Rooting depth and below ground biomass in a freshwater coastal marsh invaded by European Reed (*Phragmites australis*) compared with remnant uninvaded sites at Long Point, Ontario

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Abstract
Invasive European Reed (*Phragmites australis* subsp. *australis*) outcompetes native vegetation, reducing floristic diversity and habitat value for wildlife. Research in coastal salt marshes has indicated that *P. australis* invasion may be facilitated by its relatively deep rooting depth, but in freshwater marshes the growth pattern of below ground tissues in relation to water depth is uncertain. To determine if *P. australis* is rooting more deeply than resident wetland plant species in a freshwater coastal marsh on Lake Erie, Ontario, we measured the vertical distribution of below ground biomass in *P. australis* invaded marsh sites and compared it to the below ground biomass distribution in nearby sites not yet invaded by *P. australis*. These invaded and uninvaded sites were paired by water depth, which is known to influence resource allocation and rooting depth. Below ground biomass in invaded sites was greater than in uninvaded sites ($t_{28} = 3.528$, $P = 0.001$), but rooting depth (i.e., the depth at which 90% of total below ground biomass is accounted for) was comparable ($t_{28} = 0.992$, $P = 0.330$). Using water depth and site type, general linear models could predict below ground biomass ($F_{2,55} = 9.115$, $P < 0.001$) but not rooting depth ($F_{2,55} = 1.175$, $P = 0.316$). Rooting depth is likely affected by other factors such as substrate type and the depth of the organic soil horizon.
Key words: Below ground biomass; coastal marsh; Common Reed; ecosystem effects; invasive species; Lake Erie; rhizomes; roots; wetland

Introduction

European Reed (*Phragmites australis* (Cavanilles) Trinius *ex* Steudel subsp. *australis*) is considered highly invasive in North America (Saltonstall 2002) and has profound negative effects on both coastal and inland wetlands and shores. Researchers have reported that *P. australis* replaces native vegetation (Able *et al.* 2003; Tulbure and Johnston 2010), lowers plant biodiversity (Keller 2000), and disrupts wetland integrity and ecological function (Windham and Ehrenfeld 2003; Rothman and Bouchard 2007; Tulbure and Johnston 2010; Duke *et al.* 2015). *Phragmites australis* invasion may also lead to sediment accretion, terrain flattening, and a reduction in water-filled depressions due to the accumulation of leaf litter and rhizome biomass (Able *et al.* 2003). These invasion-driven changes in wetland habitat have consequences such as the loss of toad breeding habitat (Greenberg and Green 2013), reduced abundance of at-risk birds (Robichaud and Rooney 2017), and fewer suitable nesting areas and poor microhab-

itats for turtle eggs (Bolton and Brooks 2010; Cook 2016). Consequently, *P. australis* was named the worst invasive plant species in Canada (Catling and Mitrow 2005, 2011).

In the Great Lakes region, *P. australis* has replaced thousands of hectares of freshwater coastal wetlands. Around Lake Erie alone, invasion estimates range from 2553 ha within the coastal wetlands (Carson *et al.* 2018) to 8233 ha within a 10 km buffer around the American portion of Lake Erie (Bourgeau-Chavez *et al.* 2013). At Long Point on Lake Erie, *P. australis* invasion is predicted to continue expanding rapidly until 2022 (Jung *et al.* 2017), and the wetland communities most commonly replaced are cattail, meadow marsh, sedge and grass hummocks, and other mixed emergent communities (Wilcox *et al.* 2003).

The invasion success of *P. australis* is due to advantageous morphological features and its ability to modify its environment. For example, *P. australis* stems can grow up to five metres tall, intercepting light and shading competitors (Hirtreiter and Potts

2012). With its large seed heads, *P. australis* can produce hundreds of wind-dispersed seeds (Tulbure and Johnston 2010), which is an important strategy for creating new individuals (Albert *et al.* 2015). However, local expansion mainly occurs by vegetative growth (Albert *et al.* 2015), using stolon fragments and rhizomes (Mal and Narine 2004; Tulbure and Johnston 2010). Rhizomes are also important storage organs that enable *P. australis* to send up spring ramets in advance of resident species and to manage nitrogen limitation (Granéli *et al.* 1992).

Below ground, *P. australis* engineers its habitat to optimize its competitive advantage over native species (Minchinton *et al.* 2006). For example, a study on *P. australis* roots reported that hypodermal layers around roots and rhizomes protect against toxic organic compounds and anoxia (Armstrong and Armstrong 1988). Aerenchyma channels, which send atmospheric oxygen from emergent plant tissues to plant parts in anoxic soils, also allow *P. australis* to sustain deep rooting depths (Armstrong and Armstrong 1988). For example, studies from a marine coastal marsh gave estimates of *P. australis* roots growing from <1–4 m deep (Moore *et al.* 2012; Packer *et al.* 2017).

The deep rooting of *P. australis* may be an important strategy for invasion; species with deeper rooting depths are able to access nutrients and minerals lower in the soil profile compared to species with shallow rooting depths (Jobbágy and Jackson 2004). For example, in a New Hampshire study, *P. australis* had deeper rooting depths in more physically stressful environments that allowed it to access deeper, less saline groundwater and more available nutrients (Moore *et al.* 2012). Despite the competitive advantage that deep rooting may provide to *P. australis* in salt marshes (Moore *et al.* 2012), we are not aware of other studies quantifying its rooting depth in freshwater coastal marshes.

Other than the influence of salinity (Moore *et al.* 2012), variation in *P. australis* rooting depth may be due to differences in water depth, the frequency of water depth fluctuation, and substrate type, which may all influence redox conditions and oxygen availability. For example, in a greenhouse experiment, Hanslin *et al.* (2017) reported that increased amplitude of water level fluctuations resulted in increased *P. australis* rooting depths but decreased below ground biomass in the top soil regions. This finding has yet to be corroborated by studies of natural systems.

To the best of our knowledge, there are no studies in the Great Lakes region that quantify the vertical distribution and biomass of *P. australis* below ground tissues compared to resident vegetation, particularly

not across a gradient in water depth. Differences in rooting depth between invasive *P. australis* and resident plant communities in these freshwater wetlands may help explain the success of *P. australis* invasion. Importantly, such differences may also have implications for the ecological effects of invasion. For example, deeper rooting could expand the penetration of oxygen into saturated wetland soils (Faußer *et al.* 2016), mobilizing carbon pools and metals that were otherwise inactive (e.g., Jacob and Otte 2003). We sought to determine if freshwater coastal marsh communities dominated by invasive *P. australis* have greater below ground biomass or deeper rooting depths compared with resident uninvaded marsh. We predicted that more below ground biomass would be produced by *P. australis* than resident plant communities because *P. australis* is so productive (Rothman and Bouchard 2007). Also, because *P. australis* has deeper rooting depths than native vegetation in marine coastal marshes (Moore *et al.* 2012), we predicted that the same trend would be true in freshwater. In addition, because water depth may affect rooting depth (Hanslin *et al.* 2017), we also tested the prediction that below ground biomass and rooting depth of *P. australis*-dominated communities would be positively correlated with water depth across a naturally occurring gradient and compared this with resident vegetation communities.

Methods

Site selection

Our study was situated at Long Point, Canada (42.581°N, 80.381°W), a sand spit that sustains over 70% of the remaining intact coastal marsh on the north shore of Lake Erie (Ball *et al.* 2003). The 40 600 ha area is a designated World Biosphere Reserve by the United Nations Educational, Scientific and Cultural Organization (UNESCO), and an internationally important wetland under the Ramsar Convention (Ministry of Natural Resources and Forestry 2017). This ecologically important region is threatened by continuing expansion of high-density *P. australis* (Jung *et al.* 2017).

Sample sites within Long Point were established across a range of water depths at which *P. australis* invasion is common (13.7–55.7 cm), with sites dominated by high density *P. australis* monocultures paired by water depth with sites either dominated by cattails (*Typha* spp.; >30 cm water depth) or by meadow taxa, including graminoids, sedges, and forbs (<40 cm water depth). Sites in the 30–40 cm depth range were either meadow marsh or *Typha* spp. marsh, as the two communities stratify by depth and rarely mix. Sites were dispersed across the Crown

Marsh and Long Point Provincial Park management units, spaced between 100 and 2000 m apart. This area is representative of wet meadow and emergent lacustrine marsh in Lake Erie, with substrate ranging from organic in shallower depths to pure sand in deeper locations.

Core collection

Fieldwork was conducted in May 2017. Using a 2.54 cm diameter soil gouge auger, soil cores (0.3–0.75 m deep) were sampled from sites invaded by *P. australis* and paired uninvaded marsh sites. It was not possible to obtain cores of uniform length due to differences in the thickness of the organic horizon and difficulties penetrating the underlying sand substrate. In total 29 pairs of cores were collected. The cores were then sub-sectioned into 10 cm long segments and frozen until they could be processed. For comparison, Moore *et al.* (2012) who also examined belowground biomass trends in marsh invaded by European *P. australis*, collected 100 cm long cores from 10 tidal marshes along New Hampshire's Atlantic coast using the same diameter gouge auger and sub-sectioned them into 5 cm long segments.

Core processing

Core segments were thawed for about 24 h and then washed over two nested sieves: a coarser (1.7 mm) sieve over a finer (425 µm) sieve. All live rhizomes and all root tissues were retrieved and dried at 80°C to a constant weight (minimum 48 h). Dead roots may have been included in our weights as we did not find it possible to reliably differentiate live and dead roots. The dried below ground tissues were then weighed on a Mettler Toledo analytical balance (MS204S, Columbus, Ohio, USA) with a 0.0001 g accuracy. For comparison, Moore *et al.* (2012) picked live roots and rhizomes from trays partially filled with water and then oven dried to a constant weight at 65°C for a minimum of 48 h.

Data analysis

For the purposes of this study, rooting depth was defined as the depth (cm) at which 90% of the cumulative below ground biomass was accounted for. Below ground biomass was defined as the total root and rhizome mass per unit area (g/m^2), recognizing that the core depths varied with the thickness of the organic horizon. To test whether below ground biomass was greater in *P. australis* invaded sites compared to uninvaded sites, we used a paired-samples, one-tailed *t*-test. To test whether rooting depth was greater in *P. australis* invaded sites than uninvaded sites, we used another paired-samples, one-tailed *t*-test. Lastly, to test whether water depth is a significant predictor of below ground biomass and rooting depth, we used general linear models (GLM) with

a least squares estimation framework to model variation in below ground biomass and rooting depth based on water depth, site type (*P. australis* invaded or uninvaded), and their interaction. Models are thus represented by the general form:

$$y = \beta_1 W + \beta_2 T + \beta_3 T \times W + \beta_0 + \varepsilon,$$

where W is water depth, T is site type, and ε is error. If the interaction terms were not significant, the model would be re-run to only include the main factors: water depth and site type. In all cases, we used an alpha value of 0.05 and Type III sums of squares. Analyses were completed using IBM SPSS Statistics 20.

Results

Paired-samples t-*tests for below ground biomass and rooting depth*

Phragmites australis invaded marsh had greater below ground biomass than uninvaded marsh habitat, when meadow and *Typha* spp. marsh are considered jointly (paired-samples *t*-test, $t_{28} = 3.528$, $P = 0.001$; Figure 1a). Although the difference between *Typha* spp. dominated cattail marsh and *P. australis* invaded marsh is negligible, it revealed that the difference is primarily between *P. australis* invaded and meadow marsh sites (Figure 1a).

There is no significant difference in rooting depth between *P. australis* invaded marsh and uninvaded marsh (paired-samples *t*-test, $t_{28} = 0.992$, $P = 0.330$; Figure 1b). This appears evident in both meadow marsh and cattail marsh components of the uninvaded sites (Figure 1b).

The down-core distribution of below ground biomass suggests that core depths were sufficient to capture the bulk of total below ground tissues (Figure 2). This was true for invaded (Figure 2a) and uninvaded (Figure 2b) sites, across a range of water depth intervals between 13.7 and 55.7 cm. Below ground biomass was detected to a maximum of 80 cm soil depth yet peaked within the top 30 cm of the soil profile, regardless of site type (Figure 2).

General linear models for below ground biomass and rooting depth

For below ground biomass, the interaction term was not significant (Table S1a, Figure S1), so we removed it and re-ran the GLM as

$$below\ ground\ biomass = \beta_1 W + \beta_2 T + \beta_0 + \varepsilon.$$

This model provided a reasonable fit (adjusted $r^2 = 0.222$; GLM, $F_{2,55} = 9.115$, $P < 0.001$; details in Table S1b). Likewise, for rooting depth, the interaction term was not significant (Table S2a), so we removed it and re-ran the GLM as

$$rooting\ depth = \beta_1 W + \beta_2 T + \beta_0 + \varepsilon.$$

However, this model proved to be a poor predictor
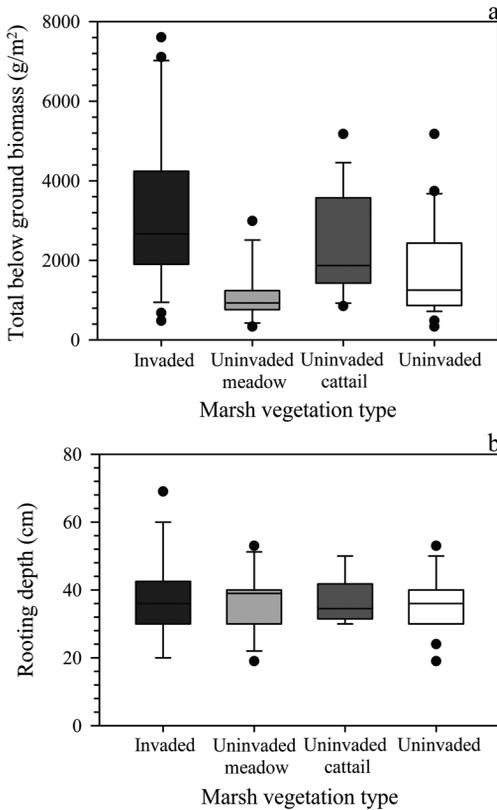
Figure 1. Total below ground biomass and rooting depth in European Reed (*Phragmites australis*) invaded and un-invaded marsh. Boxplots depicting a. total below ground biomass (g/m^2) and b. rooting depth (cm), contrasting *P. australis* invaded marsh (dark grey; *n* = 29) and uninvaded marsh (white; *n* = 29) sites. Note that uninvaded marsh is divided into shallower depth meadow marsh (light grey; *n* = 15) and deeper water cattail (*Typha* sp.) marsh (grey; *n* = 14) communities.

of rooting depth (adjusted r^2 = 0.006; GLM, $F_{2,55}$ = 1.175, P = 0.316; details in Table S2b).

Discussion

Our research objectives were to determine if *P. australis* invaded marsh produced more below ground biomass, and deeper rooting depths than uninvaded marsh in a freshwater coastal marsh, as has been observed in marine coastal marshes (e.g., Ravit *et al.* 2006; Moore *et al.* 2012). Controlling for water depth, we observed that *P. australis* invaded marsh had more below ground biomass than uninvaded marsh, however, rooting depths did not differ significantly between *P. australis* invaded and uninvaded marsh sites. Like site type, water depth was a significant predictor of below ground biomass (g/m^2) but not of rooting depth. Interestingly, although the largest difference in below ground biomass was evident between *P. australis* invaded sites and meadow marsh sites, which were restricted to shallower water depths, we detected no significant interaction between water depth and site type when predicting either below ground biomass or rooting depth.

Greater below ground biomass may provide *P. australis* a competitive advantage allowing it to usurp soil resources (van Wijk *et al.* 2003) and facilitate dispersion by vegetative reproduction (Saltonstall 2002; Tulbure and Johnston 2010; Albert *et al.* 2015). The current literature reports below ground biomass values for *P. australis* in the range of 886 g/m^2 (Rothman and Bouchard 2007) to 1368 g/m^2 (Windham 2001); for cattail marsh in the range of 742 g/m^2 (Rothman and Bouchard 2007) to 2461 g/m^2 (Ouellet-Plamondon *et al.* 2004); and for meadow species, such as Saltmeadow Cordgrass (*Sporobolus pumilus* (Roth) P.M. Peterson & Saarela) and Bluejoint Reedgrass (*Calamagrostis canadensis* (Michaux) Palisot de Beauvois), in the range of 256 g/m^2 (Ouellet-Plamondon *et al.* 2004) to 757 g/m^2 (Windham 2001). Our measures of below ground biomass show the same pattern in relative magnitude among the three communities but are noticeably higher than other published values: averaging 3137 g/m^2 for *P. australis*, 2372 g/m^2 for cattail marsh, and 1146 g/m^2 for meadow marsh. Our measurements may be high due to particularly dense growth, favourable edaphic conditions in intact freshwater coastal marsh, or because we were unable to differentiate live tissues from recently dead tissues.

When uninvaded marsh was separated into cattail and meadow marsh communities, we noted higher average below ground biomass in uninvaded cattail marsh, clearly overlapping with the below ground biomass typical of *P. australis*. This indicates that the effects of invasion on below ground biomass is likely more evident where *P. australis* replaces meadow marsh than where it invades cattail marsh. Yet, despite this difference in mean below ground biomass between cattail and meadow marsh, we fit a single slope relating the below ground biomass of uninvaded sites to water depth collectively. Future research should explicitly test for the role of resident vegetation community type on limiting the magnitude of *P. australis* invasion effects on invaded ecosystems.

Importantly, though invasion by *P. australis* in freshwater coastal marsh may increase overall below ground biomass, the concern that *P. australis* below ground tissues might penetrate more deeply than resident species and thus alter nutrient and metal fluxes in freshwater marshes is unfounded. Contrary to previous studies (e.g., Ravit *et al.* 2006; Moore *et al.* 2012), we observed no difference in rooting depth
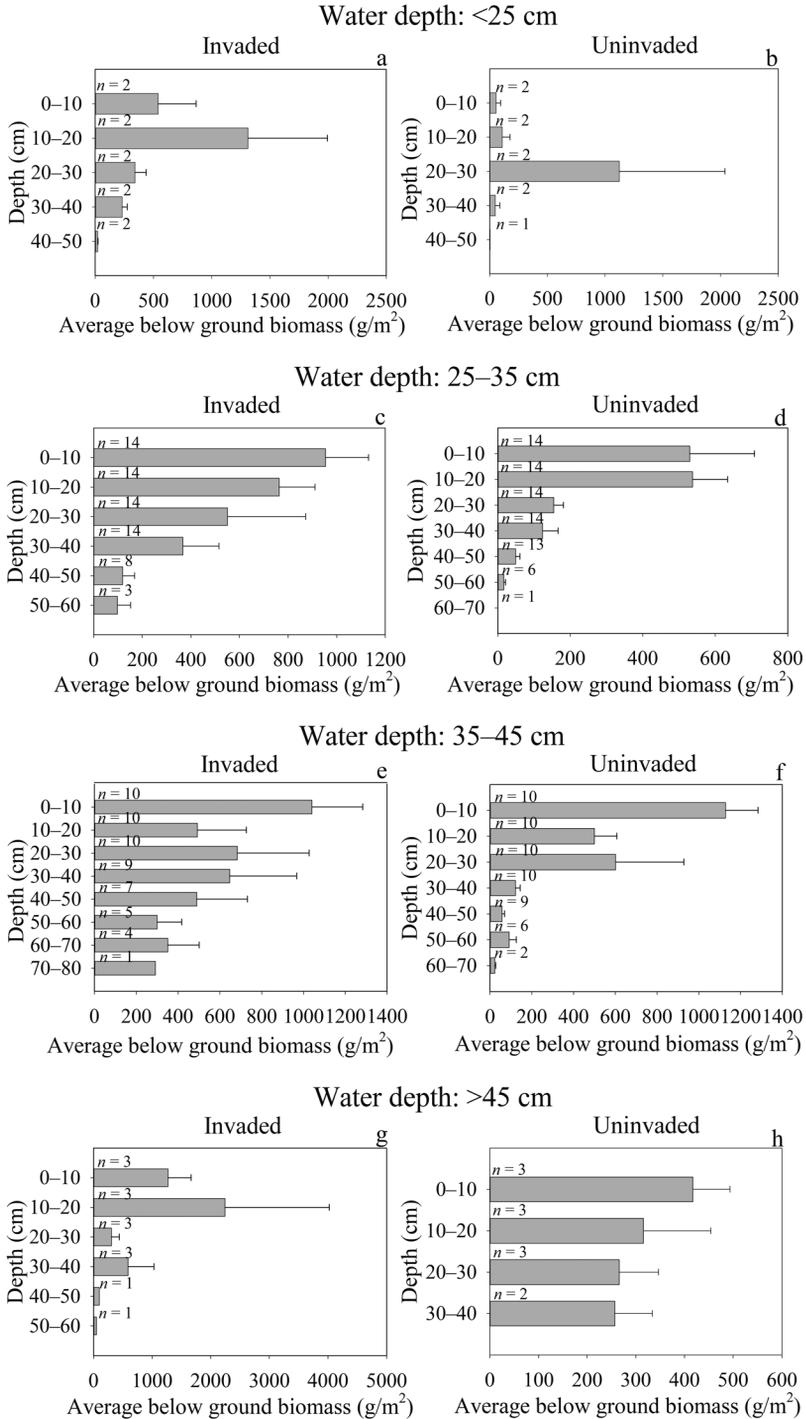
FIGURE 2. Down-core distribution of below ground biomass at different water depths. Down-core distribution of below ground biomass, contrasting European Reed (*Phragmites australis*) invaded sites (a, c, e, g) and uninvaded sites (b, d, f, h) at different water depth intervals: <25 cm (a, b), between 25–35 cm (c, d), between 35–45 cm (e, f), and >45 cm (g, h). The *n* above each bar indicates the number of cores in which living below ground tissues were detected at the indicated water and soil depth, in the indicated site type. Error bars are SE.

among the invaded and uninvaded sites. Moore *et al.* (2012) surmised that in marine coastal marsh, *P. australis* may produce deeper roots to access freshwater pockets. If this were so, it might explain why *P. australis* was not rooting more deeply than resident species in our freshwater coastal marsh. Alternatively, these published studies may differ from ours in the frequency and amplitude of water depth fluctuations that can also influence rooting depth (Hanslin *et al.* 2017). Another important factor is likely the wetland soil type and stratigraphy. Moore *et al.* (2012) reported that sandy mineral soils may inhibit deep penetration of roots. Long Point has a sand mineral soil beneath an organic horizon of variable thickness; the sand soil may have limited rooting depth for all species in our study.

Because *P. australis* produces significantly more below ground biomass in the same depth of rhizosphere as resident vegetation communities, we expect that root processes such as enhanced gas diffusion in the rhizosphere, oxidation of waterlogged anoxic soils (Armstrong and Armstrong 1988; Bart and Hartmann 2000), and the release of allelochemicals (Rudrappa *et al.* 2007) provide *P. australis* a competitive advantage and contribute to its invasion success. Yet clearly, given the equivalent rooting depths of *P. australis* invaded and uninvaded marsh, these communities experience a common rooting depth limit. This conclusion is further supported by our observation that meadow marsh, despite producing less below ground biomass than cattail marsh, nonetheless roots at an equivalent depth

Conclusion

Below ground biomass in *P. australis* invaded marsh significantly exceeded that in resident communities of meadow marsh and cattail marsh, after accounting for water depth, but rooting depths were equivalent. Consequently, root densities must be greater in *P. australis* invaded marsh, potentially contributing to its invasion success in Long Point. Because *P. australis* did not root more deeply than resident vegetation in our freshwater coastal marsh study system, concerns around invasion mobilizing deep pools of otherwise inactive carbon or metals may be generally unwarranted. The novel quantitative data presented in this study increases our understanding of *P. australis* invasion in freshwater lacustrine coastal marsh habitat and establishes the hypothesis of common limits to rooting depth in invaded and uninvaded sites that should be tested in other study systems.

Author Contributions

Conception & Design: R.C.R., S.J.Y., and C.L.; Field Work: S.J.Y.; Lab Work: C.L. and S.J.Y.; Data Analysis & Interpretation: R.C.R., S.J.Y., and C.L.; Writing – First Draft: C.L.; Writing – Review & Editing: R.C.R., S.J.Y., and C.L.; Funding Acquisition: R.C.R.

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SUPPLEMENTARY MATERIAL:

FIGURE S1. Total below ground biomass with water depth for European Reed (*Phragmites australis*) invaded sites (solid line and black triangles; $n = 29$) and uninvaded sites (dashed line and white circles; $n = 29$).

TABLE S1. Results table for GLM predicting total below ground biomass with and without interaction term.

TABLE S2. Results table for GLM predicting rooting depth with and without interaction term.