear very similar between *P. australis*, *Typha* spp. and *C. canadensis* (Fig 3.4). At higher levels of PAR, carbon assimilation rates of *P.*

australis and *Typha* spp. remain very similar, but the carbon assimilation rate of *C. canadensis* is much lower (Fig. 3.4).

The difference in maximum carbon assimilation rates among the three plant species did not depend on water depth (as measured in May or July; Table 3.7). The statistical model using the water depth measured in May had a lower AIC value, higher adjusted R^2 value and lower *p*-value compared to the model using water depth measured in July (Appendix 10). This model provided a reasonable fit (Table 3.7; Appendix 10). The maximum carbon assimilation rate differed significantly among plant species (Appendix 10); the maximum carbon assimilation rate was not significantly different between *P. australis* and *Typha* spp. but was significantly lower for *C. canadensis* (Fig. 3.5).

There was no significant interaction between plant species and water depth or significant effect of water depth (as measured in May or July) for leaf area of my target species per meter squared of wetland or maximum carbon assimilation rate at the marsh level (Appendix 10). The statistical model predicting leaf area per area of wetland using the water depth measured in May had a lower AIC value, higher adjusted R^2 value and lower *p*-value compared to the model using water depth measured in July (Appendix 10) and had a reasonable fit (Table 3.7; Appendix 10). Conversely, the statistical model predicting maximum carbon assimilation rate at the marsh level using the water depth measured in July had a lower AIC value, higher adjusted R^2 value and lower *p*-value compared to the model using water depth measured in May (Appendix 10) and had a reasonable fit (Table 3.7; Appendix 10). Leaf area of my target species per meter squared of wetland and maximum carbon assimilation rate at the marsh-level differed significantly among plant species (Appendix 10). While *C. canadensis* had significantly higher specific leaf area than *P. australis* or *Typha* spp. (Fig. 3.5A), *C. canadensis* produced the least amount of leaf

area per area of wetland (due to low primary production) and subsequently had a significantly lower maximum carbon assimilation on a marsh-level area basis than *P. australis* or *Typha* spp. (Fig. 3.5B, D). There was no significant difference in the leaf area per meter of wetland or carbon assimilation rate on a marsh-level area basis between invaded and cattail communities (Fig. 3.5C, D).

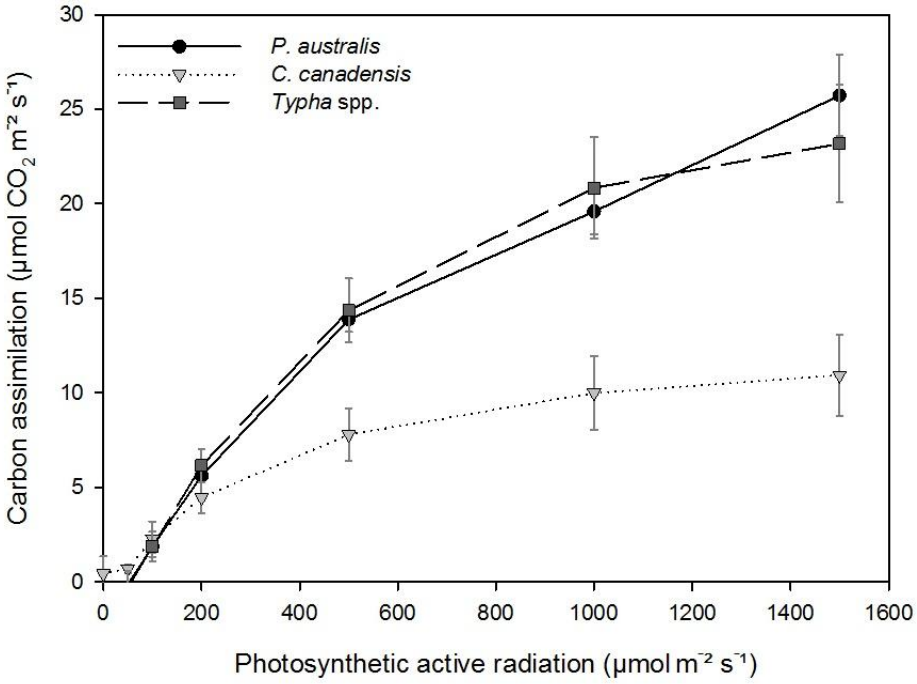

Figure 3.4 Carbon assimilation (µmol CO_2 m^{-2} s^{-1}) of *C. canadensis* (n = 5), *Typha* spp. (n = 5) and *P. australis* (n = 10) under different levels of photosynthetic active radiation (µmol m^{-2} s^{-1}) measured in June 2017 in Long Point Provincial Park using a portable infrared gas analyzer (CIRAS-III, PP Systems, MA USA). Error bars show standard error.

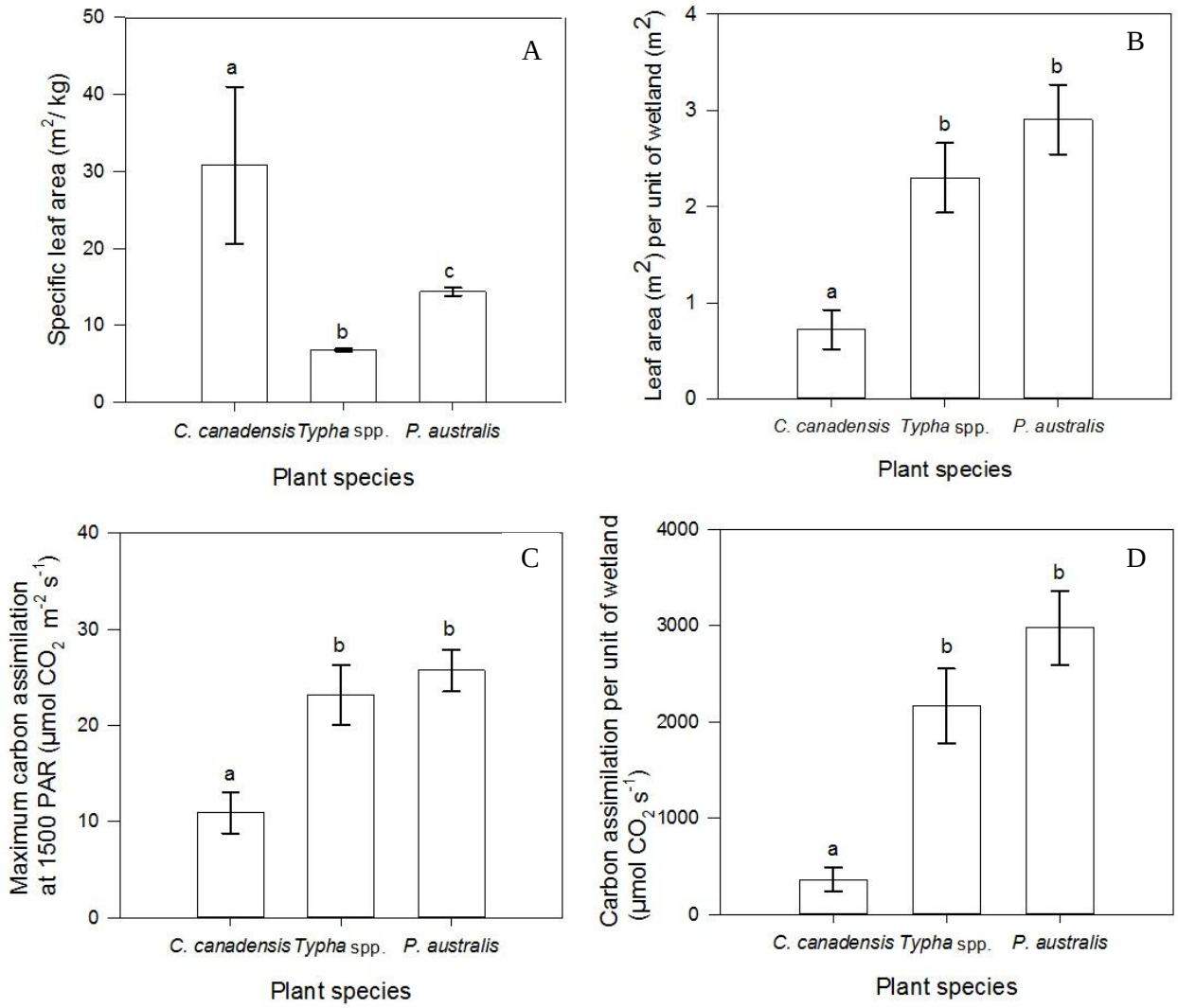

Figure 3.5 A) Average specific leaf area (m^2/ kg) of plant leaves as calculated in June 2017. B) Average leaf area (m^2) per m^2 of wetland in June 2017; calculated by determining average dry leaf weight (g) in 1 m^2 of wetland multiplied by specific leaf area (m^2/ kg). C) Maximum carbon assimilation (µmol CO_2 m^{-2} s^{-1}) as calculated in June 2017. D) Maximum carbon assimilation per unit of wetland in June 2017 based on average maximum carbon assimilation and average leaf surface area per unit of wetland. All error bars represent standard error. For *C. canadensis* n = 5, *Typha* spp. n = 5. and for *P. australis* n = 10. Measurements taken at Long Point Provincial Park (Lake Erie), Canada. Lower case letters indicate significant differences between species at $p <$ 0.05.

3.3.3 Decomposition rates

a) Litterbag transplant experiment

Two models, the single exponential and decaying coefficient exponential model, were fit to the percent mass loss of litter over 367 days in the wetland. While both models fit the data well ($R^2 >$ 0.596), 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 8). By the end of the experiment, litter loss ranged from 5.75 to 74.65%, depending upon the litter type and treatment (Table 3.8, Appendix 8). In general, submerged *P. australis* leaf litter decomposed the fastest, while the standing litter ("dry" water depth treatment) of all plant species decomposed slowest (Appendix 8).

The same model best predicted both the single exponential coefficient (k) and the initial decay coefficient (k_1). This model was: decay rate coefficient = intercept + litter type (*C. canadensis*, *Typha* spp., and *P. australis*) + site type (resident plant community, *P. australis* invaded and herbicide-treated) + water depth treatment (dry, shallow, intermediate, and deep) + site type * water depth treatment. Full models and selection criteria can be found in Appendix 8.

Decay rates (k, k_1) differed significantly among litter types (Table 3.8, Appendix 8), and *P. australis* leaf litter decomposed significantly faster than *C. canadensis* and *Typha* spp. (Fig. 3.6, Appendix 8). There was a significant interaction between site type and water depth treatment on decay rates (k, k_1; Appendix 8). In resident plant communities and *P. australis* invaded sites submerged litter decomposed fastest in deep water, but in herbicide-treated sites submerged litter decayed fastest at the intermediate water depth.

Water depth treatment had a significant effect on the single exponential coefficient (k) and initial decaying coefficient (k_1). While there was an overall trend for litter placed in deeper water depths to decay faster there was only a significant difference between submerged (shallow, intermediate, deep) and standing (dry) litter (Fig. 3.6, Appendix 8).

The initial decaying coefficient (k_1) did not significantly differ among sites (Appendix 8). The single exponential coefficient (k) differed significantly among sites and appeared to initially decay slightly faster in submerged *P. australis* invaded locations and slower in dry *P. australis* invaded locations than in resident plant communities and herbicide-treated sites (Fig. 3.6).

Table 3.8 Summary of single exponential coefficient (k) and initial decaying coefficient (k_1) of litter (*C. canadensis, P. australis. Typha* spp.), in different sites (resident plant community, invaded, herbicide-treated) and water depths (shallow, intermediate, deep). Standing litter ("dry" water treatment) is summarized separately for litter type and site. Replicates of litter from marshes in Long Point (Lake Erie) were collected over a period of 367 days beginning May 12 - 14, 2017.

Category		Decay environment	n	k	k_1	k_2	% remaining at 367 days
Litter type	*C. canadensis*	Submerged	9	-0.004 ±0.001	-0.010 ±0.001	-0.012 ±0.002	40.99 ±3.94
	Typha spp.		9	-0.004 ±0.000	-0.011 ±0.001	-0.014 ±0.001	44.04 ±2.48
	P. australis		9	-0.009 ±0.001	-0.021 ±0.001	-0.017 ±0.003	26.46 ±4.07
	C. canadensis	Standing litter	3	-0.001 ±0.000	-0.002 ±0.000	-0.006 ±0.000	70.94 ±1.18
	Typha spp.		3	-0.001 ±0.000	-0.002 ±0.000	-0.005 ±0.001	68.76 ±1.59
	P. australis		3	-0.002 ±0.000	-0.004 ±0.000	-0.009 ±0.001	63.92 ±3.07
Site	Resident plant community	Submerged	9	-0.006 ±0.001	-0.013 ±0.003	-0.013 ±0.003	37.16 ±5.25
	P. australis invaded		9	-0.005 ±0.001	-0.011 ±0.001	-0.010 ±0.001	33.79 ±4.05
	Herbicide-treated		9	-0.006 ±0.001	-0.017 ±0.002	-0.019 ±0.002	40.53 ±4.69
	Resident plant community	Standing litter	3	-0.001 ±0.000	-0.003 ±0.001	-0.007 ±0.001	68.39 ±0.00
	P. australis invaded		3	-0.002 ±0.000	-0.003 ±0.001	-0.007 ±0.000	62.15 ±0.01
	Herbicide-treated		3	-0.001 ±0.000	-0.002 ±0.000	-0.007 ±0.002	73.09 ±0.00
Water depth	Dry (standing dead)		9	-0.001 ±0.000	-0.003 ±0.000	-0.007 ±0.001	67.87 ±4.74
	Shallow		9	-0.005 ±0.001	-0.015 ±0.003	-0.018 ±0.003	43.61 ±2.65
	Intermediate		9	-0.006 ±0.001	-0.013 ±0.002	-0.013 ±0.001	39.76 ±4.02
	Deep		9	-0.007 ±0.001	-0.013 ±0.002	-0.011 ±0.002	28.11 ±4.57

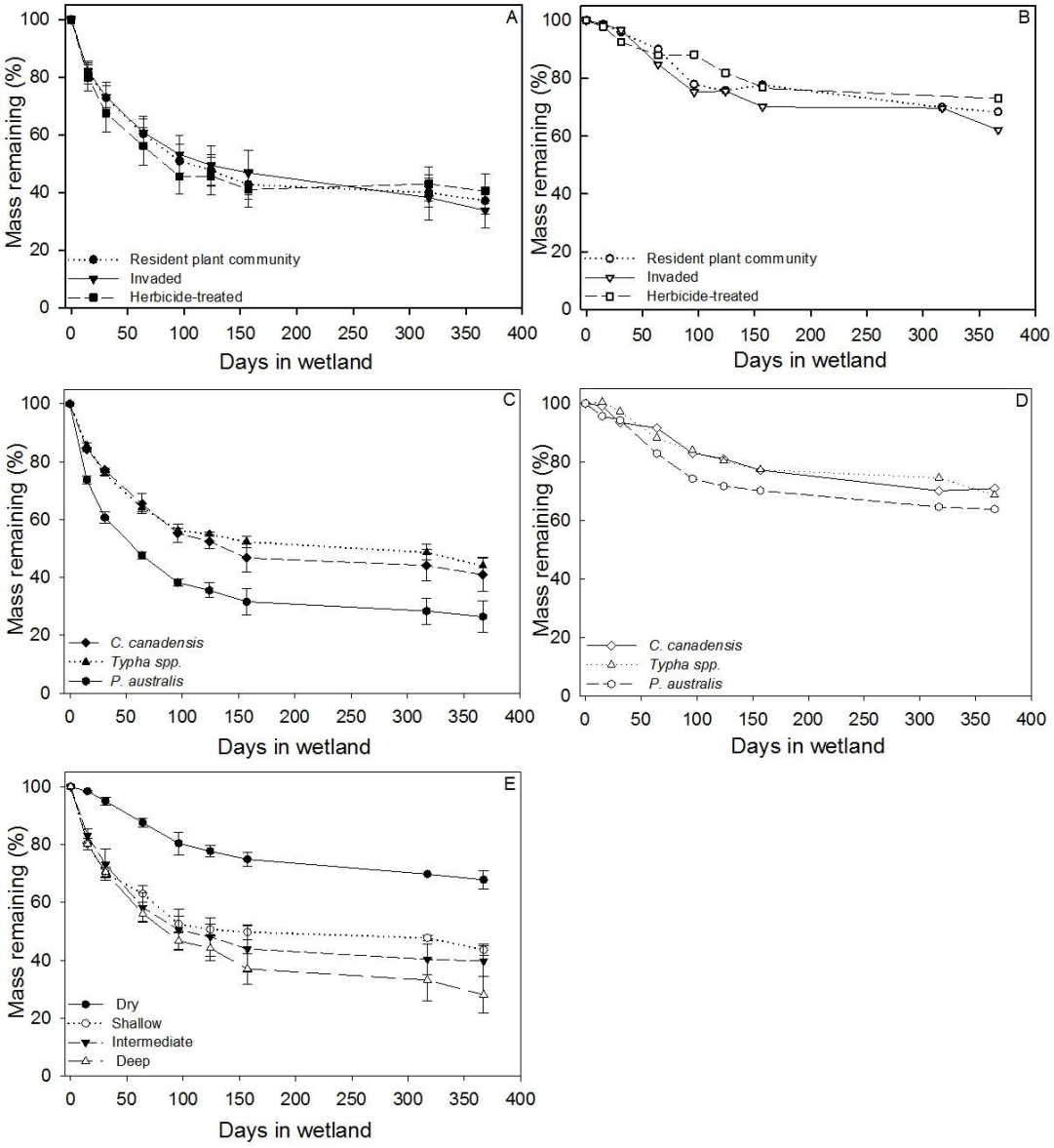

Figure 3.6 Change in the percent of mass remaining (% dry weight; mean ±SE) of *C. canadensis* leaf and stem litter, *Typha* spp. leaf litter and *P. australis* leaf litter over 367 days (day 0: May 12-14, 2017). A) Change in % mass remaining of submerged litter (average mass loss of all plant species litter in shallow, intermediate and deep water depths) in resident plant communities, invaded and herbicide-treated sites (n = 9). B) Change in % mass remaining of standing litter (average mass loss of all plant species litter in the dry water depth treatment) in resident plant communities, *P. australis* invaded and herbicide-treated sites (n = 3). C) Change in % mass remaining of *C. canadensis*, *Typha* spp. and *P. australis* litter (average mass loss of litter across shallow, intermediate and deep water depths and sites; n = 9). D) Change in % mass remaining of *C. canadensis*, *Typha* spp. and *P. australis* standing litter (averaged across site type in the dry water depth treatment, n = 3). E) Change in mass remaining of standing and submerged litter (average mass loss across all plant species and site types) where dry refers to standing litter and shallow, intermediate and deep water depths refer to submerged litter (n = 12).

b) Soil carbon dioxide efflux

I measured soil carbon dioxide efflux rate (CO_2 µmol mol^{-1} min^{-1}) once per month at each litterbag site from June to October 2017 and the rate of soil carbon dioxide efflux released per meter-squared per day ($m^{-2}d^{-1}$) was calculated (Appendix 11). The model predicting soil carbon dioxide efflux (CO_2 $m^{-2}d^{-1}$) based on site type (resident plant communities, *P. australis* invaded and herbicide-treated), the water depth during the soil carbon dioxide measurement (cm) and their interaction provided a reasonable fit ($F_{5,39}$ = 2.925, *p*-value = 0.025, R^2 = 0.272).There was no significant interaction between water depth (cm) and site type (Appendix 11). There was also no significant difference in soil carbon dioxide efflux ($m^{-2}d^{-1}$) among uninvaded, *P. australis* invaded and herbicide treated sites, but water depth had a significant impact (Appendix 11). In general, more soil carbon dioxide efflux ($m^{-2}d^{-1}$) may be occurring in deeper sites (Appendix 11). Overall, it appears that soil carbon dioxide efflux ($m^{-2}d^{-1}$) peaked in July 2017, and decreased thereafter (Appendix 11).

In addition, soil carbon dioxide efflux rate (CO_2 $m^{-2}d^{-1}$) was measured on April 20, 2018 in cattail, *P. australis* invaded and herbicide-treated marshes located within 150 m of each other. Water temperature ranged from 5.0 - 8.0°C during measurements. The model predicting soil carbon dioxide efflux based on site type (resident plant communities, invaded and herbicide-treated) provided a reasonable fit ($F_{2,12}$ = 0.209, *p* = 0.814, R^2 = 0.034). Soil carbon dioxide efflux did not significantly differ among sites (Appendix 11).

3.4 Discussion

My research objectives were to quantify the effect of invasive *P. australis* on carbon dynamics and evaluate the immediate efficacy of herbicide-treatment at restoring carbon dynamics to the

levels found in uninvaded plant communities. Though much research has been done on the effects of invasion of cattail marsh by *P. australis* on carbon dynamics, my results extend this to where *P. australis* invades meadow marsh and displaces *C. canadensis*. In such a circumstance, the effects of invasion on primary production, litter accumulation and decomposition rates appear much more extreme than where *P. australis* displaces *Typha* spp. Importantly, my results emphasize that the effect of *P. australis* invasion on net primary production, decomposition rates and environmental covariates depends on which plant community was invaded; where increased carbon accumulation in *P. australis* invaded marsh was observed compared to meadow marsh and few changes were observed compared to cattail marsh.

The more novel contribution of my work is in documenting the immediate effects of herbicide-based control 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. For example, more than 80000 hectares of *P. australis* invaded marsh was treated with herbicide in the USA between 2005 - 2009 (Martin and Blossey 2013), and yet there is limited understanding of the consequences for carbon assimilation or environmental conditions that influence decomposition rates. I observed a net reduction in carbon assimilation in the year following herbicide treatment, but interestingly I did not detect an increase in carbon release compared to resident plant communities and *P. australis* invaded marsh. From this I conclude that the temporary reduction in carbon assimilation associated with *P. australis* control is the primary effect and presuming that the areas revegetate with emergent plants over time, it will be limited in duration.

3.4.1 Effect of herbicide-based control efforts

I was not able to directly measure carbon assimilation rates in the herbicide-treated portion of the marsh due to the underwater growth forms of most of the species present (Appendix 7). Total standing crop biomass, however, was significantly lower in herbicide-treated sites than resident plant communities or invaded sites; herbicide-treated sites produced almost four times less total biomass than resident plant communities (Fig. 3.3). Based on this lower net primary production, I conclude that carbon assimilation is significantly reduced in herbicide-treated marsh one-year post-herbicide application; resulting in a gap in carbon sequestration function in these treated marshes.

Interestingly, there was not more soil carbon dioxide efflux or an increase in decomposition rates in the herbicide-treated sites relative to the invaded and resident plant community sites, indicating site characteristic changes that occurred following control efforts did not increase overall decomposition rates. Soil carbon efflux (CO_2 $m^{-2}d^{-1}$) did increase in deeper sites within all marsh plant communities (Appendix 11), and temperature, water depth and vegetation types were previously significantly correlated to soil carbon efflux rates in diverse habitats (Chojnicki et al. 2010, Bowne and Johnson 2013, Pavelka et al. 2016). In addition, the anticipated spring pulse of soil carbon dioxide efflux was not detected when I sampled in the spring following herbicide application. This result was contrary to previous research comparing *P. australis* invaded sites with controlled sites, where increased carbon dioxide release was observed in controlled sites where the aboveground biomass was removed (Martin and Moseman-Valtierra 2017). It is possible that cool spring temperatures delayed the pulse of carbon dioxide emissions so that it was not detected during my sampling. Yet, because both *P. australis* invaded and resident plant communities comprise graminoid dominated vegetation that naturally senesces every winter, I believe that the carbon dioxide released following herbicide treatment is not

substantially greater than that which occurs naturally when annual aboveground tissues are shed and begin to decompose.

3.4.2 Plant community recovery in herbicide-treated marsh

The gap in carbon sequestration function in the herbicide-treated marsh, from decreased net primary production, may be short-lived. By July, approximately ten months after treatment, living plant cover within controlled marsh was already 41% (± 8 SD) although most of the plants present were submerged or floating aquatic vegetation (Appendix 7), and very few emergent plant individuals were present. Submersed and floating vegetation tissues may decompose faster than emergent macrophytes (Chimney and Pietro 2006, Ping et al. 2017) due to changes in chemical composition or consistent submersion of dead plant material. Thus, this community change likely has consequences for decomposition rates and carbon sequestration rates in herbicide-treated marsh.

Notably, this is only one year after the herbicide was applied. It is unclear whether the herbicide-treated areas will transition toward a state more like the vegetation in resident plant communities with time. Previous research suggests that successful restoration of native plant communities through controlling *P. australis* and letting the native seed bank re-establish maybe be possible without further restoration efforts (Ailstock et al. 2001, Carlson et al. 2009, Baldwin et al. 2010). However, without active restoration efforts, such as native species planting or seeding, there is also a possibility that these sites will be re-invaded by *P. australis* or other undesirable species (Hazelton et al. 2018). In addition, recovered plant communities may possess traits different from the resident plant community present before invasion (Alldred et al. 2016). However, a

return visit to the herbicide-treated marsh in 2018 provided visual evidence that an emergent plant community, which included some *P. australis*, was re-establishing (Appendix 7).

Several factors are influencing the establishment of emergent plant communities and subsequent recovery of net primary production and decomposition rates in herbicide-treated marsh. Water depth and variance (Keddy and Reznicek 1986, Coops and Van der Velde 1995, Casanova and Brock 2000), water temperature, and light availability (Bonnewell et al. 1983, Leck 1996, Kettenring et al. 2006) are important variables that can affect germination of wetland species. Standing dead was rolled/ mowed in the herbicide-treated sites, and the emergent macrophyte canopy was short when present (15 cm ± 14 SD, Table 3.2), so approximately 100% PAR reached the water surface in the herbicide-treated sites. This increase in solar radiation to the water surface likely accounts for the increased water temperature and daily temperature fluctuations observed within the herbicide-treated sites (Table 3.5). Increased solar radiation reaching the water surface and warmer water temperatures likely benefits the general recovery of plant communities within the herbicide-treated sites (Bonnewell et al. 1983, Leck 1996, Kettenring et al. 2006). However, Lake Erie had unusually deep lake levels in 2017 and 2018 (The Canadian Hydrographic Service 2016) and at the sites where primary productivity was measured, herbicide-controlled sites were deeper in July than resident plant communities and *P. australis* invaded sites (Table 3.2), although no significant difference in average hourly water depth was detected within a subset of these sites (Table 3.4, Appendix 9). These deeper water depths may be promoting the establishment of floating or submerged aquatic plant species instead of emergent vegetation (Euliss et al. 2004).

Even if water levels within Lake Erie decline sufficiently, the litter layer present within the herbicide-treated marsh could impede emergent plant community recovery. While the intent of

the secondary treatments was to burn the rolled or mowed *P. australis* after it was treated with herbicide, weather conditions were not favourable and burning actions were never completed (Veenhof 2017). As a result, there is an extremely dense, flattened litter layer (Table 3.2, Appendix 10). Previous work observed that removing *P. australis* litter allows for increased species richness recovery and native plant biomass recovery in the first year post-treatment (Ailstock et al. 2001, Carlson et al. 2009, Holdredge and Bertness 2011). Research documenting the negative impact of macrophyte litter on resident plant communities suggest that litter mats could decrease seedling germination by changing environmental conditions, such as temperature or light availability or by physically preventing seedlings from being able to push through the litter layer (van der Valk 1986, Holdredge and Bertness 2011).

In order for emergent plant communities to establish, this dense litter layer will need to decompose. Ideally, burning the dead biomass would quickly remove it and promote plant community recovery. However, compressing the standing dead stems in the herbicide-treated sites into the underwater litter layer will increase the decomposition rate, as there is a significant increase in decomposition of submerged versus standing stems (Fig 3.6, Table 3.8, Bedford, 2005; Dolinar et al., 2015). This emphasizes the importance of secondary mechanical control efforts, such as burning, rolling or mowing, that help remove the legacy standing dead *P. australis* biomass and open the substrate to the light and warmth necessary to encourage recovery of resident emergent species from the seed bank.

3.4.3 Role of water depth on primary productivity

Primary productivity was measured across a water depth gradient. Generally, higher net primary production, as measured by annual total (aboveground and belowground) biomass was produced

in deeper water (Appendix 10). Two factors led to increased biomass production in deeper water. First, in deeper water there was increased total biomass production within meadow, cattail and invaded marsh; previous work indicates that increased aboveground biomass is produced by *Typha* spp. and *C. canadensis* when exposed to increased water depths (Wetzel and van der Valk 2005, Duke et al. 2015). *Phragmites australis* appears to have a more variable reaction to increased water depths, which depends upon the location (e.g. freshwater versus brackish marsh) and water depth treatments (Engloner 2009). However, in my study more total biomass was produced by *P. australis* growing at deeper water depths. Secondly, the dominant plant species present in shallower (< 30 cm in July) resident plant communities was *C. canadensis* (meadow marsh), whereas in deeper resident plant communities *Typha* spp. (cattail marsh) was dominant. These two communities produce very different annual standing crops (Fig. 3.3, Chapter 2). Similarly, carbon assimilation rates were measured along the water depth gradient of resident plant communities (meadow and cattail) and *P. australis* invaded marsh. Like plant biomass measurements, significant changes in carbon assimilation rates per unit of leaf area depended upon which resident plant community was being replaced. The effect of invasion on net primary productivity is therefore dependent on whether meadow or cattail marsh is being replaced.

3.4.4 Effect of invasion on net primary productivity

Many studies have compared *P. australis* invaded and cattail marsh but there is very little published about the effects of *P. australis* invasion in meadow marsh, even though *P. australis* invades meadow marsh as much as it invades cattail marsh in Long Point (Wilcox et al. 2003). The standing crop of meadow marsh (Fig. 3.3, Chapter 2) and the maximum carbon assimilation rate was significantly lower than invaded marsh, regardless of whether measured per unit leaf area or scaled up to the marsh level. The standing crop of meadow marsh compared to cattail or

P. australis invaded marsh has never been previously investigated in the Great Lakes region, but the aboveground biomass of meadow marsh in my study is comparable to results from a greenhouse experiment (1057 ±12 g m^{-2} Ouellet-Plamondon et al., 2004). Carbon assimilation rates of *C. canadensis* re-growth have previously been reported at rates similar to my own results albeit at a much lower PAR (7.4 - 22.7 µmol CO^2 m^{-2} s^{-1} at 650 µmol m^{-2} s^{-1} PAR; Hogg and Lieffers 1991). My carbon assimilation curves indicate that *C. canadensis* does not increase its carbon assimilation rate much above 600 µmol m^{-2} s^{-1}, and so this is not unexpected.

Cattail marsh and invaded marsh in the Great Lakes did not have significantly different total or aboveground biomass (Chapter 2); and these results are reflected in the literature (cattail: 1661 - 2930 g m^{-2} and *P. australis* invaded: 1522 - 3378 g m^{-2} Duke et al., 2015; Rothman and Bouchard, 2007). Carbon assimilation rates per unit of leaf area also did not differ significantly between *P. australis* and *Typha* spp. (Fig. 3.4). My reported maximum carbon assimilation rates for *P. australis* and *Typha* spp. (Fig. 3.5C) were within the range reported in the literature (*P. australis*: approximately 15 - 28.21 µmol CO_2 $m^{-2}s^{-1,}$ *Typha* spp.: approximately 20 - 25 µmol CO_2 $m^{-2}s^{-1}$; Farnsworth and Meyerson, 2003; Tho et al., 2016). Higher foliar nitrogen is correlated with higher carbon assimilation rates on a per mass basis in a worldwide review (Reich et al. 2009). Yet despite *P. australis* having higher foliar nitrogen content than *Typha* spp. (Chapter 2), I observed that the two species had equivalent maximum carbon assimilation capacities per unit leaf area (Fig. 3.5C). This observation agrees with what other researchers comparing *P. australis* and *Typha* spp. have reported (Farnsworth and Meyerson 2003, Hirtreiter and Potts 2012).

The effect of *P. australis* invasion on marsh primary production cannot be generalized across resident plant communities because the effect is so disparate between meadow and cattail marsh.

In deep water where *P. australis* replaces cattail marsh, any increases in carbon assimilation are small and there are no significant changes in standing crop biomass. In contrast, where *P. australis* replaces meadow marsh in shallower water, there is a dramatic increase in carbon assimilation rates and total biomass as a consequence of invasion. Invasion by *P. australis* may affect these two resident plant communities differently because cattail marsh was dominated by *Typha* x. *glauca*, which is a hybrid between invasive *T. angustifolia* and native *T. latifolia*. Therefore when *P. australis* invades cattail marsh it is simply displacing another invasive species, which would share some common traits such as increased carbon assimilation and aboveground biomass production (Farnsworth and Meyerson 2003, Tho et al. 2016). The consequences of this second invasion would appear less severe because the changes in traits are less extreme. Whereas when *P. australis* replaces meadow marsh it is extirpating an assembly of native species with distinct plant traits and the consequences of the community change are more drastic.

With the similarities in carbon assimilation capacity and total standing crop biomass, it begs the question why *P. australis* has so successfully replaced *Typha* spp. dominated cattail marsh in Long Point. Though similar at the leaf-scale, integrating up to the community-level reveals the greater productivity of *P. australis*. Invaded marsh intercepted more light (Fig. 3.2), had a higher specific leaf area (Fig. 3.5A), and produced more standing leaf area per meter-squared of wetland (Fig. 3.5B). Consequently, the product of carbon assimilation rates per unit leaf area and the standing leaf area per meter squared of wetland yields a higher carbon assimilation rate per meter squared of invaded marsh than it does for cattail marsh (Fig. 3.5D).

There are three important caveats to my results on net primary production and carbon assimilation rates. First, *C. canadensis*, *Typha* spp. and *P. australis* are all rhizomatous, and *P.*

australis can root to depths of greater than one meter (Bernal et al. 2016). As a result, belowground biomass is difficult to accurately measure in the field. To restrict belowground biomass to an annual crop, I used a soil core ingrowth method, and due to logistical restraints of working in a flooded wetland, my soil cores were inserted to a relatively shallow depth (11.3 cm). Therefore my belowground biomass and root: shoot ratios reflect the annual belowground biomass (to 11.3 cm) and are much lower than those reported in the literature that typically include all prior years of production (Mason and Bryant 1975, Powelson and Lieffers 1992, Farnsworth and Meyerson 2003, Ouellet-Plamondon et al. 2004, Rothman and Bouchard 2007). Measuring belowground biomass to a depth of 40 cm would have yielded a more accurate assessment of total belowground biomass, as research in my study area reports that >90% of all belowground biomass is within the upper 40 cm of the soil profile in meadow, cattail and invaded marshes (Lei 2018). The ingrowth soil cores in my study likely captured approximately 40% of the annual biomass production, as approximately 38% ± 21 SD of belowground production was accounted for in the top 10 cm of the soil profile (Lei 2018).

My second and third caveat concern carbon assimilation rates. I scaled up to the marsh-level using the assumption that all leaves present in the canopy were exposed to 1500 µmol m^{-2} s^{-1} of PAR. This value is less than incident PAR measured between 10 am and 2 pm, but I determined that >50% of this incoming PAR is intercepted before penetrating 50% of the way down the canopy (Fig. 3.2). Thus, leaves deeper in the canopy are receiving less light than those at the top of the canopy, especially in *P. australis* stands, which intercepted the most light (Fig. 3.2). My results indicate that for all three target species, carbon assimilation per unit leaf area remains fairly steady between 1500 and 600 m^{-2} s^{-1}, but at lower light levels it begins to drop off (Fig. 3.4), so I expect that leaves lower in the canopy are not assimilating as much light as I assumed

in my calculations. Notably, Hirtreiter and Potts (2012) found that carbon assimilation rates remained consistently high in *P. australis* leaves, regardless of their position in the canopy. In contrast, *Typha* spp. carbon assimilation rates decreased in the lower canopy where less light reached (Hirtreiter and Potts 2012). Therefore, my estimates of marsh-level carbon assimilation rates are possibly high, particularly in cattail marsh. However, total biomass and plant-scaled carbon assimilation rates are strongly correlated (Sutton-Grier and Megonigal 2011), and I detected no significant difference in total biomass between cattail marsh and invaded marsh (Fig. 3.3, Chapter 2). Thus, I conclude that any differences in net primary production between *P. australis* invaded and cattail marsh are negligible, though *P. australis* is assimilating slightly more carbon per meter squared of wetland.

Lastly, meadow marsh carbon assimilation rates per meter-squared of wetland are underestimated in my study, though I am confident that they are truly significantly lower than in cattail and *P. australis* invaded marsh. Carbon assimilation rates for the meadow, cattail and *P. australis* invaded marsh on an area basis were calculated using only aboveground biomass of my target species (*C. canadensis, Typha* spp., and *P. australis*), and the contribution of other species was excluded. This disproportionately underestimates meadow marsh carbon assimilation rates because meadow marsh had a more diverse assemblage of species compared to the relative monocultures in cattail and *P. australis* invaded marsh (Table 3.2).

3.4.5 Changes to decomposition rates

The net effects of *P. australis* invasion on wetland decomposition rates are difficult to quantify because of conflicting direct (more degradable litter quality) and indirect (wetter, cooler, shadier, and more standing dead litter than in meadow marsh) effects of invasion. Duke et al. (2015)

conducted a litterbag transplant experiment using *Typha* spp. and *P. australis* litter and concluded that site characteristics in *P. australis* invaded marsh increased decomposition rates more than differences in species litter quality. However, they did not evaluate *C. canadensis*. It was suggested that faster decomposition rates in invaded marsh may be due to increased oxygen and nutrient availability to plants and microbes (Duke et al. 2015), suggesting the primacy of indirect invasion effects in determining decomposition rates. However, Windham (2001) carried out a litter transplant experiment using *Spartina patens* and *P. australis* litter and reported that *S. patens* decomposed faster, indicating that changes in litter quality following invasion had a greater effect than any alteration to environmental site characteristics.

In part, my results support those of Duke et al. (2015), in that the single largest influence on decomposition rates was whether the litter was submersed or suspended dry above the water line. Suspended litter of all species decomposed much more slowly than submerged litter, regardless of the litter type or the site type (Table 3.8, Fig. 3.6). Water depth has had a consistently positive effect on decomposition rates of *P. australis* in numerous studies in freshwater and brackish 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). Litter that is never inundated can take up to two times longer to decompose than submerged litter (Dolinar et al. 2015). Submerged litter in deeper water did appear to decompose at a faster rate than litter in shallow water but this trend was non-significant (Fig. 3.6, Table 3.8). Vymazal and Březinová (2016) also report that submerged litter decomposes at an equivalent rate, regardless of immersion depth.

Yet, considering submersed litter only, my results support those of Windham (2001), indicating that litter quality has a greater effect on decomposition rates than site characteristics. Enriquez et al. (1993) reviewed decomposition studies and reported that nutrient quality had a stronger correlation to decomposition rates when litter was submerged than when in dry sites. I observed that plant litter of a given species decayed at about the same rate regardless of its depth of inundation and regardless of whether it was situated in *P. australis* invaded habitat, cattail marsh or meadow marsh (Fig. 3.6A&B). *Phragmites australis* leaf litter had higher foliar nitrogen concentrations than *C. canadensis* leaves and stems and *Typha* spp. leaves (Chapter 2, Farnsworth and Meyerson, 2003; Hirtreiter and Potts, 2012), suggesting it would decompose significantly faster. This prediction was supported by my litter transplant experiment, wherein *P. australis* litter decomposed at a faster rate than either *Typha* spp. or *C. canadensis* litter (Fig. 3.6). I observed that *Typha* spp. and *C. canadensis* tissues decomposed at equivalent rates, which was also predicted, as the nitrogen concentration in tissues of *C. canadensis* and *Typha* spp. used in my litter bag transplant study were not significantly different (Chapter 2).

I observed several changes to environmental conditions in *P. australis* invaded marsh that could affect decomposition rates. Other published studies have observed that *P. australis* invasion led to shallower water and attributed this to increased evapotranspiration, increased belowground biomass production, or litter accumulation in invaded sites (Windham and Lathrop 1999, Rooth et al. 2003, Duke et al. 2015). In contrast, in my study system I observed that *P. australis* invaded sites retained more water than uninvaded and herbicide-treated sites during summer drawdown, particularly at shallower water depths (Appendix 9). Because the water depth at sites in May was paired among plant communities, the difference in water depth later in the growing season cannot be attributed to differences in topography or a preference for *P. australis* to grow

in deeper water. Rather, I suspect that water depths were greater in invaded sites later in the summer because invaded sites were cooler and shadier, particularly compared to meadow marsh, which may have reduced evaporation. This is supported by my measurements of light penetration and water temperature. Interestingly, I also detected an increase in hourly or daily fluctuations in water depth in deeper resident plant communities and invaded sites, which may indicate that deeper sites had greater connectivity to Lake Erie.

I suspect that the negligible net effect of these altered environmental conditions on the decomposition of submersed litter resulted because some of the changes I observed that should increase decomposition rates (i.e. increased dissolved oxygen and 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). For example, previous work by Bedford (2005) reported a small, but positive correlation between decomposition rates of *P. australis* and temperature, which was reduced by greater shading in *P. australis* 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 my study location.

The accumulation of extensive standing litter in *P. australis* invaded sites observed within my own study and others (e.g., Rooth et al. 2003) presents an apparent contradiction to my conclusion that *P. australis* leaf tissue is more easily decomposed than other plant species. However, because of its stiff culms, *P. australis* is able to remain standing for long periods post-senescence, and consequently the litter may remain suspended above the water at a lower decomposition rate. In addition, decomposition rates as a function of litter quality are specific to the tissue type used in the experiment. For example, the chemical composition of *P. australis*

culms has a much lower nitrogen concentration than *P. australis* leaf tissue (Chapter 2) and the decomposition rate of culms in the literature is approximately two times slower than leaves (Dinka et al. 2004, Bedford 2005, Ágoston-Szabó and Dinka 2008, Dolinar et al. 2015). My own pilot work in the Long Point area supports this ratio: submerged *P. australis* culms lost 38.65 % (± 7.05 SD) mass after one year, compared to 81.26% (± 8.73 SD) loss of submerged leaf mass (Appendix 8). The aboveground biomass of *P. australis* is predominately stems (leaf: stem ratio = 0.36 ± 0.10 SD) which is similar to *C. canadensis* (leaf: stem ratio = 0.34 ± 0.08 SD) and considerably lower than *Typha* spp. (leaf: stem ratio = 0.90 ± 0.33 SD). While *P. australis* leaves decomposed quicker than resident plant species litter (Fig. 3.6), the large proportion of culms in invaded marsh may lead to an overall slower rate of *P. australis* (leaf and stem) litter decomposition, especially if culms remain emergent and dry (i.e. standing dead litter).

3.4.6 Effect of invasion on soil carbon efflux

Carbon sequestration is dependent on the relative net primary production and decomposition rates. Soil carbon dioxide efflux rates demonstrate how quickly carbon is released from marsh habitat in Long Point. Despite concerns that invaded sites may return more carbon to the atmosphere than resident plant community sites because *P. australis* has a deeper rooting system than native vegetation, and could access deep carbon pools in the soil (Bernal et al. 2016) and prior reports that invasive *P. australis* released more methane than native *P. australis* (Mozdzer and Megonigal 2013), I did not observe a difference in soil carbon dioxide efflux between resident plant communities and *P. australis* invaded ones. My conclusion agrees with another Lake Erie field study, which reported a non-significant increase in soil carbon dioxide efflux in invaded sites (Duke et al. 2015).

3.5 Conclusion

My findings are relevant to decision-makers who are considering whether to employ herbicide to attempt to eradicate *P. australis*. Understanding the net effects of wetland plant invasions and control efforts on wetland functions informs decision about invasive species control efforts (e.g., Gaertner et al. 2016). Land managers face potential trade-offs from *P. australis* control efforts; biodiversity conservation may increase (Schummer et al. 2012, Markle and Chow-Fraser 2018), but carbon sequestration decreases following herbicide-application. Understanding these net effects on ecosystem functions provides necessary information to decision-makers who already must consider societal values, economic feasibility, and other uncertainties (Liu et al. 2011, Martin and Blossey 2013), when deciding whether to control *P. australis*.

Phragmites australis invasion dramatically changed the carbon budget when it replaced meadow marsh that was historically dominated by *C. canadensis*. Net primary production increased in invaded marsh, and although *P. australis* foliar litter is more degradable, at the marsh-level most of the *P. australis* biomass is composed of standing dead culms that remain in cooler, shadier sites so there was no increase in carbon efflux observed. Overall, *P. australis* invasion of meadow marsh resulted in a net increase in carbon sequestration. This represents a trade-off in ecosystem services: invasion of meadow marsh enhances carbon sequestration (Fig. 3.3, Fig. 3.5) but leads to decreases in plant species richness (Appendix 7) and wildlife value (e.g., Markle and Chow-Fraser 2018; Robichaud and Rooney 2017).

Alternatively, when *P. australis* replaced cattail marsh, which was dominated by non-native hybrid cattail, there was no significant change in total biomass, carbon assimilation, or decomposition rate. The lack of significant influence on carbon dynamics is perhaps surprising,

given that *P. australis* has more easily degraded foliar tissue, increases the duration of inundation by retaining more water during summer drawdown, intercepts light and cools and moderates the water temperature, and produces a much greater volume of stem tissue. Yet, these changes appear to offset one another resulting in a net-neutral effect of *P. australis* invasion on cattail marsh habitat carbon sequestration. Despite little change to carbon services, *P. australis* invasion of cattail marsh has well-established negative effects on wildlife and plant diversity (e.g., Keller 2000, Robichaud and Rooney 2017), indicating a net negative effect of invasion of cattail marsh overall.

Wetlands along Lake Erie have the highest diversity of wetland flora and fauna of any of Canada's Great Lakes coastal wetlands (Ball et al. 2003). Furthermore, wetlands in Long Point provide critical habitat for provincially significant plants, reptiles, amphibians and migratory birds (Ball et al. 2003). Any benefits from increased carbon sequestration in meadow marsh invaded by *P. australis* may be outweighed by the importance of these wetlands to provincially significant wetland species and clearly there is no benefit where *P. australis* invasion displaces cattail marsh. Thus, efforts to control this invader in Long Point are likely justified on the basis of asset protection.

Efforts to control *P. australis* with herbicide may be under taken to re-establish biodiversity (Martin and Blossey 2013) but these control efforts dramatically reduce total biomass and carbon assimilation in the first year post-treatment. However, despite increased water depth, water-level stability, and temperature in herbicide-treated sites, no increase in decomposition rates and no increase in soil carbon dioxide efflux was observed. Plant community recovery is crucial to increase carbon sequestration in herbicide-treated marsh, and rapid recovery of floating and submersed 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 likely 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).

4 Summary and implications

4.1 Thesis summary

Resident wetland plant communities in North America are being invaded by the invasive, European lineage of *Phragmites australis* (Catling and Mitrow 2011, Saltonstall and Meyerson 2016). Invasive *P. australis* establishes thick monocultures in invaded wetlands which replaces the resident plant communities (Keller 2000, Mal and Narine 2004, Tulbure et al. 2007) and has a negative impact on wetland herptiles (Bolton and Brooks 2010, Greenberg and Green 2013, Markle et al. 2018) and birds (Robichaud and Rooney 2017). This invasion also effects wetland ecosystem functions, such as macronutrient cycling, due to changes in the size and nutrient composition of the annual vegetative standing stock, decomposition rates, and environmental conditions (Meyerson et al. 2000, Windham 2001, Rothman and Bouchard 2007, Engloner 2009, Duke et al. 2015). My thesis work confirms that the effect of these *P. australis* invasion-based changes on macronutrients may also be dependent on site specific conditions, such as availability of nutrients and standing water depth (Table 4.1), as has been reported elsewhere (Farnsworth and Meyerson 2003, Currie et al. 2014, Duke et al. 2015).

As a result of the changes *P. australis* invasion can cause to wetland flora, fauna, and ecosystem processes, extensive efforts to control *P. australis*, mainly through the use of herbicide, have been made (Martin and Blossey 2013, Hazelton et al. 2014). The first herbicide-based control effort of *P. australis* over standing water in Canada occurred in Long Point in August 2016. Restoring the ecological integrity of invaded wetlands requires the recovery of ecosystem processes to within pre-invasion ranges (Karr 1993), and while previous research has reported on the efficacy of *P. australis* control efforts (Lombard et al. 2012, Quirion et al. 2018) and the

recovery of plant communities (Ailstock et al. 2001, Breen et al. 2014), the ability of control efforts to restore macronutrient dynamics to pre-invasion ranges has not been comprehensively studied. The objective of my thesis is to quantify the changes in macronutrient pools and fluxes in annual vegetative standing stocks as a result of *P. australis* invasion of meadow and cattail marsh in Long Point (Lake Erie), and subsequent herbicide-based control efforts. I summarize the results of my research in table 4.1.

Table 4.1 Effect of *P. australis* invasion on uninvaded meadow (*C. canadensis*) and cattail (*Typha* spp.) marsh and the effect of herbicide-based control efforts on meadow, cattail and *P. australis* invaded marsh. Data collected in Long Point, ON in 2017.

		Effect of *P. australis* invasion		Effect of control efforts		
Wetland traits		Meadow marsh (*C. canadensis*)	Cattail (*Typha* spp.)	Meadow marsh (*C. canadensis*)	Cattail (*Typha* spp.)	Invaded (*P. australis*)
Site characteristics	Water depth	+	+	=	=	-
	Water fluctuations	+	+	=	=	-
	Water temperature	-	=	+	+	+
	Incident light	-	=	+	+	+
Soil nutrients	Carbon	=	=			
	Nitrogen	=	=			
	Phosphorus	=	=			
	Potassium	=	=			
	Magnesium	=	=			
	Calcium	=	=			
Plant tissue nutrient concentration	Carbon	=	=			
	Nitrogen	+	+			
	Phosphorus	+	=			
	Potassium	+	=			
	Magnesium	=	=			
	Calcium	=	-			
Net primary productivity	Aboveground biomass	+	=	-	-	-
	Belowground biomass	+	-	+	-	=
	Carbon assimilation	+	=			
Biomass accumulation	Standing dead	+	=	-	-	-
	Litter	+	=	+	+	+
	Decomposition rate (litter quality)	+	+			

In my first chapter, I provided a literature review describing wetland ecosystem processes, with a focus on macronutrient cycling. I also depicted the history of *P. australis* invasion in North America and the effects of this invasion on carbon and other macronutrient pools and fluxes. Lastly, I summarized the current literature on *P. australis* control efforts. This literature review provided context for my second and third chapter.

In my second chapter, I focussed on the effect of *P. australis* invasion on macronutrient storage in annual vegetation standing stocks. I compared meadow marsh, cattail marsh and *P. australis* invaded communities in a high nutrient and low nutrient wetland environment and across a water depth gradient. It is generally thought that *P. australis* invasion can increase the annual vegetative nutrient stocks because *P. australis* has high net primary production (Windham 2001, Rothman and Bouchard 2007, Duke et al. 2015), high foliar nitrogen content (Findlay et al. 2002, Hirtreiter and Potts 2012) and assimilates carbon at a high rate (Farnsworth and Meyerson 2003, Tho et al. 2016). In addition, *P. australis* is used in constructed wetlands in its native range to remove nutrient pollution (Gumbricht 1993, Bhatia and Goyal 2014), which suggests it could provide water quality improvements in invaded areas. Furthermore, *P. australis* invasion may have a greater effect on macronutrients in high nutrient conditions; previous research suggests the biomass production of *P. australis* may increase more than resident plant communities under high nitrogen conditions (Caplan et al. 2015). The effect of invasion may also differ along a water depth gradient; Duke et al. (2005) reported that *P. australis* produced less biomass than *Typha* spp. in wetter years. As eutrophication and climate change are threats to Lake Erie (Watson et al. 2016, Jarvie et al. 2017, Environment and Climate Change Canada and the U.S. Environmental Protection Agency 2017), the capacity of a plant, regardless of whether it is invasive or not, to store macronutrients is an important ecosystem function.

Within this chapter, I quantified invasion-driven changes in these ecosystem functions by measuring above and belowground biomass, nutrient tissue concentration and annual nutrient vegetative stocks in meadow marsh dominated by *C. canadensis*, cattail marsh dominated by *Typha* spp. and invaded marsh dominated by *P. australis*. I also evaluated whether the effect of invasion on annual nutrient vegetative standing stocks was altered in high versus low nutrient environments or along a water depth gradient. My results indicated that *P. australis* invasion of meadow marsh increased the annual nutrient vegetative stock of nitrogen, carbon, phosphorus and potassium by increasing tissue concentrations and the total biomass in the wetland (Table 4.1). When *P. australis* replaced cattail marsh, I did not observe a significant change in annual nutrient vegetative stock for nitrogen, phosphorus, potassium, despite differences in the nitrogen tissue concentrations (Table 4.1). Interestingly, cattail marsh had the greatest annual nutrient standing stock of calcium and magnesium (Table 4.1). Generally, the effect of *P. australis* invasion did not differ in high versus low nutrient environments or across the water depth gradient, indicating that abiotic factors do not have a large influence on invasion-driven changes to macronutrient storage. Overall, the results from my second chapter support the conclusion that invaded marshes appear to provide similar macronutrient storage as those currently provided by cattail marsh in Long Point, but store significantly more nutrients than meadow marsh.

In my third chapter, I evaluated the effect of *P. australis* invasion in meadow and cattail marsh, and herbicide-based *P. australis* control efforts, on carbon sequestration along a water depth gradient. *Phragmites australis* invasion can affect wetland carbon storage by changing the net primary productivity of the marsh and the decomposition rate of litter. Generally, *P. australis* has high rates of carbon assimilation and biomass production (Windham 2001, Farnsworth and Meyerson 2003, Duke et al. 2015) and relatively slow decomposition rates (van der Valk et al.

1991, Rothman and Bouchard 2007, Duke et al. 2015), which could increase carbon storage. In addition, *P. australis* invasion can change abiotic conditions of the marsh that affect carbon dynamics, including decreasing water levels (Lathrop et al. 2003, Hunter et al. 2006), restricting water sheet flow (Weinstein and Balletro 1999), increasing shading and decreasing edaphic temperatures (Rooth et al. 2003, Holdredge and Bertness 2011, Hirtreiter and Potts 2012).

I first quantified the effect of *P. australis* invasion on the carbon assimilation rate at the marsh-level and annual aboveground and belowground biomass production. My results indicated that, averaged across the water depth gradient, *P. australis* invasion increased the carbon assimilation rate and biomass production in the wetland (Table 4.1). However, there were significant differences in biomass production and carbon assimilation rate between uninvaded meadow marsh (present at shallower depths) and cattail marsh (present in deep water depths). Therefore, the effect of invasion on net primary productivity was strongly dependent on which marsh community was replaced. Biomass production and carbon assimilation rates were similar in cattail and invaded marsh, but when *P. australis* replaced meadow marsh there was a significant increase in biomass and carbon assimilation.

The effect of *P. australis* invasion on decomposition rates has been reported to depend on changes to the litter quality (Windham 2001) and site conditions (Duke et al. 2015). In my third chapter I used a litterbag transplant experiment to determine the relative effect of changes in litter quality (high nitrogen in *P. australis* leaf litter versus *C. canadensis* leaf and stem litter and *Typha* spp. leaf litter) compared to changes in environmental conditions in uninvaded meadow, cattail, and invaded plant communities along a water depth gradient. Invaded sites were cooler, shadier and experienced less seasonal drawdown than uninvaded sites and had greater water fluctuations throughout the growing season (Table 4.1). My results indicated that changes in

litter quality had a strong effect; *P. australis* leaves were more highly degradable than *C. canadensis* or *Typha* spp. litter. Site characteristics did not appear to effect decomposition rates; litter of a given species decomposed at a similar rate regardless of whether it was in an uninvaded meadow, cattail or *P. australis* invaded site. In addition, no differences in soil carbon dioxide efflux were recorded among plant communities, although there was an increase in efflux at deeper water depths.

At the marsh level, however, *P. australis* invaded marshes accumulated more dead biomass than uninvaded meadow marsh. My results indicated that this accumulation of biomass in invaded marshes, despite having more degradable leaf litter, likely resulted from two characteristics of *P. australis*. First, the majority of the aboveground biomass of *P. australis* is formed by culms instead of leaves. These culms have nitrogen and phosphorus concentrations that do not significantly differ from *C. canadensis* and *Typha* spp. stems. Furthermore, submerged culms decomposed much slower than submerged leaves in Long Point during a pilot litterbag transplant experiment. Secondly, standing dead in *P. australis* invaded marsh increase in density over time (Rooth et al. 2003); most of the culms in *P. australis* invaded marsh remain standing for multiple years . These standing dead stems are not submerged in the standing water. Litterbags that I placed above the standing water level to mimic standing dead litter decomposed significantly slower than litter that was submerged throughout my study. These characteristics of invaded marsh likely explain the discrepancy between my conclusion that *P. australis* leaf litter decomposed faster than other plant species and the accumulation of dead biomass in invaded marshes.

The last objective of my third chapter was to assess the immediate effect of herbicide-based control efforts at returning net primary production, decomposition rates and abiotic conditions to

ranges found in adjacent uninvaded meadow and cattail marsh. Total biomass was significantly reduced in herbicide-treated areas one-year post-herbicide application, resulting in a gap in carbon sequestration in the marsh. However, this gap may be short lived; I observed 41 % plant cover the herbicide-treated area, although the majority of that vegetation was submerged or floating aquatic vegetation and few emergent plants were present. No change in soil carbon dioxide efflux or in the rate of decomposition of *P. australis*, *C. canadensis* or *Typha* spp. litter was observed in herbicide-treated sites compared to uninvaded or invaded marsh despite increased water depth, stability and temperature in herbicide-treated sites. However, due to the changed plant community I concluded there would likely be differences in decomposition rates in herbicide-treated areas because of changes in litter quality and submersion of the recovering plant community. The submerged and floating aquatic vegetation re-growing in herbicide-treated areas of the marsh may decompose faster than emergent macrophytes (Chimney and Pietro 2006, Ping et al. 2017) due to changes in chemical composition or continual submersion of dead biomass.

4.2 Implications and significance

My thesis work contributes to the body of knowledge concerning the effects of *P. australis* invasion in several ways. Few previous studies have considered the effect of *P. australis* invasion on macronutrients other than nitrogen, phosphorus and carbon. I presented evidence that *P. australis* invasion also changes the potassium annual vegetative standing stock compared to meadow marsh and the calcium and magnesium annual vegetative standing stock compared to meadow and cattail marsh. In addition, I deliberately conducted my study across a range of abiotic site conditions. I examined nutrient tissue concentrations and biomass in high and low nutrient environments, and biomass, carbon assimilation, decomposition rates, soil carbon

dioxide efflux, and site characteristics across a water depth gradient. Therefore, I was able to highlight how abiotic conditions in the marsh influence invasion-driven changes. These under-reported abiotic conditions may account for some of the variation in net primary production results reported in the literature (see Chapter 1).

Another uncertainty in the *P. australis* invasion literature is whether invasion affects decomposition rates more through changes in litter quality or through changes in environmental conditions. My results indicate that, considering submerged litter, changes in litter quality are most important; *P. australis* leaf litter, which contained a higher nitrogen concentration, decomposed significantly faster than *C. canadensis* or *Typha* spp. litter, regardless of where the litter was situated. Changes in environmental conditions in invaded marsh, such as increased dissolved oxygen, increased standing water levels, higher water fluctuations and shading or decreased temperatures did not significantly change decomposition rates. However, my results did confirm that submersion of wetland plant species litter increases the decomposition rate, with rates of decomposition for all tissue types significantly lower in suspended litter bags than in submersed ones.

My research contributes to our understanding of how invasion can lead to a trade-off in ecosystem services. Alldred et al. (2016) recently suggested that invasion by *P. australis* causes a variety of opposing changes in wetland ecosystem services that reflect trade-offs among service types. The results of my research showed clear trade-offs in ecological functions when *P. australis* invaded meadow marsh. Meadow marsh is a diverse and at risk (Imperiled [S2]; Ministry of Natural Resources and Forestry 2018) plant community, and provides valuable habitat for wetland wildlife (e.g., Robichaud and Rooney 2017). Despite this, no previous work evaluated the effect of *P. australis* invasion on macronutrients in meadow marsh. My results

provided evidence that invasion of meadow marsh by *P. australis* significantly increased the storage of macronutrients in the annual vegetative standing stock, and for carbon specifically, increased carbon sequestration.

I was also able to examine the effects of *P. australis* invasion on macronutrient storage at the marsh-level, which better captures invasion-driven changes. For example, nutrient concentrations at the tissue level were not significantly different between *P. australis* and *C. canadensis* (except for foliar nitrogen) but there were significant differences among all six macronutrients at the marsh level. Scaling up also allowed for comparisons to be made at drainage-basin scales. *Phragmites australis* is estimated to cover between from 2553 ha within Lake Erie coastal wetlands (Carson et al. 2018) to 8233 ha invaded within 10 km of the American side of Lake Erie (Bourgeau-Chavez et al. 2013). Using these estimates, the replacement of *C. canadensis* dominated meadow marsh (assuming it previously dominated that area) with *P. australis* represents an estimated increase of $580,354 - $4,561,898 USD of annual carbon storage and an increase of approximately 1 % of the nitrogen and phosphorus loading into Lake Erie. However, these benefits must be weighed against the loss of biodiversity and other ecosystem services. The meadow marsh community in Long Point, already deemed at risk, has high plant species richness and provides essential habitat for provincially rare plant and bird species (Riffell et al. 2001, Ball et al. 2003). In Long Point, *P. australis* is also replacing cattail marsh, which is dominated by non-native *Typha* x. *glauca* (Freeland et al. 2013). While there were no significant change in net primary productivity, macronutrient storage or decomposition rates, *P. australis* invaded marshes are more detrimental to plant diversity and wildlife than cattail marshes in these coastal marshes (e.g., Keller 2000, Robichaud and Rooney 2017). Furthermore, *P. australis* invasion negatively affects at-risk turtles (Bolton and Brooks 2010, Markle and Chow-Fraser 2018), amphibians

(Greenberg and Green 2013) and has the potential to negatively affect fish (Able and Hagan 2000, Hunter et al. 2006). Considering the importance of intact coastal marshes for wetland flora and fauna, and the stress that human development, agriculture, and climate change places on these systems, the negative effects of *P. australis* may outweigh any benefit from marginally increased carbon sequestration where *P. australis* replaces S2 categorized meadow marsh habitat.

To my knowledge, there are no other comprehensive studies examining whether control efforts are sufficient to return net primary productivity, decomposition rates, and environment conditions to within their pre-invasion range. My results provided evidence that, overall, there was a reduction in carbon sequestration services in herbicide-treated sites one-year post treatment. As *P. australis* control-efforts are often undertaken to restore biodiversity (Martin and Blossey 2013), this reduction in carbon sequestrations services once again represents a trade-off in ecosystem services. To increase carbon sequestration in herbicide-treated marsh, the rapid recovery of emergent plant communities in the herbicide-treated area will be crucial. However, I observed recovery of floating and submersed aquatic vegetation in the herbicide-treated marsh that provides evidence that this gap in carbon sequestration services may be temporary. Emergent plant community recovery, however, may be restricted by higher water levels (van der Valk et al. 1994, Euliss et al. 2004), and in 2017 water levels in Lake Erie were relatively high (The Canadian Hydrographic Service 2016). Furthermore, secondary treatment of the herbicide-treated marsh included the rolling and mowing of standing dead *P. australis* biomass into the litter layer. While this opened the surafce of the water to increased levels of light, the dense litter layer may also be preventing emergent plant recovery because seedling germination is decreased as a result of changing environmental conditions, such as temperature or light availability, or by

physically preventing seedlings from being able to push through the litter layer (van der Valk 1986, Holdredge and Bertness 2011).

Decomposition of the remnant *P. australis* litter layer in the herbicide-treated marsh may be necessary for emergent plant community recovery. The time it will take for all of the remnant litter to decompose can be estimated using the average decay rate of *P. australis* leaf litter in the herbicide-treated marsh ($k = 0.011$) and solving for time in the single exponential model ($W_t = W_0 \exp(-kt)$). This yields an estimate of complete decomposition of *P. australis* leaf litter in approximately 432 days, assuming the decomposition rate is constant. *Phragmites australis* culms, however, decompose much slower. In a preliminary study examining the decay rate of submerged *P. australis* culms and leaf litter the mass loss of the culms was twice as slow as the mass loss of the leaves (Appendix 8). Other studies also report that *P. australis* culms take approximately twice as long to decompose (Dinka et al. 2004, Bedford 2005, Ágoston-Szabó and Dinka 2008, Dolinar et al. 2015). Therefore, I estimate that the remnant dead *P. australis* in the litter layer of the herbicide-treated marsh may take up to 864 days, or more than two years, to fully decompose.

My findings are also relevant to land managers in the Great Lakes region who are considering whether to attempt to eradicate *P. australis*. Understanding the net effects of wetland plant invasions, and the net effects of control efforts on wetland functions and ecosystems services, is vital to inform decisions about invasive species control efforts (e.g., Gaertner et al. 2016). In North America, efforts to eradicate *P. australis* from large areas have been generally unsuccessful (e.g., Lombard et al. 2012, Quirion et al. 2018), despite immense efforts to control invasive *P. australis* (Martin and Blossey 2013, Hazelton et al. 2014). If eradication of *P. australis* is not possible, then land managers face potential trade-offs in between biodiversity

conservation that results from *P. australis* control efforts (Schummer et al. 2012, Markle and Chow-Fraser 2018), and decreased carbon sequestration following herbicide-application (for at least one year post-treatment). Understanding these net effects on ecosystem functions and services provides valuable information to decision-makers who already must balance social values, economic feasibility, and outcome uncertainties (Liu et al. 2011, Martin and Blossey 2013), when deciding whether to control an invasive species.

4.3 Future work

The macronutrient cycling in wetlands is complex; I was only able to assess a limited portion of the cycles. Overall, I evaluated the annual macronutrient standing stock of vegetation (including carbon), soil nutrients and decomposition rates in meadow and cattail marsh, *P. australis* invaded marsh, and herbicide-treated marsh. My results support the conclusion that *P. australis* invaded marshes store more macronutrients in the annual vegetative standing stock than meadow marsh, and have similar macronutrient storage functions as cattail marsh. Furthermore, while decomposition of *P. australis* leaves is more rapid than *C. canadensis* or *Typha* spp., decomposition of *P. australis* culms appears to be slower. However, I was not able to assess the relative storage/ release of macronutrients from the litter during decomposition. This represents an important knowledge gap. For example, if *P. australis* is storing more macronutrients in its annual tissues than resident plants, but releases the bulk of these tissues back into the wetland during decomposition, *P. australis* invasion may not truly provide an ecosystem service in terms of macronutrient storage.

Future work should also focus on plant community recovery in the herbicide-treated marshes. Long term monitoring of herbicide-treated areas is necessary to evaluate if carbon dynamics

return to uninvaded ranges. Moreno-Mateos et al. (2012) determined in a study of 621 restored wetlands throughout the world that even after a century, restored wetlands had biological structures and biochemical functions that differed from reference wetlands. More research is required to determine if the plant communities that establish in herbicide-treated areas in the Great Lakes region have rates of net primary productivity, tissue nutrient concentrations and decomposition rates similar to those in uninvaded, adjacent, residential plant communities.

References

Able, K. W., and S. M. Hagan. 2000. Effects of common reed (*Phragmites australis*) invasion on marsh surface macrofauna: response of fishes and decapod crustaceans. Estuaries 23:633–646.

Ágoston-Szabó, E., and M. Dinka. 2008. Decomposition of *Typha angustifolia* and *Phragmites australis* in the littoral zone of a shallow lake. Biologia 63:1104–1110.

Agriculture and Food Laboratory University of Guelph. 2017. Soil and nutrient laboratory service list.

Ailstock, M. S., C. M. Norman, and P. J. Bushmann. 2001. Common reed *Phragmites australis*: control and effects upon biodiversity in freshwater nontidal wetlands. Restoration Ecology 9:49–59.

Albert, A., J. Brisson, F. Belzile, J. Turgeon, and C. Lavoie. 2015. Strategies for a successful plant invasion: the reproduction of *Phragmites australis* in north-eastern North America. Journal of Ecology 103:1529–1537.

Alldred, M., S. B. Baines, and S. Findlay. 2016. Effects of invasive-plant management on nitrogen-removal services in freshwater tidal marshes. PLOS ONE 11:e0149813.

Baldwin, A. H., K. M. Kettenring, and D. F. Whigham. 2010. Seed banks of *Phragmites australis*-dominated brackish wetlands: Relationships to seed viability, inundation, and land cover. Aquatic Botany 93:163–169.

Ball, H., J. Jalava, T. King, L. Maynard, B. Potter, and T. Pulfer. 2003. The Ontario Great Lakes coastal weltand atlas: a summary of information (1983-1997). Page Environment Canada.

Barton, K. 2018. MuMIn: Multi-Model Inference. R package version 1.40.4.

Bedford, A. P. 2004. A modified litter bag design for use in lentic habitats. Hydrobiologia 529:187–193.

Bedford, A. P. 2005. Decomposition of *Phragmites australis* litter in seasonally flooded and exposed areas of a managed reedbed. Wetlands 25:713–720.

Berg, B., G. Ekbohm, and C. McClaugherty. 1984. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long-term decomposition in a Scots pine forest. IV. Canadian Journal of Botany 62:2540–2550.

Bernal, B., J. P. Megonigal, and T. J. Mozdzer. 2016. An invasive wetland grass primes deep soil carbon pools. Global Change Biology.

Bernal, B., and W. J. Mitsch. 2012. Comparing carbon sequestration in temperate freshwater wetland communities. Global Change Biology 18:1636–1647.

Bernal, B., and W. J. Mitsch. 2013. Carbon sequestration in freshwater wetlands in Costa Rica and Botswana. Biogeochemistry 115:77–93.

Bertness, M. D., and T. C. Coverdale. 2013. An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod. Ecology 94:1937–1943.

Bhatia, M., and D. Goyal. 2014. Analyzing remediation potential of wastewater through wetland plants: a review. Environmental Progress and Sustainable Energy 33:9–27.

Bolton, R. M., and R. J. Brooks. 2010. Impact of the seasonal invasion of *Phragmites australis* (common reed) on turtle reproductive success. Chelonian Conservation and Biology 9:238–243.

Bonnewell, V., W. L. Koukkari, and D. C. Pratt. 1983. Light, oxygen, and temperature requirements for *Typha latifolia* seed germination. Canadian Journal of Botany 61:1330–1336.

Borrelli, N., M. Fernández Honaine, S. M. Altamirano, and M. Osterrieth. 2011. Calcium and silica biomineralizations in leaves of eleven aquatic species of the Pampean Plain, Argentina. Aquatic Botany 94:29–36.

Bourgeau-Chavez, L. L., K. P. Kowalski, M. L. Carlson Mazur, K. A. Scarbrough, R. B. Powell, C. N. Brooks, B. Huberty, L. K. Jenkins, E. C. Banda, D. M. Galbraith, Z. M. Laubach, and K. Riordan. 2013. Mapping invasive *Phragmites australis* in the coastal Great Lakes with ALOS PALSAR satellite imagery for decision support. Journal of Great Lakes Research 39:65–77.

Bowne, D. R., and E. R. Johnson. 2013. Comparison of soil carbon dioxide efflux between residential lawns and corn fields. Soil Science Society of America Journal 77:856.

Braun, H. A., K. P. Kowalski, and K. Hollins. 2016. Applying the collective impact approach to address non-native species: a case study of the Great Lakes *Phragmites* Collaborative. Biological Invasions 18:1–10.

Breen, D. B., S. D. Bailey, and H. A. Violi. 2014. Managing remnant and reemerging common reed (*Phragmites australis*) infestations to improve treatment efficacy and mitigate damage to native plants. Invasive Plant Science and Management 7:445–453.

Brisson, J. 2010. Roadside as invasion pathway for common reed (*Phragmites australis*). Invasive Plant Science and Management 3:506–514.

Brix, H., B. K. Sorrell, and B. Lorenzen. 2001. Are *Phragmites*-dominated wetlands a net source or net sink of greenhouse gases? Aquatic Botany 69:313–324.

Caplan, J. S., R. N. Hager, J. P. Megonigal, and T. J. Mozdzer. 2015. Global change accelerates carbon assimilation by a wetland ecosystem engineer. Environmental Research Letters 10:1–12.

Carlson, M. L., K. P. Kowalski, and D. A. Wilcox. 2009. Promoting species establishment in a *Phragmites*-dominated Great Lakes coastal wetland. Natural Areas Journal 29:263–280.

Carson, B. D., S. C. Lishawa, N. C. Tuchman, A. M. Monks, B. A. Lawrence, and D. A. Albert. 2018. Harvesting invasive plants to reduce nutrient loads and produce bioenergy: an assessment of Great Lakes coastal wetlands. Ecosphere 9:e02320.

Casanova, M. T., and M. A. Brock. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecology 147:237–250.

Catling, P. M., and S. Carbyn. 2006. Recent invasion, current status, and invasion pathway of the alien race of common reed (*Phragmites australis* (Cav.) Trin. ex Steud. var. *australis*) in the Southern Ottawa District. The Canadian Field-Naturalist 120:307–312.

Catling, P. M., and G. Mitrow. 2011. The recent spread and potential distribution of *Phragmites australis* subsp. *australis* in Canada. The Canadian Field-Naturalist 125:95–104.

CBS News. 2018. Toxic algae leads Ohio to designate western Lake Erie as impaired. https://www.cbsnews.com/news/toxic-algae-leads-ohio-to-designate-western-lake-erie-as-impaired/.

Chimney, M. J., and K. C. Pietro. 2006. Decomposition of macrophyte litter in a subtropical constructed wetland in south Florida (USA). Ecological Engineering 27:301–321.

Chojnicki, B. ., M. Michalak, M. Acosta, R. Juszczak, J. Augustin, M. Drösler, and J. Olejnik. 2010. Measurements of carbon dioxide fluxes by chamber method at the Rzecin wetland ecosystem, Poland. Polish Journal of Environmental Studies 19:283–291.

Christensen, J. R., W. G. Crumpton, and A. G. van der Valk. 2009. Estimating the breakdown and accumulation of emergent macrophyte litter: A mass-balance approach. Wetlands 29:204–214.

Chu, H., J. F. Gottgens, J. Chen, G. Sun, A. R. Desai, Z. Ouyang, C. Shao, and K. Czajkowski. 2015. Climatic variability, hydrologic anomaly, and methane emission can turn productive freshwater marshes into net carbon sources. Global Change Biology 21:1165–1181.

Coops, H., and G. Van der Velde. 1995. Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. Freshwater Biology 34:13–20.

Croft, M. V, and P. Chow-Fraser. 2007. Use and development of the wetland macrophyte index to detect water quality impairment in fish habitat of Great Lakes coastal marshes. Journal of Great Lakes Research 33:172–197.

Currie, W. S., D. E. Goldberg, J. Martina, R. Wildova, E. Farrer, and K. J. Elgersma. 2014. Emergence of nutrient-cycling feedbacks related to plant size and invasion success in a wetland community–ecosystem model. Ecological Modelling 282:69–82.

Davis, M. A., M. K. Chew, R. J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, M. L. Rosenzweig, M. R. Gardener, S. P. Carroll, K. Thompson, S. T. A. Pickett, J. C. Stromberg, P. Del Tredici, K. N. Suding, J. G. Ehrenfeld, J. Philip Grime, J. Mascaro, and J. C. Briggs. 2011. Don't judge species on their origins. Nature 474:153–154.

Department of Finance Canada. 2018. Equality and Growth - a strong middle class. Her Majesty the Queen in Right of Canada.

Dinka, M., E. Ágoston-Szabá, and I. Tóth. 2004. Changes in nutrient and fibre content of decomposing *Phragmites australis* litter. International Review of Hydrobiology 89:519–535.

Dolinar, N., M. Regvar, D. Abram, and A. Gaberščik. 2015. Water-level fluctuations as a driver of *Phragmites australis* primary productivity, litter decomposition, and fungal root colonisation in an intermittent wetland. Hydrobiologia 774:69–80.

Duke, S. T., S. N. Francoeur, and K. E. Judd. 2015. Effects of *Phragmites australis* invasion on carbon dynamics in a freshwater marsh. Wetlands 35:311–321.

Economic impacts of invasive species to Ontario municipalities and Conservation Authorities. 2018.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523.

Ehrenfeld, J. G. 2010. Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics 41:59–80.

Elzhov, T. V., K. M. Mullen, A.-N. Spiess, and B. Bolker. 2016. minpack.lm: R Interface to the Levenberg-Marquardt Nonlinear Least-Squares Algorithm found in MINPACK, Plus Support for Bounds. R package version 1.2-1.

Engle, V. D. 2011. Estimating the provision of ecosystem services by Gulf of Mexico coastal wetlands. Wetlands 31:179–193.

Engloner, A. I. 2009. Structure, growth dynamics and biomass of reed (*Phragmites australis*) – a review. Flora - Morphology, Distribution, Functional Ecology of Plants 204:331–346.

Enriquez, S., C. Duarte, and K. Sand-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C: N: P content. Oecologia 94:457–471.

Environment and Climate Change Canada and the U.S. Environmental Protection Agency, 2017. State of the Great Lakes 2017 Technical Report: indicators to assess the status and trends of the Great Lakes ecosystem.

Essex Region Conservation Authority. 2013. Big Creek watershed plan.

Euliss, N. H., J. W. Labaugh, L. H. Fredrickson, D. M. Mushet, M. K. Laubhan, G. A. Swanson, T. C. Winter, D. O. Rosenberry, and R. D. Nelson. 2004. The wetland continuum: a conceptual framework for interpreting biological studies. Wetlands 24:448–458.

Farnsworth, E. J., and L. A. Meyerson. 2003. Comparative ecophysiology of four wetland plant species along a continuum of invasiveness. Wetlands 23:750–762.

Findlay, S. E. G., S. Dye, and K. A. Kuehn. 2002. Microbial growth and nitrogen retention in litter of *Phragmites australis* compared to *Typha angustifolia*. Wetlands 22:616–625.

Finocchiaro, R., B. Tangen, and R. Gleason. 2014. Greenhouse gas fluxes of grazed and hayed wetland catchments in the U.S. Prairie Pothole Ecoregion. Wetlands Ecological Management 22:305–324.

Franceschi, V. R., and H. T. Horner. 1980. Calcium oxalate crystals in plants. The Botanical Review 46:361–427.

Fraser, L. H., and J. P. Karnezis. 2005. A comparative assessment of seedling survival and biomass accumulation for fourteen wetland plant species grown under minor water-depth differences. Wetlands 25:520–530.

Freeland, J., C. Ciotir, and H. Kirk. 2013. Regional differences in the abundance of native, introduced, and hybrid *Typha* spp. in northeastern North America influence wetland invasions. Biological Invasions 15:2651–2665.

Furlanetto, L. M., C. Palma-Silva, M. B. Perera, and E. F. Albertoni. 2018. Potential carbon gas production in southern Brazil wetland sediments: possible implications of agricultural land use and warming. Wetlands:1–11.

Gaertner, M., B. M. H. Larson, U. M. Irlich, P. M. Holmes, L. Stafford, B. W. Van Wilgen, and D. M. Richardson. 2016. Managing invasive species in cities: a framework from Cape Town, South Africa. Landscape and Urban Planning 151:1–9.

Galatowitsch, S. M., D. L. Larson, and J. L. Larson. 2016. Factors affecting post-control reinvasion by seed of an invasive species, *Phragmites australis*, in the central Platte River, Nebraska. Biological Invasions 18:2505–2516.

Godshalk, G. L., R. G. Wetzel, and W. K. Kellogg. 1978. Decomposition of aquatic angiosperms. II. Particulate components. Aquatic Botany 5:301–327.

Goyal, R., S. Gray, A. Churie Kallhauge, S. Nierop, T. Berg, and P. Leuschner. 2018. State and trends of carbon pricing 2018.

Grabas, G. P., and D. Rokitnicki-Wojcik. 2015. Characterizing daily water-level fluctuation intensity and water quality relationships with plant communities in Lake Ontario coastal wetlands. Journal of Great Lakes Research 41:136–144.

Graham, S. A., and I. A. Mendelssohn. 2016. Contrasting effects of nutrient enrichment on below-ground biomass in coastal wetlands. Journal of Ecology 104:249–260.

Greenberg, D. A., and D. M. Green. 2013. Effects of an invasive plant on population dynamics in toads. Journal of the Society for Conservation Biology 27:1049–1057.

Grutters, B. M. C., B. J. A. Pollux, W. C. E. P. Verberk, and E. S. Bakker. 2015. Native and non-native plants provide similar refuge to invertebrate prey, but less than artificial plants. PLoS One 10:p.e0124455.

Gumbricht, T. 1993. Nutrient removal processes in freshwater submersed macrophyte systems. Ecological Engineering Elsevier Science Publishers B.V 2:1–30.

Hazelton, E. L. G., R. Downard, K. M. Kettenring, M. K. McCormick, and D. F. Whigham. 2018. Spatial and temporal variation in brackish wetland seedbanks: implications for wetland restoration following *Phragmites* control. Estuaries and Coasts 41:S68–S84.

Hazelton, E. L. G., T. J. Mozdzer, D. M. Burdick, K. M. Kettenring, and D. F. Whigham. 2014. *Phragmites australis* management in the United States: 40 years of methods and outcomes. AoB PLANTS 6:plu001.

Hershner, C., and K. J. Havens. 2008. Managing invasive aquatic plants in a changing system: strategic consideration of ecosystem services. Conservation Biology 22:544–550.

Hirtreiter, J. N., and D. L. Potts. 2012. Canopy structure, photosynthetic capacity and nitrogen distribution in adjacent mixed and monospecific stands of *Phragmites australis* and *Typha latifolia*. Plant Ecology 213:821–829.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24:599–605.

Hogg, E. H., and V. J. Lieffers. 1991. Seasonal changes in shoot regrowth potential in *Calamagrostis canadensis*. Oecologia 85:596–602.

Holdredge, C., and M. D. Bertness. 2011. Litter legacy increases the competitive advantage of invasive *Phragmites australis* in New England wetlands. Biological Invasions 13:423–433.

Hunter, K. L., D. A. Fox, L. M. Brown, and K. W. Able. 2006. Responses of resident marsh fishes to stages of *Phragmites australis* invasion in three mid Atlantic estuaries 29:487–498.

Jarvie, H. P., L. T. Johnson, A. N. Sharpley, D. R. Smith, D. B. Baker, T. W. Bruulsema, and R. Confesor. 2017. Increased soluble phosphorus loads to Lake Erie: unintended consequences of conservation practices? Journal of Environment Quality 46:123–132.

Jodoin, Y., C. Lavoie, P. Villeneuve, M. Theriault, J. Beaulieu, and F. Belzile. 2008. Highways as corridors and habitats for the invasive Common Reed *Phragmites australis* in Quebec, Canada. Journal of Applied Ecology 45:459–466.

Jung, J. A., D. Rokitnicki-Wojcik, and J. D. Midwood. 2017. Characterizing past and modelling future spread of *Phragmites australis* ssp. *australis* at Long Point Peninsula, Ontario, Canada. Wetlands 37:961–973.

Kao, J. T., J. E. Titus, and W.-X. Zhu. 2003. Differential nitrogen and phosphorus retention by five wetland plant species. Wetlands 23:979–987.

Karr, J. R. 1993. Defining and assessing ecological integrity: beyond water quality. Environmental Toxicology and Chemistry 12:1521–1531.

Kayranli, B., M. Scholz, A. Mustafa, and Å. Hedmark. 2010. Carbon storage and fluxes within freshwater wetlands: a critical review. Wetlands 30:111–124.

Keddy, P. A., and A. A. Reznicek. 1986. Great lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. Journal of Great Lakes Researchs 12:25–36.

Keller, B. E. M. 2000. Plant diversity in *Lythrum*, *Phragmites*, and *Typha* marshes, Massachusetts, U.S.A. Wetlands Ecology and Management 8:391–401.

Kennedy, E., L. G. Leff, and F. A. de Szalay. 2012. Herbiciding *Phragmites australis*: effects on litter decomposition, microbial biomass, and macroinvertebrate communities. Fundamental and Applied Limnology 180:309–319.

Kettenring, K. M., G. Gardner, and S. M. Galatowitsch. 2006. Effect of light on seed germination of eight wetland *Carex* species. Annals of Botany 98:869–874.

Kirk, H., C. Connolly, and J. R. Freeland. 2011. Molecular genetic data reveal hybridization between *Typha angustifolia* and *Typha latifolia* across a broad spatial scale in eastern North America. Aquatic Botany 95:189–193.

Kiviat, E. 2013. Ecosystem services of *Phragmites* in North America with emphasis on habitat functions. AoB PLANTS 5:plt008.

Kopf, R. K., D. G. Nimmo, P. Humphries, L. J. Baumgartner, M. Bode, N. R. Bond, A. E. Byrom, J. Cucherousset, R. P. Keller, A. J. King, H. M. McGinness, P. B. Moyle, and J. D. Olden. 2017. Confronting the risks of large-scale invasive species control. Nature Ecology & Evolution 1:172.

Kvet, J., J. Pokorny, and H. Cizkova. 2008. Carbon accumulation by macrophytes of aquatic and wetland habitats with standing water. Proceedings of the National Academy of Sciences India Section B-Biological Sciences 78:91–98.

Larkin, D. J., M. J. Freyman, S. C. Lishawa, P. Geddes, and N. C. Tuchman. 2012. Mechanisms of dominance by the invasive hybrid cattail *Typha* × *glauca*. Biological Invasions 14:65–77.

Lathrop, R. G., L. Windham, and P. Montesano. 2003. Does *Phragmites* expansion alter the structure and function of marsh landscapes? Patterns and processes revisited. Estuaries 26:423–435.

Lawrence, B. A., S. C. Lishawa, N. Hurst, B. T. Castillo, and N. C. Tuchman. 2017. Wetland invasion by *Typha* × *glauca* increases soil methane emissions. Aquatic Botany 137:80–87.

League, M. T., E. P. Colbert, D. M. Seliskar, and J. L. Gallagher. 2006. Rhizome growth dynamics of native and exotic haplotypes of *Phragmites australis* (common reed). Estuaries and Coasts 29:269–276.

Leck, M. A. 1996. Germination of macrophytes from a Delaware River tidal freshwater wetland. Bulletin of the Torrey Botanical Club 123:48.

Lei, C. 2018. Rooting depth in coastal marshes invaded by *Phragmites australis* compared with remnant uninvaded sites. University of Waterloo.

Lelong, B., C. Lavoie, Y. Jodoin, and F. Belzile. 2007. Expansion pathways of the exotic Common Reed (*Phragmites australis*): a historical and genetic analysis. Diversity and Distributions 13:430–437.

Li, H., Y. Liu, J. Li, X. Zhou, and B. Li. 2016. Dynamics of litter decomposition of dieback *Phragmites* in *Spartina*-invaded salt marshes. Ecological Engineering 90:459–465.

Liao, C. Z., R. H. Peng, Y. Q. Luo, X. H. Zhou, X. W. Wu, C. M. Fang, J. K. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. The New phytologist 177:706–14.

Liu, S., A. Sheppard, D. Kriticos, and D. Cook. 2011. Incorporating uncertainty and social values in managing invasive alien species: a deliberative multi-criteria evaluation approach. Biological Invasions 13:2323–2337.

Lombard, K. B., D. Tomassi, and J. Ebersole. 2012. Long-term management of an invasive plant: lessons from seven years of *Phragmites australis* control. Northeast Naturalist 19:181–193.

Lou, Y., Y. Pan, C. Gao, M. Jiang, X. Lu, and Y. Jun Xu. 2016. Response of plant height, species richness and aboveground biomass to flooding gradient along vegetation zones in floodplain wetlands, Northeast China. PLoS ONE 11:153972.

Mal, T. K., and L. Narine. 2004. The biology of Canadian weeds. 129. *Phragmites australis* (Cav.) Trin. ex Steud. Canadian Journal of Plant Science 84:365–396.

Maltby, E., and T. Barker, editors. 2009. The Wetlands Handbook. First edition. Wiley-Blackwell, West Sussex.

Maraccio, J. V., and P. Chow-Fraser. 2016. Mapping options to track distribution of invasive *Phragmites australis* in the Great Lakes basin in Canada. Pages 75–82*in* P. Gâştescu and P. Bretcan, editors.3rd International Conference - Water resources and wetlands.

Markle, C. E., G. Chow-fraser, and P. Chow-fraser. 2018. Long-term habitat changes in a protected area : implications for herpetofauna habitat management and restoration. PLOS ONE 13:1–15.

Markle, C. E., and P. Chow-Fraser. 2018. Effects of European common reed on Blanding's turtle spatial ecology. The Journal of Wildlife Management 82:857–864.

Martin, L. J., and B. Blossey. 2013. The runaway weed: costs and failures of *Phragmites australis* management in the USA. Estuaries and Coasts 36:626–632.

Martin, R. M., and S. Moseman-Valtierra. 2017. Effects of transient *Phragmites australis* removal on brackish marsh greenhouse gas fluxes. Atmospheric Environment 158:51–59.

Mason, C. F., and R. J. Bryant. 1975a. Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. Journal of Ecology 63:71–95.

Meyer, S. W., S. S. Badzinski, S. A. Petrie, and C. D. Ankney. 2010. Seasonal abundance and species richness of birds in common reed habitats in Lake Erie. Journal of Wildlife Management 74:1559–1567.

Meyerson, L. A., K. Saltonstall, L. Windham, E. Kiviat, and S. Findlay. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetlands Ecology and Management 8:89–103.

Middleton, B. A., A. G. Van Der Valk, and C. B. Davis. 2015. Responses to water depth and clipping of twenty-three plant species in an Indian monsoonal wetland. Aquatic Botany 126:38–47.

Miller, R. C., and J. B. Zedler. 2013. Responses depth of native and invasive wetland plants to hydroperiod and water. Plant Ecology 167:57–69.

Minchinton, T. E., and M. D. Bertness. 2003. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. Ecological Applications 13:1400–1416.

Ministry of Natural Resources and Forestry. 2017. Five-year review of progress towards the protection and recovery of Ontario's Species at Risk 2017.

Ministry of Natural Resources and Forestry. 2018. Get natural heritage information. https://www.ontario.ca/page/get-natural-heritage-information.

Ministry of Natural Resources and Forestry, N. H. S. Natural Resource Conservation Policy Branch, and S. Z. Southern Region, Aylmer District Ontario Parks. 2017. Invasive *Phragmites* control at Long Point region and Rondeau Provincial Park: implementation plan.

Ministry of Natural Resources and Forestry, Natural Resource Conservation Policy Branch, and Ontario Parks. 2016. Invasive *Phragmites* control at Long Point and Rondeau Provincial Park. Report:1–18.

Mitsch, W. J., B. Bernal, A. M. Nahlik, Ü. Mander, L. Zhang, C. J. Anderson, S. E. Jørgensen, and H. Brix. 2013. Wetlands, carbon, and climate change. Landscape Ecology 28:583–597.

Moore, G. E., D. M. Burdick, C. R. Peter, and D. R. Keirstead. 2012. Belowground biomass of *Phragmites australis* in coastal marshes. Northeastern Naturalist 19:611–626.

Moreno-Mateos, D., M. E. Power, F. A. Comín, and R. Yockteng. 2012. Structural and functional loss in restored wetland ecosystems. PLoS Biology 10.

Mozdzer, T. J., J. Brisson, and E. L. G. Hazelton. 2013. Physiological ecology and functional traits of North American native and Eurasian introduced *Phragmites australis* lineages.

Mozdzer, T. J., C. J. Hutto, P. A. Clarke, and D. P. Field. 2008. Efficacy of imazapyr and glyphosate in the control of non-native *Phragmites australis*. Restoration Ecology 16:221–224.

Mozdzer, T. J., and J. P. Megonigal. 2013. Increased methane emissions by an introduced *Phragmites australis* lineage under global change. Wetlands 33:609–615.

Neill, C. 1992. Comparison of soil coring and ingrowth methods for measuring belowground production. Ecology 73:1918–1921.

Nichols, D. S. 1983. Capacity of natural wetlands to remove nutrients from wastewater. Water Pollution Control Federation 55:495–505.

Norkko, J., D. C. Reed, K. Timmermann, A. Norkko, B. G. Gustafsson, E. Bonsdorff, C. P. Slomp, J. Carstensen, and D. J. Conley. 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. Global Change Biology 18:422–434.

Olivares, E., D. Vizcaíno, and A. Gamboa. 2002. Mineral nutrition of three aquatic emergent macrophytes in a managed wetland in Venezuela. Journal of Plant Nutrition 25:475–496.

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

OMECC. 2017. Partnering in phosphorus control: achieving phosphorus reductions in Lake Erie from Canadian sources. The Canada-Ontario Draft Action Plan. Page Ontario Ministry of Environment and Climate Change (OMECC).

Ouellet-Plamondon, C. M., J. Brisson, Y. Comeau, and D. J.L. 2004. Effect of macrophyte species on subsurface flow wetland performance in cold climate. Pages 8–15Proceedings of the 2004 Self-Sustaining Solutions for Streams, Wetlands, and Watersheds Conference.

Parzych, A. E., M. Cymer, J. Jonczak, and S. Szymczyk. 2015. The ability of leaves and rhizomes of aquatic plants to accumulate macro- and micronutrients. Journal of Ecological Engineering 16:198–205.

Pavelka, M., E. Darenova, and J. Dusek. 2016. Modeling of soil CO_2 efflux during water table fluctuation based on in situ measured data from a sedge-grass marsh. Applied Ecology and Environmental Research 14:423–437.

Ping, Y., X. Pan, L. Cui, W. Li, Y. Lei, J. Zhou, and J. Wei. 2017. Effects of plant growth form and water substrates on the decomposition of submerged litter: evidence of constructed wetland plants in a greenhouse experiment. Water 9:827.

Powelson, R. A., and V. J. Lieffers. 1992. Effect of light and nutrients on biomass allocation in *Calamagrostis canadensis*. Ecography 15:31–36.

Powles, S. B. 2008. Evolved glyphosate-resistant weeds around the world: lessons to be learnt. Pest Management Science 64:360–365.

Quirion, B., Z. Simek, A. Dávalos, and B. Blossey. 2018. Management of invasive *Phragmites australis* in the Adirondacks: a cautionary tale about prospects of eradication. Biological Invasions 20:59–73.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P. B., J. Oleksyn, and I. J. Wright. 2009. Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross-biome analysis of 314 species. Oecologia 160:207–212.

Reid, K., editor. 1998. Soil Fertility Handbook. OMAFRA Publication.

Reznicek, A. A., and P. M. Catling. 1989. Flora of Long Point, Ontario. Michigan Botanical Club 28:99–175.

Riffell, S. K., B. E. Keas, and T. M. Burton. 2001. Area and habitat relationships of birds in Great Lakes coastal wet meadows. Wetlands 21:492–507.

Robertson, D. M., and D. A. Saad. 2013. Nutrient inputs to the Laurentian Great Lakes by source and watershed estimated using SPARROW watershed models". Journal of the American Water Resources Association 49:725–734.

Robertson, G. P. 1999. Standard soil methods for long-term ecological research. Oxford University Press.

Robichaud, C. D., and R. C. Rooney. 2017. Long-term effects of a *Phragmites australis* invasion on birds in a Lake Erie coastal marsh. Journal of Great Lakes Research 43:141–149.

Rong, M., Z. Xinhou, and S. Changchun. 2014. Effects of nitrogen addition on plant functional traits in freshwater wetland of Sanjiang Plain, Northeast China. Chinese Geographical Science 24:674–681.

Rooth, J. E., J. C. Stevenson, and J. C. Cornwell. 2003. Increased sediment accretion rates following invasion by *Phragmites australis*: the role of litter. Estuaries 26:475–483.

Rothman, E., and V. Bouchard. 2007. Regulation of carbon processes by macrophyte species in a Great Lakes coastal wetland. Wetlands 27:1134–1143.

Rubio, G., G. Casasola, and R. S. Lavado. 1995. Adaptations and biomass production of two grasses in response to waterlogging and soil nutrient enrichment. Oecologia 102:102–105.

Rubio, G., and R. S. Lavado. 1999. Acquisition and allocation of resources in two waterlogging-tolerant grasses. New Phytologist 143:539–546.

Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proceedings of the National Academy of Sciences 99:2445–2449.

Saltonstall, K., and L. A. Meyerson. 2016. *Phragmites australis*: from genes to ecosystems. Biological Invasions 18:2415–2420.

Saltonstall, K., P. M. Peterson, and R. J. Soreng. 2004. Recognition of *Phragmites australis* subsp. *americanus* (Poaceae: Arundinoideae) in North America: evidence from morphological and genetic analysis. Sida 21:683–692.

Sax, D. F., and S. D. Gaines. 2003. Species diversity: from global decreases to local increases. Trends in Ecology and Evolution 18:561–566.

Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The potential conservation value of non-native species. Conservation Biology 25:428–437.

Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2012. Toward a more balanced view of non-native species. Conservation Biology 26:1156–1158.

Schlesinger, W. H., and E. S. Bernhardt. 2013. Biogeochemistry: an analysis of global change. 3rd edition. Academic Press, Waltham.

Schultz, R., S. Andrews, L. O'Reilly, V. Bouchard, and S. Frey. 2011. Plant community composition more predictive than diversity of carbon cycling in freshwater wetlands. Wetlands 31:965–977.

Schummer, M. L., J. Palframan, E. McNaughton, T. Barney, and S. A. Petrie. 2012. Comparisons of bird, aquatic macroinvertebrate, and plant communities among dredged ponds and natural wetland habitats at Long Point, Lake Erie, Ontario. Wetlands 32:945–953.

Simard, R. . 1993. Ammonium Acetate-Extractable Elements. Pages 39–42*in* M. R. Carter, editor.Soil Sampling and Methods of Analysis. Canadian Society of Soil Science. Lewis Publishers.

Simberloff, D. 2011. How common are invasion-induced ecosystem impacts? Biological Invasions 13:1255–1268.

Smith, V. H., S. B. Joye, and R. W. Howarth. 2006. Eutrophication of freshwater and marine ecosystems. Limnology and Oceanography 51:351–355.

Sutton-Grier, A. E., and J. P. Megonigal. 2011. Plant species traits regulate methane production in freshwater wetland soils. Soil Biology and Biochemistry 43:413–420.

The Canadian Hydrographic Service. 2016. Monthly and yearly mean water levels. http://tides-marees.gc.ca/C&A/NetworkMeans2017.pdf.

Tho, B. T., B. K. Sorrell, C. Lambertini, F. Eller, H. Brix, B. Truong, T. Brian, C. Lambertini, F. Eller, and H. Brix. 2016. *Phragmites australis*: how do genotypes of different phylogeographic origins differ from their invasive genotypes in growth, nitrogen allocation and gas exchange? Biological Invasions 18:2563–2576.

Trebitz, A. S. 2006. Characterizing seiche and tide-driven daily water level fluctuations affecting coastal ecosystems of the Great Lakes. Journal of Great Lakes Research 32:102–116.

Tulbure, M. G., and C. A. Johnston. 2010. Environmental conditions promoting non-native *Phragmites australis* expansion in Great Lakes coastal wetlands. Wetlands 30:577–587.

Tulbure, M. G., C. A. Johnston, and D. L. Auger. 2007. Rapid invasion of a Great Lakes coastal wetland by non-native *Phragmites australis* and *Typha*. Journal of Great Lakes Research 33:269–279.

United States - Canada. 2013. Great Lakes Water Quality Agreement.

van der Valk, A. G. 1986. The impact of litter and annual plants on recruitment from the seed bank of a lacustrine wetland. Aquatic Botany 24:13–26.

van der Valk, A. G., J. M. Rhymer, and H. R. Murkin. 1991. Flooding and the decomposition of litter of four emergent plant species in a prairie wetland. Wetlands 11:1–16.

van der Valk, A. G., L. Squires, and C. H. Welling. 1994. Assessing the impacts of an increase in water level on wetland vegetation. Ecological Applications 4:525–534.

Veenhof, D. 2017. *Phragmites australis* control projects at Long Point and Rondeau: Emergency Use Registration for application of herbicide over water.

Venter, O., N. N. Brodeur, L. Nemiroff, B. Belland, I. J. Dolinsek, and J. W. A. Grant. 2006. Threats to endangered species in Canada. BioScience 56:903–910.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14:702–708.

Vitule, J. R. S., C. A. Freire, D. P. Vazquez, M. A. Nuñez, and D. Simberloff. 2012. Revisiting the potential conservation value of non-native species. Conservation Biology 26:1153–1155.

Vymazal, J., and T. D. Březinová. 2016. Decomposition of *Phragmites australis* in relation to depth of flooding. Pages 57–68*in* J. Vymazal, editor.Natural and Constructed Wetlands. Springer International Publishing.

Watson, S. B., C. Miller, G. Arhonditsis, G. L. Boyer, W. Carmichael, M. N. Charlton, R. Confesor, D. C. Depew, T. O. Hö, S. A. Ludsin, G. Matisoff, S. P. Mcelmurry, M. W. Murray, R. P. Richards, Y. R. Rao, M. M. Steffen, and S. W. Wilhelm. 2016. The re-eutrophication of Lake Erie: harmful algal blooms and hypoxia. Harmful Algae 56:44–66.

Weinstein, M. P., and J. H. Balletro. 1999. Does the common reed, *Phragmites australis*, affect essential fish habitat? Estuaries 22:793–802.

Wetzel, P. R., and A. G. van der Valk. 2005. The biomass and nutrient levels of *Calamagrostis canadensis* and *Carex stricta* under different hydrologic and fungicide regimes. Canadian Journal of Botany 83:124–130.

Wilcox, K. L., S. a. Petrie, L. a. Maynard, and S. W. Meyer. 2003. Historical distribution and abundance of *Phragmites australis* at Long Point, Lake Erie, Ontario. Journal of Great Lakes Research 29:664–680.

Windham, L. 2001. Comparison of biomass production and decomposition between *Phragmites australis* (common reed) and *Spartina patens* (salt hay grass) in brackish tidal marshes of New Jersey, USA. Wetlands 21:179–188.

Windham, L., and J. G. Ehrenfeld. 2013. Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. Ecological Applications 13:883–897.

Windham, L., and R. Lathrop. 1999. Effect of *Phragmites australis* (common reed) invasion on aboveground biomass and soil properties in brackish tidal marsh of Mullica River, New Jersey. Estuaries 22:927–935.

Zapfe, L., and J. R. Freeland. 2015. Heterosis in invasive F1 cattail hybrids (*Typha* × *glauca*). Aquatic Botany 125:44–47.

Zedler, J. B., and S. Kercher. 2005. Wetland resources: status, trends, ecosystem services, and restorability. Pages 39–74Annual Review of Environment and Resources. Annual Reviews, Palo Alto.

Appendix 1. Water depths in meadow, cattail and *P. australis* invaded marsh in Long Point Provincial Park and Big Creek NWA in 2016 and 2017.

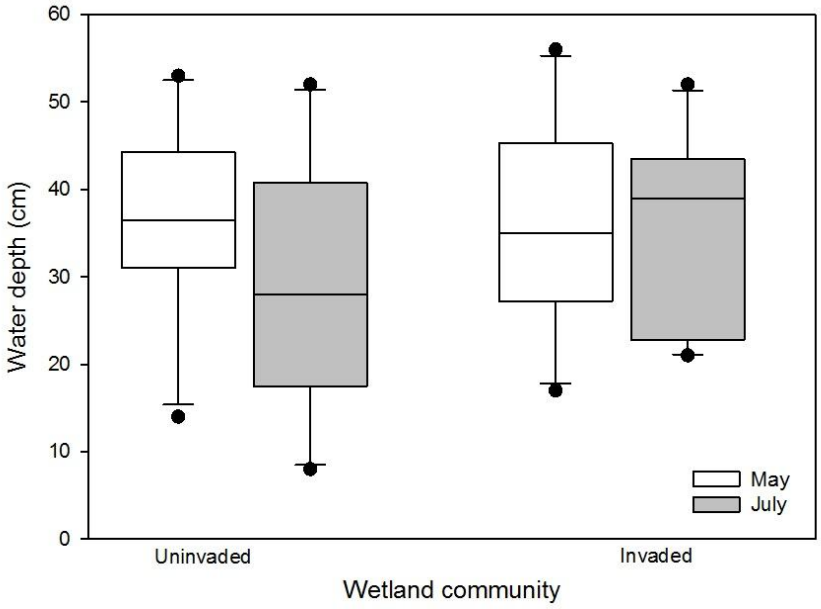

Figure 1. Average water depth (cm) of resident plant communities (n = 10) and *P. australis* invaded sites (n = 10) across a water depth gradient in May 2017 during site establishment and in July 2017 during peak aboveground biomass in Long Point (Lake Erie), Canada. Boxes represent the 25- 75 percentile, whiskers show the 10 - 90 percentile, horizontal lines are median, and circles are outliers.

Table 1. Minimum and maximum water depth (cm) measured in different meadow, cattail and *P. australis* invaded marsh sites sampled in coastal wetlands of the Long Point peninsula in July 2016 and 2017.

Plant community	2016 Big Creek National Wildlife Area			2016 Long Point Provincial Park			2017 Long Point Provincial Park		
	Meadow	Cattail	Invaded	Meadow	Cattail	Invaded	Meadow	Cattail	Invaded
n	5	5	5	5	5	5	5	5	10
July water depth (cm)	10 - 27	11 - 20	18 - 23	0 - 9	11 -20	6 - 30	8 - 26	30 - 52	21 - 52

Appendix 2. Peak biomass calculations. Picture of target species included.

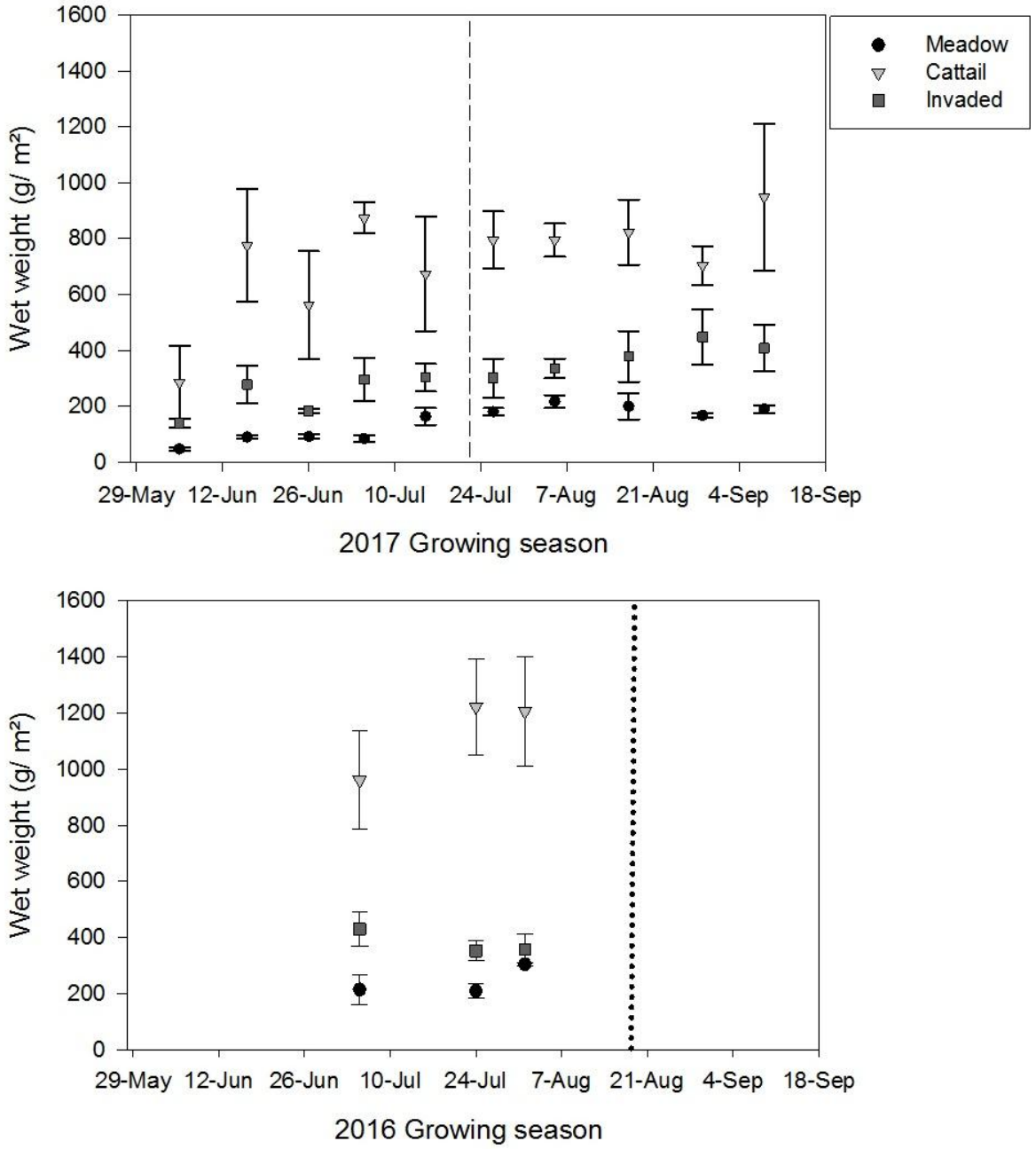

Figure 1. Measurements of average wet weight (g m^{-2}) of meadow, cattail and *P. australis* invaded sites (n = 3 quadrats from each community on each sample date) in Long Point Provincial Park during the 2016 and 2017 growing season. Dashed line shows approximate date of 2017 biomass harvest in study, dotted line shows approximate 2016 biomass harvest.

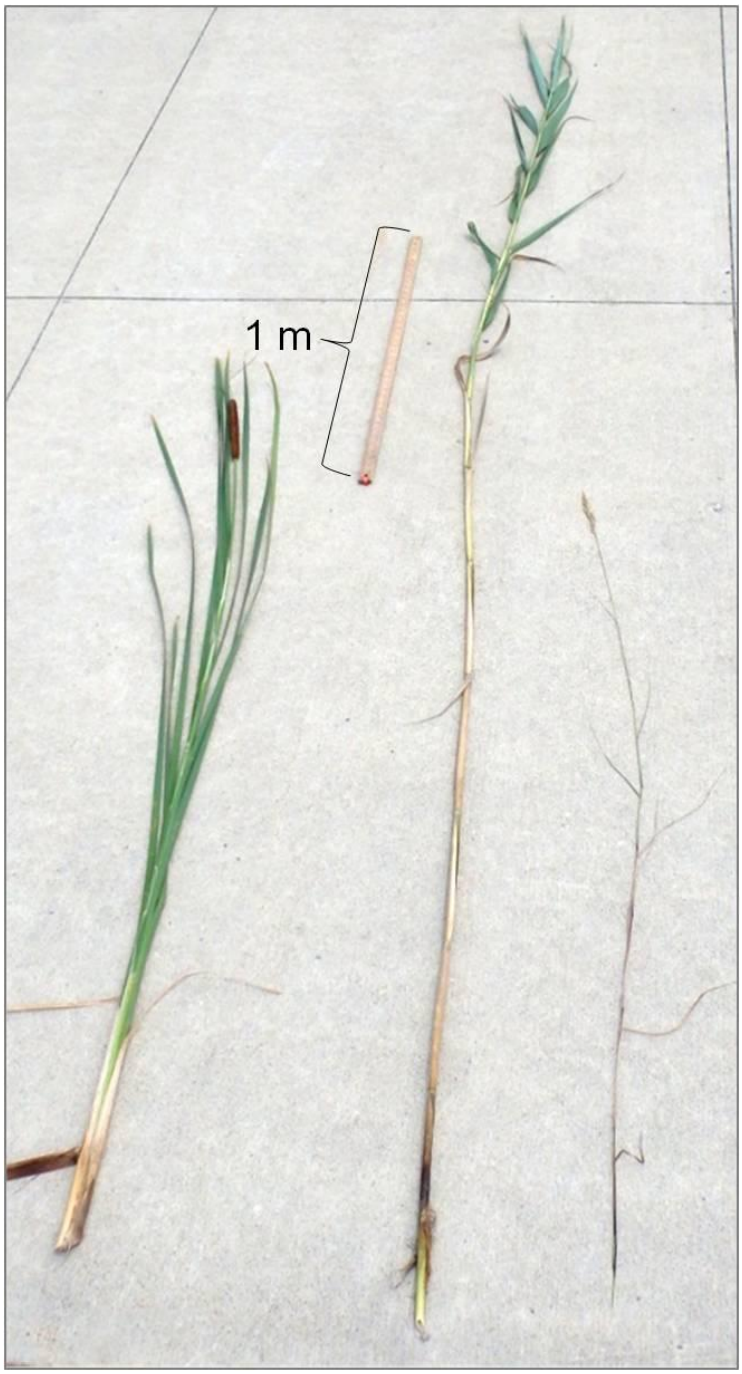

Figure 2. A single ramete of *Typha* spp. (left), *P. australis* (middle) and *C. canadensis* (right) taken from Long Point Provincial Park in July 2017. Note morphological differences between species.

Appendix 3. Summary of general linear models

Summaries of general linear models for comparing between 2016 and 2017 biomass measurements. Sample size for 2016 is n = 15, where 5 samples were taken from each plant community (meadow, cattail, *P. australis* invaded) from Long Point Provincial Park. Sample size for 2017 is n = 20, where 5 samples were taken from meadow and cattail and 10 samples from *P. australis* invaded marsh in Long Point Provincial Park.

Table 1. Summary of general linear model for belowground biomass (square root transformed) in Long Point Provincial Park as a function of plant community and year of collection, where plant community refers to meadow marsh (n = 10), emergent cattail (n = 10) and *P. australis* invaded (n = 15), and year refers to 2016 or 2017. The category *P. australis* was withheld as a reference for plant community variable and 2016 was withheld as reference for year. Residual standard error for the model = 3.830, $F_{5, 29}$ = 5.091, *p*-value = <0.002, R^2 = 0.467.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	10.824	1.713	6.319	<0.001
Plant community: meadow	-1.325	2.422	-0.547	0.589
Plant community: cattail	-6.831	2.422	-2.820	0.009
Year: 2017	0.097	2.098	0.046	0.963
Meadow*2017	-4.867	3.204	-1.519	0.140
Cattail* 2017	-3.592	3.204	-1.121	0.272

Table 2. Summary of general linear model for aboveground biomass in Long Point Provincial Park as a function of plant community and year of collection, where plant community refers to meadow marsh (n = 10), emergent cattail (n = 10) and *P. australis* invaded (n = 10), and year refers to 2016 or 2017. The category *P. australis* was withheld as a reference for plant community variable and 2016 was withheld as reference for year. Residual standard error for the model = 294.500, $F_{5, 29}$ = 8.968, *p*-value = <0.001, R^2 = 0.607.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1349.980	131.700	10.182	<0.001
Plant community: meadow	-901.18	186.260	-4.838	<0.001
Plant community: cattail	-182.239	186.260	-0.978	0.336
Year: 2017	-86.58	161.300	-0.537	0.596
Meadow*2017	3.210	246.400	0.013	0.990
Cattail* 2017	212.580	246.400	0.863	0.395

Summaries of general linear models for 2016 biomass measurements. Sample size is n = 30, where 5 samples are taken from each plant community (meadow, cattail, *P. australis* invaded) from each wetland (Big Creek NWA and Long Point Provincial Park).

Table 3. Summary of general linear model for aboveground biomass as a function of plant community and nutrient environment variables, where plant community refers to meadow marsh (n = 10), emergent cattail (n = 10) and *P. australis* invaded sites (n = 10), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 251.900, $F_{5,24}$ = 23.340, *p*-value = <0.001, R^2 = 0.829.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	2087.380	112.650	18.530	<0.001
Plant community: meadow	-970.000	159.310	-6.089	<0.001
Plant community: cattail	-528.100	159.310	-3.315	0.003
Nutrient environment: low	-746.400	159.310	-4.685	<0.001
Meadow * low nutrient environment	68.830	225.290	0.305	0.763
Cattail * low nutrient environment	345.800	225.290	1.535	0.138

Table 4. Summary of general linear model for belowground biomass (square-root transformed) to a depth of 11.3 cm as a function of plant community and nutrient environment variables, where plant community refers to meadow marsh (n = 10), emergent cattail (n = 10) and *P. australis* invaded sites (n = 10), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 4.486, $F_{5,24}$ = 4.252, *p*-value = 0.007, R^2 = 0.470.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	9.054	2.006	4.513	<0.001
Plant community: meadow	-3.907	2.837	-1.377	0.181
Plant community: cattail	3.123	2.837	1.101	0.282
Nutrient environment: low	1.770	2.837	0.624	0.539
Meadow * low nutrient environment	2.582	4.012	0.644	0.526
Cattail * low nutrient environment	3.708	4.012	0.924	0.365

Table 5. Summary of general linear model for total biomass as a function of plant community and nutrient environment variables, where plant community refers to meadow marsh (n = 10), emergent cattail (n = 10) and *P. australis* invaded sites (n = 10), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 317.500, $F_{5,24}$ = 15.200, *p*-value = <0.001, R^2 = 0.760.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	2178.410	142.010	15.340	<0.001
Plant community: meadow	-1020.560	200.830	-5.082	<0.001
Plant community: cattail	-454.200	200.800	-2.262	0.033
Nutrient environment: low	-713.320	200.830	-3.552	0.002
Meadow * low nutrient environment	89.090	284.010	0.314	0.756
Cattail * low nutrient environment	506.000	284.010	1.782	0.087

Table 6. Summary of general linear model for root:shoot ratio (square root transformed; where belowground biomass was measured to a depth of 11.3 cm) as a function of plant community and nutrient environment variables. Plant community refers to meadow marsh (n = 10), emergent cattail (n = 10) and *P. australis* invaded sites (n = 10), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 0.129, $F_{5,24}$ = 6.017, *p*-value = 0.001, R^2 = 0.556.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.196	0.058	3.398	0.002
Plant community: meadow	-0.036	0.082	-0.447	0.659
Plant community: cattail	0.111	0.082	1.365	0.185
Nutrient environment: low	0.101	0.082	1.235	0.229
Meadow * low nutrient environment	0.210	0.115	1.823	0.081
Cattail * low nutrient environment	0.101	0.115	0.873	0.391

Summaries of general linear models for 2017 biomass measurements. Sample size is n = 20, where five sites are in meadow, five sites are in cattail and 10 sites in *P. australis* invaded marsh. Resident plant community and invaded sites are placed along a water gradient which was measured in May when sites were established and again in July when biomass was harvested. General linear models were run with May water depth measurements and then with July water depth measurements. The final model was determined by comparing the AICc value of the model using the May water depth measurement with the AICc value of the model using the July water depth measurement. The lower value model was selected.

Table 7. Summary of general linear model for aboveground biomass as a function of plant community along the water depth gradient (as measured in May 2017). Plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded sites (n = 10). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 385.900, $F_{5,14}$ = 2.250, *p*-value = 0.106, R^2 = 0.446. AICc = 311.184, d.f. = 7.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1071.985	409.838	2.616	0.020
Plant community: meadow	-815.210	707.413	-1.152	0.268
Plant community: cattail	289.305	1230.293	0.235	0.818
May water depth	5.110	10.959	0.466	0.648
Meadow * May water depth	5.123	21.260	0.241	0.813
Cattail * May water depth	-11.697	28.613	-0.409	0.689

Table 8. Summary of general linear model for aboveground biomass as a function of plant community along the water depth gradient (as measured in July 2017). Plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded sites (n = 10). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 305.800, $F_{5,14}$ = 5.250, *p*-value = 0.006, R^2 = 0.652. AICc = 301.871, d.f. = 7.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	274.225	359.556	0.763	0.458
Plant community: meadow	-63.270	539.930	-0.117	0.908
Plant community: cattail	1244.528	831.054	1.498	0.157
July water depth	27.077	9.567	2.830	0.013
Meadow * July water depth	-6.683	23.783	-0.281	0.783
Cattail * July water depth	-37.944	20.433	-1.857	0.085

Table 9. Summary of general linear model for belowground biomass to a depth of 11.3 cm (square root transformed) as a function of plant community along the water depth gradient (as measured in May 2017). Plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded sites (n = 10). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 2.050, $F_{5,14}$ = 10.080, *p*-value = <0.001, R^2 = 0.783. AICc = 101.628, d.f. = 7.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	6.974	2.175	3.207	0.006
Plant community: meadow	-4.790	3.754	-1.276	0.223
Plant community: cattail	-17.055	6.528	-2.613	0.020
May water depth	0.111	0.058	1.901	0.078
Meadow * May water depth	0.016	0.113	0.142	0.889
Cattail * May water depth	0.419	0.152	2.757	0.015

Table 10. Summary of general linear model for belowground biomass to a depth of 11.3 cm (square root transformed) as a function of plant community along the water depth gradient (as measured in July 2017). Plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded sites (n = 10). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 2.820, $F_{5,14}$ = 4.000, *p*-value = 0.018, R^2 = 0.589. AICc = 114.388, d.f. = 7.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	6.762	3.312	2.041	0.061
Plant community: meadow	-3.120	4.975	-0.628	0.540
Plant community: cattail	-2.399	7.657	-0.313	0.759
July water depth	0.115	0.088	1.304	0.213
Meadow * July water depth	0.021	0.219	0.096	0.925
Cattail * July water depth	0.094	0.188	0.499	0.625

Table 11. Summary of general linear model for total biomass as a function of plant community along the water depth gradient (as measured in May 2017). Plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded sites (n = 10). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 409.500, $F_{5,14}$ = 2.640, *p*-value = 0.070, R^2 = 0.485. AICc = 313.552, d.f. = 7.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1110.079	434.834	2.553	0.023
Plant community: meadow	-859.440	750.558	-1.145	0.271
Plant community: cattail	-141.550	1305.329	-0.108	0.915
May water depth	7.553	11.628	0.650	0.526
Meadow * May water depth	4.168	22.556	0.185	0.856
Cattail * May water depth	-0.958	30.358	-0.032	0.975

Table 12. Summary of general linear model for total biomass as a function of plant community along the water depth gradient (as measured in July 2017). Plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded sites (n = 10). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 326.300, $F_{5,14}$ = 5.770, *p*-value = 0.004, R^2 = 0.673. AICc = 304.464, d.f. = 7.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	308.036	383.637	0.803	0.435
Plant community: meadow	-86.870	576.092	-0.151	0.882
Plant community: cattail	1157.971	886.713	1.306	0.213
July water depth	29.605	10.207	2.900	0.012
Meadow * July water depth	-7.567	25.376	-0.298	0.770
Cattail * July water depth	-34.783	21.802	-1.595	0.133

Table 13. Summary of general linear model for root: shoot ratio (square root transformed, where belowground biomass was captured to a depth of 11.3 cm) as a function of plant community along the water depth gradient (as measured in May 2017). Plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded sites (n = 10). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 0.080, $F_{5,14}$ = 4.190, *p*-value = 0.015, R^2 = 0.599. AICc = -30.205, d.f. = 7.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.250	0.081	3.107	0.008
Plant community: meadow	-0.087	0.139	-0.629	0.540
Plant community: cattail	-0.611	0.242	-2.527	0.024
May water depth	0.002	0.002	0.920	0.373
Meadow * May water depth	0.001	0.004	0.326	0.749
Cattail * May water depth	0.015	0.006	2.756	0.015

Table 14. Summary of general linear model for belowground root: shoot ratio (square root transformed, where belowground biomass was captured to a depth of 11.3 cm) as a function of plant community along the water depth gradient (as measured in July 2017). Plant community refers to meadow marsh (n = 5), emergent cattail (n = 5) and *P. australis* invaded sites (n = 10). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 0.100, $F_{5,14}$ = 1.520, *p*-value = 0.247, R^2 = 0.352. AICc = -20.581, d.f. = 7.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.375	0.113	3.308	0.005
Plant community: meadow	-0.133	0.170	-0.783	0.447
Plant community: cattail	-0.340	0.262	-1.297	0.216
July water depth	-0.002	0.003	-0.497	0.627
Meadow * July water depth	0.003	0.008	0.367	0.719
Cattail * July water depth	0.010	0.006	1.611	0.129

Summaries of general linear models for 2016 soil nutrient measurements. Sample size is n = 18, where 3 samples are taken from each plant community (meadow, cattail, *P. australis* invaded) from each wetland (Big Creek NWA and Long Point Provincial Park).

Table 15. Summary of general linear model for total nitrogen in the soil as a function of plant community and nutrient environment variables, where plant community where plant community refers to meadow marsh (n = 6), emergent cattail (n = 6) and *P. australis* invaded sites (n = 6), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 0.421, $F_{5, 12}$ = 11.370, *p*-value = <0.001, R^2 = 0.826.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	2.210	0.243	9.098	<0.001
Plant community: meadow	-0.163	0.344	-0.475	0.643
Plant community: cattail	-0.410	0.344	-1.193	0.256
Nutrient environment: low	-1.583	0.344	-4.609	0.001
Meadow * low nutrient environment	-0.233	0.486	-0.480	0.640
Cattail * low nutrient environment	0.733	0.486	1.509	0.157

Table 16. Summary of general linear model for total carbon in the soil as a function of plant community and nutrient environment variables, where plant community where plant community refers to meadow marsh (n = 6), emergent cattail (n = 6) and *P. australis* invaded sites (n = 6), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 5.448, $F_{5, 12}$ = 9.490, *p*-value = <0.001, R^2 = 0.798

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	28.613	3.146	9.097	<0.001
Plant community: meadow	-4.153	4.448	-0.934	0.369
Plant community: cattail	-5.997	4.448	-1.348	0.203
Nutrient environment: low	-19.923	4.448	-4.479	0.001
Meadow * low nutrient environment	-0.347	6.291	-0.055	0.957
Cattail * low nutrient environment	10.527	6.291	1.673	0.120

Table 17. Summary of general linear model for phosphorus in the soil as a function of plant community and nutrient environment variables, where plant community where plant community refers to meadow marsh (n = 6), emergent cattail (n = 6) and *P. australis* invaded sites (n = 6), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 2.965, $F_{5, 12}$ = 7.943, *p*-value = 0.002, R^2 = 0.768.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	14.433	1.712	8.430	<0.001
Plant community: meadow	-2.337	2.421	-0.965	0.354
Plant community: cattail	-2.033	2.421	-0.840	0.418
Nutrient environment: low	-9.243	2.421	-3.817	0.002
Meadow * low nutrient environment	-0.843	3.424	-0.246	0.810
Cattail * low nutrient environment	4.293	3.424	1.254	0.234

Table 18. Summary of general linear model for potassium in the soil as a function of plant community and nutrient environment variables, where plant community where plant community refers to meadow marsh (n = 6), emergent cattail (n = 6) and *P. australis* invaded sites (n = 6), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 24.070, $F_{5, 12}$ = 5.866, *p*-value = 0.006, R^2 = 0.710.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	93.600	13.900	6.736	<0.001
Plant community: meadow	-16.900	19.650	-0.860	0.407
Plant community: cattail	0.900	19.650	0.046	0.964
Nutrient environment: low	-41.030	19.650	-2.088	0.059
Meadow * low nutrient environment	-23.830	27.790	-0.858	0.408
Cattail * low nutrient environment	-19.770	27.790	-0.711	0.491

Table 19. Summary of general linear model for magnesium in the soil as a function of plant community and nutrient environment variables, where plant community where plant community refers to meadow marsh (n = 6), emergent cattail (n = 6) and *P. australis* invaded sites (n = 6), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 169.400, $F_{5, 12}$ = 11.920, *p*-value = <0.001, R^2 = 0.832.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	792.00	97.823	8.096	<0.001
Plant community: meadow	34.667	138.343	0.251	0.806
Plant community: cattail	-27.667	138.343	-0.200	0.845
Nutrient environment: low	-530.333	138.343	-3.833	0.002
Meadow * low nutrient environment	-226.367	195.647	-1.157	0.270
Cattail * low nutrient environment	6.667	195.647	0.034	0.973

Table 20. Summary of general linear model for calcium in the soil as a function of plant community and nutrient environment variables, where plant community where plant community refers to meadow marsh (n = 6), emergent cattail (n = 6) and *P. australis* invaded sites (n = 6), and nutrient environment refers to high nutrient (Big Creek NWA) and low nutrient (Long Point Provincial Park) in 2016. The category *P. australis* invaded was withheld as a reference for plant community variable and high nutrient environment (Big Creek NWA) was withheld as reference for nutrient environment. Residual standard error for the model = 1021.000, $F_{5, 12}$ = 10.090, *p*-value = <0.001, R^2 = 0.808.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	7943.300	589.400	13.477	<0.001
Plant community: meadow	-913.300	833.600	-1.096	0.295
Plant community: cattail	-370.000	833.600	-0.444	0.665
Nutrient environment: low	-3230.000	833.600	-3.875	0.002
Meadow * low nutrient environment	-726.700	1178.800	-0.616	0.549
Cattail * low nutrient environment	1873.300	1178.800	1.589	0.138

Summaries of general linear models for nutrients in plant tissue. Sample size is n = 30, where four samples were taken from leaf tissue, four samples from stem tissue, and two samples from roots and rhizomes from each plant species (*C. canadensis*, *Typha* spp., and *P. australis*).

Table 21. Summary of general linear model for nitrogen in plant tissues (% dry weight) as a function of tissue type (leaf, stem and belowground biomass) and plant species (*C. canadensis*, *Typha* spp., and *P. australis*). The category *P. australis* was withheld as a reference for plant species variable and leaf was withheld as reference for tissue type. Residual standard error for the model = 0.215, $F_{8, 21}$ = 51.480, *p*-value = <0.001, R^2 = 0.952.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	2.838	0.108	26.400	<0.001
Plant species: *C. canadensis*	-1.100	0.152	-7.237	<0.001
Plant species: *Typha* spp.	-1.105	0.152	-7.270	<0.001
Tissue: root	-1.893	0.186	-10.166	<0.001
Tissue: stem	-2.290	0.152	-15.066	<0.001
C. canadensis * root	1.140	0.263	4.330	<0.001
Typha spp. * root	1.025	0.263	3.893	0.001
C. canadensis * stem	1.028	0.215	4.780	<0.001
Typha spp. * stem	1.088	0.215	5.059	<0.001

Table 22. Summary of general linear model for carbon in plant tissues (% dry weight) as a function of tissue type (leaf, stem and belowground biomass) and plant species (*C. canadensis*, *Typha* spp., and *P. australis*). The category *P. australis* was withheld as a reference for plant species variable and leaf was withheld as reference for tissue type. Residual standard error for the model = 0.773, $F_{8, 21}$ = 2.288, *p*-value = 0.062, R^2 = 0.466.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	45.723	0.386	118.338	<0.001
Plant species: *C. canadensis*	-0.030	0.546	-0.055	0.957
Plant species: *Typha* spp.	0.955	0.546	1.748	0.095
Tissue: root	1.263	0.669	1.887	0.073
Tissue: stem	-0.010	0.546	-0.018	0.986
C. canadensis * root	-0.940	0.946	-0.993	0.332
Typha spp. * root	-3.710	0.946	-3.920	<0.001
C. canadensis * stem	0.303	0.773	0.391	0.699
Typha spp. * stem	-0.600	0.773	-0.776	0.446

Table 23. Summary of general linear model for phosphorus in plant tissues (% dry weight) as a function of tissue type (leaf, stem and belowground biomass) and plant species (*C. canadensis*, *Typha* spp., and *P. australis*). The category *P. australis* was withheld as a reference for plant species variable and leaf was withheld as reference for tissue type. Residual standard error for the model = 0.027, $F_{8, 21}$ = 10.380, *p*-value = <0.001, R^2 = 0.798

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.157	0.013	11.694	<0.001
Plant species: *C. canadensis*	-0.053	0.019	-2.796	0.011
Plant species: *Typha* spp.	-0.031	0.019	-1.609	0.123
Tissue: root	-0.095	0.023	-4.081	0.001
Tissue: stem	-0.114	0.019	-5.987	<0.001
C. canadensis * root	0.066	0.033	2.010	0.057
Typha spp. * root	0.064	0.033	1.934	0.067
C. canadensis * stem	0.039	0.027	1.436	0.166
Typha spp. * stem	0.022	0.027	0.811	0.426

Table 24. Summary of general linear model for carbon: nitrogen ratio in plant tissues (% dry weight) as a function of tissue type (leaf, stem and belowground biomass) and plant species (*C. canadensis*, *Typha* spp., and *P. australis*). The category *P. australis* was withheld as a reference for plant species variable and leaf was withheld as reference for tissue type. Residual standard error for the model = 10.500, $F_{8, 21}$ = 32.020, *p*-value = <0.001, R^2 = 0.924.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	16.398	5.250	3.123	0.005
Plant species: *C. canadensis*	10.125	7.425	1.364	0.187
Plant species: *Typha* spp.	10.873	7.425	1.464	0.158
Tissue: root	33.767	9.094	3.713	0.001
Tissue: stem	69.890	7.425	9.413	<0.001
C. canadensis * root	-12.185	12.861	-0.947	0.354
Typha spp. * root	-8.972	12.861	-0.698	0.493
C. canadensis * stem	2.383	10.501	0.227	0.823
Typha spp. * stem	-9.635	10.501	-0.918	0.369

Table 25. Summary of general linear model for nitrogen: phosphorus ratio in plant tissues (% dry weight) as a function of tissue type (leaf, stem and belowground biomass) and plant species (*C. canadensis*, *Typha* spp., and *P. australis*). The category *P. australis* was withheld as a reference for plant species variable and leaf was withheld as reference for tissue type. Residual standard error for the model = 5.320, $F_{8, 21}$ = 1.381, *p*-value = 0.261, R^2 = 0.345

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	18.136	2.660	6.818	<0.001
Plant species: *C. canadensis*	0.827	3.762	0.220	0.828
Plant species: *Typha* spp.	-4.265	3.762	-1.134	0.270
Tissue: root	-2.339	4.607	-0.508	0.617
Tissue: stem	-5.292	3.762	-1.407	0.174
C. canadensis * root	-0.848	6.516	-0.130	0.898
Typha spp. * root	-2.408	6.516	-0.370	0.715
C. canadensis * stem	7.499	5.320	1.410	0.173
Typha spp. * stem	7.138	5.320	1.342	0.194

Table 26. Summary of general linear model for potassium in plant tissues (% dry weight) as a function of tissue type (leaf, stem and belowground biomass) and plant species (*C. canadensis*, *Typha* spp., and *P. australis*). The category *P. australis* was withheld as a reference for plant species variable and leaf was withheld as reference for tissue type. Residual standard error for the model = 0.164, $F_{8, 21}$ = 16.240, *p*-value = <0.001, R^2 = 0.861

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.248	0.082	15.253	<0.001
Plant species: *C. canadensis*	-0.335	0.116	-2.896	0.009
Plant species: *Typha* spp.	-0.303	0.116	-2.615	0.016
Tissue: root	-0.763	0.142	-5.383	<0.001
Tissue: stem	-0.775	0.116	-6.700	<0.001
C. canadensis * root	0.075	0.200	0.374	0.712
Typha spp. * root	0.408	0.200	2.034	0.055
C. canadensis * stem	0.240	0.164	1.467	0.157
Typha spp. * stem	0.100	0.164	0.611	0.548

Table 27. Summary of general linear model for magnesium in plant tissues (% dry weight) as a function of tissue type (leaf, stem and belowground biomass) and plant species (*C. canadensis*, *Typha* spp., and *P. australis*). The category *P. australis* was withheld as a reference for plant species variable and leaf was withheld as reference for tissue type. Residual standard error for the model = 0.034, $F_{8, 21}$ = 13.490, *p*-value = <0.001, R^2 = 0.837.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.168	0.017	9.941	<0.001
Plant species: *C. canadensis*	-0.033	0.024	-1.364	0.187
Plant species: *Typha* spp.	-0.005	0.024	-0.210	0.836
Tissue: root	0.003	0.029	0.086	0.933
Tissue: stem	-0.135	0.024	-5.665	<0.001
C. canadensis * root	0.073	0.041	1.757	0.094
Typha spp. * root	0.050	0.041	1.211	0.239
C. canadensis * stem	0.028	0.034	0.816	0.424
Typha spp. * stem	0.073	0.034	2.151	0.043

Table 28. Summary of general linear model for calcium in plant tissues (% dry weight) as a function of tissue type (leaf, stem and belowground biomass) and plant species (*C. canadensis*, *Typha* spp., and *P. australis*). The category *P. australis* was withheld as a reference for plant species variable and leaf was withheld as reference for tissue type. Residual standard error for the model = 0.082, $F_{8, 21}$ = 112.500, *p*-value = <0.001, R^2 = 0.977.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.740	0.041	18.063	<0.001
Plant species: *C. canadensis*	-0.193	0.058	-3.323	0.003
Plant species: *Typha* spp.	0.413	0.058	7.120	<0.001
Tissue: root	-0.115	0.071	-1.621	0.120
Tissue: stem	-0.678	0.058	-11.694	<0.001
C. canadensis * root	0.493	0.100	4.908	<0.001
Typha spp. * root	0.348	0.100	3.463	0.002
C. canadensis * stem	0.220	0.082	2.685	0.014
Typha spp. * stem	0.715	0.082	8.727	<0.001

Summaries of general linear models for nutrient annual standing stock. Sample size is n = 50, where 15 sites are in meadow and cattail each and 20 sites are in *P. australis* invaded communities.

Table 29. Summary of general linear model for annual standing stock of nitrogen (g m^{-2}) in three plant communities (meadow, cattail and *P. australis* invaded). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 6.585, $F_{2, 47}$ = 14.840, *p*-value = <0.001, R^2 = 0.387.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	17.004	1.472	11.549	<0.001
Plant community: meadow	-10.864	2.249	-4.830	<0.001
Plant community: cattail	0.464	2.249	0.206	0.838

Table 30. Summary of general linear model for annual standing stock of carbon (g m^{-2}) in three plant communities (meadow, cattail and *P. australis* invaded). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 204.400, $F_{2, 47}$ = 16.450, *p*-value = <0.001, R^2 = 0.412.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	713.728	45.708	15.615	<0.001
Plant community: meadow	-361.590	69.820	-5.179	<0.001
Plant community: cattail	0.559	69.820	0.008	0.994

Table 31. Summary of general linear model for annual standing stock of phosphorus (g m^{-2}) in three plant communities (meadow, cattail and *P. australis* invaded). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 0.537, $F_{2, 47}$ = 14.330, *p*-value = <0.001, R^2 = 0.379.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.083	0.120	9.016	<0.001
Plant community: meadow	-0.707	0.184	-3.854	<0.001
Plant community: cattail	0.313	0.184	1.706	0.095

Table 32. Summary of general linear model for annual standing stock of potassium (g m^{-2}) in three plant communities (meadow, cattail and *P. australis* invaded). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 2.885, $F_{2, 47}$ = 29.760, *p*-value = <0.001, R^2 = 0.559.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	10.890	0.645	16.879	<0.001
Plant community: meadow	-7.109	0.986	-7.213	<0.001
Plant community: cattail	-0.609	0.986	-0.618	0.539

Table 33. Summary of general linear model for annual standing stock of magnesium (g m^{-2}; log-transformed) in three plant communities (meadow, cattail and *P. australis* invaded). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 0.223, $F_{2, 47}$ = 35.760, *p*-value = <0.001, R^2 = 0.604.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	-0.011	0.050	-0.211	0.834
Plant community: meadow	-0.355	0.076	-4.662	<0.001
Plant community: cattail	0.333	0.076	4.377	<0.001

Table 34. Summary of general linear model for annual standing stock of calcium (g m^{-2}; log-transformed) in three plant communities (meadow, cattail and *P. australis* invaded). The category *P. australis* invaded was withheld as a reference for plant community variable. Residual standard error for the model = 0.164, $F_{2, 47}$ = 150.000, *p*-value = <0.001, R^2 = 0.865.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.579	0.037	15.833	<0.001
Plant community: meadow	-0.320	0.056	-5.734	<0.001
Plant community: cattail	0.689	0.059	12.310	<0.001

Appendix 4. Measurements of biomass along a water depth gradient in meadow marsh, cattail and *P. australis* invaded plant communities.

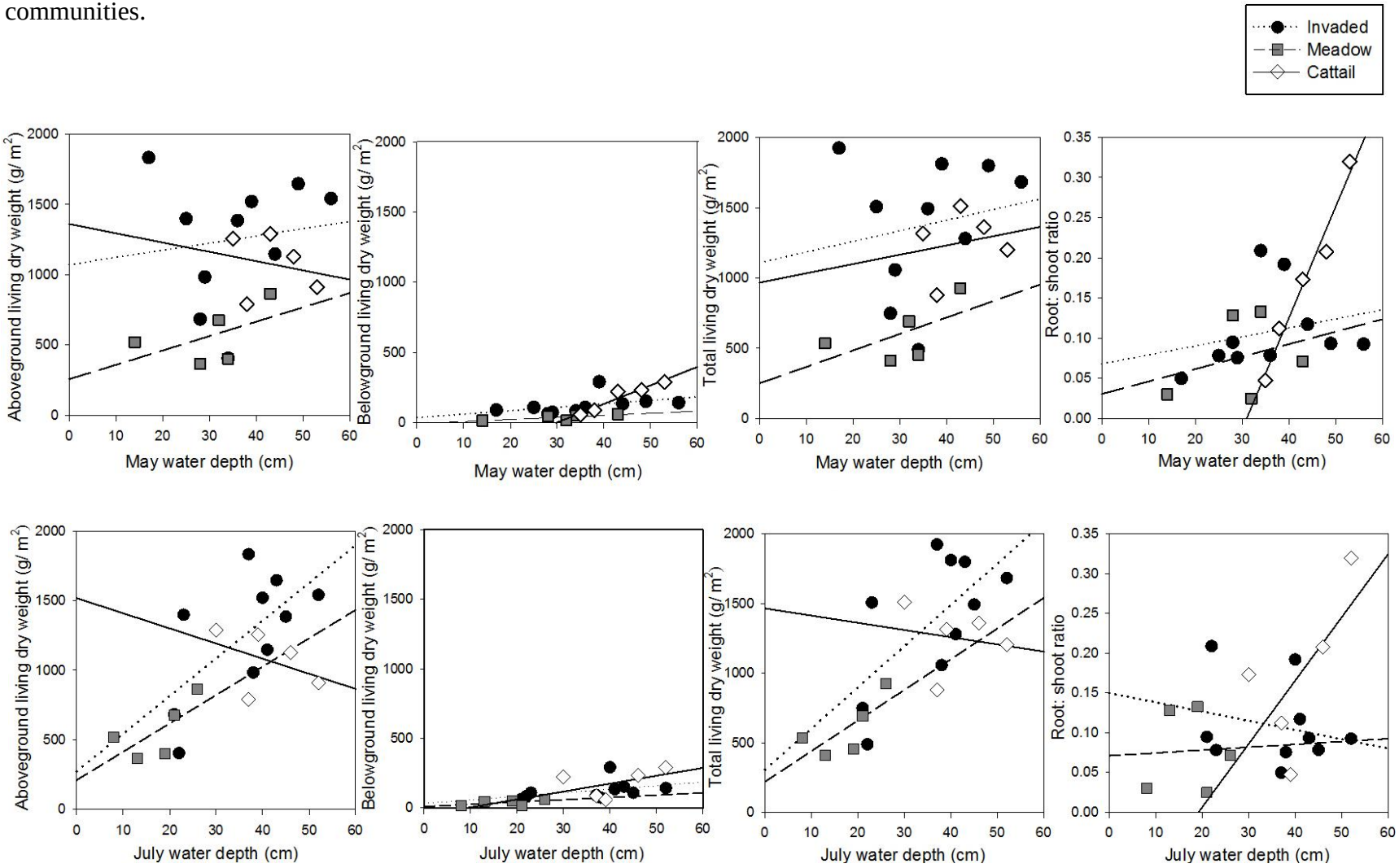

Figure 1. Dry weight of biomass (g m^{-2}) and root: shoot ratio correlated to May and July 2017 water depth (cm) in emergent cattail (n=5), meadow marsh (n = 5), and *P. australis* invaded (n = 10) sites.

Appendix 5. Soil nutrients in plant communities in high and low nutrient environments.

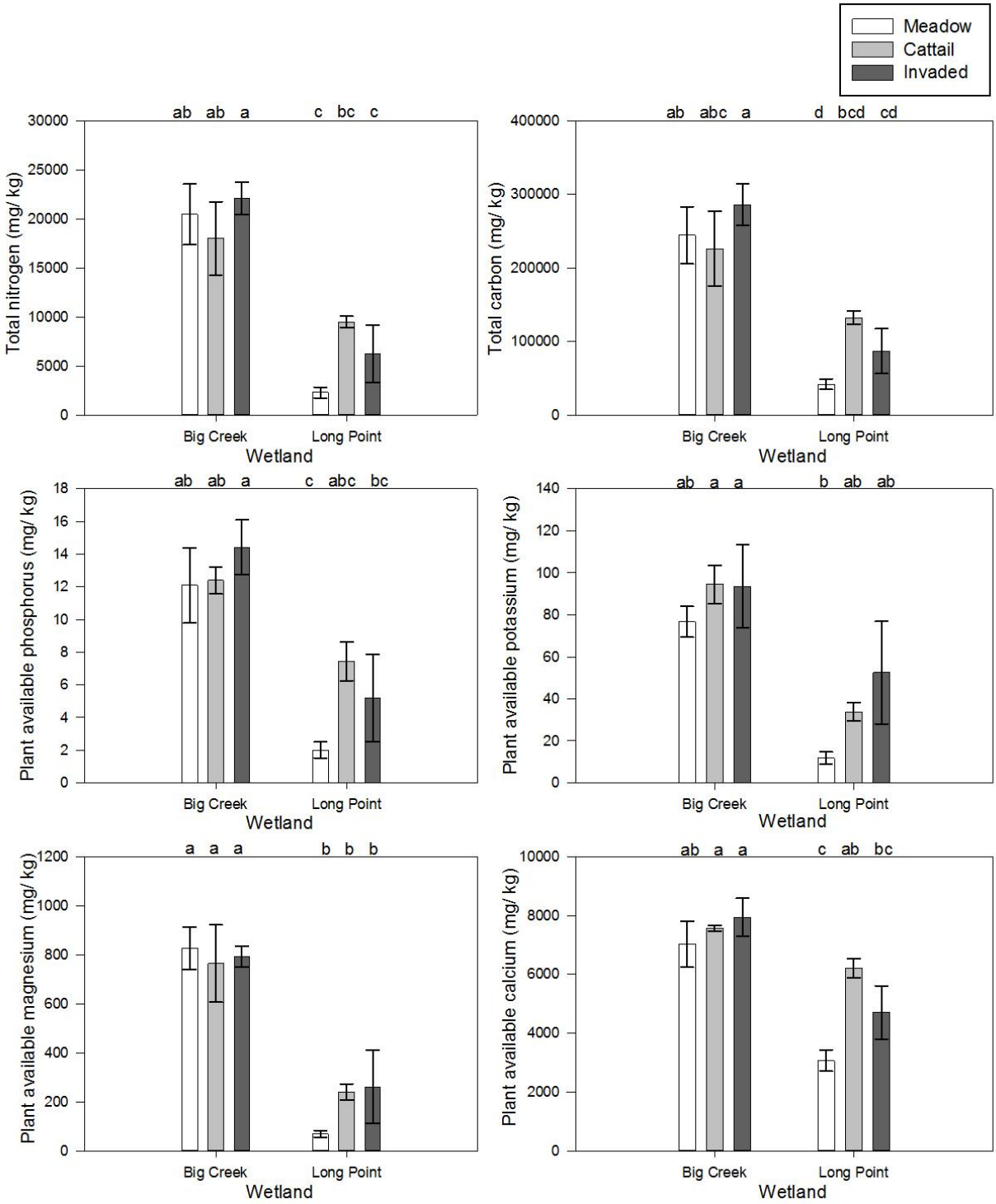

Figure 1. Average soil nutrients from meadow, cattail, and *P. australis* invaded marsh sites (n = 3 per marsh community in each wetland). Samples collected in August 2017. Error bars represent standard error. Letters indicate significant differences of soil nutrients among plant communities at $p < 0.05$.

Appendix 6. Annual nutrient standing stock estimates.

Table 1. Nutrient standing stock estimates of meadow, cattail and *P. australis* invaded marsh using biomass of the total marsh community and the estimated biomass of the target species (calculated using the percent cover of *C. canadensis*, *Typha* spp., and *P. australis* for meadow, cattail and invaded sites, respectively). Nutrient standing stock estimates calculated for meadow (n = 5/ wetland), cattail (n = 5/ wetland) and invaded (n = 5/ wetland) sites in Big Creek National Wildlife Area (BC) and Long Point Provincial Park (LP) in July 2016 and five meadow, five cattail and 10 invaded sites along a water depth gradient in Long Point Provincial Park in 2017. Standard deviation in brackets.

		Total Nitrogen (g/ m²)		**Total Carbon (g/ m²)**		**Phosphorus (g/ m²)**		**Potassium (g/ m²)**		**Calcium (g/ m²)**		**Magnesium (g/ m²)**	
Plant Community	Site	Marsh community	Target species	Marsh community	Target species	Marsh community	Target species	Marsh community	Target species	Marsh community	Target species	Marsh community	Target species
Meadow	2017	4.22 (± 1.27)	2.03 (±1.50)	273.62 (±94.78)	132.70 (±100.25)	0.16 (±0.05)	0.08 (±0.06)	2.51 (±0.81)	1.21 (±0.92)	1.53 (±0.40)	0.72 (±0.48)	0.31 (±0.08)	0.15 (±0.10)
	2016 BC	10.37 (±4.24)	9.35 (4.62)	540.02 (±214.13)	486.56 (±233.61)	0.81 (±0.34)	0.73 (±0.37)	6.72 (±2.49)	6.04 (±2.74)	2.58 (±1.40)	2.35 (±1.48)	0.84 (±0.41)	0.76 (±0.44)
	2016 LP	3.84 (±1.02)	1.57 (±1.64)	242.77 (±65.19)	99.31 (±103.45)	0.15 (±0.04)	0.06 (±0.07)	2.12 (±0.59)	0.87 (±0.90)	1.74 (±0.47)	0.71 (±0.77)	0.36 (±0.10)	0.15 (±0.16)
Cattail	2017	11.77 (±2.52)	9.62 (±3.91)	575.49 (±108.67)	469.01 (±175.16)	0.83 (±0.19)	0.68 (±0.27)	7.74 (±1.65)	6.29 (±2.47)	14.46 (±2.74)	11.76 (±4.32)	1.38 (±0.31)	1.11 (±0.40)
	2016 BC	24.90 (±5.68)	23.52 (±6.45)	791.50 (±188.78)	747.99 (±212.14)	2.20 (±0.52)	2.08 (±0.58)	12.49 (±2.85)	11.80 (±3.23)	23.34 (±5.67)	22.06 (±6.35)	3.67 (±0.88)	3.46 (±0.99)
	2016 LP	15.73 (±2.20)	14.76 (±2.76)	775.88 (±122.74)	728.21 (±147.68)	1.15 (±0.22)	1.08 (±0.25)	10.61 (±1.89)	9.96 (±2.19)	19.72 (±3.47)	18.51 (±4.04)	2.00 (±0.54)	1.88 (±0.57)
P. australis invaded	2017	13.55 (±5.34)	12.72 (±5.45)	637.03 (±222.31)	596.76 (±222.25)	0.85 (±0.32)	0.80 (±0.33)	10.58 (±3.92)	9.93 (±3.97)	3.50 (±1.33)	3.28 (±1.35)	0.83 (±0.30)	0.78 (±0.31)
	2016 BC	28.44 (±2.92)	27.60 (±2.94)	988.51 (±107.35)	959.66 (±108.58)	1.85 (±0.18)	1.79 (±0.18)	12.59 (±1.14)	12.22 (±1.13)	6.29 (±0.81)	6.11 (±0.82)	1.99 (±0.25)	1.94 (±0.26)
	2016 LP	12.49 (±2.65)	10.88 (±2.10)	592.34 (±126.80)	515.96 (±99.44)	0.79 (±0.17)	0.68 (±0.13)	9.80 (±2.11)	8.54 (±1.65)	3.26 (±0.84)	2.83 (±0.59)	0.78 (±0.20)	0.67 (±0.14)

Appendix 7. Description and photos of plant communities.

Table 1. Plant species identified in July 2017 in meadow and cattail (n = 5), invaded and herbicide-treated (n = 10) sites. Three 0.25 m^2 quadrats were used at each site. Growth form refers to emergent (e), submerged (s) or floating (f).

		Present in site?				
Scientific name	Common name	Meadow	Cattail	Invaded	Herbicide-treated	Growth form
Calamagrostis canadensis	Canada bluejoint grass	X	X	X	X	e
Campanula aparinoides	marsh bell flower	X		X	X	e
Calystegia sepium	hedge bindweed	X				e
Carex aquatilis	water sedge	X		X		e
Carex buxbaumii	dark-scaled sedge	X				e
Carex comosa	bristly sedge			X		e
Carex cryptoepis	small yellow sedge	X				e
Carex lacustris	common lakeshore sedge			X		e
Carex lanuginosa	woolly sedge	X		X		e
Carex lasiocarpa	wire sedge	X		X		e
Cladium mariscoides	twigrush	X				e
Chara spp.	muskgrass				X	s
Cornus racemosa	gray dogwood	X				e
Cornus stolonifera	red-osier dogwood	X				e
Panicum flexile	wiry witch grass	X				e
Eleocharis spp.	spike-rush	X				e
Equisetum fluviatile	water horsetail			X		e
Hydrocharis morsus-ranae	frogbit		X	X	X	f
Hypericum kalmianum	Kalm's St. John's-wort	X				e
Juncus brevicaudatus	short-tailed rush				X	e
Juncus spp.	wire rush	X				e
Lemna	duckweed			X		f
Lysimachia thyrsiflora	tufted loosestrife	X	X		X	e
Lycopus spp.	water-horehound	X				e
Phragmites australis	common reed			X	X	e
Polygonum amphibium	water smartweed		X	X		e, s, f
Polygonum spp.	smartweed			X		e, s, f
Potentilla anserina	silver-weed	X				e
Potamogeton alpinus	red pondweed				X	e, s, f
Sagittaria latifolia	broad-leaved arrowhead		X			e
Scirpus pungens	common threesquare				X	e
Solanum dulcamara	climbing nightshade			X		e
Solidago spp.	goldenrod	X				e
Thelypteris palustris	marsh fern	X				e
Toxicodendron radicans	common poison-ivy	X				e
Typha spp.	NA		X	X	X	e
unknown forb	NA	X	X			-
Utricularia intermedia	flat-leaved bladderwort		X	X	X	s
Utricularia vulgaris	common bladderwort	X	X		X	s

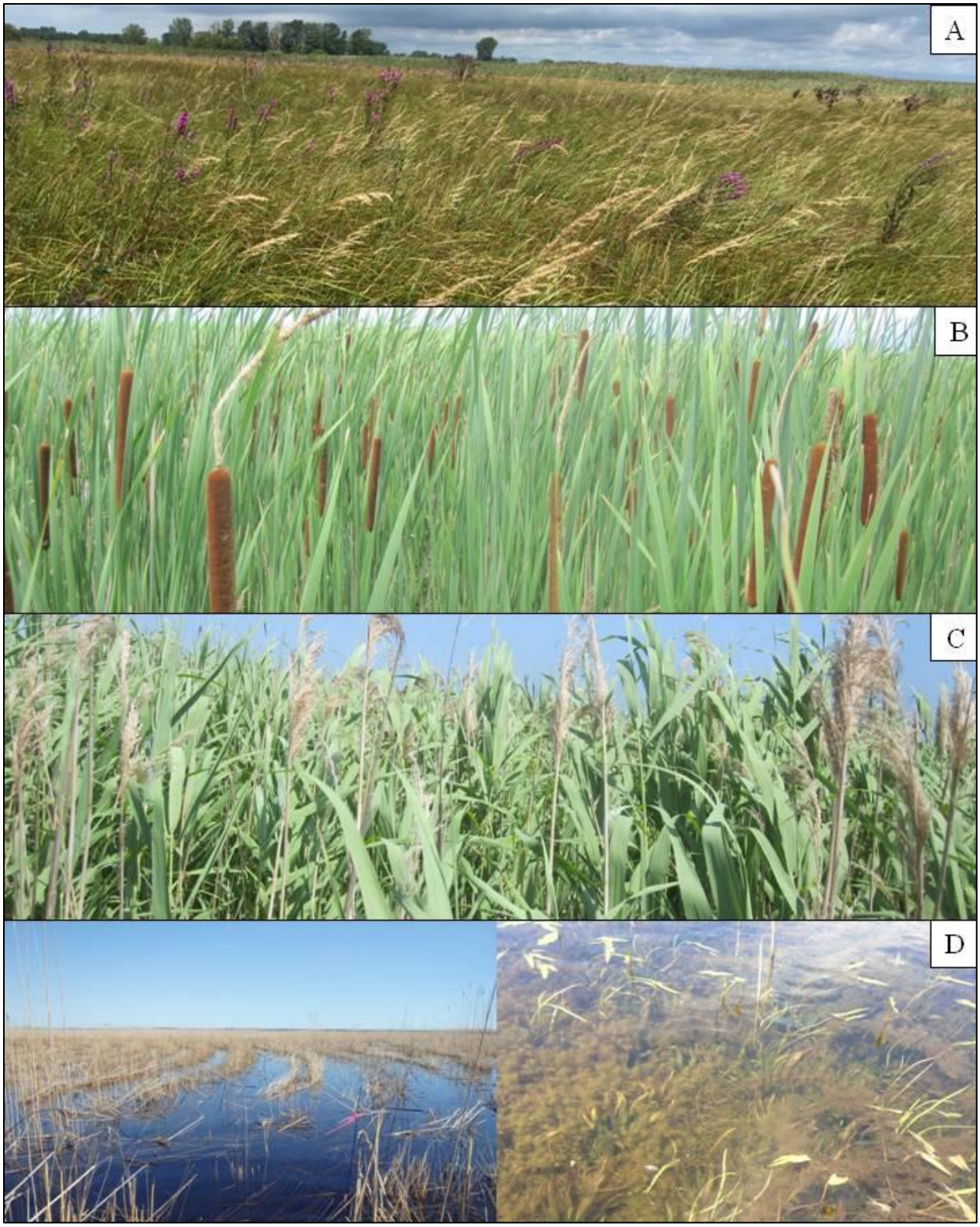

Figure 1. Photos of A) meadow marsh; B) cattail marsh; C) invaded marsh; and D) herbicide-treated marsh in Long Point in the summer of 2017.

Figure 2. Photos of the same herbicide-treated marsh site approximately one year post-herbicide application (top; August 16, 2017) and approximately two years post-herbicide application (bottom; July 27, 2018).

Appendix 8. Decomposition rate figures, tables, photos and statistical summaries.

Table 1. Single exponential model (k) and decaying coefficient model (initial decay rate: k_1; relative decay rate: k_2) of litter (*C. canadensis, P. australis. Typha* spp.), in different sites (resident plant community, *P. australis* invaded, herbicide-treated) and water depths (shallow, intermediate, deep) and standing litter ("dry" water treatment), calculated from repeated measurements of litter mass loss over a period of 367 days. Percent mass remaining indicates the percent of initial litter mass remaining after 367 days of exposure in the wetland. R^2 values for both single exponential and decaying coefficient models are reported.

Litter	Site	Water depth	k	R^2	k_1	k_2	R^2	% mass remaining
C. canadensis	Resident plants	Shallow	0.003	0.885	0.009	-0.013	0.972	48.64
C. canadensis	Resident plants	Intermediate	0.003	0.910	0.006	-0.009	0.984	50.30
C. canadensis	Resident plants	Deep	0.007	0.978	0.012	-0.007	0.998	23.31
C. canadensis	Invaded	Shallow	0.003	0.926	0.008	-0.010	0.985	42.76
C. canadensis	Invaded	Intermediate	0.004	0.929	0.010	-0.011	0.996	40.33
C. canadensis	Invaded	Deep	0.006	0.970	0.011	-0.007	0.992	21.41
C. canadensis	Herbicide-treated	Shallow	0.003	0.772	0.013	-0.023	0.995	56.89
C. canadensis	Herbicide-treated	Intermediate	0.006	0.888	0.015	-0.015	0.991	39.79
C. canadensis	Herbicide-treated	Deep	0.003	0.896	0.009	-0.011	0.988	45.45
C. canadensis	Resident plants	Dry	0.001	0.934	0.002	-0.005	0.978	70.57
C. canadensis	Invaded	Dry	0.001	0.915	0.003	-0.007	0.981	67.61
C. canadensis	Herbicide-treated	Dry	0.001	0.946	0.002	-0.005	0.980	74.65
Typha spp.	Resident plants	Shallow	0.004	0.844	0.012	-0.016	0.987	43.78
Typha spp.	Resident plants	Intermediate	0.003	0.865	0.009	-0.015	0.995	55.66
Typha spp.	Resident plants	Deep	0.005	0.961	0.010	-0.008	0.999	29.76
Typha spp.	Invaded	Shallow	0.002	0.910	0.007	-0.012	0.957	48.63
Typha spp.	Invaded	Intermediate	0.003	0.918	0.008	-0.011	0.996	45.69
Typha spp.	Invaded	Deep	0.004	0.935	0.009	-0.010	0.970	36.99
Typha spp.	Herbicide-treated	Shallow	0.003	0.845	0.013	-0.018	0.991	47.67
Typha spp.	Herbicide-treated	Intermediate	0.006	0.864	0.015	-0.016	0.988	41.08
Typha spp.	Herbicide-treated	Deep	0.003	0.814	0.013	-0.020	0.983	47.07
Typha spp.	Resident plants	Dry	0.001	0.909	0.002	-0.005	0.963	72.14
Typha spp.	Invaded	Dry	0.001	0.885	0.003	-0.007	0.950	63.31
Typha spp.	Herbicide-treated	Dry	0.001	0.945	0.002	-0.004	0.976	70.82
P. australis	Resident plants	Shallow	0.008	0.846	0.031	-0.031	0.993	33.16
P. australis	Resident plants	Intermediate	0.004	0.896	0.011	-0.014	0.995	44.04
P. australis	Resident plants	Deep	0.015	0.990	0.020	-0.007	0.992	5.75
P. australis	Invaded	Shallow	0.006	0.934	0.015	-0.013	0.997	32.40
P. australis	Invaded	Intermediate	0.009	0.972	0.016	-0.010	0.998	21.60
P. australis	Invaded	Deep	0.009	0.980	0.015	-0.008	0.991	14.31
P. australis	Herbicide-treated	Shallow	0.008	0.818	0.029	-0.030	0.997	38.54
P. australis	Herbicide-treated	Intermediate	0.015	0.969	0.027	-0.016	1.000	19.39
P. australis	Herbicide-treated	Deep	0.009	0.910	0.023	-0.020	0.990	28.91
P. australis	Resident plants	Dry	0.002	0.881	0.004	-0.009	0.973	62.45
P. australis	Invaded	Dry	0.002	0.893	0.004	-0.008	0.969	55.53
P. australis	Herbicide-treated	Dry	0.001	0.856	0.003	-0.010	0.966	73.78

Table 2. Results of AICc model selection for single exponential model coefficient (*k*) as a function of litter type (*C. canadensis, P. australis. Typha* spp.), site type (resident plant communities, *P. australis* invaded, herbicide-treated) and water depth treatment (dry, shallow, intermediate, deep; where dry refers to standing litter). The single exponential coefficient was log-transformed to meet the assumptions of normality. AICc value, difference in AICc among models, AIC degrees of freedom, model probability (w_i), and model parameters R^2, *F* (degrees of freedom) and *p*-value reported.

Model (*k*)	AICc	ΔAICc	AICc df	w_i	R^2	*F* (d.f.)	*p*-value
Intercept + Site + Water + Litter + Site*Water	-40.983	0	15	0.996	0.935	39.39 (13, 22)	<0.001
Intercept + Water + Litter	-29.764	11.219	7	0.004	0.822	33.23 (5, 30)	<0.001
Intercept + Litter + Site + Water	-22.942	18.041	9	0.000	0.809	22.23 (7, 28)	<0.001
Intercept + Water + Litter + Litter*Water	-11.295	29.688	13	0.000	0.812	14.71 (11, 24)	<0.001
Intercept + Site + Water + Litter + Litter*Site	-7.164	33.819	13	0.000	0.789	12.88 (11, 24)	<0.001
Intercept + Water	-5.829	35.154	5	0.000	0.616	19.70 (3, 32)	<0.001
Intercept + Site + Water + Litter + Litter*Water	0.039	41.022	15	0.000	0.795	11.45 (13, 22)	<0.001
Intercept + Site + Water	0.127	41.110	7	0.000	0.591	11.10 (5, 30)	<0.001
Intercept + Site + Water + Site * Water	10.933	51.916	13	0.000	0.651	6.93 (11, 24)	<0.001
Intercept + Litter	21.168	62.151	4	0.000	0.150	4.08 (2, 33)	0.026
Intercept + Litter + Site	26.754	67.738	6	0.000	0.132	1.92 (4, 31)	0.132
Intercept + Site	29.110	70.093	4	0.000	-0.060	0.01 (2, 33)	0.993
Intercept + Site + Litter + Litter * Site	40.314	81.297	10	0.000	-0.029	0.87 (8, 27)	0.547

Table 3. Results of AICc model selection for the initial decay coefficient (k_1) from the decaying coefficient model as a function of litter type (*C. canadensis, P. australis. Typha* spp.), site type (resident plant communities, *P. australis* invaded, herbicide-treated) and water depth treatment (dry, shallow, intermediate, deep; where dry refers to standing litter). The initial decay coefficient was square-root transformed to meet the assumptions of normality. AICc value, difference in AICc among models, AIC degrees of freedom, model probability (w_i), and model parameters R^2, F (degrees of freedom) and p-value reported.

Model (k_1)	AICc	ΔAICc	AICc df	w_i	R^2	F (d.f.)	p-value
Intercept + Site + Water + Litter + Site*Water	-57.247	0	15	0.996	0.963	70.14 (13, 22)	<0.001
Intercept + Water + Litter	-39.164	18.082	7	0.000	0.877	50.69 (5, 30)	<0.001
Intercept + Litter + Site + Water	-38.486	18.761	9	0.000	0.889	40.96 (7, 28)	<0.001
Intercept + Site + Water + Litter + Litter*Site	-23.141	34.106	13	0.000	0.878	23.94 (11, 24)	<0.001
Intercept + Water + Litter + Litter*Water	-16.981	40.266	13	0.000	0.856	19.83 (11, 24)	<0.001
Intercept + Water	-13.047	44.200	5	0.000	0.718	30.63 (3, 32)	<0.001
Intercept + Site + Water + Litter + Litter*Water	-12.236	45.010	15	0.000	0.869	18.88 (13, 22)	<0.001
Intercept + Site + Water	-9.476	47.771	7	0.000	0.718	18.85 (5, 30)	<0.001
Intercept + Site + Water + Site * Water	3.692	60.938	13	0.000	0.743	10.22 (11, 24)	<0.001
Intercept + Litter	27.025	84.272	4	0.000	0.101	2.97 (2, 33)	0.065
Intercept + Litter + Site	31.908	89.155	6	0.000	0.062	1.58 (4, 31)	0.205
Intercept + Site	32.367	89.614	4	0.000	0.043	0.28 (2, 33)	0.755
Intercept + Site + Litter + Litter * Site	45.575	102.821	10	0.000	0.070	0.72 (8, 27)	0.677

Table 4. Summary of general linear model for single exponential model coefficient (*k*) as a function of litter type (*C. canadensis, P. australis. Typha* spp.), site type (resident plant communities, invaded, herbicide-treated) and water depth treatment (dry, shallow, intermediate, deep; where dry refers to standing litter). The single exponential coefficient was log-transformed to meet the assumptions of normality. The category *P. australis* was withheld as a reference for litter, invaded was withheld as a reference for site type variable and the category deep water depth 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
Litter: *C. canadensis*	-0.282	0.034	-8.358	<0.001
Litter: *Typha* spp.	-0.317	0.034	-9.379	<0.001
Site: herbicide-treated	-0.113	0.676	-1.667	0.110
Site: resident plant	0.141	0.676	2.081	0.049
Water: dry	-0.590	0.676	-8.737	<0.001
Water: shallow	-0.211	0.676	-3.126	0.005
Water: intermediate	-0.091	0.676	-1.342	0.193
Site: herbicide-treated * Water: dry	-0.014	0.096	-0.145	0.886
Site: resident plant * Water: dry	-0.213	0.096	-2.227	0.036
Site: herbicide-treated * Water: shallow	0.160	0.096	1.676	0.108
Site: resident plant * Water: shallow	-0.039	0.096	-0.405	0.690
Site: herbicide-treated * Water: intermediate	0.327	0.096	3.427	0.002
Site: resident plant * Water: intermediate	-0.352	0.096	-3.682	0.001

Table 5. Summary of general linear model for initial decay coefficient (k_1) from the decaying coefficient model as a function of litter type (*C. canadensis, P. australis. Typha* spp.), site type (resident plant communities, invaded, herbicide-treated) and water depth treatment (dry, shallow, intermediate, deep; where dry refers to standing litter). initial decay coefficient was square-root transformed to meet the assumptions of normality The category *P. australis* was withheld as a reference for litter, invaded was withheld as a reference for site type variable and the category deep water depth 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
Litter: *C. canadensis*	-0.284	0.027	-10.555	<0.001
Litter: *Typha* spp.	-0.272	0.027	-10.094	<0.001
Site: herbicide-treated	0.098	0.054	1.821	0.082
Site: resident plant	0.078	0.054	1.449	0.162
Water: dry	-0.526	0.054	-9.750	<0.001
Water: shallow	-0.070	0.054	-1.302	0.206
Water: intermediate	-0.000	0.054	-0.007	0.994
Site: herbicide-treated * Water: dry	-0.260	0.076	-3.409	0.003
Site: resident plant * Water: dry	-0.163	0.076	-2.144	0.043
Site: herbicide-treated * Water: shallow	0.151	0.076	1.985	0.060
Site: resident plant * Water: shallow	0.132	0.076	1.737	0.096
Site: herbicide-treated * Water: intermediate	0.124	0.076	1.632	0.117
Site: resident plant * Water: intermediate	-0.187	0.076	-2.455	0.022

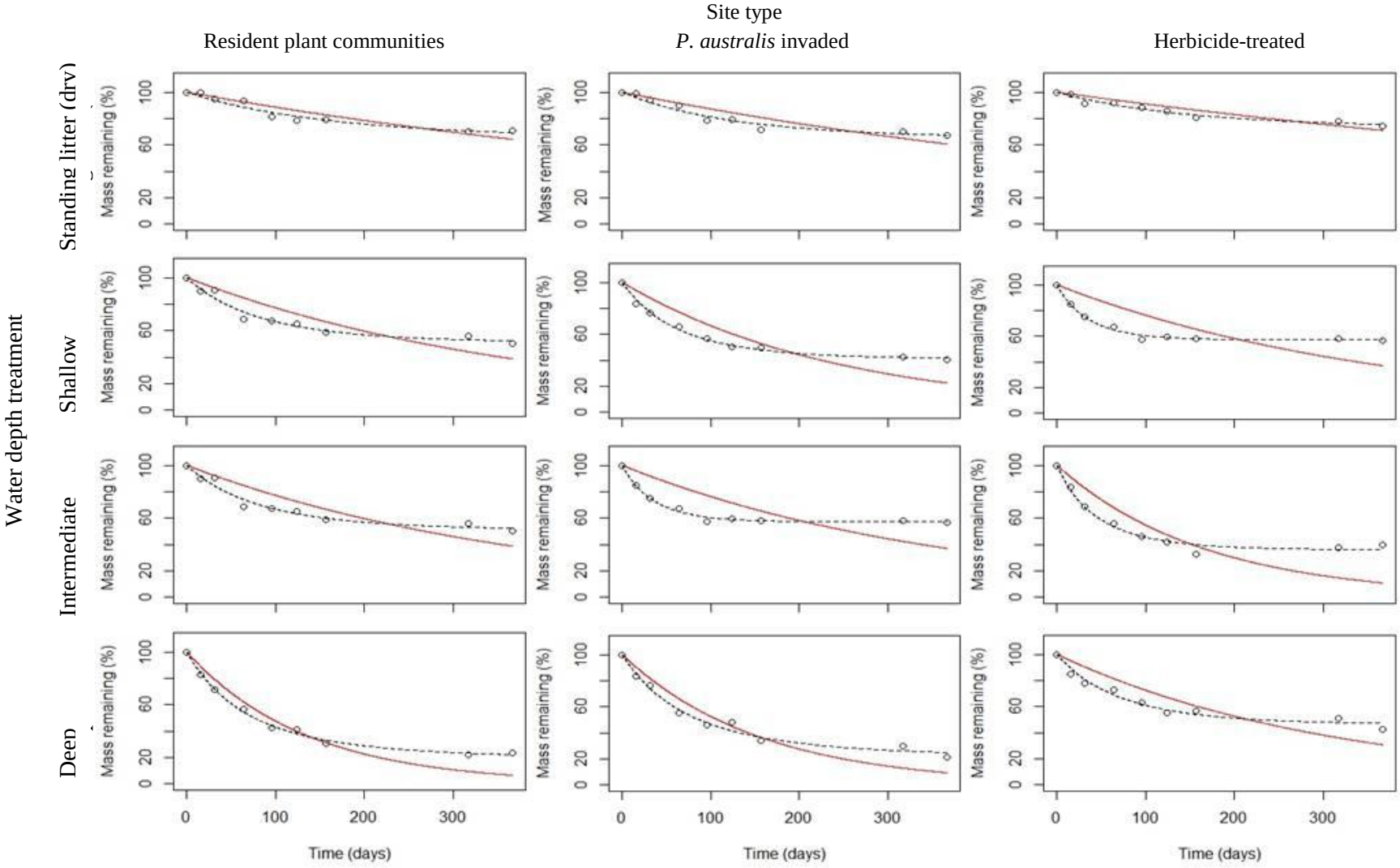

Figure 1. Mass loss (%) of *C. canadensis* leaf and stem litter (5 g) over 367 days in the wetland. Single exponential decay model (red, solid line) and decaying coefficient model (black, dashed line) calculated using the Levenberg-Marquardt method in R Studio.

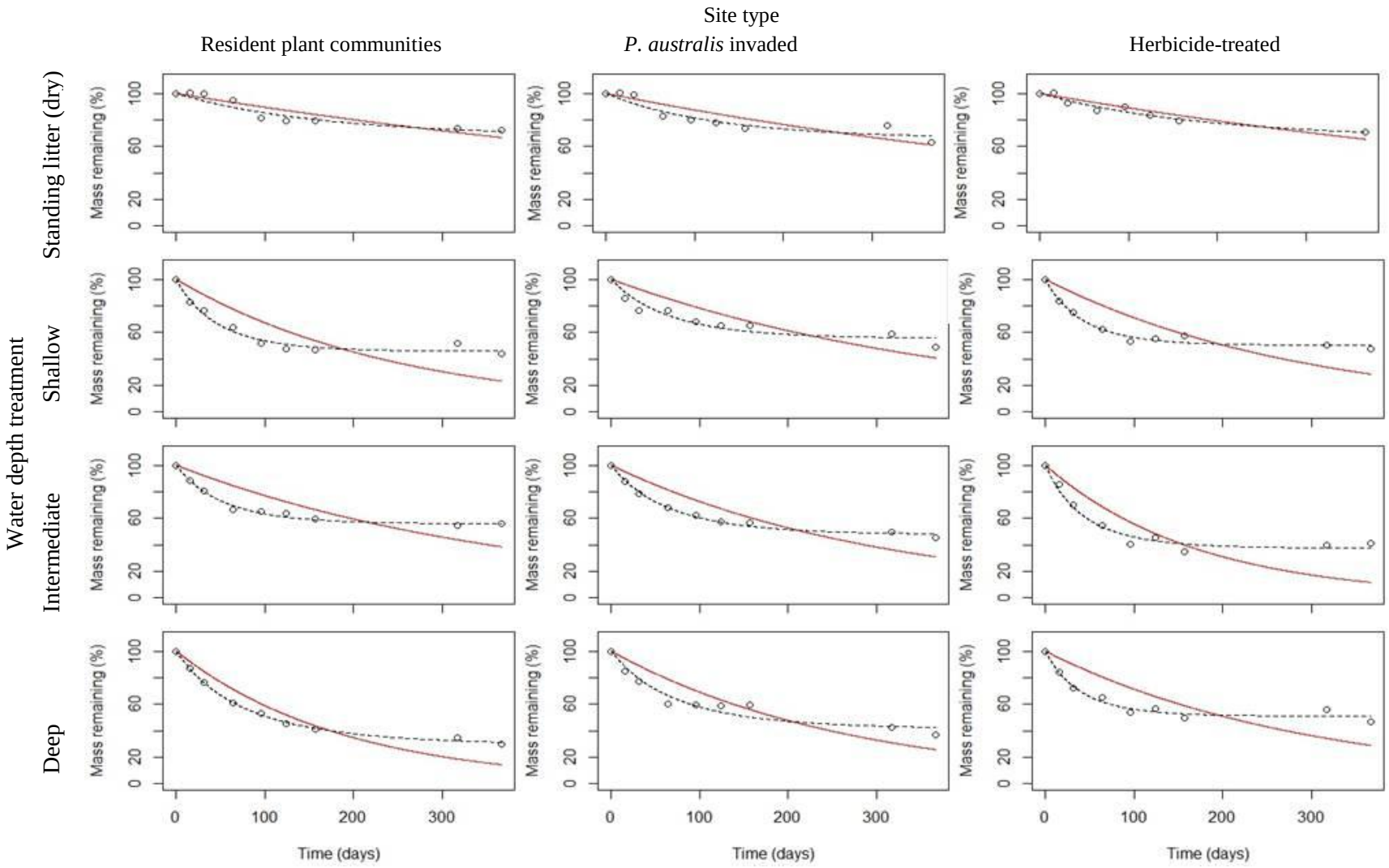

Figure 2. Mass loss (%) of *Typha* spp. leaf litter (5 g) over 367 days in the wetland. Single exponential decay model (red, solid line) and decaying coefficient model (black, dashed line) calculated using the Levenberg-Marquardt method in R Studio.

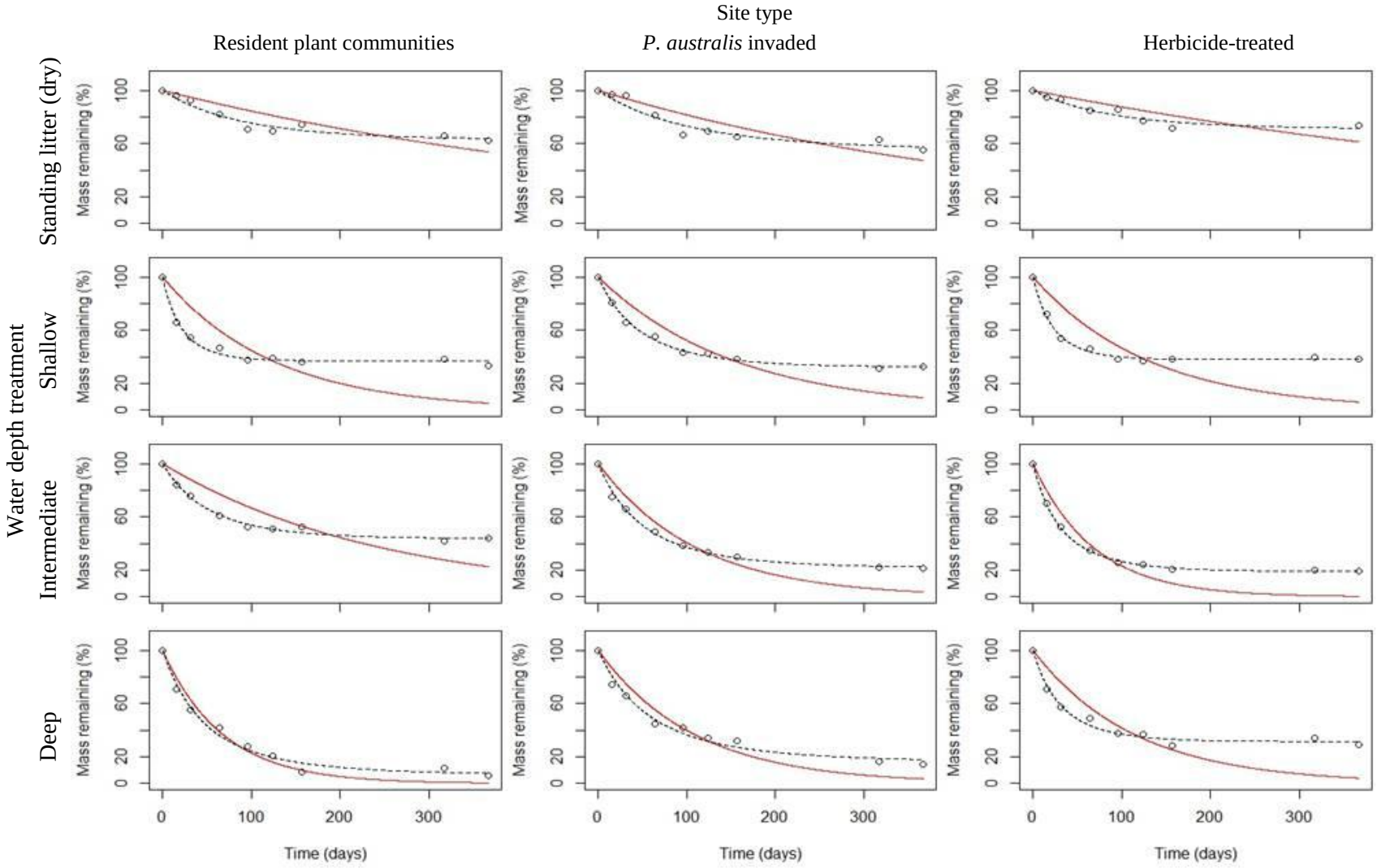

Figure 3. Mass loss (%) of *P. australis* leaf litter (5 g) over 367 days in the wetland. Single exponential decay model (red, solid line) and decaying coefficient model (black, dashed line) calculated using the Levenberg-Marquardt method in R Studio.

Figure 4. Photos of submerged litterbags in A) resident plant communities; B) *P. australis* invaded; C) herbicide-treated marsh; D) standing litter in resident plant communities (left), *P. australis* invaded (middle) and herbicide-treated (right).

Table 6. Percent mass remaining of 2.5 g of *P. australis* leaf and stem tissue after 315 days of exposure in the wetland; day 0: May 7, 2016. Data from litterbag transplant pilot work in Long Point Provincial Park. *Phragmites australis* litter was placed on the ground in meadow, cattail and *P. australis* invaded marsh (n = 4 sites/ plant community).

	% mass remaining	
Site	stem tissue	leaf tissue
Cattail	64.79	13.05
	52.77	5.05
	64.89	13.18
	67.98	22.12
Meadow	65.75	20.44
	53.41	27.68
	67.40	34.46
	59.32	29.12
P. australis invaded	47.01	11.78
	58.49	10.27
	64.16	16.98
	65.40	19.25

Appendix 9. Water depth, water temperature and light insolation characteristics figures, tables and statistical summaries for resident plant communities, invaded and herbicide-treated sites.

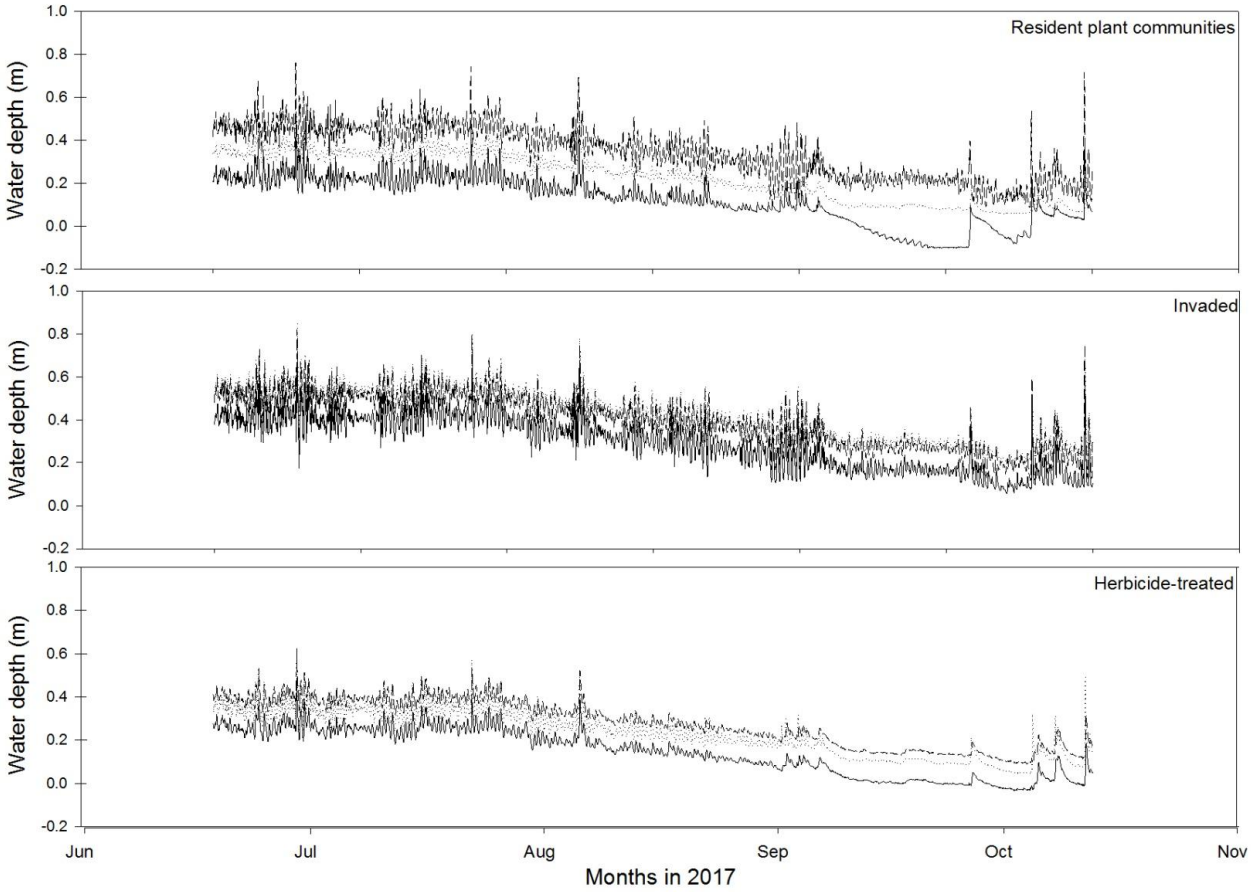

Figure 1. Hourly water depth (m) from June 14 to October 16, 2017 in nine sites in Long Point Provincial Park and Crown Marsh. Plant growth and subsequent water use throughout the day may account for some of the fluctuations in hourly water depth. Dashed lines are the deep water sites, dotted lines are the intermediate water depth sites and solid lines represent the shallow water sites.

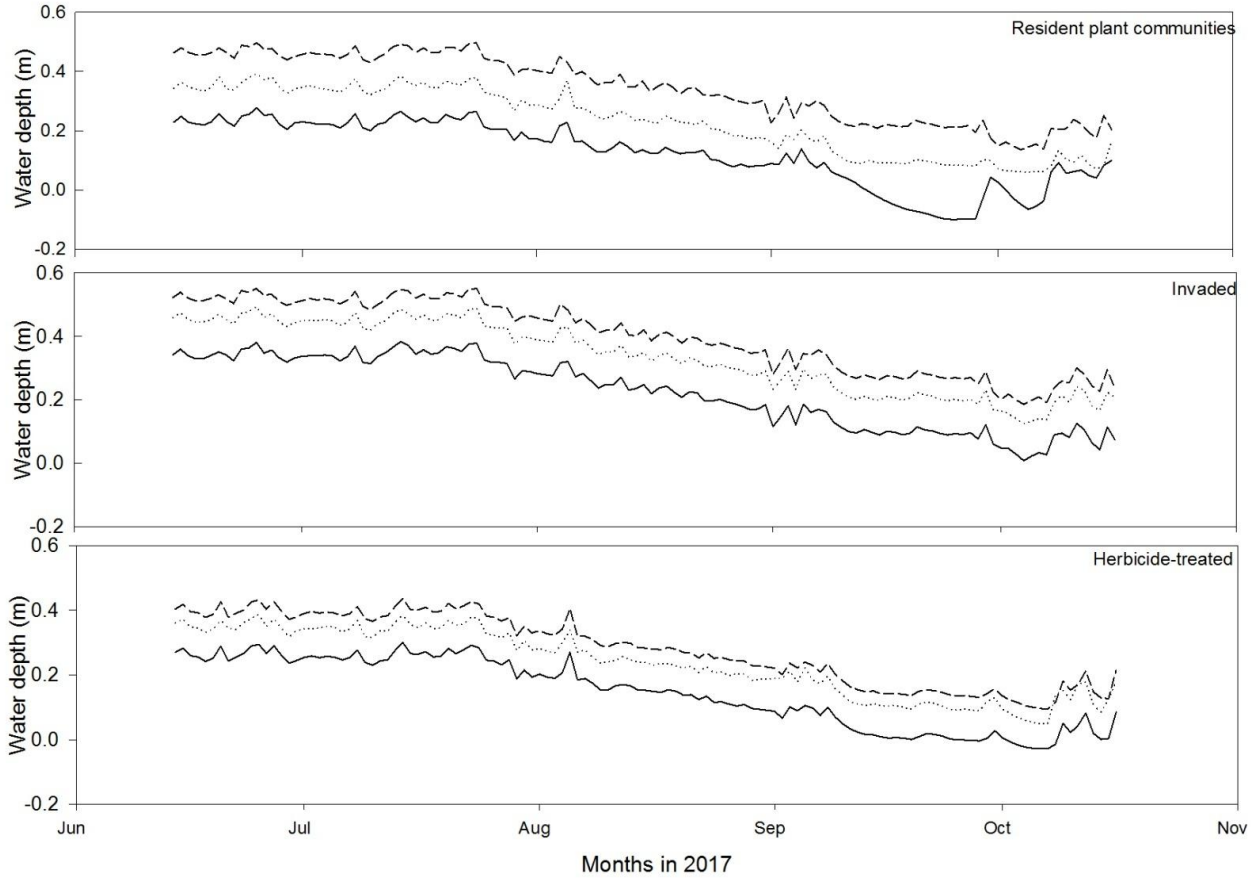

Figure 2. Hourly water depth (m) averaged to daily values from June 14 to October 16, 2017 in nine sites in Long Point Provincial Park and Crown Marsh. Seiche events may account for the variation in daily water depths. Dashed lines are the deep water sites, dotted lines are the intermediate water depth sites and solid lines represent the shallow water sites.

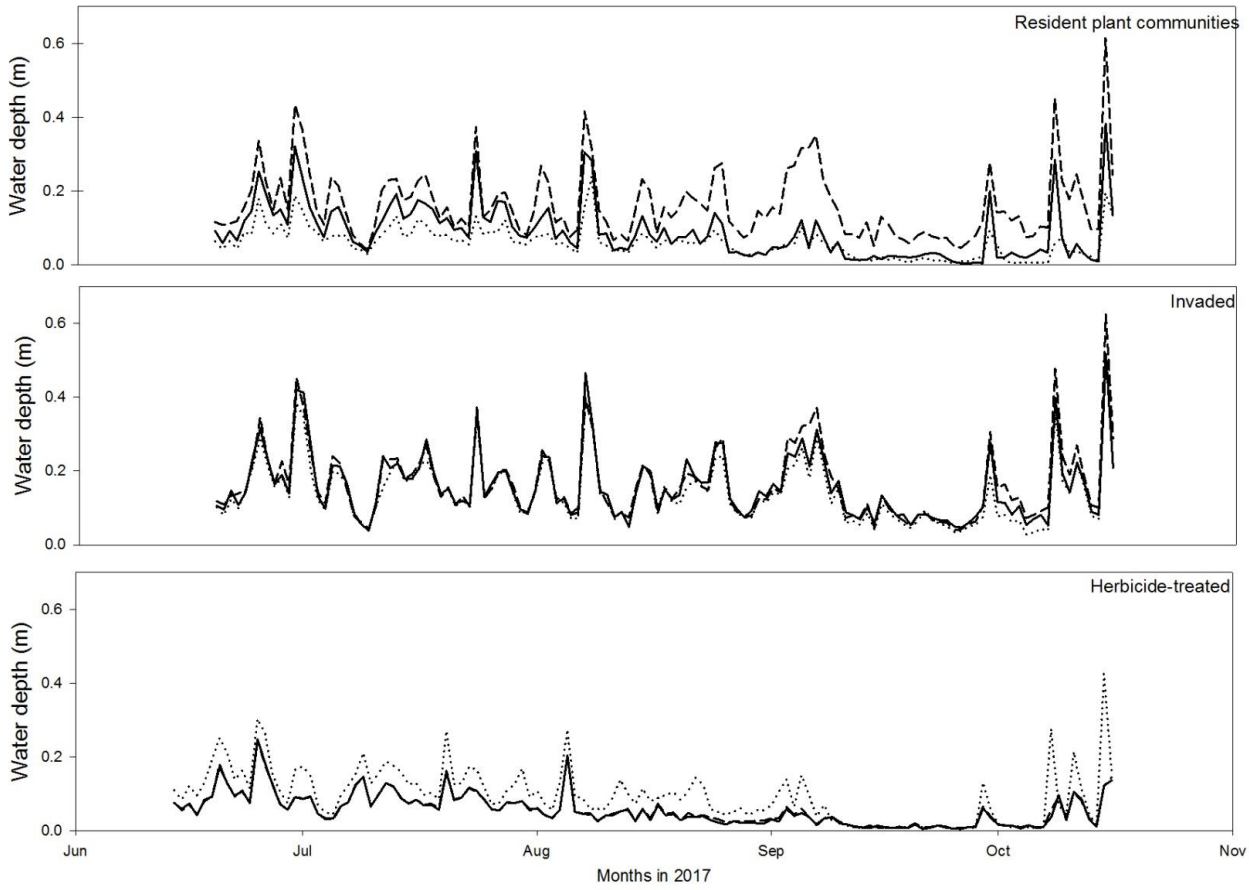

Figure 3. Daily range in water depth (maximum - minimum) from June 14 to October 16, 2017 in nine sites in Long Point Provincial Park and Crown Marsh. Dashed lines are the deep water sites, dotted lines are the intermediate water depth sites and solid lines represent the shallow water sites.

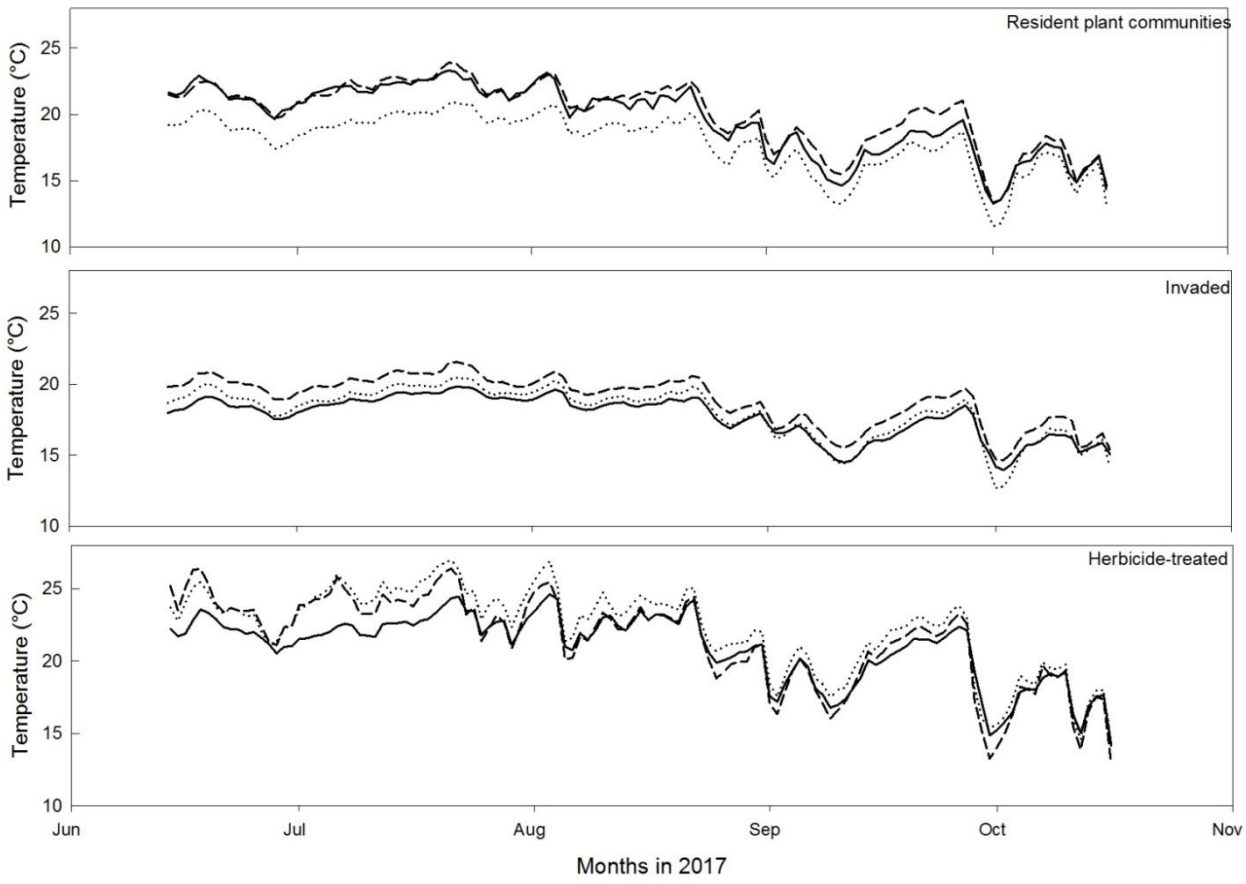

Figure 4. Hourly water temperature (°C) averaged per day from June 14 to October 16, 2017 in nine sites in Long Point Provincial Park and Crown Marsh. Dashed lines are the deep water sites, dotted lines are the intermediate water depth sites and solid lines represent the shallow water sites.

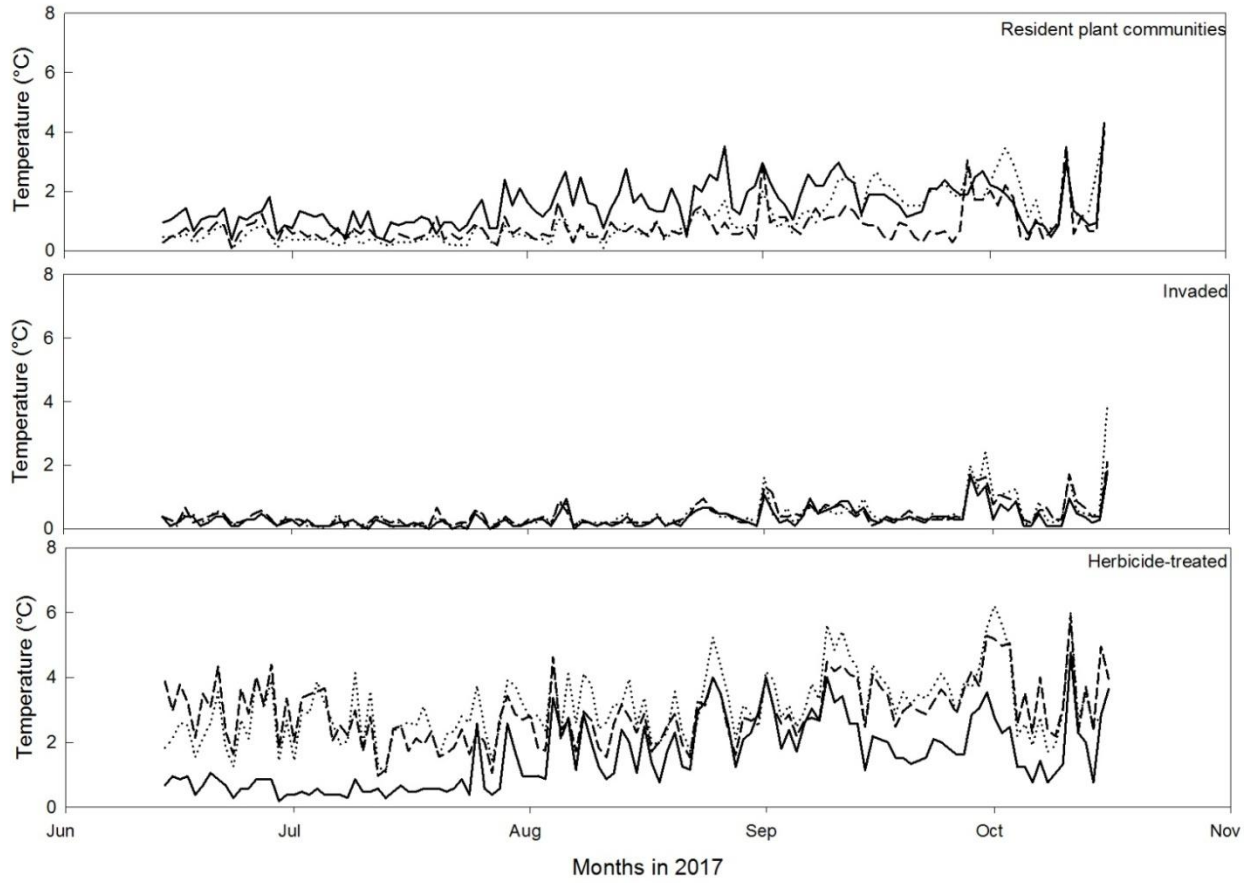

Figure 5. Daily range in temperature (maximum - minimum) from June 14 to October 16, 2017 in nine sites in Long Point Provincial Park and Crown Marsh. Dashed lines are the deep water sites, dotted lines are the intermediate water depth sites and solid lines represent the shallow water sites.

Table 1.Light levels (PAR; 400-700 nm), descending in 50 cm increments from the top of the canopy to the soil or water surface in meadow, cattail and *P. australis* invaded marsh in June 2017. Average canopy height is shortest in meadow marsh (102 cm ± 26 SD) intermediate in cattail marsh (266 cm ± 14 SD), and tallest in *P. australis* invaded marsh (350 cm ± 48 SD). Standard error shown. These data were used to calculate % insolation reaching the soil or water surface.

	Position from top of canopy (cm)															
Plant community	0 PAR	n	-50 PAR	n	-100 PAR	n	-150 PAR	n	-200 PAR	n	-250 PAR	n	-300 PAR	n	Bottom PAR	n
Meadow	1381.1 ± 282.1	5	630.7 ± 263.2	4											170.1 ± 146.5	9
Cattail	1605.2 ± 193.5	5	1055.0 ± 243.4	5	782.2 ± 318.2	5	251.2 ± 140.8	5							231.9 ± 370.6	4
Invaded	1638.6± 126.8	10	1128.7 ± 154.4	10	292.7 ± 44.7	10	332.3 ± 124.5	10	122.9 ± 32.5	9	57.2 ± 11.6	4	3.6	1	111.1 ± 35.2	5

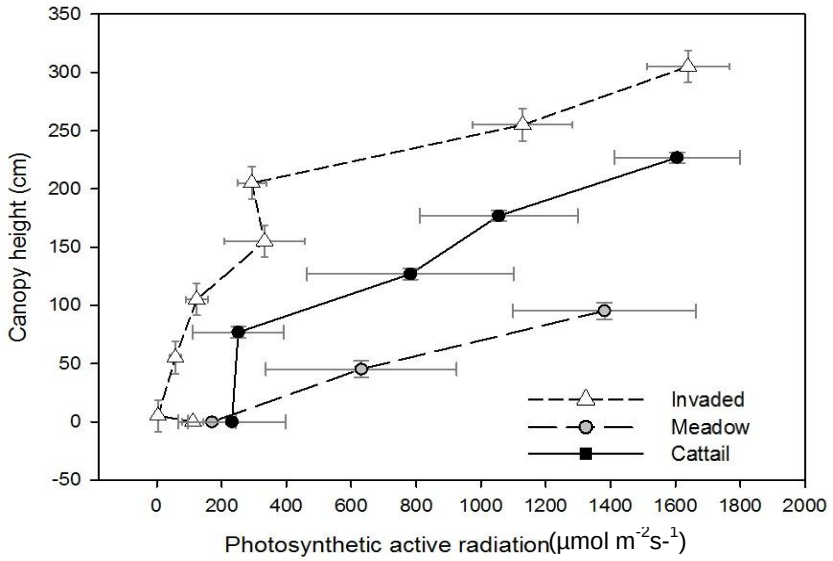

Figure 6. Light levels (PAR; 400-700 nm), descending in 50 cm increments from the top of the canopy to the soil or water surface in meadow, cattail and *P. australis* invaded marsh in June 2017. Standard error shown.

Table 2. Summary of general linear model for daily water depth (cm) from June 14 - October 16, 2017 at the nine decomposition sites as a function of site type (resident plant communities: n = 3, invaded: n = 3, herbicide-treated: n = 3). The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 0.132, $F_{2,1122}$ = 61.600, *p*-value = <0.001, R^2 = 0.099.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.319	0.007	46.832	<0.001
Site: herbicide-treated	-0.098	0.010	-10.172	<0.001
Site: resident plants	-0.086	0.010	-8.932	<0.001

Table 3. Summary of general linear model for daily water depth fluctuations (maximum - minimum water depth; cm) from June 14 - October 16, 2017 at the nine decomposition sites as a function of site type (resident plant communities: n = 3, invaded: n = 3, herbicide-treated: n = 3) crossed with water depth category (shallow, intermediate, deep). Daily water depth fluctuations was square root transformed to meet normality assumptions. The category invaded was withheld as a reference for site type variable and the category deep water depth was withheld as a reference for water depth variable. Residual standard error for the model = 0.106, $F_{8,1116}$ = 62.760, *p*-value = <0.001, R^2 = 0.310.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.393	0.009	41.391	<0.001
Site: herbicide-treated	-0.169	0.013	-12.581	<0.001
Site: resident plants	-0.003	0.013	-0.192	0.848
Water depth: intermediate	-0.030	0.013	-2.249	0.025
Water depth: shallow	-0.008	0.013	-0.620	0.535
Site: herbicide-treated * Water depth: intermediate	0.091	0.019	4.807	<0.001
Site: resident plants * Water depth: intermediate	-0.129	0.019	-6.818	<0.001
Site: herbicide-treated * Water depth: shallow	0.004	0.019	0.236	0.814
Site: resident plants * Water depth: shallow	-0.107	0.019	-5.668	<0.001

Table 4. Summary of general linear model for daily water temperature (°C) from June 14 - October 16, 2017 at the nine decomposition sites as a function of site type (resident plant communities: n = 3, invaded: n = 3, herbicide-treated: n = 3) crossed with water depth category (shallow, intermediate, deep). The category invaded was withheld as a reference for site type variable and the category deep water depth was withheld as a reference for water depth variable. Residual standard error for the model = 2.339, $F_{8,1116}$ = 61.710, *p*-value = <0.001, R^2 = 0.307.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	18.965	0.209	90.667	<0.001
Site: herbicide-treated	2.535	0.296	8.571	<0.001
Site: resident plants	1.139	0.296	3.852	<0.001
Water depth: intermediate	-0.906	0.296	-3.062	0.002
Water depth: shallow	-1.216	0.296	-4.109	<0.001
Site: herbicide-treated * Water depth: intermediate	1.640	0.418	3.921	<0.001
Site: resident plants * Water depth: intermediate	-1.265	0.418	-3.023	0.003
Site: herbicide-treated * Water depth: shallow	0.685	0.418	1.638	0.102
Site: resident plants * Water depth: shallow	0.777	0.418	1.857	0.064

Table 5. Summary of general linear model for daily water temperature fluctuations (maximum - minimum water depth; °C) from June 14 - October 16, 2017 at the nine decomposition sites as a function of site type ((resident plant communities: n = 3, invaded: n = 3, herbicide-treated: n = 3) crossed with water depth category (shallow, intermediate, deep). Daily water temperature fluctuations was square root transformed to meet normality assumptions. The category invaded was withheld as a reference for site type variable and the category deep water depth was withheld as a reference for water depth variable. Residual standard error for the model = 0.309, $F_{8,1116}$ = 369.000, *p*-value = <0.001, R^2 = 0.659.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.599	0.028	21.688	<0.001
Site: herbicide-treated	1.088	0.039	27.844	<0.001
Site: resident plants	0.277	0.039	7.086	<0.001
Water depth: intermediate	-0.007	0.039	-0.167	0.868
Water depth: shallow	-0.076	0.039	-1.943	0.052
Site: herbicide-treated * Water depth: intermediate	0.051	0.055	0.920	0.358
Site: resident plants * Water depth: intermediate	0.072	0.055	1.312	0.190
Site: herbicide-treated * Water depth: shallow	-0.428	0.055	-7.743	<0.001
Site: resident plants * Water depth: shallow	0.405	0.055	7.325	<0.001

Table 6. Summary of general linear model of % insolation (PAR; 400-700 nm) reaching the soil or water surface canopy in meadow (n = 5), cattail (n = 5), and invaded marsh (n = 10) in June 2017, located in Long Point Provincial Park. The category invaded was withheld as a reference for site type variable. Average canopy height is shortest in meadow marsh (102 ± 26 cm) intermediate in cattail marsh (266 ± 14 cm), and tallest in invaded marsh (350 ± 48 cm). Residual standard error for the model = 0.497, $F_{2,16}$ = 1.195, *p*-value = 0.328, R^2 = 0.130.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	-1.357	0.157	-8.640	<0.001
Meadow	0.454	0.294	1.544	0.142
Cattail	0.151	0.272	0.555	0.586

Appendix 10. Standing crop biomass and water depth gradient figures and statistical modelling.

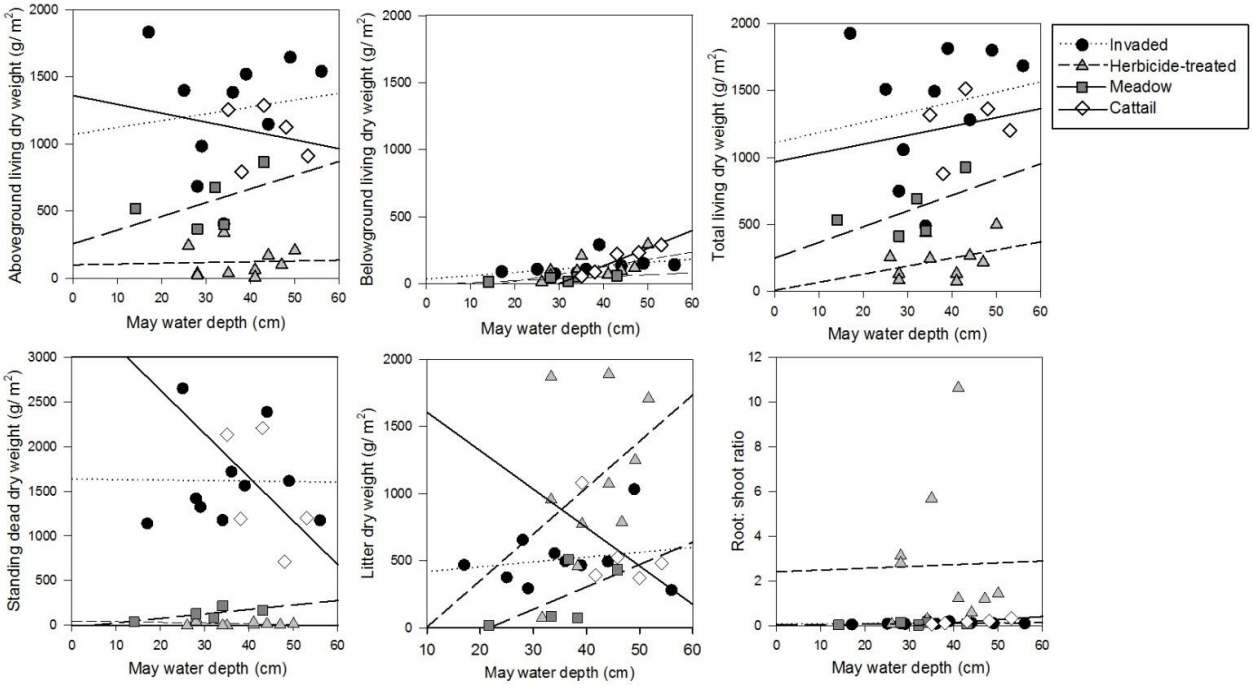

Figure 1. Dry weight of biomass (g/ m²) and root: shoot ratio correlated to May 2017 water depth (cm) in cattail and meadow (n = 5) and invaded and herbicide-treated (n = 10) sites.

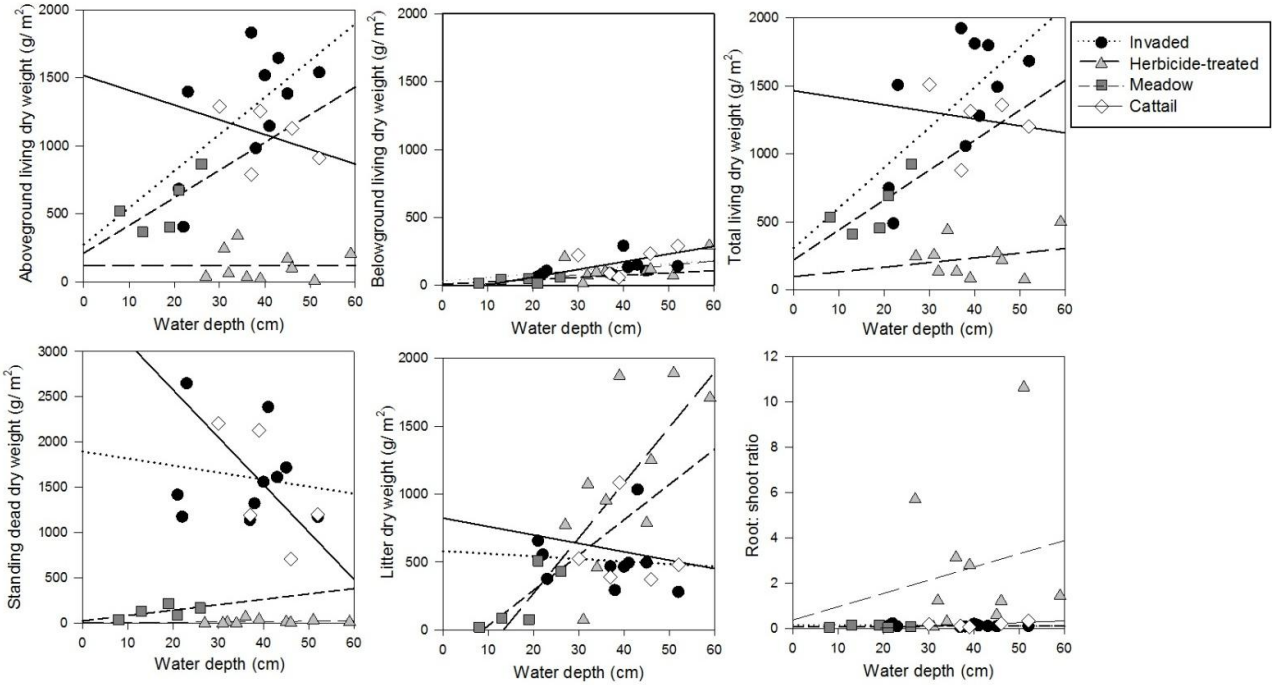

Figure 2. Dry weight of biomass (g/ m²) and stem count (m^{-2}) correlated to July 2017 water depth (cm) in cattail and meadow (n = 5) and invaded and herbicide-treated (n = 10) sites.

Table 1. Summary of model competition outcomes, comparing models including and excluding an interaction term between water depth and site type when the interaction term was not itself statistically significant, as well as comparing models where water depth is based on July measurements against models where water depth is based on May measurements. The optimal model is indicated by an asterisk and a Δ AICc value of 0.00. If the Δ AICc value for a model was > 2, I concluded that the best fitting model was superior. If the Δ AICc was < 2, I concluded that the was some evidence supporting the model, but favoured the simpler model.

Response variable	Water measure	Interaction in model?	Interaction significant?	Model adjusted R^2	Model *p*-value	AICc	Δ AICc	AICc df
Aboveground	May	Yes	No	0.753	<0.001	206.054	11.666	7
	July	Yes	No	0.817	<0.001	196.937	2.549	7
	May	No	-	0.760	<0.001	200.936	6.548	5
	July*	No	-	0.807	<0.001	194.388	0.000	5
Belowground	May	Yes	No	0.453	0.001	157.430	0.861	7
	July	Yes	No	0.330	0.011	163.521	6.952	7
	May*	No	-	0.389	0.001	156.569	0.000	5
	July	No	-	0.332	0.004	159.242	2.673	5
Total live	May	Yes	No	0.722	<0.001	203.402	12.879	7
	July	Yes	No	0.801	<0.001	193.324	2.801	7
	May	No	-	0.723	<0.001	199.091	8.567	5
	July*	No	-	0.792	<0.001	190.523	0.000	5
Root: shoot	May	Yes	No	0.411	0.003	62.431	6.764	7
	July	Yes	No	0.427	0.002	61.609	5.942	7
	May	No	-	0.454	<0.001	55.950	0.282	5
	July*	No	-	0.459	<0.001	55.667	0.000	5
Standing dead	May	Yes	Yes	0.755	<0.001	228.302	8.295	7
	July*	Yes	Yes	0.814	<0.001	220.006	0.000	7
Litter	May	Yes	No	0.383	0.004	219.691	6.618	7
	July*	Yes	No	0.505	<0.001	213.073	0.000	7
	May	No	-	0.367	0.002	216.258	3.184	5
	July	No	-	0.430	0.000	213.116	0.043	5
Maximum carbon assimilation rate	May	Yes	No	0.480	0.012	146.634	5.177	7
	July	Yes	No	0.386	0.033	149.955	8.498	7
	May*	No	-	0.448	0.006	141.457	0.000	5
	July	No	-	0.429	0.007	142.106	0.649	5
Specific leaf area	May	Yes	No	0.669	0.001	-5.341	8.110	7
	July	Yes	No	0.654	0.001	-4.447	9.004	7
	May	No	-	0.695	<0.001	-13.347	0.104	5
	July*	No	-	0.696	<0.001	-13.451	0.000	5
Leaf area per meter of wetland	May	Yes	No	0.508	0.008	28.553	7.936	7
	July	Yes	No	0.554	0.004	26.610	5.994	7
	May*	No	-	0.545	0.001	20.617	0.000	5
	July	No	-	0.524	0.002	21.495	0.878	5
Carbon assimilation rate per meter of	May	Yes	No	0.694	<0.001	164.578	6.049	7
	July	Yes	No	0.704	<0.001	163.902	5.373	7
	May	No	-	0.685	<0.001	158.764	0.235	5
	July*	No	-	0.689	<0.001	158.529	0.000	5

Summary of general linear models for biomass, plant morphology and carbon assimilation measurements. Resident plant communities, invaded and herbicide-treated sites are placed along a water gradient which was measured once in May and again in July. General linear models were run with May water depth measurements and then with July water measurements. If the interaction term was not significant, the interaction term was removed and the models (May and July water depths) were run again. The final model was determined by comparing the AICc value of the models.

Table 2. Summary of general linear model for aboveground biomass (square root transformed) as a function of site type crossed with water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for the site type variable. Residual standard error for the model = 6.102, $F_{5,24}$ = 18.640, *p*-value = <0.001, R^2 = 0.795. AICc = 206.054.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	31.582	6.480	4.873	<0.001
Site: herbicide-treated	-24.477	11.250	-2.176	0.040
Site: resident plants	-15.958	9.574	-1.667	0.109
May water depth	0.089	0.173	0.516	0.611
Site: herbicide-treated* May water depth	-0.017	0.296	-0.056	0.956
Site: resident plants* May water depth	0.249	0.253	0.983	0.335

Table 3. Summary of general linear model for aboveground biomass (square root transformed) as a function of site type crossed with water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 5.242, $F_{5,24}$ = 26.970, *p*-value = <0.001, R^2 = 0.849, AICc = 196.937.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	18.882	6.164	3.063	0.005
Site: herbicide-treated	-9.307	9.437	-0.986	0.334
Site: resident plants	0.213	7.301	0.029	0.977
July water depth	0.439	0.164	2.677	0.013
Site: herbicide-treated* July water depth	-0.433	0.239	-1.811	0.083
Site: resident plants* July water depth	-0.131	0.204	-0.640	0.528

Table 4. Summary of general linear model for aboveground biomass (square root transformed) as a function of site type along the water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 6.009, $F_{3,26}$ = 31.630, *p*-value = <0.001, R^2 = 0.785. AICc = 200.936.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	28.442	4.364	6.518	<0.001
Site: herbicide-treated	-25.246	2.694	-9.372	<0.001
Site: resident plants	-6.904	2.690	-2.567	0.016
May water depth	0.177	0.110	1.612	0.119

Table 5. Summary of general linear model for aboveground biomass (square root transformed) as a function of site type along the water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 5.387, $F_{3, 26}$ = 41.460, *p*-value = <0.001, R^2 = 0.827, AICc = 194.388.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	24.965	3.599	6.937	<0.001
Site: herbicide-treated	-25.974	2.432	-10.679	<0.001
Site: resident plants	-4.785	2.488	-1.923	0.065
July water depth	0.271	0.088	3.094	0.005

Table 6. Summary of general linear model for belowground biomass (square root transformed) as a function of site type crossed with water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 2.714, $F_{5,24}$ = 5.799, *p*-value = 0.001, R^2 = 0.547, AICc = 157.430.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	6.974	2.882	2.420	0.024
Site: herbicide-treated	-6.636	5.002	-1.326	0.197
Site: resident plants	-10.829	4.257	-2.544	0.018
May water depth	0.111	0.077	1.435	0.164
Site: herbicide-treated* May water depth	0.151	0.132	1.145	0.264
Site: resident plants* May water depth	0.251	0.112	2.231	0.035

Table 7. Summary of general linear model for belowground biomass (square root transformed) as a function of site type crossed with water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 3.004, $F_{5,24}$ = 3.851, *p*-value = 0.011, R^2 = 0.445, AICc = 163.521.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	6.762	3.532	1.915	0.068
Site: herbicide-treated	-2.592	5.407	-0.479	0.636
Site: resident plants	-5.001	4.183	-1.195	0.244
July water depth	0.115	0.094	1.223	0.233
Site: herbicide-treated* July water depth	0.034	0.137	0.246	0.808
Site: resident plants* July water depth	0.149	0.117	1.274	0.215

Table 8. Summary of general linear model for belowground biomass (square root transformed) as a function of site type along the water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 2.868 $F_{3,26}$ = 7.143, *p*-value = 0.001, R^2 = 0.452. AICc = 156.569.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	2.514	2.083	1.207	0.238
Site: herbicide-treated	-1.207	1.286	-0.938	0.357
Site: resident plants	-1.735	1.284	-1.351	0.188
May water depth	0.236	0.053	4.483	<0.001

Table 9. Summary of general linear model for belowground biomass (square root transformed) as a function of site type along the water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 2.999, $F_{3,26}$ = 5.795, *p*-value = 0.004, R^2 = 0.401, AICc = 159.242.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	3.825	2.003	1.909	0.067
Site: herbicide-treated	-1.551	1.354	-1.146	0.262
Site: resident plants	-0.084	1.385	-0.060	0.952
July water depth	0.196	0.049	4.021	<0.001

Table 10. Summary of general linear model for total live biomass (square root transformed) as a function of site type crossed with water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 5.839, $F_{5,24}$ = 16.060, *p*-value = < 0.001, R^2 = 0.770, AICc = 203.402.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	32.362	6.200	5.219	<0.001
Site: herbicide-treated	-24.517	10.763	-2.278	0.032
Site: resident plants	-18.759	9.160	-2.048	0.052
May water depth	0.116	0.166	0.702	0.490
Site: herbicide-treated* May water depth	0.068	0.284	0.240	0.812
Site: resident plants* May water depth	0.324	0.242	1.338	0.193

Table 11. Summary of general linear model for total live biomass (square root transformed) as a function of site type crossed with water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 4.936, $F_{5,24}$ = 24.380, *p*-value = <0.001, R^2 = 0.836, AICc = 193.324.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	20.152	5.804	3.472	0.002
Site: herbicide-treated	-8.466	8.886	-0.953	0.350
Site: resident plants	-1.477	6.874	-0.215	0.832
July water depth	0.452	0.154	2.927	0.007
Site: herbicide-treated* July water depth	-0.376	0.225	-1.669	0.108
Site: resident plants* July water depth	-0.070	0.192	-0.363	0.720

Table 12. Summary of general linear model for total live biomass (square root transformed) as a function of site type along the water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 5.827 $F_{3,26}$ = 26.40, *p*-value = <0.001, R^2 = 0.752. AICc = 199.091.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	27.582	4.231	6.518	<0.001
Site: herbicide-treated	-22.196	2.612	-8.497	<0.001
Site: resident plants	-6.992	2.608	-2.681	0.013
May water depth	0.250	0.107	2.345	0.027

Table 13. Summary of general linear model for total live biomass (square root transformed) as a function of site type along the water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 5.051, $F_{3,26}$ = 37.770, *p*-value = <0.001, R^2 = 0.813, AICc = 190.523.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	24.658	3.374	7.307	<0.001
Site: herbicide-treated	-23.015	2.281	-10.092	<0.001
Site: resident plants	-4.392	2.333	-1.882	0.071
July water depth	0.328	0.082	3.989	<0.001

Table 14. Summary of general linear model for root: shoot ratio (square root transformed) as a function of site type crossed with water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 0.557, $F_{5,24}$ = 5.045, *p*-value = 0.003, R^2 = 0.512, AICc = 62.431.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.250	0.592	0.423	0.676
Site: herbicide-treated	0.934	1.027	0.910	0.372
Site: resident plants	-0.243	0.874	-0.278	0.783
May water depth	0.002	0.016	0.125	0.901
Site: herbicide-treated* May water depth	0.004	0.027	0.142	0.889
Site: resident plants* May water depth	0.007	0.023	0.295	0.771

Table 15. Summary of general linear model for root: shoot ratio (square root transformed) as a function of site type crossed with water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 0.550, $F_{5,24}$ = 5.318, *p*-value = 0.002, R^2 = 0.526, AICc = 61.609.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.375	0.646	0.581	0.567
Site: herbicide-treated	0.364	0.989	0.368	0.716
Site: resident plants	-0.212	0.765	-0.276	0.785
July water depth	-0.002	0.017	-0.087	0.931
Site: herbicide-treated* July water depth	0.018	0.025	0.721	0.478
Site: resident plants* July water depth	0.007	0.021	0.338	0.738

Table 16. Summary of general linear model for root: shoot ratio (square root transformed) as a function of site type along the water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 0.536 $F_{3,26}$ = 9.044, *p*-value = <0.001, R^2 = 0.511. AICc = 44.950.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.131	0.389	0.337	0.739
Site: herbicide-treated	1.072	0.240	4.458	<0.001
Site: resident plants	0.004	0.240	0.017	0.987
May water depth	0.005	0.010	0.541	0.593

Table 17. Summary of general linear model for root: shoot ratio (square root transformed) as a function of site type along the water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model =0.534, $F_{3,26}$ = 9.211, *p*-value = <0.001, R^2 = 0.515, AICc = 55.667.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.090	0.357	0.252	0.803
Site: herbicide-treated	1.056	0.241	4.385	<0.001
Site: resident plants	0.055	0.246	0.224	0.825
July water depth	0.006	0.009	0.736	0.468

Table 18. Summary of general linear model for standing dead (square root transformed) as a function of site type crossed with water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 8.842, $F_{5,24}$ = 18.830, *p*-value = <0.001, R^2 = 0.797, AICc = 228.302.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	39.656	9.389	4.223	<0.001
Site: herbicide-treated	-35.675	16.299	-2.189	0.039
Site: resident plants	-44.166	13.872	-3.184	0.004
May water depth	0.003	0.251	0.013	0.990
Site: herbicide-treated* May water depth	-0.020	0.429	-0.046	0.963
Site: resident plants* May water depth	0.781	0.366	2.133	0.043

Table 19. Summary of general linear model for standing dead (square root transformed) as a function of site type crossed with water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 7.700, $F_{5,24}$ = 26.350, *p*-value = <0.001, R^2 = 0.846, AICc = 220.006.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	42.695	9.054	4.715	<0.001
Site: herbicide-treated	-43.649	13.862	-3.149	0.004
Site: resident plants	-40.871	10.724	-3.811	0.001
July water depth	-0.081	0.241	-0.335	0.741
Site: herbicide-treated* July water depth	0.189	0.351	0.537	0.596
Site: resident plants* July water depth	0.855	0.300	2.851	0.009

Table 20. Summary of general linear model for litter (square root transformed) as a function of site type crossed with water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 7.660, $F_{5,24}$ = 4.601, *p*-value = 0.004, R^2 = 0.489, AICc = 219.691.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	20.343	8.134	2.501	0.020
Site: herbicide-treated	-11.382	14.120	-0.806	0.428
Site: resident plants	-18.605	12.017	-1.548	0.135
May water depth	0.053	0.218	0.243	0.810
Site: herbicide-treated* May water depth	0.545	0.372	1.464	0.156
Site: resident plants* May water depth	0.396	0.317	1.247	0.224

Table 21. Summary of general linear model for litter (square root transformed) as a function of site type crossed with water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 6.860, $F_{5,24}$ = 6.922, *p*-value = <0.001, R^2 = 0.591, AICc = 213.073.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	24.489	8.066	3.036	0.006
Site: herbicide-treated	-20.423	12.349	-1.654	0.111
Site: resident plants	-18.085	9.554	-1.893	0.071
July water depth	-0.062	0.215	-0.291	0.774
Site: herbicide-treated* July water depth	0.743	0.313	2.378	0.026
Site: resident plants* July water depth	0.470	0.267	1.757	0.092

Table 22. Summary of general linear model for litter (square root transformed) as a function of site type along the water depth gradient (as measured in May 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 0.7.757 $F_{3,26}$ = 6.612, *p*-value = 0.002, R^2 = 0.433. AICc = 216.258.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	10.939	5.633	1.942	0.063
Site: herbicide-treated	8.539	3.477	2.456	0.021
Site: resident plants	-4.324	3.473	-1.245	0.224
May water depth	0.316	0.142	2.227	0.035

Table 23. Summary of general linear model for litter (square root transformed) as a function of site type along the water depth gradient (as measured in July 2017). Site type refers to resident plant communities (n = 10), invaded (n = 10) and herbicide-controlled (n = 10) plots. The category invaded was withheld as a reference for site type variable. Residual standard error for the model =7.361 $F_{3,26}$ = 8.299, *p*-value = <0.001, R^2 = 0.489, AICc = 213.116.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	9.694	4.917	1.971	0.059
Site: herbicide-treated	7.761	3.323	2.335	0.028
Site: resident plants	-1.517	3.400	-0.446	0.659
July water depth	0.346	0.120	2.894	0.008

Table 24. Summary of general linear model for maximum carbon assimilation rate as a function of plant species crossed with water depth gradient (as measured in May 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 6.309, $F_{5,14}$ = 4.504, *p*-value = 0.012, R^2 = 0.617, AICc = 146.634.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	20.346	6.699	3.037	0.009
Plant species: *C. canadensis*	-19.653	11.564	-1.700	0.111
Plant species: *Typha* spp.	26.805	20.111	1.333	0.204
May water depth	0.151	0.179	0.840	0.415
Plant species: *C. canadensis* * May water depth	0.188	0.348	0.541	0.597
Plant species: *Typha* spp.* May water depth	-0.703	0.468	-1.503	0.155

Table 25. Summary of general linear model for maximum carbon assimilation rate as a function of plant species crossed with water depth gradient (as measured in July 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 6.855, $F_{5,14}$ = 3.386, *p*-value = 0.033, R^2 = 0.547, AICc = 149.955.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	26.894	8.061	3.337	0.005
Plant species: *C. canadensis*	-24.036	12.104	-1.986	0.067
Plant species: *Typha* spp.	-5.518	18.631	-0.296	0.771
July water depth	-0.032	0.214	-0.151	0.882
Plant species: *C. canadensis* * July water depth	0.496	0.533	0.930	0.368
Plant species: *Typha* spp.* July water depth	0.077	0.458	0.167	0.870

Table 26. Summary of general linear model for maximum carbon assimilation rate as a function of plant species along the water depth gradient (as measured in May 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 6.501, $F_{3,16}$ = 6.131, *p*-value = 0.006, R^2 = 0.535. AICc = 141.457.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	21.574	5.705	3.782	0.002
Plant species: *C. canadensis*	-14.161	3.654	-3.876	0.001
Plant species: *Typha* spp.	-3.434	3.741	-0.918	0.372
May water depth	0.116	0.149	0.779	0.447

Table 27. Summary of general linear model for maximum carbon assimilation rate as a function of plant species along the water depth gradient (as measured in July 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model =6.607 $F_{3,16}$ = 5.765, *p*-value = 0.007, R^2 = 0.519, AICc = 142.106.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	24.015	6.508	3.690	0.002
Plant species: *C. canadensis*	-13.915	4.832	-2.880	0.011
Plant species: *Typha* spp.	-2.757	3.703	-0.745	0.467
July water depth	0.047	0.170	0.277	0.786

Table 28. Summary of general linear model for specific leaf area as a function of plant species crossed with water depth gradient (as measured in May 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 0.141, $F_{5,14}$ = 8.667, *p*-value = 0.001, R^2 = 0.756, AICc = -5.341.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.209	0.150	8.062	<0.001
Plant species: *C. canadensis*	0.057	0.259	0.219	0.830
Plant species: *Typha* spp.	-0.281	0.450	-0.624	0.543
May water depth	-0.002	0.004	-0.377	0.712
Plant species: *C. canadensis* * May water depth	0.006	0.008	0.834	0.418
Plant species: *Typha* spp.* May water depth	-<0.001	0.010	-0.062	0.952

Table 29. Summary of general linear model for specific leaf area as a function of plant species crossed with water depth gradient (as measured in July 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 0.144, $F_{5,14}$ = 8.166, *p*-value = 0.001, R^2 = 0.745, AICc = -4.447.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.176	0.170	6.924	<0.001
Plant species: *C. canadensis*	0.269	0.255	1.054	0.310
Plant species: *Typha* spp.	-0.254	0.392	-0.648	0.528
May water depth	-0.001	0.005	-0.127	0.901
Plant species: *C. canadensis* * July water depth	-0.001	0.011	-0.095	0.926
Plant species: *Typha* spp.* July water depth	-0.002	0.010	-0.161	0.874

Table 30. Summary of general linear model for specific leaf area as a function of plant species along the water depth gradient (as measured in May 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 0.136, $F_{3,16}$ = 15.400, *p*-value = < 0.001, R^2 = 0.743. AICc = -13.347.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.157	0.119	9.724	<0.001
Plant species: *C. canadensis*	-0.261	0.076	3.420	0.004
Plant species: *Typha* spp.	-0.320	0.078	-4.101	0.001
May water depth	-0.000	0.003	-0.017	0.987

Table 31. Summary of general linear model for specific leaf area as a function of plant species along the water depth gradient (as measured in July 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model =0.135 $F_{3,16}$ = 15.510, *p*-value = <0.001, R^2 = 0.744, AICc = -13.451.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.191	0.133	8.944	<0.001
Plant species: *C. canadensis*	0.242	0.099	2.447	0.026
Plant species: *Typha* spp.	-0.316	0.076	-4.167	<0.001
July water depth	-0.001	0.003	-0.289	0.776

Table 32. Summary of general linear model for leaf area for target species per meter of wetland (square root transformed) as a function of plant species crossed with water depth gradient (as measured in May 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 0.330, $F_{5,14}$ = 4.923, *p*-value = 0.008, R^2 = 0.637, AICc = 28.553.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	2.018	0.350	5.766	<0.001
Plant species: *C. canadensis*	-1.370	0.604	-2.268	0.040
Plant species: *Typha* spp.	0.058	1.050	0.055	0.957
May water depth	-0.010	0.009	-1.034	0.319
Plant species: *C. canadensis* * May water depth	0.015	0.018	0.835	0.418
Plant species: *Typha* spp.* May water depth	-0.004	0.024	-0.149	0.883

Table 33. Summary of general linear model for leaf area for target species per meter of wetland (square root transformed) as a function of plant species crossed with water depth gradient (as measured in July 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 0.314, $F_{5,14}$ = 5.711, *p*-value = 0.004, R^2 = 0.671, AICc = 26.610.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.325	0.369	3.591	0.003
Plant species: *C. canadensis*	-0.634	0.554	-1.144	0.272
Plant species: *Typha* spp.	1.261	0.853	1.478	0.162
May water depth	0.010	0.010	0.977	0.345
Plant species: *C. canadensis* * July water depth	-0.003	0.024	-0.104	0.918
Plant species: *Typha* spp.* July water depth	-0.036	0.021	-1.730	0.106

Table 34. Summary of general linear model for leaf area for target species per meter of wetland (square root transformed) as a function of plant species along the water depth gradient (as measured in May 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 0.317, $F_{3,16}$ = 8.582, *p*-value = 0.001, R^2 = 0.617. AICc = 20.617.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.905	0.278	6.849	<0.001
Plant species: *C. canadensis*	-0.895	0.178	-5.023	<0.001
Plant species: *Typha* spp.	-0.125	0.182	-0.687	0.502
May water depth	-0.007	0.007	-0.895	0.384

Table 35. Summary of general linear model for leaf area for target species per meter of wetland (square root transformed) as a function of plant species along the water depth gradient (as measured in July 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 0. 324 $F_{3,16}$ = 7.984, *p*-value = 0.002, R^2 = 0.600, AICc = 21.495.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	1.588	0.319	4.975	<0.001
Plant species: *C. canadensis*	-0.815	0.237	-3.439	0.003
Plant species: *Typha* spp.	-0.186	0.182	-1.025	0.321
July water depth	0.002	0.008	0.281	0.782

Table 36. Summary of general linear model for carbon assimilation scaled up to marsh-level (square root transformed) as a function of plant species crossed with water depth gradient (as measured in May 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 9.880, $F_{5,14}$ = 9.614, *p*-value = <0.001, R^2 = 0.775, AICc = 164.578.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	57.711	10.492	5.500	<0.001
Plant species: *C. canadensis*	-51.036	18.110	-2.818	0.014
Plant species: *Typha* spp.	28.385	31.496	0.901	0.383
May water depth	-0.115	0.281	-0.409	0.689
Plant species: *C. canadensis* * May water depth	0.470	0.544	0.864	0.402
Plant species: *Typha* spp.* May water depth	-0.814	0.733	-1.111	0.285

Table 37. Summary of general linear model for carbon assimilation scaled up to marsh-level (square root transformed) as a function of plant species crossed with water depth gradient (as measured in July 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 9.714, $F_{5,14}$ = 10.040, *p*-value = <0.001, R^2 = 0.782, AICc = 163.902.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	41.604	11.423	3.642	0.003
Plant species: *C. canadensis*	-32.657	17.154	-1.904	0.078
Plant species: *Typha* spp.	33.010	26.403	1.250	0.232
May water depth	0.332	0.304	1.092	0.293
Plant species: *C. canadensis* * July water depth	0.155	0.756	0.205	0.840
Plant species: *Typha* spp.* July water depth	-1.038	0.649	-1.599	0.132

Table 38. Summary of general linear model for carbon assimilation scaled up to marsh-level (square root transformed) as a function of plant species along the water depth gradient (as measured in May 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 10.020, $F_{3,16}$ = 14.780, *p*-value = <0.001, R^2 = 0.735. AICc = 158.764.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	57.005	8.793	6.483	<0.001
Plant species: *C. canadensis*	-36.721	5.632	6.520	<0.001
Plant species: *Typha* spp.	-7.093	5.766	-1.230	0.236
May water depth	-0.095	0.230	-0.413	0.685

Table 39. Summary of general linear model for carbon assimilation scaled up to marsh-level (square root transformed) as a function of plant species along the water depth gradient (as measured in July 2017). Plant species refers to *P. australis* (n = 10), *C. canadensis* (n = 5) and *Typha* spp. (n = 5). The category *P. australis* was withheld as a reference for plant species variable. Residual standard error for the model = 9.961, $F_{3,16}$ = 15.020, *p*-value = <0.001, R^2 = 0.738, AICc = 158.529.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	48.028	9.813	4.894	<0.001
Plant species: *C. canadensis*	-33.297	7.284	-4.571	<0.001
Plant species: *Typha* spp.	-8.534	5.582	-1.529	0.146
July water depth	0.154	0.257	0.601	0.556

Appendix 11. Soil carbon dioxide efflux figures and statistical models.

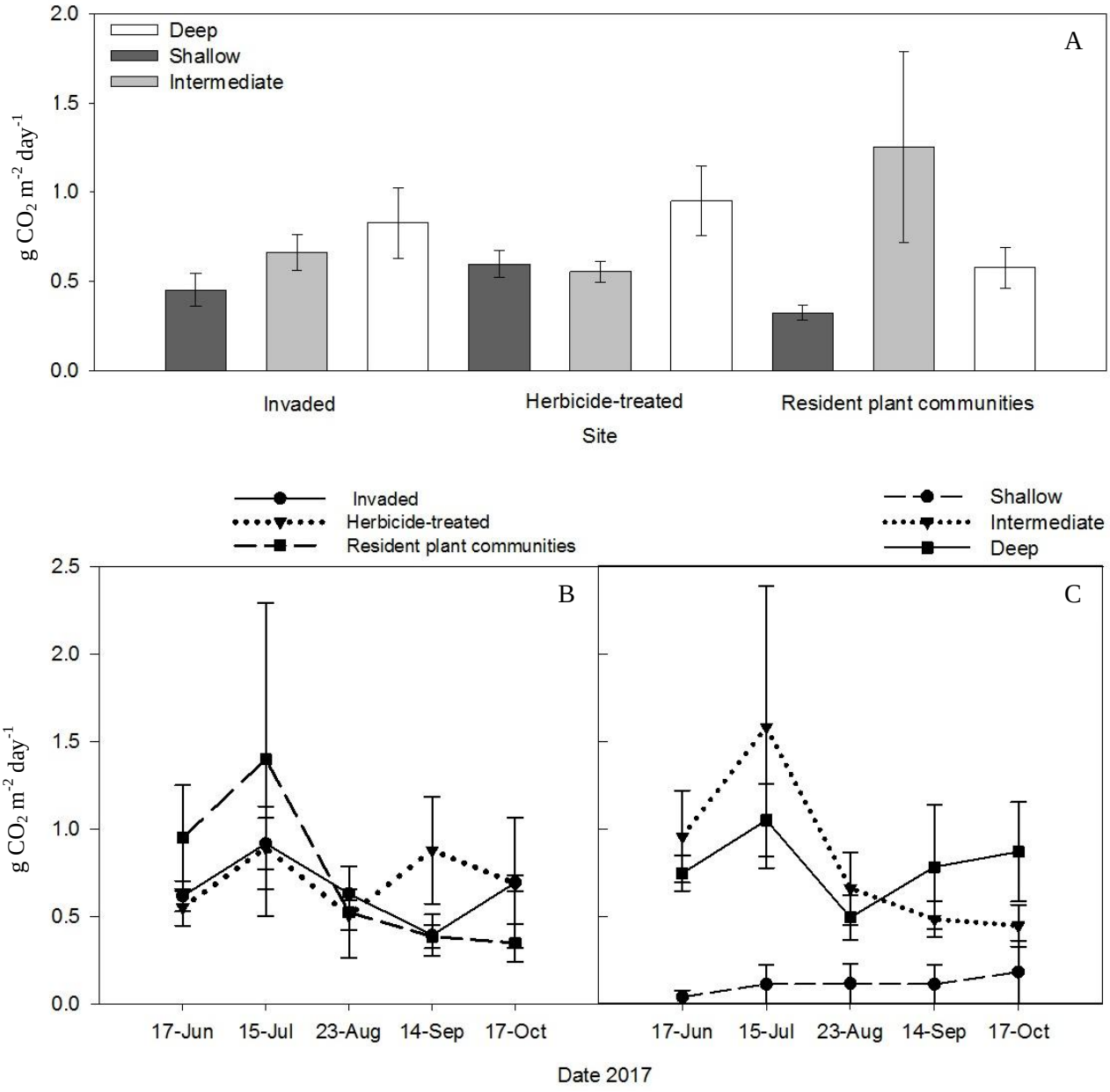

Figure 1. Soil carbon dioxide efflux measured from June to October 2017 in 9 sites in Long Point Provincial Park A) soil carbon dioxide efflux (g CO_2 m^{-2} day^{-1}) at each site, averaged across sampling dates; B) soil carbon dioxide efflux (g CO_2 m^{-2} day^{-1}) of *P. australis* invaded (n = 3), herbicide-treated (n = 3), and resident plant communities (n = 3) sites, averaged across water depths; and C) soil carbon dioxide efflux (g CO_2 m^{-2} day^{-1}) at shallow (n = 3), intermediate (n = 3) and deep (n =3) , averaged across site types. Error bars represent standard error.

Table 1. Summary of general linear model for soil carbon dioxide efflux (g CO_2 $m^{-2}d^{-1}$) measured from June to October 2017 as a function of site type with water depth as a covariate (measured during each efflux measurement). Soil carbon dioxide efflux was log transformed to meet normality assumptions. Site type refers to resident plant community (n = 3), invaded (n = 3) and herbicide-treated (sprayed in 2016; n = 3). The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 0.226, $F_{5,39}$ = 2.925, *p*-value = 0.025, R^2 = 0.272.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	-0.483	0.116	-4.144	<0.001
Water depth	0.008	0.003	2.414	0.021
Site: herbicide-treated	0.290	0.183	1.582	0.122
Site: resident plants	-0.024	0.154	-0.157	0.876
Site: herbicide-treated * water depth	-0.008	0.006	-1.364	0.180
Site: resident plants* water depth	0.003	0.005	0.587	0.560

Table 2. Summary of general linear model for soil carbon dioxide efflux (g CO_2 $m^{-2}d^{-1}$) measured in April 2018 as a function of site type. Site type refers to cattail (n = 5), invaded (n = 5) and herbicide-treated (sprayed in 2017; n = 5). The category invaded was withheld as a reference for site type variable. Residual standard error for the model = 0.006, $F_{2,12}$ = 0.209, *p*-value = 0.814, R^2 = 0.034.

Term	Coefficient	Standard error	*t*-value	*p*-value
Intercept	0.033	0.003	13.014	<0.001
Site: cattail	0.002	0.004	0.627	0.542
Site: herbicide-treated	0.001	0.004	0.178	0.862