

**Belowground plant material and its contribution to soil
volume in a St. Lawrence salt marsh, QC, Canada**

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Abstract

Accumulation of belowground plant material (live roots, rhizomes, and dead material) is critical to vertical accretion of tidal salt marsh soils and their ability to maintain elevation with respect to sea-level rise. Many studies utilize a single, global relationship between soil organic carbon and belowground volume, which does not include the pore space created by belowground growth, thus does not appropriately reflect the contribution of vegetation to soil accretion. This thesis reports on research that seeks to address this gap.

Chapter 1 is an introduction and literature review that describes tidal marshes vegetation typical of Northwest Atlantic tidal salt marshes. This chapter describes the importance of living biomass (roots and rhizomes) and dead material of the dominant marsh species in soil vertical accretion for marsh resiliency to keep up with sea-level changes.

Chapter 2 is written in manuscript style including methods and results of a study of the relationship of the volume of live roots and rhizomes to their dry biomass. The study focuses on four species in a Quebec salt marsh. The species, *Spartina alterniflora*, *Spartina patens*, and invasive *Phragmites australis* were identified in the aboveground growth, while only tubers and roots of *Cyperus esculentus* were found. Cores of the top 30 cm of soil were collected and cut into 0-15 and 15-30 cm sections from the *S. alterniflora* –dominated low marsh, the *S. patens*–dominated high marsh, and the upper *S. patens* marsh invaded by *P. australis*. The soil was washed over a 1 mm sieve, and the organic matter was retained. The live material was sorted into fractions of roots and rhizomes by species. The volume of all components was measured by displacement in water before drying to obtain mass. An overall conversion factor of 8.2 g cm⁻³ reflects the volumetric contribution of live roots, rhizomes, and organic matter (OM) of all

species studied. The relationship varies by species, with *S. alterniflora* contributing the greatest volume per unit mass (8.9 g cm^{-3}), followed by *S. patens* (7.9 g cm^{-3}), then *P. australis* and *C. esculentus*, both at 5.6 g cm^{-3} . The results of this thesis not only demonstrate that the total mass and volume of each species for each component (rhizomes, roots, and dead material) are strongly correlated but that measurements of simple carbon density underestimate the actual contribution of salt marsh plants to the soil volume.

Chapter 3 presents final conclusions, limitations of the study reported on in Chapter 2, and identifies directions that would be valuable for future research.

Résumé

L'accumulation de matériel végétal souterraine (racines vivantes, rhizomes vivantes et matériel mort) est essentielle à l'accrétion verticale des sols des marais salés de marée et à leur capacité à maintenir leur élévation par rapport à l'élévation du niveau de la mer. De nombreuses études utilisent une relation unique et globale entre le carbone organique du sol et le volume souterrain, qui n'inclut pas l'espace poreux créé par la croissance souterraine, ce qui ne reflète pas de manière appropriée la contribution de la végétation à l'accrétion du sol. Cette thèse rend compte d'une recherche qui cherche à combler cette lacune.

Le chapitre 1 est une introduction et une revue de la littérature qui décrit la végétation des marais salés tidaux de l'Atlantique Nord-Ouest. Ce chapitre décrit l'importance de la biomasse vivante (racines et rhizomes) et du matériel mort des espèces dominantes des marais dans l'accrétion verticale du sol pour la résilience des marais face aux changements du niveau de la mer.

Le chapitre 2 est rédigé dans le style d'un manuscrit et comprend les méthodes et les résultats d'une étude sur la relation entre le volume des racines vivants et des rhizomes vivants et leur biomasse sèche. L'étude porte sur quatre espèces dans un marais salé du Québec. Les espèces, *Spartina alterniflora*, *Spartina patens*, et l'envahissante *Phragmites australis* ont été identifiées dans la croissance aérienne, tandis que seuls les tubercules et les racines de *Cyperus*

esculentus ont été trouvés. Des carottes des 30 premiers cm de sol ont été prélevées et coupées en sections de 0-15 et 15-30 cm dans le bas marais dominé par *S. alterniflora*, le haut marais dominé par *S. patens*, et le haut marais de *S. patens* envahi par *P. australis*. Le sol a été lavé sur un tamis de 1 mm, et la matière organique a été retenue. Le matériel vivant a été trié en fractions de racines et de rhizomes par espèce. Le volume de tous les composants a été mesuré par déplacement dans l'eau avant d'être séché pour obtenir la biomasse. Un facteur de conversion global de $8,2 \text{ g cm}^{-3}$ reflète la contribution volumétrique des racines vivantes, des rhizomes, et de la matière organique (MO) souterraine vivante de toutes les espèces étudiées. Le rapport varie selon les espèces, *S. alterniflora* contribuant le plus grand volume par unité de masse ($8,9 \text{ g cm}^{-3}$), suivi de *S. patens* ($7,9 \text{ g cm}^{-3}$), puis de *P. australis* et *C. esculentus*, tous deux à $5,6 \text{ g cm}^{-3}$. Les résultats de cette thèse démontrent non seulement que la masse totale et le volume de chaque composant (rhizomes, racines et matériel mort) sont fortement corrélés mais aussi que les mesures de la simple densité de carbone sous-estiment la contribution réelle des plantes des marais salés au volume du sol.

Le chapitre 3 présente les conclusions finales, les limites de l'étude rapportée au chapitre 2, et identifie les orientations qui seraient utiles pour les recherches futures.

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Chapter 1: Introduction and Literature Review

1.1 Introduction

Tidal salt marshes are wetlands located on marine coasts in the upper margins of the intertidal zone. These ecosystems possess unique, salt-tolerant vegetation. They are recognized as natural climate solutions due to their potential to capture and sequester carbon in their soils at rates higher than terrestrial forests (e.g., Adame et al. 2015; Griscom et al., 2017; Mcleod et al., 2011). At the same time, they provide other, valuable ecosystem services such as habitat for waterfowl, water purification, erosion control, and coastal protection, among others (e.g., Barbier et al., 2011; Chmura et al., 2012; Costanza et al., 2014; Griscom et al., 2017; Howard et al., 2017; Mitsch and Gosselink, 2000).

To continue to provide these ecosystem services, the surface elevation of salt marshes must stay around the level of mean high water and thus keep pace with rising sea levels (Kirwan and Megonigal, 2013; Morris et al., 2002). Increased rates of vertical accretion of salt marsh soils are required to preserve marsh stability in the face of increasing rates of sea-level rise. Accretion is achieved by deposition of mineral sediments, belowground biomass and organic matter (Craft et al., 1993; DeLaune et al., 1983; Hatton et al., 1983; Morris et al., 2002; Nyman et al., 1990).

The influence of matter accumulation on salt marsh vertical accretion was demonstrated by Turner et al. (2002). They found a strong relationship between vertical accretion rates and the rate of the mass of organic matter accumulation for >141 salt marshes from New England to the Gulf of Mexico. Most studies considering the relationship between organic matter accumulation and vertical accretion rates have concentrated on the mass of organic matter in salt marsh soils, making general assumptions regarding its contribution to soil volume, yet there has been limited

study of this relationship (e.g., Chmura and Hung, 2004; Morris et al., 2016; Neubauer et al. 2002; Nyman et al. 2006; Turner et al., 2002).

Smith (1943) reported a range from 1.41 to 1.90 g cm⁻³ for organic matter density among different types of upland soils. He used the pycnometer method, which employs a vacuum to push water into air spaces of the sample, omitting pore spaces in plant tissues from volumetric measurements. Later, Brady (1984) reported that the organic particle density varied between 1.10-1.40 g cm⁻³ for mineral soils. Citing the work of Smith (1943), Delaune et al. (1983) used an organic particle density of 1.14 g cm⁻³ to calculate the volumetric contribution of soil biomass in a Louisiana tidal marsh dominated by *Spartina patens*. Citing the work of Delaune et al. (1983), Bricker-Urso et al. (1989) then used the value of 1.1 g cm⁻³ to estimate the volumetric contribution of soil biomass to *Spartina alterniflora* salt marshes in Rhode Island. Later, Craft et al. (1993) reported an average organic density of 1.29 g cm⁻³ for an irregularly flooded marsh dominated by *Juncus roemerianus*, *Distichlis spicata*, *Spartina patens* and *Spartina cynosuroides* located on the North Carolina coast. Since then, a constant relationship between organic matter mass and its volumetric contribution in salt marshes has been generally assumed (e.g., Boyd et al., 2017; Callaway et al., 1997; Unger et al., 2016).

The results of some studies have challenged the assumption of a constant relationship between belowground plant material (live roots, rhizomes, and dead) mass and its volumetric contribution to salt marsh soils. For example, Blum et al. (2021) observed that the contribution of roots to surface elevation change varied with marsh elevation and species in a Virginia salt marsh. It could be argued that organic densities vary with species since most of the data for belowground and soil vertical accretion studies comes from studies in Atlantic salt marshes of the USA which have different dominant species than on other coasts (De la Cruz and Hackney,

1977; Gallagher and Plumley, 1979; Valiela et al., 1976). Additionally, making the assumption that 1 cm³ of any belowground plant material component has a mass of 1.1 g may misrepresent the degree to which belowground mass contributes to the volume of salt marsh soils. Blum and Davey (2013) demonstrated that the volume of the top 25 cm of soil in an *S. alterniflora*-dominated marsh mainly was taken up by roots and rhizomes, despite it being mineral-rich in two salt marshes at the Virginia Coast Reserve Long Term Ecological Research Site.

A better understanding of the volumetric contributions of belowground plant material component (such as living roots, rhizomes, and dead) by different salt marsh species is needed to understand marsh accretion processes properly. The widely employed assumption that 1.1 cm⁻³ of belowground component has a mass of 1 g has not been tested to determine if it is an accurate predictor of the volumetric contribution of living roots, rhizomes, and dead material. In this thesis, my objective is to examine whether all components of belowground plant material have the mass/volume relationship of 1.1 g cm⁻³ in soil- using the example of a salt marsh on the St. Lawrence River Estuary (Quebec). As the dominant vegetation of this salt marsh is generally characteristic of salt marshes on the NW Atlantic, the results should be widely transferable. I compared the volume and mass of live roots, rhizomes and dead material of *Cyperus esculentus*, *S. alterniflora*, *S. patens*, and *Phragmites australis*, as well as an aboveground standing crop to the belowground plant material of the latter three.

The following presents an overview of tidal salt marsh vegetation characteristics, especially on the northwestern Atlantic, and the importance of vertical soil accretion in this ecosystem to maintain marsh equilibrium with sea-level rise.

1.2 Literature Review

1.2.1 Tidal Salt Marsh Vegetation

In his review of the world's salt marshes, Chapman (1960) noted the similarities in the vegetation of marshes along the coast of eastern North America. The low marsh is mainly dominated by *Spartina alterniflora* associated with *Salicornia* spp., followed by *Spartina patens* in the upper elevations, termed "high marsh." In Canadian tidal salt marshes, it is common to find *S. patens* mixed with some forbs such as *Glaux maritima* (= *Lysimachia maritima*), *Plantago oliganthos* (= *Plantago maritima*), *Triglochin gaspense*, *Suaeda maritima* and *Salicornia europaea* (Chapman, 1976). In recent years it also is common to also find invasive *Phragmites australis* in the high marsh (Mal and Narine, 2003).

Salt marsh vegetation on other coasts can be dominated by other plant communities distributed and the following species' distributions are noted by Chapman (1960 and 1976). Marshes of boreal and Arctic Canada, Alaska, Greenland, Iceland, northern Scandinavia, and Russia are dominated by the grass *Puccinellia phryganodes* and various species of the sedge *Carex*. However, *Salicornia* and *Suaeda* dominate some of the southwestern coast of Alaska. In western European salt marshes, the dominant species are *Halimione portulacoides* (= *Atriplex portulacoides*), *Puccinellia maritima*, *Juncus maritimus*, *Salicornia* spp., and the invasive *Spartina anglica* and *Spartina townsendii*. While on the west coast of the United Kingdom, as well as the Baltic Sea coast, the dominant species are *Festuca rubra*, *Agrostis stolonifera*, *Carex paleacea*, *Juncus bufonius*, *Desmoschoenus bottanica*, and *Scirpus* spp. Mediterranean salt marshes are dominated by *Sarcocornia fruticosa*, *Limonium vulgare*, *Juncus* spp., and *Salicornia* spp. Asian salt marshes are dominated by *Triglochin maritima*, *Limonium japonicum*, *Salicornia*, and *Zoysia macrostachya*. On the coast of New Zealand, Tasmania and Australia, salt marshes

are dominated by *Sporobolus virginicus*, *Sarcocornia quinqueflora*, and *Suaeda australis* and invasive *Spartina anglica*. On the Atlantic coast of South American salt marshes are mainly dominated by *Spartina densiflora*, *Limonium brasiliense*, *Distichlis spicata*, *Juncus californicus*, *Heterostachys*, and *Allenrolfea*. Along the west coast of South America, salt marshes are dominated by *Batis maritima*, *Sesuvium portulacastrum*, *D. spicata*, *Salicornia fruticosa*, *S. densiflora*, *Schoenoplectus americanus* (Ampuero et al., 2020; Fariña et al., 2018).

Most studies of salt marsh mass show that live belowground plant material is considerably greater than that aboveground. At Dipper Harbour marsh on the Bay of Fundy, Connor and Chmura (2000) measured the end-of-season standing crop of *S. alterniflora* as $460 \pm 92 \text{ g m}^{-2}$ and the maximum belowground biomass was 17 times higher ($8044 \pm 562 \text{ g m}^{-2}$). This greater biomass belowground than aboveground also was reported by Gross et al. (1991) for *S. alterniflora* in salt marshes from Georgia to Nova Scotia. However, Kennedy et al. (2013) reported ratios of below- to aboveground biomass for tidal marshes according to climate domains and regions, which ranged from 1.15 for temperate freshwater tidal marshes to 3.65 for subtropical marshes. Overall, the production of vascular salt marsh plants varies widely, and belowground production (roots and rhizomes) is an important component in many marshes (Chmura, 2009). For example, the range of root-to-shoot ratios was 4.2:1 and 4.4:1 for tidal marshes dominated by *S. patens* and *S. alterniflora*, respectively, on Delaware Bay (Roman and Daiber, 1984).

Similar relationships of below- to aboveground biomass have been reported for *S. patens* marsh. Connor and Chmura (2000) measured the aboveground standing crop of *S. patens* at Dipper Harbour, New Brunswick. Their measurement of $379 \pm 82 \text{ g m}^{-2}$ was similar to the average of 371 g m^{-2} reported by Gordon et al. (1985) for marshes at the head of the Bay of

Fundy. Connor and Chmura (2000) reported that the mass of live roots and rhizomes (2696 ± 370 g m⁻²) was seven times greater than the aboveground, while dead belowground mass (3891 ± 1232 g m⁻²) was even higher. Tripathee and Schäfer (2015) found that, in a New Jersey salt marsh, belowground biomass (11600 g m⁻²) of *S. patens* was about five times greater than aboveground (2300 g m⁻²). They also observed that their roots represented almost 80% of the total belowground mass (Tripathee and Schäfer, 2015). In contrast, microtidal Mediterranean coastal marshes dominated by *Arthrocnemum macrostachyum* had a R:S ratio less than 1:1 in Ebre Delta (Ibañez et al., 2000). Thus, with some exceptions, such as forb-dominated marshes, belowground vascular biomass is frequently larger than aboveground in salt marshes over a wide range of latitudes.

Invasive *P. australis* has been encroaching into *S. patens*-dominated salt marshes of Eastern North America (e.g., Windham and Lathrop, 1999; Gu et al., 2020) and when both species compete, the invasive *P. australis* has higher belowground biomass, allowing it to contribute more to soil volume. In a New Jersey tidal marsh co-dominated by *S. patens* and *P. australis*, Windham (2001) reported that *P. australis* produced three times more aboveground biomass and two times more belowground biomass than *S. patens* in a single growing season. In contrast, Gu et al. (2020) found that at a salt marsh on the St. Lawrence River estuary, that invasive *P. australis* produced 1.3 times less aboveground biomass but greater belowground biomass than *S. patens*. Moore et al. (2012) reported that, in a New Hampshire salt marsh, the invasive *P. australis* had a total live belowground biomass of 6250 g m⁻² over 100 cm depth in which rhizome biomass represented 93% of the total. They noted that living roots and rhizomes could be found to depths greater than the native species. Moreover, Windham (2001) reported that the rhizomes of *P. australis* represented more than 70% of the total belowground biomass.

Cyperus esculentus is a native species along water bodies and in some marshes and bogs in southeastern Canada, especially in the upper and lower St. Lawrence River (e.g., Hudon, 2004; Mulligan and Junkins, 1976). This species is also considered a difficult-to-control weed plant in cultivated fields (Soltani et al. 2018) and an introduced species in British Columbia (Brouillet et al. 2010). Its tubers can overwinter while its roots and rhizomes do not survive the winter (Mulligan and Junkins, 1976). This species (with only 10% of areal coverage) was also found in a seasonally flooded wetland in Missouri in association with other species, where its tubers, found predominantly in the upper 15 cm (Mulligan and Junkins, 1976), comprised 85% of its belowground biomass (Kelley, 1990). There has been no report of its biomass in tidal salt marshes.

1.2.2 Soil Vertical Accretion

Soil vertical accretion in salt marshes is controlled by the interplay of sea-level rise (thus flooding frequency), and depositional and vegetative processes. At high latitudes (e.g., Atlantic Canada and Maine), ice rafting can enhance marsh sediment accretion (Chmura et al., 2001). With an acceleration of the rate of global mean sea-level rise (Church et al., 2013), increased rates of salt marsh vertical soil accretion are critical for marsh resiliency (e.g., Byrd et al., 2016; Cahoon et al., 2021; Morris et al., 2002; Schile et al., 2014). For example, Chmura et al. (2001) calculated that historical rates (~170 years) of salt marsh soil vertical accretion increased and kept up with sea-level changes in the outer Bay of Fundy. However, the authors reported that some marshes evaluated were highly vulnerable to short-term changes in relative sea level.

Redfield (1972) first suggested that each component of belowground plant material is an essential contributor to the vertical accretion of soil marshes, and many studies since have confirmed its importance (e.g., Cahoon et al. 2021; Chmura and Hung, 2004; Neubauer et al.,

2002; Nyman et al., 2006; Turner et al., 2002). Therefore, it is necessary to include these biological feedbacks in vertical accretion studies (Kirwan et al., 2010).

Many studies have used a constant conversion factor between belowground plant material mass and its volumetric contribution when calculating the contribution of organic matter to salt marsh accretion (e.g., Boyd et al., 2017; Callaway et al., 1997; Unger et al., 2016). Based on the methodology of Smith (1943) for terrestrial soils, DeLaune et al. (1983) calculated an organic matter density of 1.14 g cm^{-3} for a Louisiana marsh dominated by *S. patens*. Bricker-Urso et al. (1989) used 1.1 g cm^{-3} from DeLaune et al. (1983) as the organic density to calculate the total average sediment accumulation in Rhode Island salt marshes dominated by *Spartina alterniflora*. The factor 1.1 or 1.14 g cm^{-3} for organic sediment density has been used to calculate the organic contribution to accretion in salt marshes regardless of the plant species (e.g., Boyd et al., 2017; Callaway et al., 1997; Unger et al., 2016).

Blum et al. (2021) emphasized that root and rhizomes made a considerable contribution to surface accretion rates over as much as a decadal time frame. They also reported that vertical accretion rates in the low marsh were higher than in high marsh soils, indicating that accretion rates varied with marsh elevation and, therefore, with the species.

1.2.3 Marsh Equilibrium Model

The marsh equilibrium model (MEM) is a one-dimensional model that predicts changes in marsh surface elevation as a function of physical (e.g., mean and initial rate sea-level rise, etc.) and biological (e.g., OM decay rate, max root depth, root and rhizome shoot ratios, biomass production, etc.) inputs for long-term marsh stability and productivity with sea-level rise (Byrd et al., 2016; Morris et al., 2002). The model is based upon vegetation modulating marsh elevation in equilibrium with mean sea level, assuming there is an optimal rate of relative sea-level rise for

every marsh and an optimum elevation where a marsh plant species is most productive. The long-term prediction of MEM in a scenario of rising sea-level rates is reduced primary productivity, thus a decline of marsh elevation. However, the MEM was calibrated only to an *S. alterniflora*-dominated marsh in South Carolina, where sediment accretion was linked to primary productivity and relative sea-level rise (Morris et al., 2002).

Schile et al. (2014) emphasized the importance of including belowground mass in marsh accretion models to get more accurate marsh predictions of marsh response to the increased rates of sea-level rise expected in this century. Vegetation feedbacks in MEM have shown that for tidal inundation depths less than 80 cm, vertical accretion is dominated by root and rhizome contributions to soil volume (Cahoon et al., 2021). However, other studies reported that in MEM, there is a lack of feedback between marsh vertical accretion and the impact of higher CO₂ levels in the atmosphere, warmer temperatures, and other aspects of climate change (e.g., Kirwan et al., 2016; Langley et al., 2009) that could change the predictions. Langley et al. (2009) conducted a two-year greenhouse experiment in a Chesapeake Bay marsh, dominated by *Schoenoplectus americanus*, *S. patens* and *D. spicata* with elevated CO₂. They reported that, as CO₂ levels rose, root thickness doubled and fine root production significantly increased, contributing to an increase in marsh surface elevation. However, when marsh plants were exposed to different sea level treatments below- and aboveground production ratios were decreased after they reached their threshold of flooding tolerance at a higher sea level (Langley et al., 2013).

Preface and Contribution of Authors to Chapter 2

Chapter 2 “Potential Mass Contribution of Belowground Plant Material to Salt Marsh Soil Volume” intended to be submitted for publication in the journal *Estuarine, Coastal and Shelf Science*. As such, there will necessarily be repetition of some material from the thesis literature review and final conclusions chapters.

I am the lead author of this manuscript. I co-designed the research, developed and carried out the majority of the field work, as well as laboratory work and statistical analysis. Dr. Chmura suggested the project, assisted in the planning, design and implementation of the field and lab work, as well as editing the manuscript.

Chapter 2: Potential Mass Contribution of Belowground Plant Material to Salt Marsh Soil Volume

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2.1. Introduction

The contributions of sediment deposition and belowground growth to vertical accumulation of tidal salt marshes soils known as biophysical feedbacks (Kirwan and Megonigal, 2013) are critical to maintaining their surface elevation in equilibrium with mean sea level rise (e.g., Bricker-Urso et al., 1989; Delaune et al., 1983; Hatton et al., 1983; Morris et al., 2002; Redfield, 1972). Bricker-Urso et al. (1989) reported that the organic component of Rhode Island salt marsh soils made a greater contribution than mineral matter to vertical accretion. Callaway et al. (1997) found a statistical relationship between the vertical accretion rate and organic accumulation in five Gulf of Mexico coastal wetlands. Nyman et al. (1993) also found that organic matter (OM) made a significant contribution to soil volume in 15 salt or brackish marshes in Louisiana. Supporting the observations by previous studies, Turner et al. (2006) reported that soil OM deposition had dominated vertical accretion over the last 100 years in salt marsh soils and suggested this was due to contributions from the live roots but did not measure this component. Emphasizing the significance of roots and rhizomes inputs, Cahoon et al. (2021) reported that their contributions substantially increase soil volume, allowing for further vertical accretion of salt marshes fostering their resistance to sea-level rise.

Many researchers have simply used organic sediment mass to calculate the contribution of organic matter to salt marsh accretion (Boyd et al., 2017; Callaway et al., 1997; Unger et al., 2016), assuming a constant relationship between organic matter mass and its volumetric contribution. Delaune et al. (1983), for a *Spartina patens*-dominated marsh in Louisiana, reported that organic matter obtained a higher percentage of volume than mineral. However, water and entrapped gases occupied a greater proportion of the total soil volume. For their volumetric calculations, they utilized an organic particle density of 1.14 g cm^{-3} based on work on terrestrial soils by Smith (1943). Bricker-Urso et al. (1989) used this value (1.1 g cm^{-3}) to determine the contribution of belowground organic matter to the total average sediment volume of *Spartina alterniflora* salt marshes in Rhode Island. And, Turner et al. (2002) used 1.2 g cm^{-3} , an average of the factors reported by DeLaune et al. (1983), Craft et al. (1993) and Callaway et al. (1997), for Gulf of Mexico and western North Atlantic salt marshes. Since then, researchers have used this value as a conversion factor for their studies of belowground organic matter volume attributed to their mass (e.g., Carey et al., 2017; Craft and Richardson, 1993; Thorne et al., 2018; Wang et al., 2017).

Studies suggest that salt marsh accretion varies with root growth and organic matter accumulation. Blum et al. (2021) observed the contribution of roots to surface elevation change varied with marsh elevation and species in a Virginia salt marsh. Ford et al. (1999) suggested that seasonal increases in belowground biomass production may have contributed to the uplift of the marsh soil surface, based on the faster rate of soil elevation change. Turner et al. (2006) found that belowground biomass was greater than dead material, thus making a greater contribution to vertical accretion.

Although widely employed, the assumption that 1 g of belowground mass has a volume of 1.1 cm^3 has not been tested to determine if it is an accurate predictor of the volumetric contribution of roots, rhizomes, or dead material. In this study, we test the hypothesis that all components of belowground plant material have the same mass/volume relationship of 1.1 g cm^{-3} . We examine the relationship of the mass and volume of each component of belowground plant material in soils from a salt marsh on the St. Lawrence River Estuary (Quebec), where the dominant vegetation is generally characteristic of salt marshes on the NW Atlantic. We compare the volume and mass of living roots, rhizomes, and dead material of *Cyperus esculentus*, *S. alterniflora*, *S. patens*, and *Phragmites australis*, as well as an aboveground standing crop to the belowground plant material of the latter three.

2.2. Methods

2.2.1. Study Site

The study site ($47^{\circ}22'34''\text{N}$, $70^{\circ}03'21''\text{W}$) is located on the lower shore of the St. Lawrence estuary, at la Pocatière, approximately 110 km northeast of Quebec City (Figure 2.1). In this portion of the estuary, waters are mesohaline, and the tide is mixed semidiurnal and with an amplitude of 5 m (Fisheries and Oceans Canada, 2020). The daily average temperature varies from -12.4°C in winter and 18.3°C in summer, and the average annual precipitation is 996 mm (Environment Canada, 2020).

The vegetation here is typical of salt marshes in the NW Atlantic (Duncan and Duncan, 1987; Roland and Smith 1969; Thompson, 1991; Wigand et al., 2012). *Spartina alterniflora* dominates the vegetation in the low marsh with a minor occurrence of *Salicornia europaea*. At elevations immediately above the *S. alterniflora*, *S. patens* dominate with occasional patches of

Lysimachia maritima, *Plantago maritima*, *Triglochin maritima*, *Schoenoplectus bolbosonous*, and *Salicornia europaea*. At higher elevations, an invasive form of *P. australis* (hereafter referred to as *Phragmites*) has been replacing *S. patens* (Gu et al., 2020). Here, we also found some patches of *L. maritima*, *S. europaea* and *S. patens*.

2.2.2. Field Sampling

Fieldwork took place in late August 2020. Circular plots (25 cm-diameter) were located in conjunction with a greenhouse gas flux study (Comer-Warner et al., *in prep*). Plots were located to ensure a consistent representation of species within each of three vegetation zones: *S. alterniflora*, *S. patens*, and the *Phragmites* transition zone. We defined the transition zone as locations with ~ 20% *Phragmites* cover within the *S. patens* (hereafter, Phrag/Spat zone). We harvested all standing biomass within each plot. We sampled belowground biomass by collecting a 30 cm deep soil core in the middle of each plot using a 54 mm diameter Dutch gouge corer. We collected 10 cores in each zone, and each core was sectioned in the field at intervals of 0-15 and 15-30 cm, resulting in a total of 60 soil samples. Samples were kept chilled until analysis.

2.2.3. Laboratory Analyses

Aboveground vegetation was washed and sorted by species. The soil sections were washed over a 1 mm sieve to retain living roots, rhizomes and dead material. The belowground plant material was sorted into the dead, live root, and live rhizome fractions. Live material was identified by its often light color, turgidity and was usually floating, while dead material sunk to the bottom of the water-filled basin. Live rhizomes were sorted by species using the key of

Niering et al. (1977). Roots were removed from live rhizomes. The volume of the three belowground plant components, live roots, live rhizomes and dead material, was measured by water displacement in a graduated cylinder with a precision of 5 ml. This method compares well and is more efficient than other direct methods such as computer-aided tomography (CT) imaging (Blum and Davey, 2013) and WinRHIZO root-scanning software (Pang et al., 2011). However, CT imaging can pick up fine roots that may not be caught on a 1 mm sieve (Blum and Davey, 2013). All above- and belowground plant material was dried at 60°C to constant weight for mass.

2.2.4. Statistical Analyses

Data for mass and volume were analyzed statically using IBM SPSS. We used the Shapiro-Wilk test to verify normality and the Levene test to assure homoscedasticity of variances ($p < 0.05$ for both tests). Analysis of Variance (ANOVA, Tukey's test) was performed to test for differences in above- and belowground mass (live roots, rhizomes and dead material) between vegetation zones at each soil depth (0-15 cm and 15-30 cm). Linear regression analysis was used to determine the relationship between volume and mass, and for all, the intercept was set at zero.

2.3. Results

2.3.1. Aboveground Biomass

The aboveground biomass of all species in the three vegetation zones is reported in Table 2.1. The Phrag/Spat zone had the highest total aboveground biomass, followed by the *S. patens*, and *S. alterniflora* zone. *Spartina patens* in the Phrag/Spat zone had the highest aboveground biomass and was significantly different from the rest of the species. In all the zones, the forbs *L. maritima* and *S. europaea* had considerably lower belowground biomass than other species.

2.3.2. Belowground Mass

In the upper 15 cm of soil (Figure 2.2a), *C. esculentus* and *Phragmites* had significantly lower rhizome biomass ($p \leq 0.001$) than other species, and *S. alterniflora* had the highest rhizome biomass. The root biomass of *S. patens* in the *S. patens* zone and *S. alterniflora* was similar and significantly higher than that of other species ($p \leq 0.001$). In the 0-15 cm soil sections, rhizomes of all species had higher biomass than their roots except for *S. patens* in the *S. patens* zone. In contrast, the root biomass of *S. patens* in the *S. patens* zone was almost three times greater than in the Phrag/Spat zone. The dead mass was greatest in the Phrag/Spat zone (1449 g m⁻²), although this difference was not significant compared to the other vegetation zones. The total mean root biomass of the three vegetation zones together contributed only 30% to the total belowground plant material, and rhizome biomass (35.5%) contributed slightly more than the dead material (35%). *Spartina alterniflora* had the highest mass where its roots and rhizomes independently were significantly different ($p \leq 0.001$), but not its dead mass.

In the 15-30 cm soil section, *C. esculentus* and *Phragmites* had the lowest live belowground biomass (Figure 2.2b). However, only the biomass of *C. esculentus* rhizomes in the *S. patens* zone was significantly lower ($p \leq 0.05$) than the other species. *Spartina patens* in the Phrag/Spat zone had the highest root biomass (1203 g m⁻²), but it was not significantly different from the *S. patens* zone (1106 g m⁻²). *S. patens* species had the largest root biomass of all species. Except for Phrag/Spat zone, the total biomass in the rest of the vegetation zones was double that of the dead material. In this deeper soil interval, the total root biomass had the larger portion of the total belowground plant material in all vegetation zones, followed by the dead material then rhizome biomass. The mass of dead material of the three zones combined

comprised 35% of the total belowground mass. The *S. alterniflora* zone had the highest mean dead belowground biomass, but this difference was not statistically significant with the other two zones.

The proportion of belowground plant material varied in the two soil intervals. In the upper soil interval, the rhizomes had the highest averaged contribution (36%), and root biomass represented 39% of the mass of the total belowground plant material in the 15–30 soil interval. Within the 30 cm depth of soil sampled, the total live MOM biomass was double that of the dead material. The highest total mass of belowground plant material occurred in the Phrag/Spat zone, and the least was in the *S. patens* zone. The total belowground mass was between 5 to 10 times greater than the total aboveground biomass in all the three vegetation zones and was greatest in the Phrag/Spat zone. In addition, the total living roots and rhizomes mass constituted more than 50% of the total belowground mass of plant material in all species.

2.3.3. Belowground MOM Volume

Volumes generally followed a similar pattern in all three vegetation zones, with the greatest volume contributed by dead material and the least by rhizomes of most species (Figure 2.3). Apart from *C. esculentus* whose tubers and root volumes were minor constituents in both soil depths, *Phragmites* also had the lowest rhizome and root volume. Living roots and rhizomes volumes of both species were significantly ($p \leq 0.05$) lower than *S. alterniflora* except for roots in the lower soil interval where there were no significant differences. The dead material constituted a greater portion of the belowground mass volume in the three vegetation zones, except for roots in the *S. patens* zone within the lower interval, but the difference was not significant.

Figure 2.3a shows the volumes of belowground plant material in the upper 15 cm. The mean rhizome volume of *S. alterniflora* in all cores within 15 cm (26 cm³ of the auger volume of 344 cm³) was significantly higher ($p \leq 0.001$) than the other species. Except for *Phragmites* and *C. esculentus*, root volumes were higher than that of rhizomes. Although *S. alterniflora* had the highest roots volume (34 cm³), the difference was only significant ($p \leq 0.05$) with upper marsh species in the Phrag/Spat zone and *C. esculentus* ($p \leq 0.001$) in the *S. patens* zone. Dead material contributed substantially to belowground volume. The highest volume of dead MOM was in the Phrag/Spat zone (42 cm³), following by the *S. alterniflora* (40 cm³) and *S. patens* (26 cm³) zones, but the differences were not significant. Figure 2.3b shows the volumes of belowground plant material in the lower soil section where there was more minor variation in volumes of rhizomes among the different species.

In La Pocatière salt marsh, the total volume of belowground plant material, i.e., volume of live roots, rhizomes and dead material varied with species zone and depth. The total belowground plant material volume in the top 15-cm of the *S. alterniflora* zone was nearly twice that in the lower interval, while in the Phrag/Spat zone, the total living volume of *S. patens* in the deeper section was 1.3 times that of the upper section, was due to the recent invasion of *Phragmites* and colonization of the upper soil layer. In the lower soil interval, the total belowground plant material volume of Phrag/Spat zone was 1.13 greater than the first 15 cm, representing 43% of the 15 cm soil depth total organic volume (185 cm³). However, the total mean volume of live roots, rhizomes and dead material (230 cm³) in all zones was more concentrated in the upper soil interval.

We calculated the volumetric contributions of total live roots and rhizomes to the total soil volume and found that they contributed >65% to the soil volume within the 30-cm of soil

examined. Generally, the volume contribution of living roots and rhizomes was greater in the upper interval (0-15 cm) than in the lower one (15-30 cm). The exception is the living roots and rhizomes of *S. alterniflora* that contributed more to the total volume in the upper 15 cm than the lower section. The dead material decreased with depth.

2.3.4. Mass-Volume Relationship of the Live Roots, Rhizomes and Dead Material

A linear regression of the mass of living roots and rhizomes and dead material of all samples revealed that mass is a significant predictor of volume (Figure 2.4, Table 2.2). The relationship improves if the analysis is restricted to dead OM or total live belowground components by species, except for *S. patens* (Figure 2.5, Table 2.1).

Generally, rhizome mass (and tubers for *C. esculentus*) had a stronger relationship to its volume than roots (Figure 2.5). *Cyperus esculentus* and *S. alterniflora* rhizomes had a strong relationship between their mass and volume with an R^2 of 98% and 95%, respectively. *Spartina patens* rhizome mass explained slightly less variability (82%) in volume than *Phragmites* (93%).

The degree to which root biomass explained variability in its volume also varied with species. The relationship between *C. esculentus* root mass and volume was not as strong (70%) as with rhizomes. The mass of *S. alterniflora* roots explained the greatest variability in their volume (96%), and the mass of *S. patens* roots explained less (72%).

2.4. Discussion

Connor and Chmura (2000) examined seasonal patterns of belowground mass of *S. patens* and *S. alterniflora* at Dipper Harbour, on the Bay of Fundy, where climate and growing season are similar to that on the St. Lawrence estuary. Our average total belowground plant material of

S. patens over the 30 cm depth (5246 g m^{-2}) is comparable to the $6587 \pm 1602 \text{ g m}^{-2}$ reported by Connor and Chmura at the end of the growing season. However, the contribution of living and dead mass of *S. patens* to the total belowground mass of plant material was different. For example, at la Pocatière, living roots and rhizomes constituted 70% of the total belowground mass, while they were only 41% on the Bay of Fundy. The dead material had a higher contribution, 59%, on the Bay of Fundy, while at La Pocatière the contribution was 30%. In our study site, *S. alterniflora* dead mass was 2.3 times higher than in the Bay of Fundy salt marsh. Nevertheless, roots and rhizomes of *S. alterniflora* represented more than 60% of the total belowground mass in both salt marshes.

Our results refute the hypothesis that all components of belowground plant material have the same mass/volume relationship (1.1 or 1.14 g cm^{-3}) as assumed in many other studies (e.g., Boyd et al. 2017; Unger et al. 2016). The three species we examined had a different coefficient in the predictive equation for the relationship between live roots, rhizomes, and dead material mass and volume. The total live plant material volume/mass relationships we measured are 8.1, 7.2 and 5.1 times higher than the assumption of 1.1 for *S. alterniflora*, *S. patens*, and *Phragmites*, respectively.

Callaway et al. (1997) assumed the relationship of 1.14 g cm^{-3} to examine the relationship of OM accumulation to vertical soil accretion rates in *S. alterniflora* marshes on the Gulf of Mexico. From their data (see their figure 3a) for Aransas and San Bernard National Wildlife Refuges of soil profiles up to 50 cm depth graph (see their figure 3a), we calculated the volumetric contribution of *S. alterniflora* roots and rhizomes to the soil using the relationship we estimated. For example, within the upper 30 cm of soil in the low marsh, the organic content ranged from 7 to 21% multiplied by the bulk density would indicate an OM volume of ~7 to

15%. The volume of mineral matter ranged from ~20 to 45%, based on a mineral density of 2.61 g cm⁻³. The remainder (~50-75%), and the majority, of the core volume, was determined to be pore space. Using our relationship of 8.9 g cm⁻³ for the volumetric contribution of live belowground *S. alterniflora* material to the soil, we calculate that it would have roughly contributed from ~57% to 90% and ~40% to 60% for Aransas and San Bernard National Wildlife Refuge low marshes, respectively. These OM volumetric results are in the range of the OM plus pore space at both their study sites.

Our factor of 8.9 g cm⁻³ for *S. alterniflora* OM contribution to the total soil volume, including its water and pore space, can be applied to other soil marshes. For example, on the mid-Atlantic coast of the US, Unger et al. (2016) used a 1.1 g cm⁻³ factor calculating an average OM volume of *S. alterniflora* less than 10% through a depth of 50 cm in six salt marshes with water and pore space ranging from ~60 to 85%. Using 8.9 g cm⁻³, we calculated a total OM volumetric contribution from ~70 to 90%, similar to the total of OM volume plus the pore space reported by Unger et al. (2016). In comparison, Boyd et al. (2017) reported the volume of OM as between 7 and 18%, with 12 to 80 % of water-filled pore space for *S. alterniflora* in the Delaware Bay marshes. At La Pocatière, the average OM volume in *S. alterniflora* was 21 cm³. If we used the 1.1 factor would have provided a result of 2.53 cm³, underestimating the actual volume.

Morris et al. (2016) examined organic matter density in soils from sediment bulk density as a function of loss-on-ignition (LOI) in soils from salt marshes on the west and east coasts of the US. For their marsh accretion model, they used 0.085 ±0.001 g cm⁻³ for the bulk density of organic matter Using the factor of Morris et al., Gu et al. (2020) estimated *Phragmites*'s roots and rhizomes contribution to soil accretion and compared them with their mass/volume ratios

calculations including decomposition. Gu et al. (2020) reported that the 0.085 g cm^{-3} factor overestimated their results for *Phragmites* (estimated age 6-12 years) contribution to soil accretion at La Pocatière marsh by an average of 1.43 cm y^{-1} .

Live root and rhizome dynamics are crucial for marsh elevation adjustment and are part of the ecogeomorphic feedbacks as marshes adaptation to sea-level changes (Kirwan et al., 2016). For example, Blum et al. (2021) reported that the elevations of the low, middle and high marsh zones varied over a 20-year-old salt marsh in Virginia, where roots contributed significantly to these increases. In *S. patens* and *Schoenoplectus americanus* marshes in the Chesapeake Bay, Kirwan and Guntenspergen (2012) reported a positive relationship between mass of roots and rhizomes and flooding regulated the salt marsh response to sea-level rise through soil organic accumulation. Using species-specific factors for living roots and rhizomes will provide more accurate predictions of vertical accretion as rapid responses to sea-level change.

The Marsh Equilibrium Model (Morris et al. 2002) predicts salt marsh surface elevation and biomass production over time in response to changes in sea level. It does not include root and rhizome volumetric contributions; instead, it is based on the mass of recalcitrant material. However, the immediate response of soil elevation to sea level rise is dependent upon the volume of roots and rhizomes produced and based upon our results, the inclusion of only the mass of recalcitrant material would probably not reflect the elevation change of the salt marsh soil surface over the decadal scale. It is over this time frame that most assessments of salt marsh resiliency are made. For example, Chmura et al. (2001) reported that 15 cm of soil likely accumulates over 30 years in Eastern Canadian salt marshes. Thus, our higher conversion factors indicate that, despite decomposition, the uncompressed and labile carbon contributes to soil volume for at least 30 years.

2.5. Conclusions

Our study at La Pocatière demonstrates that the mass and volume of belowground plant material (living roots, rhizomes and dead material) in salt marsh soil are strongly correlated. The relationship of total belowground plant material volume to mass has a slope about 9.5 times greater than the relationship of 1.1 g cm^{-3} conventionally used. Values of 1.1 and 1.14 for organic matter density do not reflect the space occupied by the living roots and rhizomes, thus considerably underestimate the contribution of belowground growth to marsh accretion rates over decadal periods. Assuming a conversion factor of 1.1 for organic matter density underestimates the volumetric contribution of live belowground plant material to marsh accretion. A general conversion factor of 8.2 would more accurately indicate the volumetric contribution. However, the contribution of each component of the belowground plant material to salt marsh soil volume varies with species. When the dominant marsh species is known, the volume of live belowground of *Phragmites*, *S. patens*, *C. esculentus* and *S. alterniflora* would be better predicted by the species' specific factors 5.6, 7.9 5.6 and 8.9, respectively.

2.6. Tables

Table 2.1. Average (\pm sd) aboveground biomass (g m^{-2}) harvested in 0.05 m^2 plots in three vegetation zones. *indicates a significant difference among species in a zone ($p < 0.001$).
n=number of plots per vegetation zone, species.

Species	Vegetation zones		
	<i>Phragmites/S. patens</i> n=10	<i>S. patens</i> n=10	<i>S. alterniflora</i> n=10
<i>Phragmites</i>	404 \pm 148.4*	0	0
<i>S. patens</i>	901.0 \pm 220.8*	651.0 \pm 265.6*	0
<i>L. maritima</i>	42.0 \pm 33.7	45.0 \pm 30.9	0
<i>S. europaea</i>	0.3 \pm 0.3	3.0 \pm 5.8	2.0 \pm 1.9
<i>S. alterniflora</i>	0	0	622.0 \pm 192.3*
Total aboveground	1347.3 \pm 403.2	699.0 \pm 302.3	624.0 \pm 194.2

Table 2.2. Belowground plant material mass as a predictor of volume within 30-cm soil depth.

All relationships are significant at $p < 0.001$ with the intercept set at zero. n= the number of samples in which roots and rhizomes were found.

Species (only live roots and rhizomes)	n	R ²	equation
all	185	0.78	$y = 8.2x$
<i>Phragmites</i>	35	0.86	$y = 5.6x$
<i>S. patens</i>	80	0.68	$y = 7.9x$
<i>C. esculentus</i>	30	0.97	$y = 5.6x$
<i>S. alterniflora</i>	40	0.94	$y = 8.9x$
Vegetation zones (only dead material)	n	R ²	equation
all	60	0.93	$y = 13.8x$
<i>Phragmites/S. patens</i>	20	0.92	$y = 15.2x$
<i>S. patens</i>	20	0.94	$y = 10.9x$
<i>S. alterniflora</i>	20	0.97	$y = 13.3x$

2.7. Figures

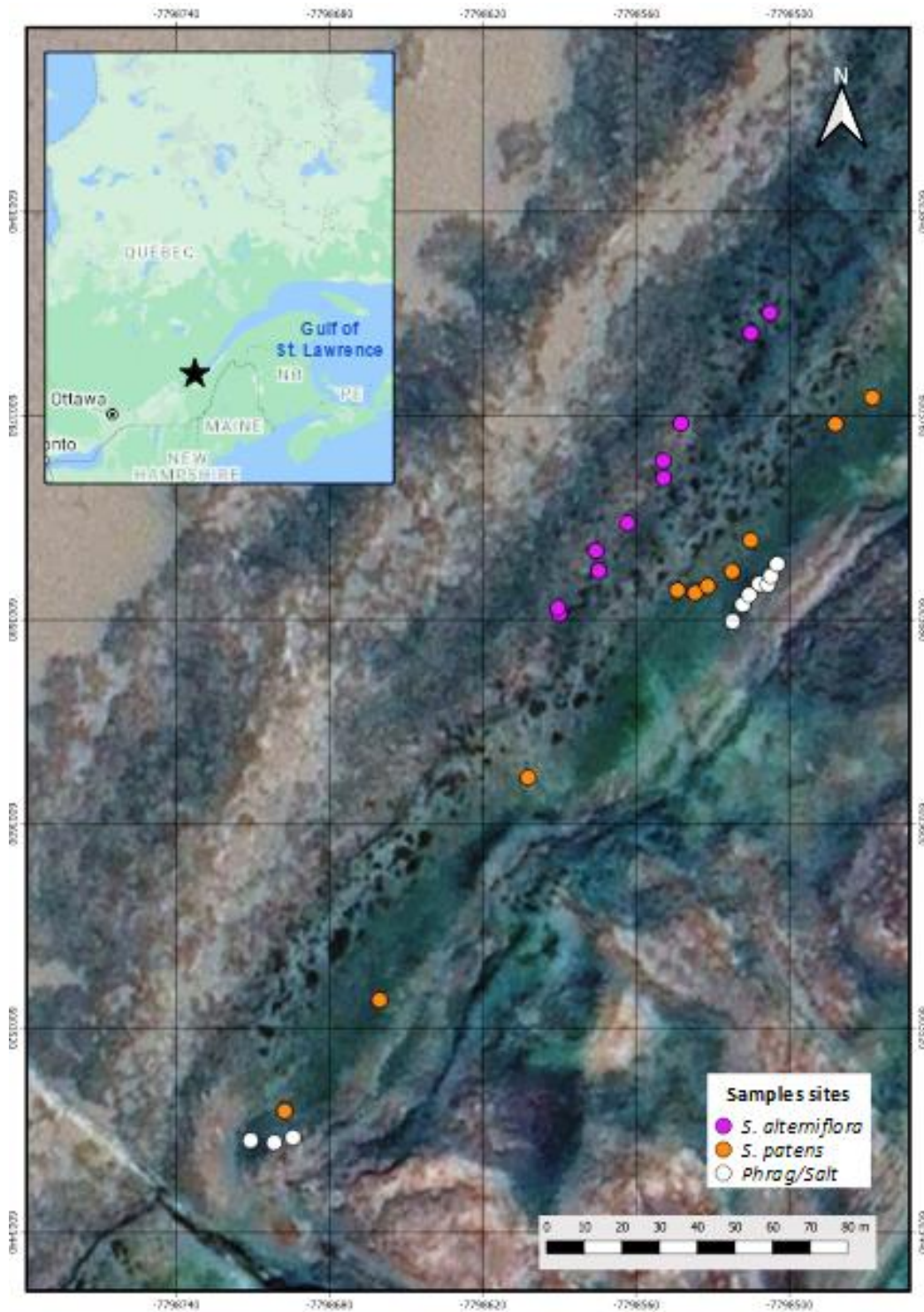


Figure 2.1. Inset map showing the location of the La Pocatière salt marsh on the St. Lawrence River Estuary, Quebec, Canada. Colored dots indicate the location of sample plots. Source: Google Earth.

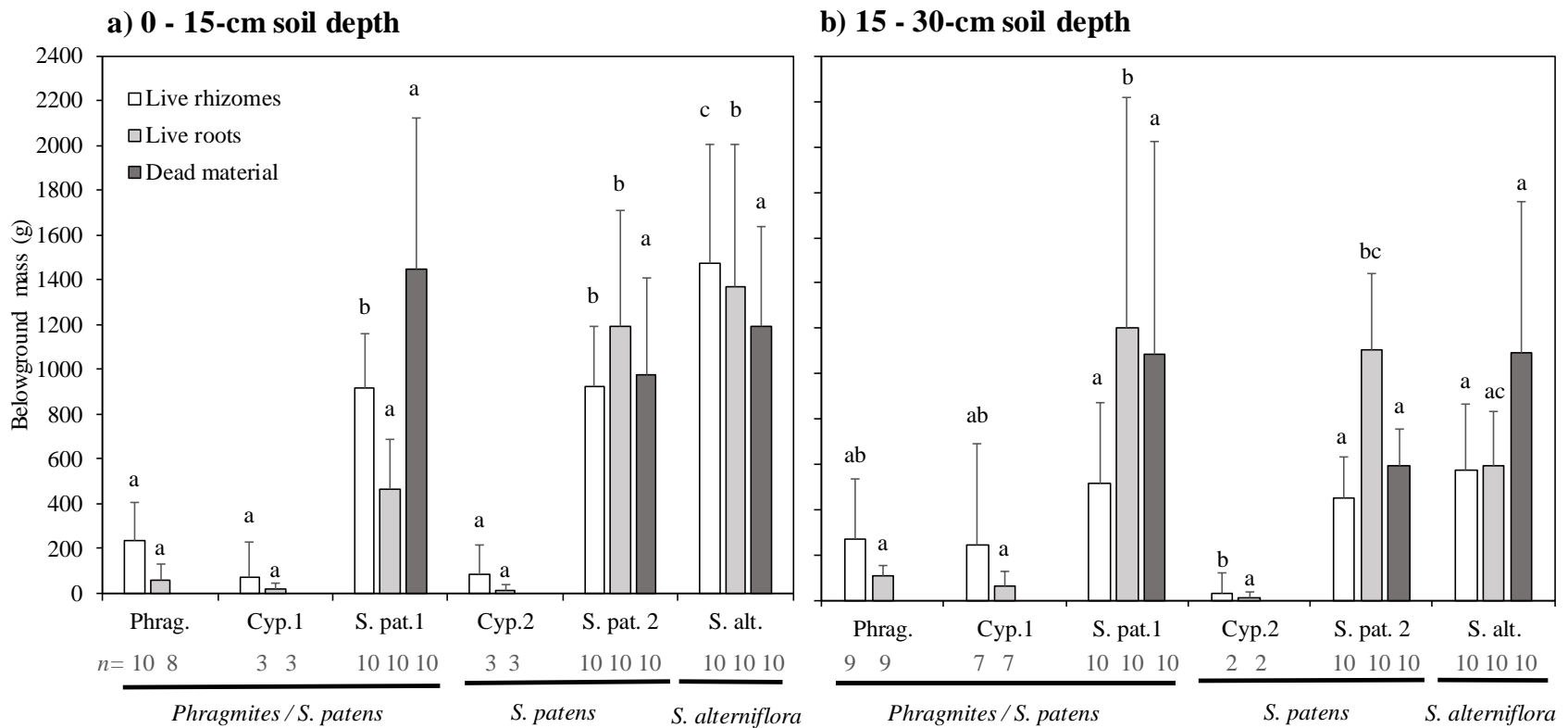


Figure 2.2. Average belowground mass (\pm sd) in the three vegetation zones. a) upper 15 cm soil interval and b) lower 15–30 cm soil interval. Means labeled with the same letters are not significantly different at $p \leq 0.05$. n indicates the number of plots in which the species' plant material was found.

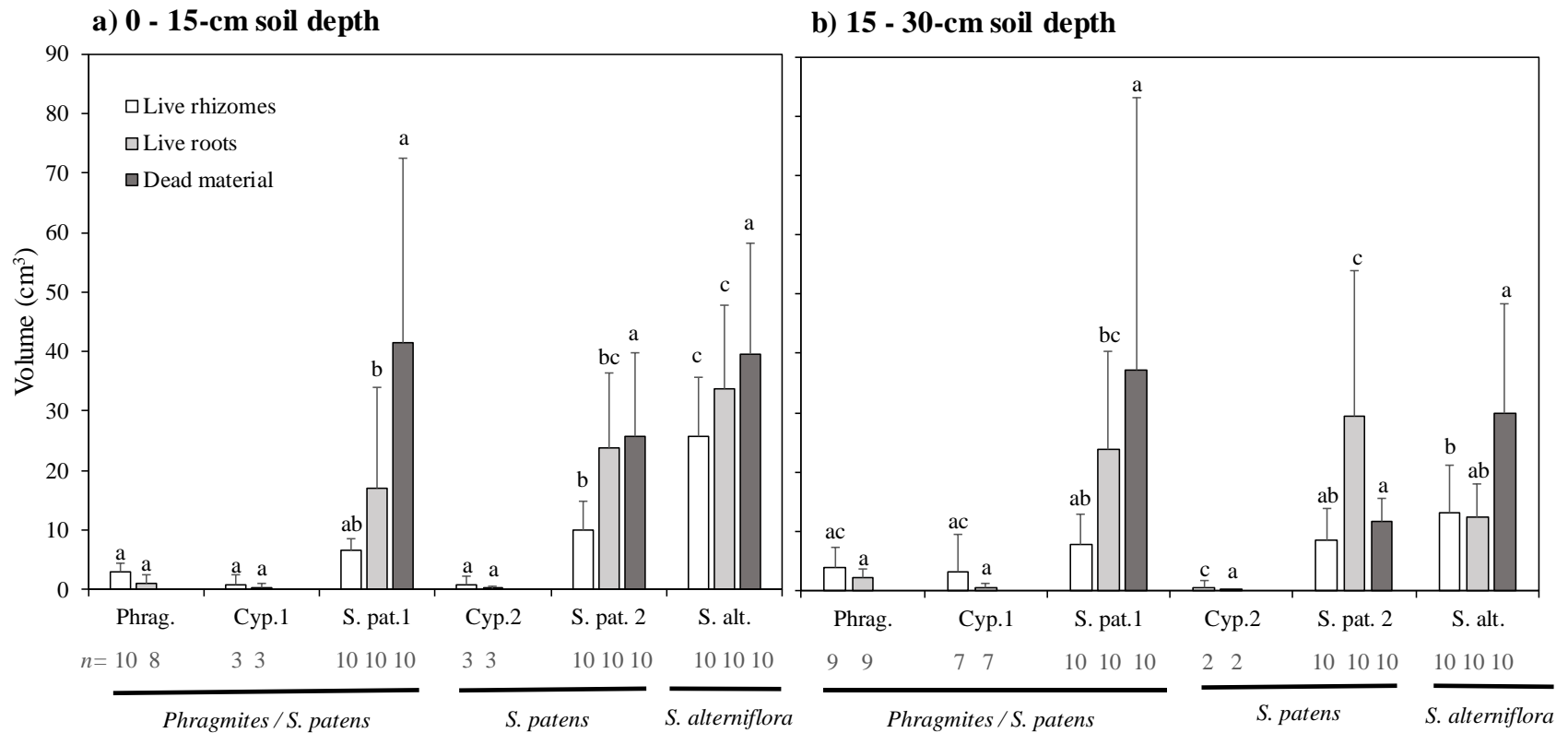


Figure 2.3. Average (\pm sd) belowground plant material volume (within a volume of 344 cm³) in the three vegetation zones. a) upper 15 cm soil interval and b) the 15–30 cm soil interval. Means labeled with the same letters are not significantly different at $p \leq 0.05$. n indicates the number of plots in which a species' plant material was found.

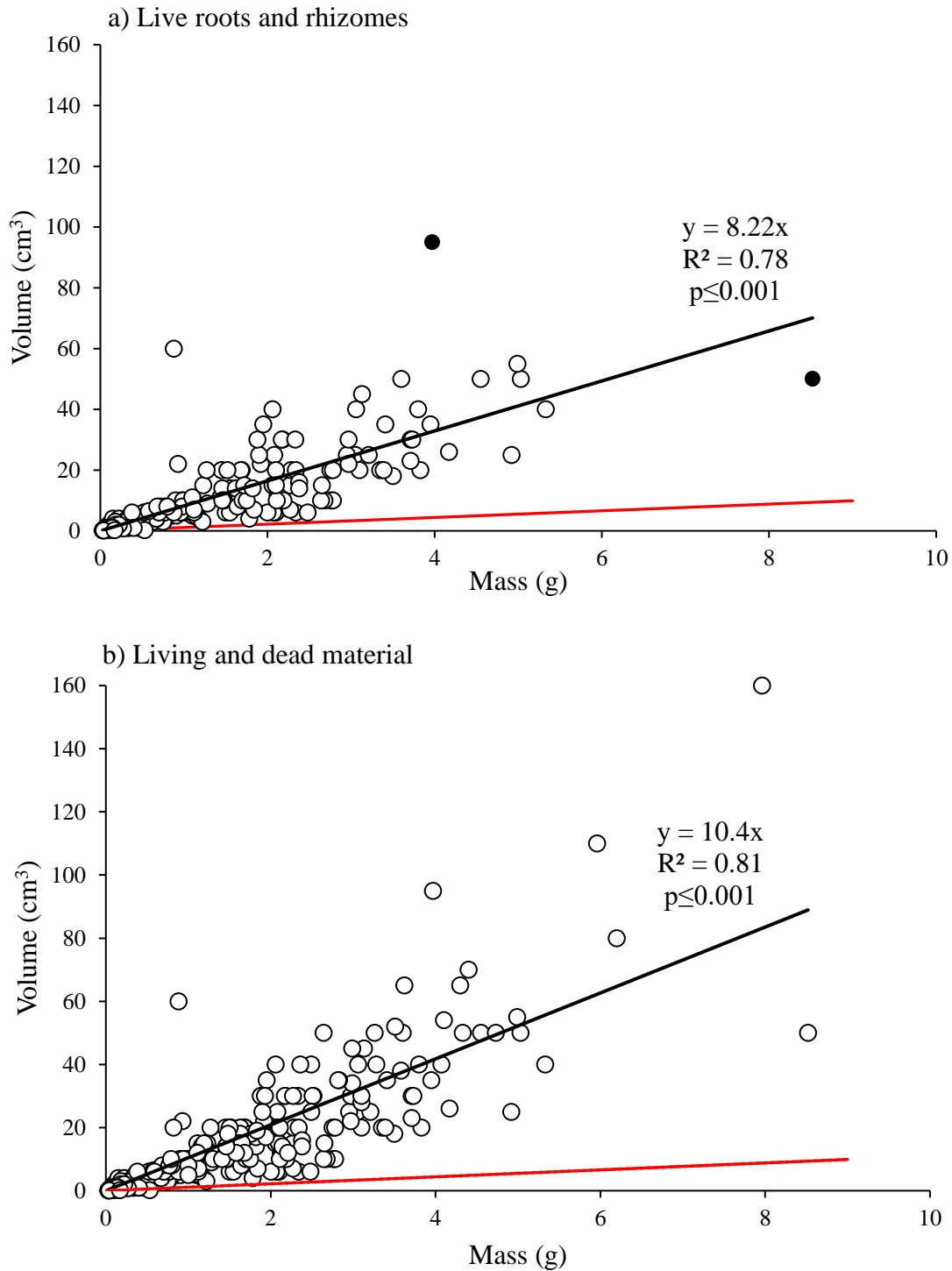


Figure 2.4. Relationship between volume and dry weight for all belowground; a) live roots and rhizomes, b) living and dead material. Solid black circles in a) represent outliers, which when removed gives a similar $R^2=0.81$, but a predictive equation of $y=8.1x$. The red line represents the relationship if 1.1 g of belowground plant material had the volume of 1 cm⁻³.

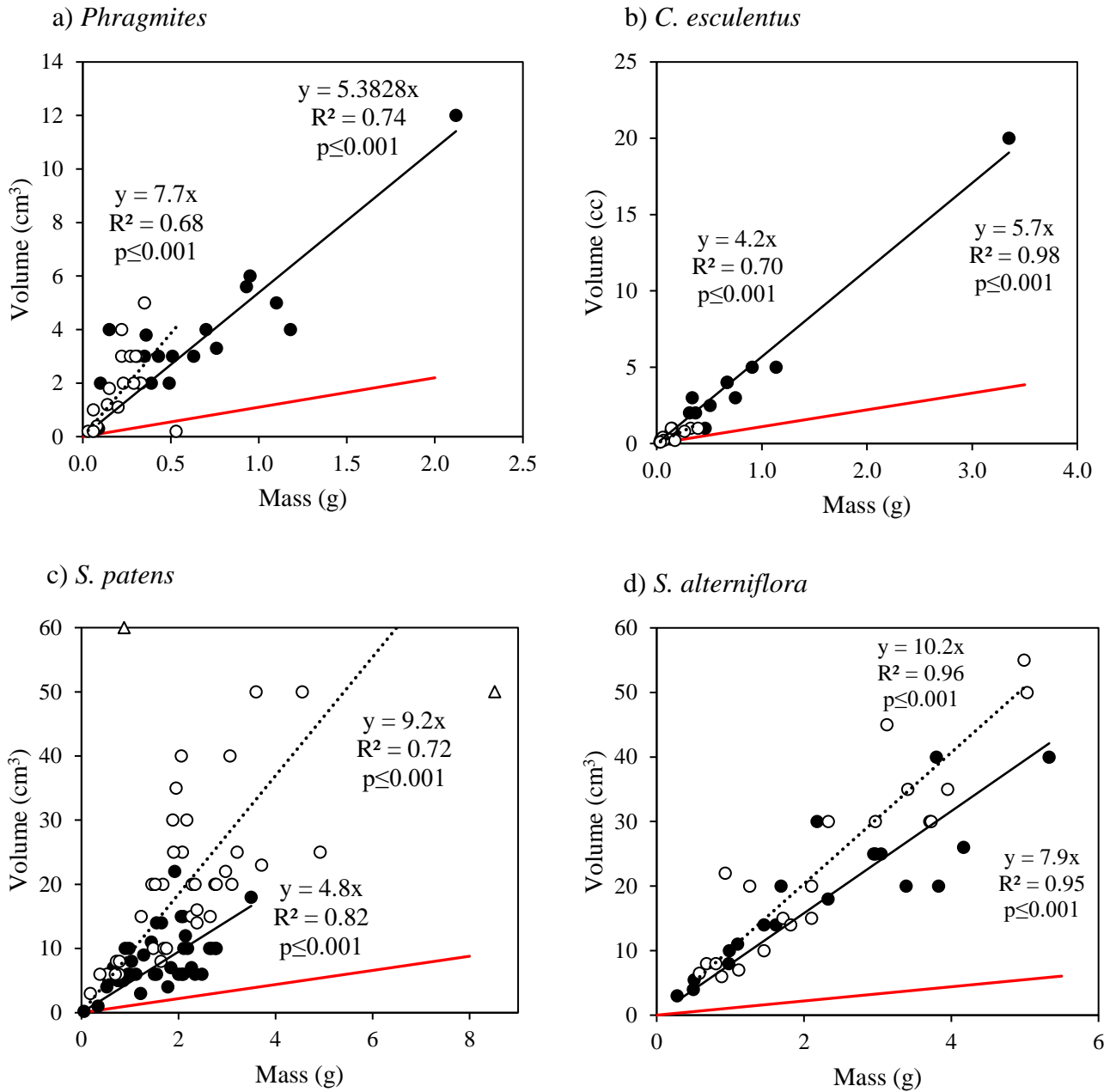


Figure 2.5. Relationship of mass and volume of live roots and rhizomes for each species; a) *Phragmites*, b) *C. esculentus*, c) *S. patens*, and d) *S. alterniflora*. Filled circles represent rhizomes and the solid line is the trendline for the regression. Open symbols represent roots and the dashed line is the trendline for the regression. The triangle represents an outlier for roots, which when removed an $R^2=0.79$ and predictive equation of $y=10.1x$. The red line represents the relationship if 1.1 g of belowground plant material has the volume of 1 cm³.

Chapter 3: Summary and Final Conclusions

Vertical soil accretion, required for salt marshes to keep pace with sea-level rise, is mainly driven by belowground plant material accumulation (i.e., live roots and rhizomes as well as dead material).

This thesis tests the widely held assumption that 1 g of belowground OM has a volume of 1.1 cm³ in any species or marsh, a relationship that excludes the role of roots and rhizomes in soil volume. Thus, a conversion factor of 1.1 for organic matter density underestimates the volumetric contribution of live belowground organic matter to marsh accretion. The results of this thesis demonstrate that the mass and volume of organic matter in salt marsh soil are strongly correlated. The relationship of total belowground plant material volume to mass has a slope about 9.5 times greater than the relationship of 1.1 g cm⁻³ conventionally used.

In this thesis, the volume of belowground plant material was measured using water displacement in a graduated cylinder. Because most roots and rhizomes have a cut end, one of the limitations was that part of the pore space would be filled by water. Thus, the conversion factor values calculated may be underestimated. However, it has been shown that this method compares well with other direct techniques, such as computer-aided tomography (CT) imaging and WinRHIZO root-scanning software.

Another of the limitation of the research was the fact that in our field site the *S. patens* was found in competition with invasive *P. australis*. This invasive's encroachment might affect the results for *S. patens* in Phrag/Spat zone.

The inclusion of only the mass of recalcitrant material, based on my study, would most likely not capture the elevation change of the salt marsh soil surface on a decadal timeframe. A

general conversion factor of 8.2 would more accurately indicate the volumetric contribution. However, the contribution of any belowground plant material component to salt marsh soil volume varies with species. When the dominant marsh species is known, the volume of live roots and rhizomes of *Phragmites*, *S. patens*, *C. esculentus*, and *S. alterniflora* would be better predicted by the species-specific factors of 5.6, 7.9 5.6 and 8.9, respectively.

Future studies should examine the mass/volume relationships for dominant species of salt marshes on other coastlines. For example, on the west coast of the United Kingdom and the Baltic Sea coast marsh vegetation includes no native *Spartina* but other graminoid species such as *Festuca rubra*, *Agrostis stolonifera*, *Carex paleacea*, *Juncus bufonius*, *Desmoschoenus botanica*, and *Scirpus* spp. which might have different mass/volume relationships. More importantly, the annual herbaceous forbs (*Salicornia* and *Suaeda*) of the marshes on the Alaska coast are likely to contribute less to soil volume and have different belowground mass / volume relationships as compared to graminoids.

It would be an interesting expansion of the Marsh Equilibrium Model (MEM) to incorporate species-specific volume to mass relationships of belowground production as these would be valid over decadal scales. Since the dominant salt marsh species vary globally, research on mass/volume relationships of additional species would be valuable for further development of the MEM and understanding of marsh vertical accretion in general.

Literature Cited

- Adame, M.F., Santini, N.S., Tovilla, C., et al., 2015. Carbon stocks and soil sequestration rates of tropical riverine wetlands. *Biogeosciences* 12(12), 3805–3818.
<https://doi.org/10.5194/bg-12-3805-2015>
- Ampuero, W., Aponte, H., 2020. Estimación del carbono almacenado en un juncal de *Schonoeplectus americanus* en el humedal costero Los Pantanos de Villa (Lima-Perú). *Arnaldoa* 27(1), 267-282
- Barbier, E.B., Hacker, S.D., et al., 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81(2), 169–193.
- Blum, M.J., Bando, K.J., Katz, M., Strong, D.R., 2007. Geographic structure, genetic diversity and source tracking of *Spartina alterniflora*. *Journal of Biogeography* 34(12), 2055–2069.
- Blum, L.K., Davey, E., 2013. Below the salt marsh surface: Visualization of plant roots by computer-aided tomography. *Oceanography* 26(3), 85–87.
<http://dx.doi.org/10.5670/oceanog.2013.49>.
- Blum, L.K., Christian, R.R., Cahoon, D.R., Wiberg, P.L., 2021. Processes influencing marsh elevation change in low- and high-elevation zones of a temperate salt marsh. *Estuaries and Coasts* 44, 818–833. <https://doi.org/10.1007/s12237-020-00796-z>
- Boyd, B.M., Sommerfield, C.K., Eelsey-Quirk, T., 2017. Hydrogeomorphic influences on salt marsh sediment accumulation and accretion in two estuaries of the U.S. Mid-Atlantic coast. *Marine Geology* 383, 132–145. <https://doi.org/10.1016/j.margeo.2016.11.008>
- Brady, N.C., 1984. *The nature and properties of soils*. 9th ed. New York, Macmillan.

- Bricker-Urso, S., Nixon, S.W., Cochran, J.K., Hirschberg, D.J., Hunt, C., 1989. Accretion rates and sediment accumulation in Rhode Island salt marshes. *Estuaries* 12, 300–317.
<https://doi.org/10.2307/1351908>
- Brouillet et al., 2010. *Cyperus esculentus* Linnaeus in VASCAN, the Database of Vascular Plants of Canada. <http://data.canadensys.net/vascan/taxon/5211> (accessed on 2021-03-04)
- Byrd, K.B., Windham-Myers, L., Leeuw, T., Downing, B., Morris, J.T., Ferner, M.C., 2016. Forecasting tidal marsh elevation and habitat change through fusion of Earth observations and a process model. *Ecosphere* 7, 1–27. <https://doi.org/10.1002/ecs2.1582>
- Cahoon, D.R., McKee, K.L., Morris, J.T., 2021. How plants influence resilience of salt marsh and mangrove wetlands to sea-level rise. *Estuaries and Coasts* 883–898.
<https://doi.org/10.1007/s12237-020-00834-w>
- Callaway, J.C., DeLaune, R.D., Patrick, W.H., 1997. Sediment accretion rates from four coastal wetlands along the Gulf of Mexico. *Journal of Coastal Research* 13, 181–191.
- Carey, J.C., Moran, S.B., Kelly, R.P., Kolker, A.S., Fulweiler, R.W., 2017. The declining role of organic matter in New England salt marshes. *Estuaries and Coasts* 40, 626–639.
<https://doi.org/10.1007/s12237-015-9971-1>
- Chapman, V.J. 1960. Salt marshes and salt deserts of the world. Leonard Hill Books, London, 392 pp.
- Chapman, V.J., 1976. Coastal vegetation (2nd ed). Pergamon Press, Oxford, UK. 300 pp.
- Chmura, G.L., Helmer, L.L., Beecher, C.B., Sunderland, E.M., 2001. Historical rates of salt marsh accretion on the outer Bay of Fundy. *Canadian Journal of Earth Sciences* 38(7), 1081–1092. <https://doi.org/10.1139/e01-002>

- Chmura, G.L., and Hung, G.A., 2004. Controls on salt marsh accretion: a test in salt marshes of eastern Canada. *Estuaries* 27(1), 70–81.
- Chmura, G.L., 2009. Tidal Salt Marshes. In: Laffoley, D.d'A. and Grimsditch, G. (eds). *The management of natural coastal carbon sinks*. IUCN, Gland, Switzerland, pp. 53.
- Chmura, G.L., Burdick, D.M., Moore G.E, 2012. Recovering salt marsh ecosystem services through tidal restoration. In: Roman, C.T., Burdick, D.M. (Eds.), *Tidal marsh restoration: a synthesis of science and management*. Island Press, Washington, DC, pp. 233-521.
<https://doi.org/10.5822/978-1-61091-229-7>
- Church, J.A., Clark, P.U., Cazenave, A., Gregory, J.M., et al., 2013. Sea Level Change. In: Stocker, T.F., D. Qin, D., Plattner, G.K., et al., (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Connor, R., Chmura, G.L., 2000. Dynamics of above- and belowground organic matter in a high latitude macrotidal saltmarsh. *Marine Ecology Progress Series* 204, 101–110.
<https://doi.org/10.3354/meps204101>
- Costanza, R., Kubiszewski, I., De Groot, R., et al., 2014. Changes in the global value of ecosystem services. *Global Environmental Change* 26(1), 152–158.
<https://doi.org/10.1016/j.gloenvcha.2014.04.002>
- Craft, C.B., Richardson, C.J., 1993. Peat accretion and phosphorus accumulation along a eutrophication gradient in the northern Everglades. *Biogeochemistry* 22, 133–156.
<https://doi.org/10.1007/BF00002708>

- Craft, C.B., Seneca, E.D., Broome, S.W., 1993. Vertical accretion microtidal regularly and irregularly flooded estuarine marshes. *Estuarine, Coastal and Shelf Science* 37, 371-386.
- De La Cruz, A.A., Hackney, C.T., 1977. Energy value, elemental composition and productivity of belowground biomass of a *Juncus* tidal marsh. *Ecology* 58, 1165–1170
- Delaune, R.D., Baumann, R.H., Gosselink, J.G., 1983. Relationships among vertical accretion, coastal submergence and erosion in a Louisiana Gulf Coast marsh. *Journal of Sedimentary Petrology* 53, 147–157. <https://doi.org/10.1306/212F8175-2B24-11D7-8648000102C1865D>
- Duncan, W.H., Duncan, M.B., 1987. *The Smithsonian guide to seaside plants of the Gulf and Atlantic coasts from Louisiana to Massachusetts, exclusive of lower peninsular Florida.* Smithsonian Institution Press.
- Environment Canada, 2020. Canadian Climate Normals 1980-2010 Station Data, St. Bruno, Kamouraska. http://climate.weather.gc.ca/climate_normals/ (Accessed January 2021).
- Fariña, J.M., He, Q., Silliman, B.R., Bertness, M.D., 2018. Biogeography of salt marsh plant zonation on the Pacific coast of South America. *Journal of Biogeography* 45(1), 238–247. <https://doi.org/10.1111/jbi.13109>
- Fisheries and Oceans Canada, 2020. Tides, Currents and Water Levels from Saint Jean Port Joli, <https://www.tides.gc.ca/fra/station?type=0&date=2020%2F08%2F27&sid=3170&tz=EDT&pres=1> (Accessed January 2021).
- Ford, M.A., Cahoon, D.R., Lynch, J.C., 1999. Restoring marsh elevation in a rapidly subsiding salt marsh by thin-layer deposition of dredged material. *Ecol. Eng.* 12, 189–205. [https://doi.org/10.1016/S0925-8574\(98\)00061-5](https://doi.org/10.1016/S0925-8574(98)00061-5)

- Gallagher, J.L. and Plumley, F.G., 1979. Underground biomass profiles and productivity in Atlantic Coastal Marshes. *American Journal of Botany* 66 (2), 156–161.
- Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., et al., 2017. Natural climate solutions. *Proceedings of the National Academy of Sciences of the United States of America* 114(44), 11645–11650. <https://doi.org/10.1073/pnas.1710465114>
- Gross, M.F., Hardisky, M.A., Wolf, P.L., Klemas, V., 1991. Relationship between aboveground and belowground biomass of *Spartina alterniflora* (Smooth Cordgrass). *Estuaries* 14, 180–191. <https://doi.org/10.2307/1351692>
- Gu, J., van Ardenne, L.B., Chmura, G.L., 2020. Invasive *Phragmites* increases blue carbon stock and soil volume in a St. Lawrence Estuary Marsh. *Journal of Geophysical Research: Biogeosciences* 125 (8), 1-12. <https://doi.org/10.1029/2019JG005473>
- Hatton, R.S., DeLaune, R.D., Patrick, W.H., 1983. Sedimentation, accretion, and subsidence in marshes of Barataria Basin, Louisiana. *Limnology and Oceanography* 28, 494–502. <https://doi.org/10.4319/lo.1983.28.3.0494>
- Howard, J., Sutton-Grier, A., Herr Dorothée, et al., 2017. Clarifying the role of coastal and marine systems in climate mitigation. *Frontiers in Ecology and the Environment* 15(1), 42–50.
- Hudon, C., 2004. Shift in wetland plant composition and biomass following low-level episodes in the St. Lawrence river: looking into the future. *Canadian Journal of Fisheries and Aquatic Sciences* 61(4), 603–617. <https://doi.org/10.1139/f04-031>
- Ibañez C., Curco A., Day J.W., Prat N., 2000. Structure and productivity of microtidal Mediterranean coastal marshes, 107-137 pp. In: Weinstein M.P., Kreeger D.A. (eds).

Concepts and controversies in tidal marsh ecology. Springer, Dordrecht.

https://doi.org/10.1007/0-306-47534-0_7

Kelley, J.R., 1990. Biomass production of chufa (*Cyperus esculentus*) in a seasonally flooded wetland. *Wetlands* 10(1), 61–67. <https://doi.org/10.1007/BF03160823>

Kennedy, H.A., Alongi, D.M., Karim, A., Chen, G., Chmura, G.L., et al., 2013. Chapter 4 Coastal Wetlands In: Supplement to the 2006 IPCC Guidelines on National Greenhouse Gas Inventories: Wetlands.

Kirwan, M.L., Guntenspergen, G.R., Morris, J.T., 2009. Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. *Global Change Biology*, 15(8), 1982–1989.

Kirwan, M.L., Guntenspergen, G.R., D'Alpaos, A., Morris, J.T., et al., 2010. Limits on adaptability of coastal marshes to rising sea level. *Geophysical Research Letters* 37: 1–5.

Kirwan, M.L., Guntenspergen, G.R., 2012. Feedbacks between inundation, root production, and shoot growth in a rapidly submerging brackish marsh. *Journal of Ecology* 100(3), 764–770.

Kirwan, M.L., Megonigal, J.P., 2013. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504(7478), 53–60. <https://doi.org/10.1038/nature12856>

Kirwan, M.L., Temmerman, S., Skeeahan, E.E., Guntenspergen, G.R., Fagherazzi, S., 2016. Overestimation of marsh vulnerability to sea level rise. *Nature Climate Change* 6(3), 253–260. <https://doi.org/10.1038/nclimate2909>

Langley, J.A., McKee, K.L., Cahoon, D.R., et al., 2009. Elevated CO₂ stimulates marsh elevation gain, counterbalancing sea-level rise. *Proceedings of the National Academy of Sciences of the United States of America* 106 (15), 6182–6186.

- Langley, J.A., Mozdzer, T.J., Shepard, K.A., Hagerty, S.B., Megonigal, P.J., 2013. Tidal marsh plant responses to elevated. *Global Change Biology* 19(5), 1495–1503.
<https://doi.org/10.1111/gcb.12147>
- Mal, T., and Narine, L., 2004. The biology of Canadian weeds. 129. *Phragmites australis* (Cav.) Trin. ex Steud. *Canadian Journal of Plant Science* 84, 365–396.
- McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., et al., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment* 9(10), 552–560.
- Mitsch, W.J., Gosselink, J.G., 2000. *Wetlands*. John Wiley & Sons, New York, 920 pp.
- Moore, G.E., Burdick, D.M., Peter, C.R., Keirstead, D.R., 2012. Belowground biomass of *Phragmites australis* in coastal marshes. *Northeastern Naturalist* 19(4), 611–626.
<https://doi.org/10.1656/045.019.0406>
- Morris, J.T., Barber, D.C., Callaway, J.C., Chambers, R., Hagen, S.C., et al., 2016. Contributions of organic and inorganic matter to sediment volume and accretion in tidal wetlands at steady state. *Earth's Future* 4, 110–121. <https://doi.org/10.1002/2015EF000334>
- Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83, 2869–2877.
- Mulligan, G.A., Junkins, B.E., 1976. The biology of Canadian weeds. 17. *Cyperus esculentus* L. *Canadian Journal of Plant Science* 56(2), 339-350. <https://doi.org/10.4141/cjps76-052>
- Neubauer, S.C., Anderson, I.C., Constantine, J.A., et al., 2002. Sediment deposition and accretion in a Mid-Atlantic (U.S.A.) tidal freshwater marsh. *Estuarine, Coastal and Shelf Science* 54(4), 713–727. <https://doi.org/10.1006/ecss.2001.0854>

- Niering, W.A., Warren, R.S., Weymouth, C.G., 1977. Our dynamic tidal marshes: vegetation changes as revealed by peat analysis. Connecticut Arboretum Bulletin No. 22., New London, Connecticut, 14 pp. <http://digitalcommons.conncoll.edu/arbbulletins/21>
- Nyman, J.A., Delaune, R.D., Roberts, H.H., Patrick, W.H., 1993. Relationship between vegetation and soil formation in a rapidly submerging coastal marsh. *Marine Ecology Progress Series* 96, 269–279. <https://doi.org/10.3354/meps096269>
- Nyman, J.A., Walters, R.J., Delaune, R D., and Patrick, W.H., 2006. Marsh vertical accretion via vegetative growth. *Estuarine, Coastal and Shelf Science* 69(3), 370–380. <https://doi.org/10.1016/j.ecss.2006.05.041>
- Pang, W., Crow, W.T., Luc, J.E., McSorley, R., Giblin-Davis, R.M., Kenworthy, K.E., Kruse, J.K., 2011. Comparison of water displacement and WinRHIZO software for plant root parameter assessment. *Plant Disease* 95 (10), 1308–1310. <https://doi.org/10.1094/PDIS-01-11-0026>
- Redfield, A.C., 1972. Development of a New England salt marsh. *Ecological Monographs* 42(2), 201–237.
- Roland, A.E., Smith, E.C., 1969. *The Flora of Nova Scotia*. Halifax, NS: Nova Scotia Museum. 746 pp.
- Roman, C.T., Daiber, F.C., 1984. Aboveground and belowground primary production dynamics of two Delaware Bay tidal marshes. *Bulletin of the Torrey Botanical Club* 3(1), 34-41.
- Schile, L.M., Callaway, J.C., Morris, J.T., et al., 2014. Modeling tidal marsh distribution with sea-level rise: evaluating the role of vegetation, sediment, and upland habitat in marsh resiliency. *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0088760>

- Smith, W., 1943. Density of soil and their genetic relations. *Soil Science* 56, 263-272.
- Soltani, N., Shropshire, C., Sikkema, P.H., 2018. Yellow nutsedge (*Cyperus esculentus* l.) control in corn with various rates of halosulfuron. *Canadian Journal of Plant Science* 98(3), 628–632. <https://doi.org/10.1139/cjps-2017-0229>
- Thompson, J.D., 1991. The biology of an invasive plant. *Bioscience* 41(6), 393-401.
- Thorne, K., MacDonald, G., Guntenspergen, G., Ambrose, R., et al., 2018. U.S. Pacific coastal wetland resilience and vulnerability to sea-level rise. *Science Advances* 4(2), 1–10. <https://doi.org/10.1126/sciadv.aao3270>
- Turner, R.E., Swenson, E.M., Milan C.S., 2002. Organic and Inorganic Contributions to Vertical Accretion in Salt Marsh Sediments, 583-595. In: Weinstein M.P., Kreeger D.A. (eds) *Concepts and controversies in tidal marsh ecology*. Springer, Dordrecht. https://doi.org/10.1007/0-306-47534-0_27
- Turner, E.R., Milan, C.S., Swenson, E.M., 2006. Recent volumetric changes in salt marsh soils. *Estuarine, Coastal and Shelf Science* 69, 352–359. <https://doi.org/10.1016/j.ecss.2006.05.005>
- Tripathee, R., Schäfer, K.V.R., 2015. Above- and belowground biomass allocation in four dominant salt marsh species of the Eastern United States. *Wetlands* 35, 21–30. <https://doi.org/10.1007/s13157-014-0589-z>
- Unger, V., Eelsey-Quirk, T., Sommerfield, C., Velinsky, D., 2016. Stability of organic carbon accumulating in *Spartina alterniflora*-dominated salt marshes of the Mid-Atlantic U.S. *Estuarine, Coastal and Shelf Science* 182, 179–189. <https://doi.org/10.1016/j.ecss.2016.10.001>

- Valiela, I., Teal, J.M., Persson, N.Y., 1976. Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnology and Oceanography* 21, 245–252.
<https://doi.org/10.4319/lo.1976.21.2.0245>
- Wang, H., Steyer, G.D., Couvillion, B.R., Beck, H.J., Rybczyk, J.M., Rivera-Monroy, V.H., Krauss, K.W., Visser, J.M., 2017. Predicting landscape effects of Mississippi River diversions on soil organic carbon sequestration. *Ecosphere* 8(11), 1-15.
<https://doi.org/10.1002/ecs2.1984>
- Wigand, C., Roman, C.T., 2012. Chapter 2: North Atlantic Coastal Tidal Wetlands 13-28. In: Batzer, D.P., Baldwin, A.H. (Eds.), *Wetland habitats of North America: ecology and conservation concerns*. University of California Press, Berkeley, CA, 408 pp.
<https://doi.org/10.1525/9780520951419-004>
- Windham, L., Lathrop, R.G., 1999. Effects of *Phragmites australis* (common reed) invasion on aboveground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. *Estuaries* 22(4), 927–935.
- 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(2), 179–188.

Appendix A

Table A.1. Aboveground oven dry mass (g) of species found in the three vegetation zones in La Pocatière salt marsh. Area sampled (plot) = 0.049 m².

Vegetation zones	Plot #	<i>Phragmites</i>	<i>S. patens</i>	<i>L. maritima</i>	<i>S. europaea</i>	<i>S. alterniflora</i>
<i>Phragmites/S. patens</i>	1	15.5	50.59	3.8	0.05	
	2	23.43	60.32	1.26	0.03	
	3	16.09	41.06	0.47	0.01	
	4	11.13	32.62	5.46	0	
	5	11.5	47.3	0.87	0	
	6	18.42	32.74	0.51	0.01	
	7	23.12	27.84	1	0.02	
	8	32.8	52.96	1.35	0	
	9	29.58	55.21	2.5	0	
	10	16.51	41.72	3.18	0.02	
		Mean	19.81	44.24	2.04	0.01
	sd	20.24	10.84	1.65	0.02	
<i>S. patens</i>	11		38.60	1.00	0.01	
	12		10.28	0.90	0.38	
	13		24.77	1.05	0.21	
	14		27.02	1.84	0.00	
	15		31.06	2.47	0.00	
	16		27.83	4.27	0.00	
	17		41.77	1.08	0.00	
	18		20.21	3.77	0.87	
	19		41.73	4.82	0.00	
	20		56.30	1.08	0.04	
		Mean		31.96	2.23	0.15
	sd		13.04	1.52	0.28	

Table A.1. continued

Vegetation zones	Plot #	<i>Phragmites</i>	<i>S. patens</i>	<i>L. maritima</i>	<i>S. europaea</i>	<i>S. alterniflora</i>
<i>S. alterniflora</i>	21				0.00	23.69
	22				0.05	20.00
	23				0.05	24.50
	24				0.14	23.93
	25				0.20	35.72
	26				0.00	28.58
	27				0.04	25.90
	28				0.08	37.62
	29				0.30	51.77
	30				0.04	33.75
	<i>Mean</i>				0.09	30.55
	<i>sd</i>				0.10	9.44

Table A.2. Belowground oven dry mass (g) of species harvested in each 0.049 m² plots found in the three vegetation zones in La Pocatière salt marsh. Phrag= *P. australis*; Cyp 1 & Cyp2 = *C. esculentus*; Spat 1 & Spat 2 = *S. patens*; Salt = *S. alterniflora*.

Vegetation zones	Soil depth (cm)	Plot #	Species	Rhizomes	Roots	Dead material
Phrag/Spat	0-15	1	Phrag	1.18	0.03	5.96
Phrag/Spat	0-15	2	Phrag	0.09	0.00	2.99
Phrag/Spat	0-15	3	Phrag	0.63	0.00	3.58
Phrag/Spat	0-15	4	Phrag	0.39	0.06	6.20
Phrag/Spat	0-15	5	Phrag	0.70	0.08	3.28
Phrag/Spat	0-15	6	Phrag	1.10	0.06	2.49
Phrag/Spat	0-15	7	Phrag	0.10	0.53	2.52
Phrag/Spat	0-15	8	Phrag	0.15	0.22	1.82
Phrag/Spat	0-15	9	Phrag	0.76	0.14	2.14
Phrag/Spat	0-15	10	Phrag	0.32	0.22	2.21
Phrag/Spat	0-15	1	Spat 1	2.34	1.48	
Phrag/Spat	0-15	2	Spat 1	2.76	0.77	
Phrag/Spat	0-15	3	Spat 1	1.50	0.72	
Phrag/Spat	0-15	4	Spat 1	2.10	0.52	
Phrag/Spat	0-15	5	Spat 1	2.48	0.78	
Phrag/Spat	0-15	6	Spat 1	2.27	0.70	
Phrag/Spat	0-15	7	Spat 1	1.78	0.88	
Phrag/Spat	0-15	8	Spat 1	1.00	2.17	
Phrag/Spat	0-15	9	Spat 1	2.78	1.23	
Phrag/Spat	0-15	10	Spat 1	2.07	1.45	
Phrag/Spat	0-15	1	Cyp 1	0.00	0.00	
Phrag/Spat	0-15	2	Cyp 1	0.00	0.00	
Phrag/Spat	0-15	3	Cyp 1	0.00	0.00	
Phrag/Spat	0-15	4	Cyp 1	0.00	0.00	
Phrag/Spat	0-15	5	Cyp 1	0.00	0.00	
Phrag/Spat	0-15	6	Cyp 1	0.00	0.00	
Phrag/Spat	0-15	7	Cyp 1	0.00	0.00	
Phrag/Spat	0-15	8	Cyp 1	0.16	0.14	
Phrag/Spat	0-15	9	Cyp 1	1.14	0.18	
Phrag/Spat	0-15	10	Cyp 1	0.31	0.10	
<i>S. patens</i>	0-15	11	Spat 2	2.06	2.08	4.33

Table A.2. continued

Vegetation zones	Soil depth (cm)	Plot #	Species	Rhizomes	Roots	Dead material
<i>S. patens</i>	0-15	12	Spat 2	2.10	4.55	1.61
<i>S. patens</i>	0-15	13	Spat 2	2.00	2.75	1.93
<i>S. patens</i>	0-15	14	Spat 2	3.50	4.92	3.26
<i>S. patens</i>	0-15	15	Spat 2	1.22	1.64	1.63
<i>S. patens</i>	0-15	16	Spat 2	1.84	1.70	1.11
<i>S. patens</i>	0-15	17	Spat 2	2.64	3.06	1.76
<i>S. patens</i>	0-15	18	Spat 2	2.19	2.78	3.10
<i>S. patens</i>	0-15	19	Spat 2	2.11	2.28	1.94
<i>S. patens</i>	0-15	20	Spat 2	1.55	1.52	1.63
<i>S. patens</i>	0-15	11	Cyp 2	0.00	0.00	
<i>S. patens</i>	0-15	12	Cyp 2	0.00	0.00	
<i>S. patens</i>	0-15	13	Cyp 2	0.46	0.13	
<i>S. patens</i>	0-15	14	Cyp 2	0.75	0.00	
<i>S. patens</i>	0-15	15	Cyp 2	0.0	0.0	
<i>S. patens</i>	0-15	16	Cyp 2	0.0	0.0	
<i>S. patens</i>	0-15	17	Cyp 2	0.0	0.0	
<i>S. patens</i>	0-15	18	Cyp 2	0.0	0.0	
<i>S. patens</i>	0-15	19	Cyp 2	0.67	0.07	
<i>S. patens</i>	0-15	20	Cyp 2	0.00	0.14	
<i>S. alterniflora</i>	0-15	21	Salt	2.97	1.27	4.40
<i>S. alterniflora</i>	0-15	22	Salt	0.51	0.58	2.36
<i>S. alterniflora</i>	0-15	23	Salt	3.05	2.97	2.99
<i>S. alterniflora</i>	0-15	24	Salt	3.80	2.33	4.30
<i>S. alterniflora</i>	0-15	25	Salt	3.83	3.73	2.27
<i>S. alterniflora</i>	0-15	26	Salt	5.33	5.03	2.83
<i>S. alterniflora</i>	0-15	27	Salt	2.95	3.95	2.09
<i>S. alterniflora</i>	0-15	28	Salt	3.71	3.13	2.64
<i>S. alterniflora</i>	0-15	29	Salt	4.17	4.99	2.51
<i>S. alterniflora</i>	0-15	30	Salt	3.39	3.41	0.94
Phrag/Spat	15-30	1	Phrag	0.95	0.00	7.96
Phrag/Spat	15-30	2	Phrag	0.93	0.35	3.62
Phrag/Spat	15-30	3	Phrag	0.00	0.33	1.20
Phrag/Spat	15-30	4	Phrag	0.35	0.23	2.49
Phrag/Spat	15-30	5	Phrag	2.12	0.29	3.10
Phrag/Spat	15-30	6	Phrag	0.49	0.20	2.11
Phrag/Spat	15-30	7	Phrag	0.43	0.27	0.82

Table A.2. continued

Vegetation zones	Soil depth (cm)	Plot #	Species	Rhizomes	Roots	Dead material
Phrag/Spat	15-30	8	Phrag	0.51	0.31	1.16
Phrag/Spat	15-30	9	Phrag	0.00	0.30	1.19
Phrag/Spat	15-30	10	Phrag	0.36	0.15	1.30
Phrag/Spat	15-30	1	Spat 1	0.34	0.38	
Phrag/Spat	15-30	2	Spat 1	0.05	0.18	
Phrag/Spat	15-30	3	Spat 1	0.86	3.10	
Phrag/Spat	15-30	4	Spat 1	2.14	8.52	
Phrag/Spat	15-30	5	Spat 1	0.52	2.27	
Phrag/Spat	15-30	6	Spat 1	1.03	2.65	
Phrag/Spat	15-30	7	Spat 1	2.68	1.95	
Phrag/Spat	15-30	8	Spat 1	1.55	3.21	
Phrag/Spat	15-30	9	Spat 1	1.65	3.60	
Phrag/Spat	15-30	10	Spat 1	0.98	1.68	
Phrag/Spat	15-30	1	Cyp 1	0.00	0.00	
Phrag/Spat	15-30	2	Cyp 1	0.00	0.00	
Phrag/Spat	15-30	3	Cyp 1	0.37	0.04	
Phrag/Spat	15-30	4	Cyp 1	0.00	0.00	
Phrag/Spat	15-30	5	Cyp 1	3.35	0.32	
Phrag/Spat	15-30	6	Cyp 1	0.91	0.40	
Phrag/Spat	15-30	7	Cyp 1	0.51	0.27	
Phrag/Spat	15-30	8	Cyp 1	0.04	0.06	
Phrag/Spat	15-30	9	Cyp 1	0.34	0.22	
Phrag/Spat	15-30	10	Cyp 1	0.03	0.15	
<i>S. patens</i>	15-30	11	Spat 2	1.12	2.34	1.61
<i>S. patens</i>	15-30	12	Spat 2	0.80	1.75	1.41
<i>S. patens</i>	15-30	13	Spat 2	1.44	2.97	1.83
<i>S. patens</i>	15-30	14	Spat 2	0.56	2.38	1.11
<i>S. patens</i>	15-30	15	Spat 2	0.90	1.90	0.77
<i>S. patens</i>	15-30	16	Spat 2	0.66	2.06	1.00
<i>S. patens</i>	15-30	17	Spat 2	0.75	1.88	1.00
<i>S. patens</i>	15-30	18	Spat 2	0.96	2.38	1.65
<i>S. patens</i>	15-30	19	Spat 2	1.28	3.71	1.68
<i>S. patens</i>	15-30	20	Spat 2	1.92	3.97	1.58
<i>S. patens</i>	15-30	11	Cyp 2	0.00	0.00	
<i>S. patens</i>	15-30	12	Cyp 2	0.00	0.00	
<i>S. patens</i>	15-30	13	Cyp 2	0.00	0.00	
<i>S. patens</i>	15-30	14	Cyp 2	0.00	0.00	

Table A.2. continued

Vegetation zones	Soil depth (cm)	Plot #	Species	Rhizomes	Roots	Dead material
<i>S. patens</i>	15-30	15	Cyp 2	0.00	0.00	
<i>S. patens</i>	15-30	16	Cyp 2	0.07	0.04	
<i>S. patens</i>	15-30	17	Cyp 2	0.00	0.00	
<i>S. patens</i>	15-30	18	Cyp 2	0.00	0.00	
<i>S. patens</i>	15-30	19	Cyp 2	0.67	0.00	
<i>S. patens</i>	15-30	20	Cyp 2	0.00	0.17	
<i>S. alterniflora</i>	15-30	21	Salt	0.99	2.10	1.50
<i>S. alterniflora</i>	15-30	22	Salt	0.50	1.12	0.59
<i>S. alterniflora</i>	15-30	23	Salt	1.46	2.10	1.46
<i>S. alterniflora</i>	15-30	24	Salt	0.28	1.46	0.79
<i>S. alterniflora</i>	15-30	25	Salt	1.62	0.88	4.07
<i>S. alterniflora</i>	15-30	26	Salt	2.33	1.72	4.73
<i>S. alterniflora</i>	15-30	27	Salt	0.98	1.82	2.82
<i>S. alterniflora</i>	15-30	28	Salt	1.69	0.68	3.51
<i>S. alterniflora</i>	15-30	29	Salt	2.18	0.93	4.10
<i>S. alterniflora</i>	15-30	30	Salt	1.10	0.80	1.48

Table A.3. Volume (cm³) of live rhizomes, roots and dead material of species harvested in each 0.049 m² plots found in the three vegetation zones in La Pocatière salt marsh. Volume of soil corer = 343.53 m³. Phrag = *P. australis*; Cyp 1 & Cyp2 = *C. esculentus*; Spat 1 & Spat 2 = *S. patens*; Salt = *S. alterniflora*.

Vegetation zones	Soil depth (cm)	Plot #	Species	Rhizome	Root	Dead material
Phrag/Spat	0-15	1	Phrag	4	0.2	110
Phrag/Spat	0-15	2	Phrag	0.3	0	34
Phrag/Spat	0-15	3	Phrag	3	0	38
Phrag/Spat	0-15	4	Phrag	2	1	80
Phrag/Spat	0-15	5	Phrag	4	0.4	40
Phrag/Spat	0-15	6	Phrag	5	0.2	40
Phrag/Spat	0-15	7	Phrag	2	0.2	30
Phrag/Spat	0-15	8	Phrag	4	3	17
Phrag/Spat	0-15	9	Phrag	3.3	1.2	14
Phrag/Spat	0-15	10	Phrag	2	4	12
Phrag/Spat	0-15	1	Spat 1	6	10	
Phrag/Spat	0-15	2	Spat 1	10	6	
Phrag/Spat	0-15	3	Spat 1	6	8	
Phrag/Spat	0-15	4	Spat 1	6	6	
Phrag/Spat	0-15	5	Spat 1	6	8	
Phrag/Spat	0-15	6	Spat 1	7	6	
Phrag/Spat	0-15	7	Spat 1	4	60	
Phrag/Spat	0-15	8	Spat 1	6	30	
Phrag/Spat	0-15	9	Spat 1	10	15	
Phrag/Spat	0-15	10	Spat 1	6	20	
Phrag/Spat	0-15	1	Cyp 1	0	0	
Phrag/Spat	0-15	2	Cyp 1	0	0	
Phrag/Spat	0-15	3	Cyp 1	0	0	
Phrag/Spat	0-15	4	Cyp 1	0	0	
Phrag/Spat	0-15	5	Cyp 1	0	0	
Phrag/Spat	0-15	6	Cyp 1	0	0	
Phrag/Spat	0-15	7	Cyp 1	0	0	
Phrag/Spat	0-15	8	Cyp 1	0.6	0.8	
Phrag/Spat	0-15	9	Cyp 1	5	2	
Phrag/Spat	0-15	10	Cyp 1	2	0.4	
Phrag/Spat	15-30	1	Phrag	6	0	160
Phrag/Spat	15-30	2	Phrag	5.6	5	65

Table A.3. continued

Vegetation zone	Soil depth (cm)	Plot #	Species	Rhizomes	Roots	Dead material
Phrag/Spat	15-30	3	Phrag	0	2	14
Phrag/Spat	15-30	4	Phrag	3	2	25
Phrag/Spat	15-30	5	Phrag	12	2	30
Phrag/Spat	15-30	6	Phrag	2	1.1	20
Phrag/Spat	15-30	7	Phrag	3	3	20
Phrag/Spat	15-30	8	Phrag	3	3	14
Phrag/Spat	15-30	9	Phrag	0	3	15
Phrag/Spat	15-30	10	Phrag	3.8	1.8	10
Phrag/Spat	15-30	1	Spat 1	1	6	
Phrag/Spat	15-30	2	Spat 1	0.2	3	
Phrag/Spat	15-30	3	Spat 1	5	20	
Phrag/Spat	15-30	4	Spat 1	12	50	
Phrag/Spat	15-30	5	Spat 1	4	15	
Phrag/Spat	15-30	6	Spat 1	8	15	
Phrag/Spat	15-30	7	Spat 1	10	35	
Phrag/Spat	15-30	8	Spat 1	14	25	
Phrag/Spat	15-30	9	Spat 1	14	50	
Phrag/Spat	15-30	10	Spat 1	10	20	
Phrag/Spat	15-30	1	Cyp 1	0	0	
Phrag/Spat	15-30	2	Cyp 1	0	0	
Phrag/Spat	15-30	3	Cyp 1	2	0.2	
Phrag/Spat	15-30	4	Cyp 1	0	0	
Phrag/Spat	15-30	5	Cyp 1	20	1	
Phrag/Spat	15-30	6	Cyp 1	5	1	
Phrag/Spat	15-30	7	Cyp 1	2.5	0.8	
Phrag/Spat	15-30	8	Cyp 1	0.3	0.4	
Phrag/Spat	15-30	9	Cyp 1	3	2	
Phrag/Spat	15-30	10	Cyp 1	0.1	1	
<i>S. patens</i>	0-15	11	Spat 2	15	25	50
<i>S. patens</i>	0-15	12	Spat 2	15	50	12
<i>S. patens</i>	0-15	13	Spat 2	6	20	30
<i>S. patens</i>	0-15	14	Spat 2	18	25	50
<i>S. patens</i>	0-15	15	Spat 2	3	8	20
<i>S. patens</i>	0-15	16	Spat 2	7	10	15
<i>S. patens</i>	0-15	17	Spat 2	10	40	18
<i>S. patens</i>	0-15	18	Spat 2	10	20	28
<i>S. patens</i>	0-15	19	Spat 2	10	20	17

Table A.3. continued

Vegetation zones	Soil depth (cm)	Plot #	Species	Rhizomes	Roots	Dead material
<i>S. patens</i>	0-15	20	Spat 2	6	20	18
<i>S. patens</i>	0-15	11	Cyp 2	0	0	
<i>S. patens</i>	0-15	12	Cyp 2	0	0	
<i>S. patens</i>	0-15	13	Cyp 2	1	0.3	
<i>S. patens</i>	0-15	14	Cyp 2	3	0	
<i>S. patens</i>	0-15	15	Cyp 2	0	0	
<i>S. patens</i>	0-15	16	Cyp 2	0	0	
<i>S. patens</i>	0-15	17	Cyp 2	0	0	
<i>S. patens</i>	0-15	18	Cyp 2	0	0	
<i>S. patens</i>	0-15	19	Cyp 2	4	0.2	
<i>S. patens</i>	0-15	20	Cyp 2	0	1	
<i>S. patens</i>	15-30	11	Spat 2	6	20	15
<i>S. patens</i>	15-30	12	Spat 2	5	10	10
<i>S. patens</i>	15-30	13	Spat 2	11	22	19
<i>S. patens</i>	15-30	14	Spat 2	5	16	12
<i>S. patens</i>	15-30	15	Spat 2	10	25	8
<i>S. patens</i>	15-30	16	Spat 2	7	40	8
<i>S. patens</i>	15-30	17	Spat 2	5	30	5
<i>S. patens</i>	15-30	18	Spat 2	6	14	15
<i>S. patens</i>	15-30	19	Spat 2	9	23	12
<i>S. patens</i>	15-30	20	Spat 2	22	95	12
<i>S. patens</i>	15-30	11	Cyp 2	0	0	
<i>S. patens</i>	15-30	12	Cyp 2	0	0	
<i>S. patens</i>	15-30	13	Cyp 2	0	0	
<i>S. patens</i>	15-30	14	Cyp 2	0	0	
<i>S. patens</i>	15-30	15	Cyp 2	0	0	
<i>S. patens</i>	15-30	16	Cyp 2	0.3	0.1	
<i>S. patens</i>	15-30	17	Cyp 2	0	0	
<i>S. patens</i>	15-30	18	Cyp 2	0	0	
<i>S. patens</i>	15-30	19	Cyp 2	4	0.2	
<i>S. patens</i>	15-30	20	Cyp 2	0	0	
<i>S. alterniflora</i>	0-15	21	Salt	25	20	70
<i>S. alterniflora</i>	0-15	22	Salt	5.5	6.5	40
<i>S. alterniflora</i>	0-15	23	Salt	25	30	45
<i>S. alterniflora</i>	0-15	24	Salt	40	30	65
<i>S. alterniflora</i>	0-15	25	Salt	20	30	30
<i>S. alterniflora</i>	0-15	26	Salt	40	50	35

Table A.3. continued

Vegetation zones	Soil depth (cm)	Plot #	Species	Rhizomes	Roots	Dead material
<i>S. alterniflora</i>	0-15	27	Salt	25	35	20
<i>S. alterniflora</i>	0-15	28	Salt	30	45	50
<i>S. alterniflora</i>	0-15	29	Salt	26	55	30
<i>S. alterniflora</i>	0-15	30	Salt	20	35	10
<i>S. alterniflora</i>	15-30	21	Salt	10	20	20
<i>S. alterniflora</i>	15-30	22	Salt	4	7	6
<i>S. alterniflora</i>	15-30	23	Salt	14	15	14
<i>S. alterniflora</i>	15-30	24	Salt	3	10	10
<i>S. alterniflora</i>	15-30	25	Salt	14	6	40
<i>S. alterniflora</i>	15-30	26	Salt	18	15	50
<i>S. alterniflora</i>	15-30	27	Salt	8	14	35
<i>S. alterniflora</i>	15-30	28	Salt	20	8	52
<i>S. alterniflora</i>	15-30	29	Salt	30	22	54
<i>S. alterniflora</i>	15-30	30	Salt	11	8	18