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ORIGINAL RESEARCH

Above- and Belowground Biomass Allocation in Four Dominant Salt Marsh Species of the Eastern United States

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Abstract Measurements of aboveground and belowground biomass allocations are important for characterization of structure and function in marsh ecosystems as various processes such as carbon sequestration, gas transport, nutrient cycling, and ecosystem resilience are affected by these allocations. We measured aboveground and belowground biomass, root and rhizome characteristics, leaf area index (LAI), and carbon to nitrogen (C/N) ratio of various tissues of four tidal marsh species in New Jersey by harvesting biomass during peak growing season. The aboveground biomasses for *Spartina patens*, *S. alterniflora, Phragmites australis,* and *Distichlis spicata* were 2.3, 2.2, 1.7 and 1.2 kg m^{-2}, respectively. The ratio of belowground to aboveground biomass for *S. alterniflora* and *D. spicata*, harvested from a recently restored wetland were lower than in previous studies. LAI for *S. alterniflora, D. spicata, P. australis,* and *S. patens* were 8.4, 6.8, 4.8 and 3.7 m^2 m^{-2}, respectively. Diameter of rhizome and root, number of primary roots per node, root surface area to volume ratio, and C/N of various tissues varied with species. The measured above- and belowground biometric traits are crucial for a better understanding of carbon dynamics, and modeling greenhouse gas transport in marsh ecosystems.

Keywords Biomass · Salt marsh · Root diameter · Rhizome diameter

Introduction

Salt marshes are highly productive and one of the most valuable carbon sinks on the planet (McLeod et al. 2011; Townend et al. 2011). Flooded or saturated conditions limit oxygen availability in marsh soils causing slow decomposition of plant material (Solomon et al. 2007), resulting in the accumulation of significant amounts of organic carbon over time (Chmura et al. 2003). The addition of organic carbon to marsh soil serves as a carbon sink and also contributes to vertical accretion of marsh sediment (Nyman et al. 2006; Langley et al. 2009, 2013; Deegan et al. 2012; Kirwan and Mudd 2012). If vertical accretion is slower than relative sea level rise, shallow open water could replace tidal marshes (Roman et al. 1997; Orson et al. 1998). Thus, production of plant material in marsh ecosystems is important both for carbon sequestration and the persistence of marshes with rising sea level. Accurate measurements of both above- and belowground biomass provide a foundation for better understanding ecosystem structure and function in salt marshes.

Accurately quantifying belowground biomass of wetland plants is also important because production, consumption, and transport of greenhouse gases such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) depend largely on the amount of root biomass belowground. When roots die, they serve as substrate for the production of these gases, and exudates supplied by roots are important substrates for CH_4 production (Chanton et al. 1989). The CH_4 and N_2O produced in a hypoxic wetland soil environment are transported to the atmosphere via roots and aboveground tissue. In addition to transporting CH_4 and N_2O to the atmosphere, roots also transport oxygen (O_2) from the atmosphere to the soil via aboveground tissue (Le Mer and Roger 2001). This oxygen can be used by microbes for the decomposition of organic compounds or to oxidize CH_4, both resulting in the production of CO_2 (Mitsch and Gosselink 2007). Therefore, the diameter and length of the roots are likely to affect the transport of O_2 and greenhouse gases between the atmosphere and the soil (Segers and Leffelaar 2001). Knowledge of the vertical distribution and amount of roots as well as their length and diameter

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are important in order to better understand the role of roots in the production and transport of greenhouse gases from marsh soils to the atmosphere.

Belowground biomass production plays a key role in the accumulation of organic carbon in a wetland environment (Nyman et al. 2006; Neubauer 2008). However, usually, only aboveground biomass is used to calculate salt marsh net primary productivity (NPP), because roots and rhizomes are difficult to measure (Fahey and Knapp 2007). Even when belowground biomass estimates are made, there is a significant variation among measurements, partly due to natural variability, but also due to measurement error in terms of small core diameters and inconsistency in technique used by investigators during processing and sorting of samples (Good et al. 1982; Fahey and Knapp 2007). Previous studies have shown that variation in belowground biomass estimations were significantly larger when core diameters of 10 cm or less were used, leading to biases in the estimation of belowground production (Singh et al. 1984; Fahey and Knapp 2007). Therefore, harvesting larger volumes results in better estimates of belowground biomass. Estimates of aboveground biomass are relatively easy to obtain via harvesting, but can also be estimated via remote sensing methods (Lefsky et al. 2002). Thus, more accurate estimates of aboveground to belowground biomass ratios can be used to improve estimates of overall plant biomass production.

In this study, we characterized above- and belowground biomass as well as diameter and length of primary roots of four marsh plant species in coastal North America: *Spartina alterniflora* (Loisel.), *S. patens* ((Aiton) Muhl), *Distichlis spicata* ((L.) Greene), and *Phragmites australis* ((Cav.) Trin. ex Steud.). Comparison of allocation of biomasses in aboveground and belowground tissues for the four dominant marsh species will help to better understand carbon dynamics of marshes. The measurements of distribution of leaf area at various canopy heights as well as root and rhizome parameters can aid in modeling greenhouse gas flux (Beckett et al. 2001; Dai et al. 2004). In low marsh areas of the eastern United States, *Spartina alterniflora* is a dominant native grass. Whereby, *Spartina patens* is also a native to the eastern United States and found in high marsh areas. *Distichlis spicata* is found in high marsh areas along with *S. patens*. *Phragmites australis* is an invasive species in the eastern United States and typically outcompetes native vegetation resulting in monocultures. We hypothesized that both rhizome and root biomass are higher near the soil surface as the main nutrient source in these marshes comes from the surface water; the supply of most of the nutrients to the soil profile is therefore close to the surface, and stimulate most of the belowground biomass growth there (Valiela et al. 1976; Shin et al. 2013). Also, because *P. australis* dominated marshes has been shown to emit more CH_4 than marshes of *S. patens* (Tripathee et al. in preparation), we hypothesized that the diameter of rhizomes and roots, the number of primary roots per node and the root surface area to volume ratio are higher in *P. australis* than native *S. patens* and *D. spicata*.

Materials and Methods

Study Sites

This study was conducted in the New Jersey Meadowlands (NJM), which covers most of the Hudson Raritan estuary ecosystem and is comprised of about 35,000 ha of wetlands including tidal marshes and water bodies. These wetlands are surrounded by intense urban activities. We selected two restored (Marsh Resource Meadowlands Mitigation Bank, MRMMB; and Secaucus High School, SH) and one natural (Lyndhurst Riverside Marsh, LRM) wetland sites within this estuarine ecosystem for this study. The MRMMB site (site #1) is located in Carlstadt, Bergen County, New Jersey (40.82°N, 74.03°W). This 83.4 ha site was restored by removing *P. australis* and planting *S. alterniflora* in 1999. Despite the application of herbicides to eliminate *P. australis*, new patches have continued to appear annually. The herbicide application has limited the coverage of *P. australis* to approximately 15 % of the total coverage of this wetland, and there were no *P. australis* plants within a few meters of harvested plots. Therefore, there was no or minimal biological interaction between *S. alterniflora* and *P. australis* in the harvested area. The *P. australis* in our site is likely to be the Eurasian haplotypes as it is the most common in the region and has the most widespread distribution in North America among the haplotypes of *P. australis* (Saltonstall 2002; Howard et al. 2008). We harvested above- and belowground biomass of *S. alterniflora* from this site. The SH site (site #2) is located in Secaucus, Hudson County, New Jersey (40.80°N, 74.04°W). This 17.4 ha site was restored in 2007 by removing the monoculture of *P. australis*. Currently, *S. patens* and *D. spicata* are dominant in this high marsh system. We harvested above- and belowground biomass of *D. spicata* from this site. The LRM site (site #3) is located in Lyndhurst, Bergen County, New Jersey (40.78°N, 70.09°W) and spans 12.5 ha. This site is a natural (or non-mitigated) wetland with invasive *P. australis* as the dominant species although some remnant patches of native *S. patens* can also be found. We harvested above- and belowground biomass of both *P. australis* and *S. patens* from this site.

Above- and Belowground Biomass Harvest and Rhizome and Root Biomass at Various Depths

For each study species, three 25×25 cm plots were randomly selected in monospecific stands of *S. alterniflora* (site #1), *D. spicata* (site #2), *S. patens* and *P. australis* (site #3).

Beginning at ground level, we harvested aboveground biomass in 10 cm height increments. For every 10 cm, biomass was separated into different components: florescence, green leaves, dead leaves, leaf sheath and stem. Harvested biomass was dried in a commercial drying oven (Thermo Scientific Precision 3050 Series premium oven, Thermo Fisher Scientific, USA) for 1 week at 60 °C and weighed.

In conjunction with aboveground sampling, we harvested belowground biomass by excavating up to 55 cm below the soil surface using a shovel. At each sampling point, the harvested blocks were partitioned into 0–25 cm, 25–40 cm and 40–55 cm depth from the soil surface. These blocks were rinsed with tap water and belowground biomass for each portion was separated into rhizomes and roots. Belowground biomass was dried and weighed as above.

Measurements of Root and Rhizome Characteristics

From the uppermost belowground sampling block (25×25×25 cm), we randomly selected three average-sized plants and measured the diameter of the rhizome and the length and diameter of every root at every node of the plant using a digital caliper for diameter measurement and a ruler for length measurements (±1 mm accuracy). Root diameter was measured around the midsection of the root to account for slight variations in diameter along the root. Root surface area to volume ratio was also calculated assuming roots were approximately cylindrical.

Leaf Area Distribution and Leaf Area Index

Total leaf area per plot was calculated by multiplying specific leaf area (SLA, leaf area per unit dry mass) by total leaf dry weight. In order to determine SLA, two mature green leaves were taken from canopy mid-height from each harvested plot. We cut 15 cm long pieces from the mid portion of each harvested leaf and determined its area using a commercial scanner (Epson Perfection V30, Epson America, Inc, Long Beach, CA) and Image J software (http://rsbweb.nih.gov/ij/, National Institutes of Health). The leaves were dried as above and weighed. We calculated leaf area index (LAI, m^2 leaf area m^{-2} ground area) for various heights of the canopy by multiplying SLA with leaf weight of each particular canopy height.

%N and Total C in Leaves; C/N in Roots, Rhizomes and Leaves

To estimate %C and %N of leaves, roots and rhizomes, dried biomass samples from each species and plot were finely ground into a powder using a ball bearing mill (8000D Dual Mixer/Mill, Metuchen, NJ, USA). The ground samples (2.5–3.5 mg each) were placed in tin capsules and sent to the UC Davis Stable Isotope Facility, Department of Plant Sciences, Davis, California, USA, for analysis. The facility used a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) for the analysis of %C and %N.

Statistical Analyses

Comparisons between species were made for total aboveground, total belowground, total rhizome and total root biomasses. For each soil depth (0–25, 25–40 and 40–55 cm from the soil surface) and each belowground biomass type (root and rhizome), comparisons were made between species. We also compared belowground to aboveground biomass ratio, root length, root diameter, root surface area to volume ratio, rhizome diameter, leaf %N, leaf total C content and C/N for each tissue type and LAI between species. For each species, we also compared C/N of leaves, roots and rhizomes. Analysis of Variance (ANOVA, Tukey HSD test) was performed for all comparisons using MATLAB (MATLAB R2012a, Mathworks, Natick, MA). A P value$\leq$0.05 was considered significant.

Results

Total Above- and Belowground Biomass

Total biomass, aboveground biomass, and belowground biomass varied between species (Tables 1 and 4). For each of the biomass categories, *S. patens* had the highest and *D. spicata* had the lowest value (Fig. 1). The belowground biomasses of *S. patens* and *P. australis* were more than four times greater than their respective aboveground biomasses, whereas for *S. alterniflora* and *D. spicata,* the belowground biomasses were less than twice that of aboveground biomasses (Fig. 1). The belowground to aboveground biomass ratios were 1.7±0.1, 1.0±0.25, 4.9±0.2 and 4.9±0.9 for *S. alterniflora*, *D. spicta*, *S. patens* and *P. australis*, respectively (Table 1).

Rhizome and Root Biomass at Various Depths

For all species, the majority of the rhizome and root biomass was found close to the surface (0–25 cm below the soil surface; Figs. 2 and 3). *P. australis* had significantly greater rhizome biomass than the other three species at greater depths (40–55 cm below the soil surface). The ratio of rhizome biomass to root biomass varied with species (Table 2). For *S. alterniflora* and *D. spicata,* the ratios were greater than one, whereas the ratios were below one for *S. patens* and *P. australis*.

Table 1 Contribution of different components of above- and belowground biomass (kg m^{-2}) to the total above- and belowground biomass (kg m^{-2}), and leaf area index (LAI, m^2 m^{-2} ground area) for different species

	S.alterniflora	*D. spicata*	*S. patens*	*P. australis*
Florescence	0	0.02±0.01	0.01±0.01	0
Green leaf	0.7±0.1	0.4±0.07	0.5±0.05	0.4±0.04
Dead leaf	0.1±0.01	0.1±0.01	0.1±0.01	0.1±0.01
Green leaf sheath	0.3±0.04	0.2±0.08	0.1±0.1	0.2±0.07
Stem	0.5±0.08	0.5±0.1	1.3±0.00	1.1±0.09
Litter	0.4±0.09	0.1±0.04	0.2±0.19	0
Total aboveground	2.2 ± 0.23^{c}	1.2 ± 0.09^{b}	$2.3\pm0.21^{a,c}$	$1.7\pm0.14^{a,b,c}$
Root	$1.7\pm0.52^{a,d}$	0.5 ± 0.11^{d}	$9.2\pm1.42^{b,c}$	$5.2\pm0.61^{a,b,c}$
Rhizome	2.2 ± 0.21^{a}	0.6 ± 0.11^{b}	2.4 ± 0.48^{a}	2.8 ± 0.11^{a}
Total belowground	3.9 ± 0.69^{a}	1.2 ± 0.20^{a}	11.6 ± 1.14^{b}	8.0 ± 0.5^{b}
LAI	8.4 ± 0.9^{a}	$6.8\pm1.3^{a,b}$	3.7 ± 2.1^{b}	$4.8\pm0.4^{a,b}$

Values are mean and standard error of three replicates. Significant differences ($P\leq0.05$) between biomass and LAI of different species are indicated by different letters

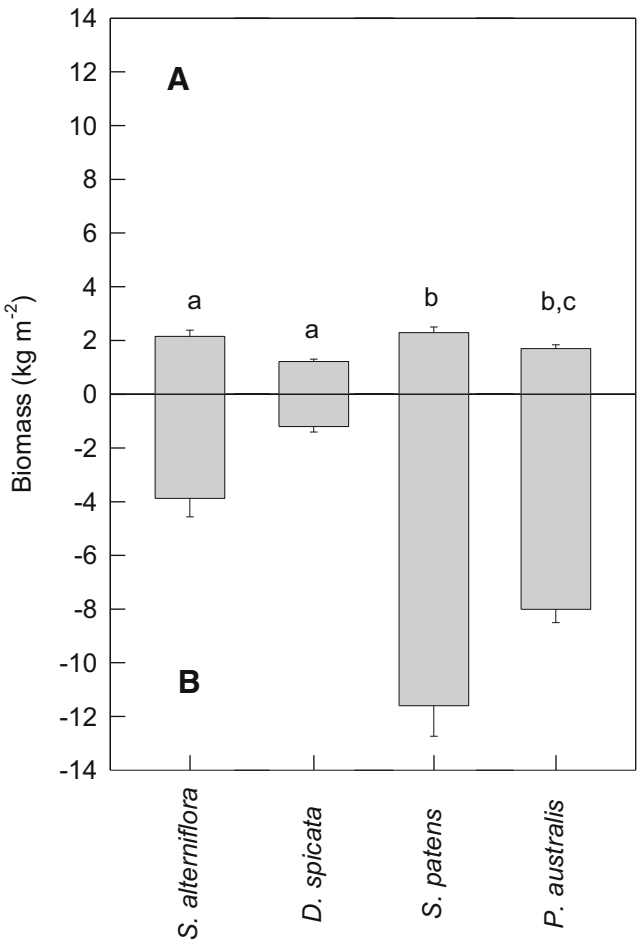

Fig. 1 Mean total biomass for different species. Positive values are for aboveground biomass (**A**) and negative values are for belowground biomass (both rhizome and root) (**B**). Significant differences ($P\leq0.05$) between the total biomass of different species are indicated by different letters. The error bars are standard errors of three replicates

Root and Rhizome Characteristics

The number of primary roots at a rhizome node varied from 2 to 5 and the highest number was found in *S. alterniflora* (Table 2). Similarly, rhizome diameter was largest in *P. australis* followed by *S. alterniflora*. Mean root diameters varied from 0.5 to 1.1 mm (Table 2). The surface areas to volume ratios of roots were significantly different from one another and varied from 44.5 to 109.7 cm^{-1}.

Leaf Area Distribution and LAI

For each investigated species, LAI varied with species and the majority of leaf area was found at canopy mid-height, although species differed significantly in their overall canopy

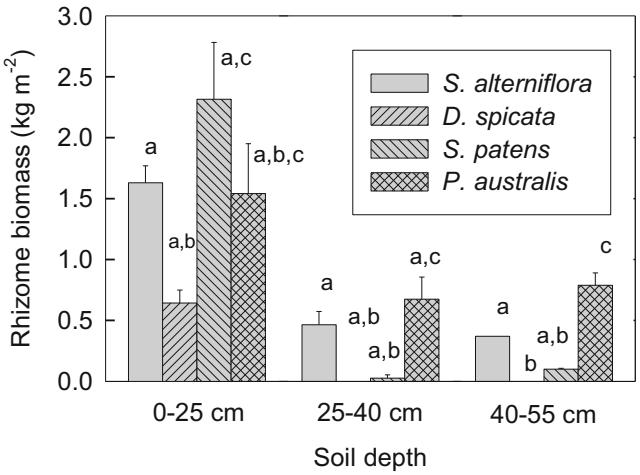

Fig. 2 Mean rhizome biomass at various depths for each species. For each depth, significant differences ($P\leq0.05$) between the biomass of different species are indicated by different letters. The error bars are standard errors of three replicates

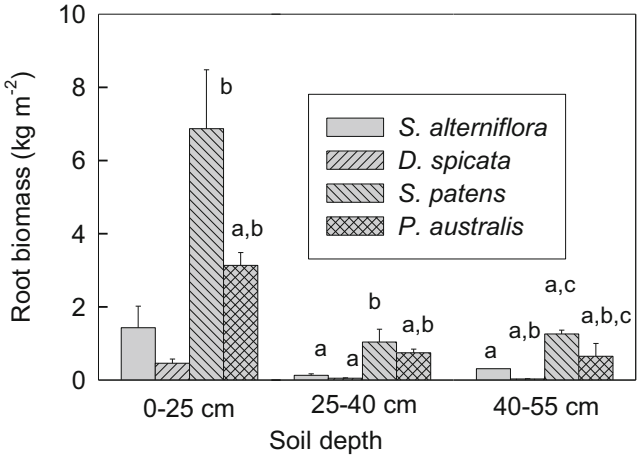

Fig. 3 Mean root biomass at various depths for each species. For each depth, significant differences ($P \leq 0.05$) between the biomass of different species are indicated by different letters. The error bars are standard errors of three replicates

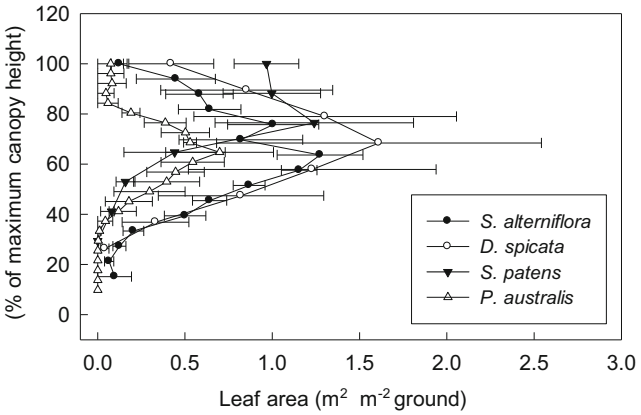

Fig. 4 Leaf area distribution of different species within their canopies (% of maximum canopy height for each 10 cm interval in height of canopy). The error bars are standard errors of three replicates

height (Fig. 4). The highest LAI was found in *S. alterniflora,* which was more than twice that of the lowest LAI found in *S. patens* (Table 1).

%N and Total C in Leaves; C/N in Roots, Rhizomes and Leaves

The %N in leaf tissue differed significantly among the studied species and was highest in leaf tissue of invasive *P. australis* (Table 3). For every species, C/N ratio was higher in rhizomes than in leaves (Tables 3 and 4). *D. spicata* had a higher C/N ratio than *S. alterniflora* and *S. patens* in root tissues (Table 3). The C/N ratio in root tissues of *D. spicata* and *P. australis* were not significantly different. For rhizomes, *S. alterniflora* and *P. australis* had higher C/N ratios than *D. spicata* and *S. patens* (Table 3). For leaves, *P. australis* had a lower C/N ratio than all other study species. When total carbon content in roots was compared between species, *S. patens* had the highest amount, followed by *P. australis*, *D. spicata*, and *S. alterniflora* (Tables 3 and 4). Likewise, rhizomes of *D. spicata* had the smallest total carbon content, compared to the other species. Total carbon content in green leaves was less than 1 kg m^{-2} for all the species (Table 3).

Discussion

Aboveground Biomass

Aboveground biomass estimation can vary depending on the method employed. For example, Shew et al. (1981) estimated a range of 0.2 to 1.0 kg of aboveground biomass per m^2 per year for *S. alterniflora* in a North Carolina marsh, depending upon the method used. This variation arises because certain methods may not take into account one or more components that affect biomass estimation. For example, in the Peak Standing Crop Method, net aboveground primary production is the single largest value of aboveground living biomass present during a 1-year growth period. In the Milner et al. (1968) Method, all positive changes in live biomass over time are summed up, thereby including a time element that is not included in the Peak Standing Crop Method. The Peak

Table 2 Ratio between rhizome biomass and root biomass, number of primary roots per node, rhizome diameter, primary root diameter and root volume for different species

	S.alterniflora	*D. spicata*	*S. patens*	*P. australis*
Rhizome biomass/Root biomass	1.5 ± 0.33^{a}	$1.2\pm0.17^{a,b}$	0.3 ± 0.1^{b}	$0.6\pm0.09^{a,b}$
No. of primary root per node	4.9 ± 0.44^{a}	1.8 ± 0.15^{b}	1.6 ± 0.13^{b}	2.8 ± 0.23^{c}
Diameter of rhizome (mm)	5.5 ± 0.2^{a}	1.9 ± 0.09^{b}	2.2 ± 0.14^{b}	6.7 ± 0.78^{a}
Diameter of primary root (mm)	0.9 ± 0.07^{a}	0.5 ± 0.02^{b}	0.6 ± 0.02^{b}	1.1 ± 0.03^{a}
Surface area to volume ratio of a root (cm^{-1})	29.1 ± 0.92^{a}	109.7 ± 4.83^{b}	83.0 ± 3.41^{c}	44.5 ± 1.35^{d}

Values are mean and standard error of three (ratio of rhizome and root biomass), 40–90 (number of primary roots per node), 9–31 (rhizome diameter), and 118–187 (primary root diameter) replicates. For surface area to volume ratio of a root, values are mean and standard error of 197 (*S. alterniflora)*, 117 (*D. spicata*), 143 (*S. patens*) and 185 (*P. australis*) roots. Significant differences ($P \leq 0.05$) between each of the parameters of different species are indicated by different letters

Table 3 %N and total C in leaves and C/N ratio in roots, rhizomes and leaves of different species. Values are mean and standard error of three replicates

	S. alterniflora	*D. spicata*	*S. patens*	*P. australis*
Root (C/N)	$53.8\pm6.66^{a,}{}_{A,B}$	$81.9\pm6.37^{b,c,}{}_{A}$	$46.4\pm5.81^{a,}{}_{A}$	$65.9\pm4.4^{a,c,}{}_{A}$
Root (C, kg m^{-2})	$0.7\pm0.39^{a,c}$	0.2 ± 0.14^{a}	4.1 ± 2.38^{b}	$2.2\pm1.29^{d,c}$
Rhizome (C/N)	$85.4\pm16.64^{a,b,}{}_{B}$	$64.6\pm4.72^{a,}{}_{A}$	$58.6\pm4.32^{a,}{}_{A,B}$	$130.4\pm12.83^{a,b,}{}_{B}$
Rhizome (C, kg m^{-2})	0.9 ± 0.52^{a}	0.3 ± 0.17^{b}	1.1 ± 0.63^{a}	1.1 ± 0.65^{a}
Green leaf (%N)	1.5 ± 0.09^{a}	1.3 ± 0.02^{a}	1.4 ± 0.1^{a}	2.5 ± 0.07^{b}
Green leaf (C/N)	$32.5\pm2.55^{a,}{}_{A}$	$32.8\pm1.41^{a,}{}_{B}$	$31.0\pm2.91^{a,}{}_{A,C}$	$19.3\pm1.2^{b,}{}_{C}$
Green leaf (C, kg m^{-2})	0.3 ± 0.02^{a}	0.1 ± 0.02^{b}	$0.2\pm0.01^{a,b}$	0.2 ± 0.01^{b}

Significant differences ($P\leq0.05$) between each of the parameters of different species (lower case, superscript), and C/N of various tissues within species (upper case, subscript) are indicated by different letters

Table 4 Analysis of Variance (ANOVA) for all the plant tissues measured of the different species

	DF	*F*	*P*
Aboveground biomass	3	7.49	0.01
Total root biomass	3	21.11	0.0007
Total rhizome biomass	3	9.99	0.05
Belowground biomass	3	31.44	0.0002
Total Biomass	3	19.17	0.002
Belowground/aboveground	3	15.51	0.003
Rhizome biomass, 0–25 cm	3	4.53	0.04
Rhizome biomass, 25–40 cm	3	9.8	0.005
Rhizome biomass, 40–55 cm	3	45.11	0.0005
Root biomass, 0–25 cm	3	23.91	0.004
Root biomass, 25–40 cm	3	6.86	0.01
Root biomass, 40–55 cm	3	5.92	0.03
LAI	3	5.43	0.03
Rhizome biomass/root biomass	3	7.31	0.01
No. of primary root per node	3	39.86	<0.0001
Diameter of rhizome (mm)	3	61.3	<0.0001
Diameter of primary root (mm)	3	28.34	<0.0001
Surface area to volume ratio of a root	3	3.69	0.01
Root (C/N)	3	6.98	0.01
Root (Total C)	3	23.53	0.003
Rhizome (C/N)	3	8.77	0.006
Rhizome (Total C)	3	10.89	0003
Green leaf (%N)	3	45.84	<0.0001
Green leaf (C/N)	3	9.03	0.006
Green leaf (total C)	3	7.98	0.009
*C/N (root, rhizome, leaf, *S. alterniflora*)	2	6.47	0.03
*C/N (root, rhizome, leaf, *D. spicata*)	2	28.73	0.008
*C/N (root, rhizome, leaf, *S. patens*)	2	9.4	0.01
*C/N (root, rhizome, leaf, *P. australis*)	2	50.31	0.002

Comparisons within the species are indicated by "*". Comparisons without "*" are between species. *P* values≤0.05 are considered significant

Standing Crop Method does not take into account decomposition, mortality or growth occurring after peak growth and the Milner and Hughes Method does not take into account decomposition or dead material. Likewise, another method, the Smalley Method (1959), does not account for decomposition, but records changes in live and dead plant material over time.

For a given species, the variation in productivity between various studies is not solely the result of differences in methodology, as other factors also determine productivity levels. Marshes of lower latitude are generally more productive than marshes of higher latitude, due to longer growing seasons and warmer climates in lower latitudes (Turner 1976). Reviews of past studies regarding aboveground biomass showed great variation depending upon harvest method, location of marsh, and year of harvest (Table 5). Aboveground biomass varied from 0.2 to 3.7, 0.1–3.7, 0.5–0.9, and 1.1–3.7 kg m^{-2} $year^{-1}$ for *S. alterniflora*, *S. patens*, *D. spicata*, and *P. australis,* respectively. The highest aboveground biomasses for *S. alterniflora* and *D. spicata* were recorded in Louisiana (Pezeshki and Delaune 1991), which could be due to a longer growing season as well as nitrogen enrichment (Turner 1976; Valiela et al. 1976; Goolsby et al. 2001). Year to year disparity in productivity of the same marsh is due to changes in physical and chemical properties of marsh sediment caused by variation in climate and tidal events that vary from year to year (Mendelssohn and Morris 2000).

Aboveground biomass for *S. alterniflora*, *D. spicata*, *S. patens* and *P. australis* in our study were 2.2±0.23, 1.2±0.09, 2.3±0.21, and 1.7±0.14 kg m^{-2}, respectively. Except for *D. spicata,* the biomass estimates for different species in our study falls within the range of the biomass estimates in other studies (Table 5).

Belowground Biomass, Root and Rhizome Characteristics

Generally, belowground biomass estimates are made by harvesting biomass many times a year throughout the season. Net belowground primary productivity is calculated by subtracting minimum recorded biomass from maximum

Table 5 Comparison of aboveground and belowground biomasses of our study with past studies

Marsh and/or location	Aboveground (kg m^{-2} $year^{-1}$)	Belowground (kg m^{-2} $year^{-1}$)	References
S. alteniflora			
Great Sippewissett Salt Marsh, Cape Cod	0.4–0.7	NA	(Valiela et al. 1975)
Great Sippewissett Salt Marsh, Cape Cod	0.4	3.5	(Valiela et al. 1976)
New Jersey marsh	0.4–0.5	11.0	(Smith et al. 1979)
Brunswick County, North Carolina	0.2 to 1.0	NA	(Shew et al. 1981)
Canary Creek Marsh and Black Bird Creek Marsh, Delaware Bay	0.5–1.5	4.3–7.7	(Roman and Daiber 1984)
Louisiana Gulf Coast	2.0–3.7	NA	(Pezeshki and Delaune 1991)
Narragansett Bay, various sites	0.3–2.4	3.5–17	(Wigand 2008)
New Jersey Meadowlands (*S. alterniflora* and *P. australis* were intermingling on the site)	0.7	0.6	(Windham et al. 2003)
MRMMB site, New Jersey Meadowlands	2.2±0.23	3.9±0.69	Our study
S. patens			
Great Sippewissett Salt Marsh, Cape Cod	0.5–0.7	NA	(Valiela et al. 1975)
Great Sippewissett Salt Marsh, Cape Cod	0.6	2.5	(Valiela et al. 1976)
Canary Creek Marsh and Black Bird Creek Marsh, Delaware Bay	0.1–1.4	2.5–7.3	(Roman and Daiber 1984)
Louisiana Gulf Coast	3.7	NA	(Pezeshki and Delaune 1991)
Narragansett Bay, various sites	0.2–1.1		(Wigand 2008)
LRM site, New Jersey Meadowlands	2.3±0.21	11.6±1.14	Our study
D. spicata			
Canary Creek Marsh, Delaware Bay	0.5–0.9	NA	(Roman and Daiber 1984)
SHS site, New Jersey Meadowlands	1.2±0.09	1.2±0.2	Our Study
Phragmites australis			
Black Bird Creek Marsh, Delaware Bay	1.7–3.7	5.1–6.4	(Roman and Daiber 1984)
New Jersey Meadowlands (*S. alterniflora* and *P. australis* were intermingling on the site)	1.1	1.2	(Windham et al. 2003)
LRM, New Jersey Meadowlands	1.7±0.14	8.0±0.5	Our study

recorded biomass (Roman and Daiber 1984; Darby and Turner 2008). However, our biomass harvest occurred during the mid-growing season (July).

Estimates of belowground biomass using a range of core diameters have shown that cores with a smaller diameter underestimate belowground biomass (Gross et al. 1991). In comparison to the area and depth harvested in many studies (Smith et al. 1979; Roman and Daiber 1984; Kirwan and Mudd 2012), greater area (25 cm by 25 cm plot) and greater depth (up to 55 cm down from soil surface) were reached in our study. Therefore, we assume that our harvest is giving a better estimate for belowground biomass than the belowground biomass estimates performed using a smaller core reaching only to a shallower soil depth.

As in aboveground biomass, review of past studies showed large variation in belowground biomass productivity depending on the location of the marsh and the year of harvest (Table 5). In these past studies, the belowground biomasses for *S. alterniflora*, *S. patens* and *P. australis* were 3.5–17, 2.5–7.3 and 1.2–6.4 kg m^{-2} $year^{-1}$, respectively. In our study, belowground biomasses for *S. patens* and *P. australis*, were greater than the biomasses reported in the past studies. The belowground biomass was estimated from a single harvest during the peak growing season, instead of estimating the belowground productivity by subtracting minimum recorded biomass from maximum recorded biomass from harvests done at different times of the year. This could have contributed to the high belowground biomass estimates for the two species in our study. We do not know how much belowground biomass is retained year to year in the marshes we studied, but in some other marshes, about 12–70 % of maximum belowground biomass is retained annually (Roman and Daiber 1984). The aboveground and belowground biomass estimates for *S. alterniflora* and belowground biomass for *P. australis* in our study are higher than estimates done in a different marsh of the NJM a decade earlier by Windham et al. (2003). They harvested the biomasses from a mixed patch of the same two species reaching only up to 30 cm below the soil surface using

a smaller corer. Conversely, we harvested *S. alterniflora* from a pure patch of a restored wetland and *P. australis* from a natural high marsh of the NJM. Also, we reached greater depth covering a greater area for belowground biomass estimates. Therefore, differences in location, species composition, depth and size of the harvested area, and the year of harvest between their and our study could have contributed for the differences in biomass estimates between the two studies. Except Windham et al. (2003), in all the other studies we reviewed (Table 5), biomasses were harvested from pure patches of a particular species. When our harvest data were compared with the biomass harvested from pure patches, belowground biomass in our study was at the lower end of the range reported in past studies for *S. alterniflora*. Belowground biomass of *D. spicata* was similar to aboveground biomass (Table 5). *Spartina alterniflora* and *D. spicata* were harvested from wetlands restored in 1999 and 2007, respectively. We expected that the plants growing in these recently restored wetlands have not had as much time as natural wetlands to accrue belowground biomass, resulting in lower belowground biomass for the species. Due to lower belowground biomass, the ratios of belowground to aboveground biomass were also lower for *S. alterniflora* and *D. spicata* in comparison to *S. patens* and *P. australis* harvested from a natural wetland in our study, as well as various past studies. We harvested belowground biomass up to 55 cm below the soil surface and found that most of the belowground biomass (both root and rhizome) was present closer to the soil surface (0–25 cm soil profile). This was also found by Darby and Turner (2008) for all the species, thus confirming our first hypothesis. The presence of the majority of the belowground biomass close to the soil surface suggests that most of the root effect on production, consumption and transport of CH_4 takes place at the wetland sediment to atmosphere interface. Porewater CH_4 measurements from one of our sites (site # 1; Reid et al. 2013) showed higher CH_4 concentration in deeper soil layers confirming that the root effect on methane oxidation and/or transportation should be lower in deeper soil due to a decreased root biomass in this region.

P. australis had more belowground biomass in the deeper soil region than any other species. Thus, the effect of belowground biomass on CH_4 dynamics should be greater for *P. australis* than the other plant species in the deeper soil profile. Our second hypothesis was that the diameters of rhizome and root, number of primary roots per node, and root surface area to volume ratio would be higher in *P. australis* than native *S. patens* and *D. spicata*. This hypothesis was partially confirmed. The number of primary roots per node was higher in *P. australis* than in *D. spicata* and *S. patens* but lower than in *S. alterniflora*. For rhizome and root diameters, *P. australis* was not different from *S. alterniflora,* but diameters were higher in *P. australis* than in *D. spicata* and *S. patens*. Davey et al. (2011) measured root and rhizome diameter of *S. alterniflora* at a marsh in Jamaica Bay, New York and found higher rhizome and root diameter in a deteriorating marsh than in a stable marsh in 10–20 cm soil depth. In 10–20 cm soil depth, only rhizome diameters were higher in a deteriorating marsh than in stable marsh. The rhizome diameter of *S. alterniflora* in our study was similar to the deteriorating marsh but root diameter in our study was smaller than in the marsh of Jamaica Bay.

In this study, root surface area to volume ratios were higher in *P. australis* than in *S. alterniflora,* but lower than in *D. spicata* and *S. patens*. Variation in rhizome and root diameters and number of primary roots per node of rhizome and root surface area to volume ratio could cause differences in surface area availability for CH_4 and O_2 exchange between wetland sediment and plant tissue. Differences in surface area might be one of the contributing factors that causes variation in production and release of CH_4 from wetlands that are dominated by different species (Emery and Fulweiler 2014), while the root and rhizome parameters can be useful for modeling CH_4 flux from the plant (Beckett et al. 2001).

Leaf Area Distribution and LAI

The leaf area distribution at various heights of canopy showed that most of the leaves were found at the mid-height of canopy in all studied species. A significant part of CH_4 produced in wetland sediment is transported by root and rhizome and released either from leaves or stems into the atmosphere (Van der Nat et al. 1998). The presence of most of the leaf area at canopy mid-height suggests that the leaf mediated CH_4 release from plant to atmosphere occurs mainly from mid-height of the plant canopy. The highest LAI in *S. alterniflora* and the lowest LAI in *S. patens* indicate that the former species has higher leaf area for CH_4 and other greenhouse gases release per unit ground area than the latter. Leaf area distribution at various heights of the canopy can be useful for modeling stomatal mediated greenhouse gas flux (Dai et al. 2004).

%N and Total C in Leaves; C/N in Roots, Rhizomes and Leaves

Quality of decomposing plant materials, as indicated by C/N ratio and C/lignin ratio, is an important factor affecting the affinity of decomposers to litter, which then affects CH_4 production as methanogens prefer litter low in C/N and C/lignin (Valentine et al. 1994; de Neiff et al. 2006). Higher C/N ratios in rhizomes than in leaves of the studied species suggests that methanogens prefer leaf litter over rhizomes. Although the nitrogen concentrations in leaf tissue of *S. alterniflora* and *P. australis* were similar to a previous study carried out in a different marsh of the NJM (Windham et al. 2003), they exhibited the opposite trend with *S. alterniflora*

having higher N than *P. australis*. In a previous study, it was shown that *P. australis* decomposes more slowly than *S. alterniflora*, thus building up more litter and sediment over time (Windham et al. 2004). In our study, the opposite response may be expected due to a lower C/N ratio in *P. australis* than *S. alterniflora*.

Conclusion

The aboveground biomass of *S. alterniflora*, *S. patens* and *P. australis* in this study were within the range of biomasses reported in the literature from various locations. *D. spicata* had higher aboveground biomass than earlier studies. Likewise, belowground biomass for *S. patens* and *P. australis,* which were harvested from natural wetlands, were greater than previously estimated. This higher biomass could be due to harvesting belowground biomass from a single harvest in peak season, rather than estimating belowground productivity by subtracting minimum recorded biomass from maximum recorded biomass by harvesting the biomass multiple times a year. However, *S. alterniflora* and *D. spicata*, which were harvested from recently restored wetlands, have had low belowground biomass, resulting in a lower belowground to aboveground biomass ratio than previous studies indicate. Recently restored wetlands do not have as much time as natural wetlands to accrue belowground biomass, likely contributing to the low belowground to aboveground biomass ratio in *S. alterniflora* and *D. spicata*. The majority of the belowground biomass (both root and rhizome) were found in the region close to the soil surface, suggesting that most of the effect of belowground biomass on production, consumption and transport of CH_4 and other greenhouse gases takes place in the soil close to its surface. In a deeper soil region, the effect of belowground biomass on CH_4 dynamics is likely to be greater under *P. australis* than under other species, as *P. australis* had more belowground biomass than the other species at this soil region. For all species, most of the leaf area was found at canopy mid-height, suggesting that most of the leaf-mediated greenhouse gas emission occurs in this region. Variation in rhizome and root diameter, number of primary roots per node of rhizome, and root surface area to volume ratio between species may be some of the contributing factors that lead to variations in CH_4 release from wetlands of different species as root and rhizome characteristics affect CH_4 and O_2 exchange between wetland sediment and plant tissue. Above- and belowground tissues of the species differ in substrate quality, suggesting that different species can have different effects on methanogenic activity, even if they have the same amount of a particular tissue. More importantly, the belowground plant characteristics as well as LAI we reported in this study can be useful for modeling CH_4 and other greenhouse gas transport.

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