



Estimation of short-term C-fixation in a New England temperate tidal freshwater wetland



Gailynn Milligan^a, Helen M. Poulos^{b,*}, Martha S. Gilmore^a, Graeme P. Berlyn^c, Joseph Milligan^{a,d}, Barry Chernoff^{a,b,e}

^a Department of Earth and Environmental Sciences, Wesleyan University, Middletown, CT 06459, United States

^b College of the Environment, Wesleyan University, Middletown, CT 06459, United States

^c Yale School of Forestry and Environmental Studies, New Haven, CT 06511, United States

^d Department of Geology, Baylor University, Waco, TX 76798, United States

^e Biology Department, Wesleyan University, Middletown, CT 06459, United States

ARTICLE INFO

Keywords:

Environmental science
Plant biology
Ecology

ABSTRACT

Wetlands provide myriad ecosystem services, yet the C-cycling of vegetation within interior freshwater tidal wetlands remains poorly understood. To this end, we estimated species-specific plant carbon-fixation rates for the six dominant wetland plant species in a large temperate freshwater wetland in Connecticut, USA. We integrated field C-fixation rates for dominant marsh plant species with satellite-derived leaf area index and wetland aerial extent data to: 1) quantify seasonal and species-level differences in wetland plant C-fixation rates; and 2) estimate whole-marsh emergent aquatic plant C-fixation rates over the growing season. Photosynthetic rates differed significantly by species and month ($P < 0.05$). *Acorus calamus* had the highest photosynthetic rate between May and September, and *Acer saccharinum* had the lowest. By integrating field photosynthetic data with wetland aerial extents, we estimated that the total annual C uptake by the vegetation in this wetland, which was 2868 Mg C. Herbaceous vegetation contributed to most of that stock (herbaceous vegetation = 2099.2 Mg C, forest = 769.6 Mg C), although soil respiration likely offset those numbers substantially. Our results demonstrate the importance of short-term above-ground freshwater wetland C-fixation, and that the emergent vegetative component of these wetland systems are key components of the tidal freshwater wetland C cycle.

1. Introduction

Wetlands are major global carbon sinks that continue to be threatened by a variety of anthropogenic stressors (Mitra et al., 2005; Bridgman et al., 2006; Kayranli et al., 2010; Mitsch et al., 2013). Over half of the world's wetlands have been lost over the last two centuries, and 98% of these losses have occurred in freshwater wetlands (Zedler and Kercher, 2005). Large-scale wetland conversion to other land uses converts a global C-sink to a source (Pant et al., 2003; Mitsch and Gosselink, 2007). Thus, the world's remaining freshwater wetlands provide an important ecosystem service; they mitigate global climate change by fixing C from the atmosphere and storing it in plant tissues and below-ground sediments (Mcleod et al., 2011; Mitsch et al., 2013).

Wetland ecosystems sequester carbon over decades in biomass, and for centuries to millennia in sediments (Lavery et al., 2013; Chmura et al., 2016). While the organic carbon storage capacity of wetland sediments

accounts for nearly one-third of the world's total soil organic carbon pool to 1 m depth (450×10^{15} g out of the estimated 1550×10^{15} g) (Mitsch and Gosselink, 2000; Lal, 2008), the above-ground carbon fixation potential of wetland vegetation is also considerable via photosynthesis (Lal, 1997; Adhikari et al., 2009), and root exudation of photosynthate into wetland sediments (Wu et al., 2012). Wetlands ameliorate the effects of climatic change by sequestering, accreting, and holding large amounts of C in pools that often exceed terrestrial C sinks (Mitsch and Gosselink, 2000; Chmura et al., 2003; Duarte et al., 2005; Mcleod et al., 2011). While the anoxic conditions of most wetlands also make them a CH₄ emissions source (Whiting and Chanton, 2001; Weston et al., 2014), Mitsch et al. (2013) demonstrated that the world's wetland vegetation serves as a net C sink, and that the net wetland C accumulation rate offsets up to 12% of annual global fossil fuel combustion.

The 2013 IPCC Wetlands Supplement provided a first estimate of the wetland C stocks and their various compartments (Hiraishi et al., 2014).

* Corresponding author.

E-mail address: hpoulos@wesleyan.edu (H.M. Poulos).

<https://doi.org/10.1016/j.heliyon.2019.e01782>

Received 8 January 2019; Received in revised form 25 February 2019; Accepted 17 May 2019

2405-8440/© 2019 Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

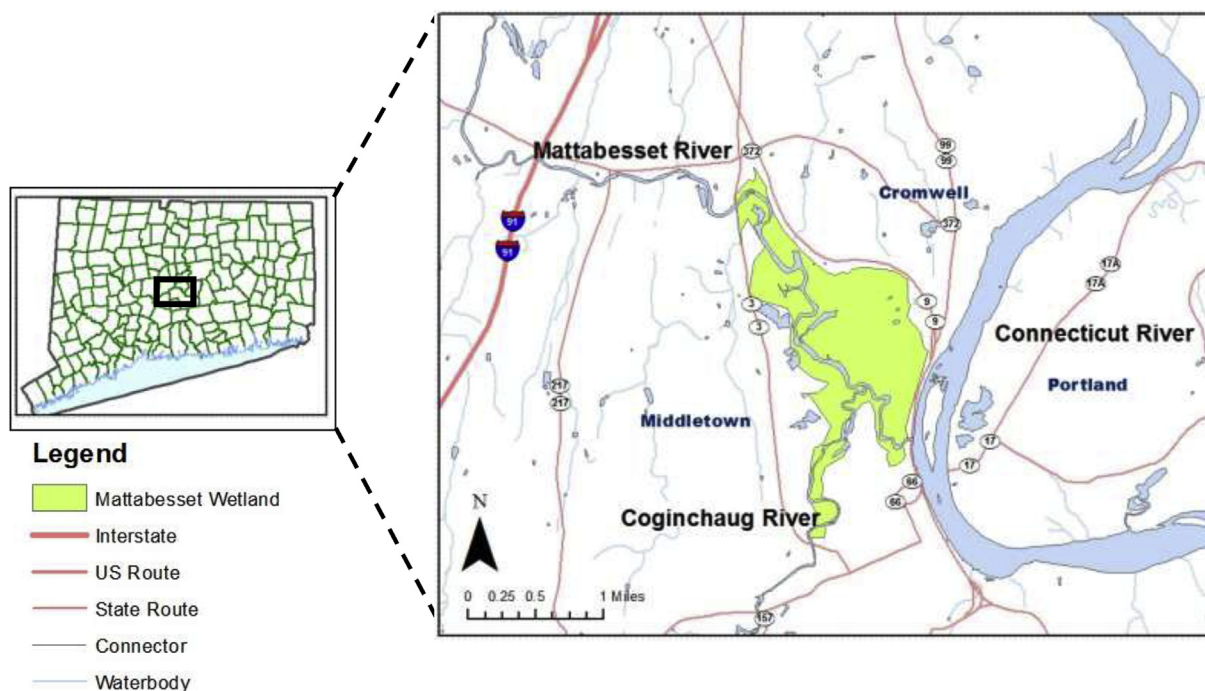


Fig. 1. Map of the Mattabesett wetland in Connecticut, U.S.A.

However, IPCC values in the supplement were focused on soil and biomass C content only, and not on C-fixation rates of aboveground wetland vegetation. Although, wetlands have been recognized as important C sinks over the last few decades (Grimsditch et al., 2013; Siikamäki et al., 2013; Thomas, 2014), wetland carbon sequestration capacity can vary substantially due to differences in wetland plant species composition, area, climate, and environmental setting (Mitsch and Gosselink, 2000; Junk, 2002; Bernal and Mitsch, 2008, 2012).

Wetland carbon cycle science has focused heavily on mangroves, salt marshes, and seagrass beds, although freshwater wetlands account for a significant portion ($5.3 \times 10^6 \text{ km}^2$) of total wetland area (Matthews and Fung, 1987), and they comprise some of the most productive ecosystems in the world (Odum et al., 1984a; Odum, 1988; Mcleod et al., 2011). Freshwater tidal wetlands, in particular, lack the stressful salinity levels of coastal wetlands, which promotes high productivity, high photosynthetic rates, and species diversity (Odum, 1988; Megonigal and Neubauer, 2009; Pasternack, 2009).

Wetlands have a large standing stock of biomass that contributes to the C pool through C-fixation, as demonstrated by eddy covariance measurements across a global set of wetland sites (Lu et al., 2017). Yet, species-specific C-fixation rates and their contributions to whole-marsh C-cycling remain poorly understood in tidal freshwater wetlands (Weston et al., 2014). Landscape-scale assessments of above-ground plant C-fixation rates have the potential to refine local- and regional-scale estimates of C-cycling in understudied compartments of the C-pool, such as that which is fixed and stored in fringe forest and emergent aquatic vegetation. Moreover, field-based measurements of plant photosynthetic rates in wetlands are few because wetland fieldwork is extremely labor intensive, costly, time-consuming and many areas are often difficult to sample due to poor accessibility and frequent inundation (Adam et al., 2009; Samaritani et al., 2011).

In this study, we examined species-specific differences in plant photosynthetic rates among six wetland plants in the tidal Mattabesett Freshwater Wetland in central Connecticut, USA. We then extrapolated these measurements to the wetland-scale using aerial extents of fringe forest and emergent aquatic vegetation to estimate the C-sequestration potential of the vegetative component of the wetland over the growing season. The objectives of this study were to: i) quantify the

photosynthetic rates and C-sequestration of the six dominant wetland plant species in the Mattabesett Wetland; and ii) extrapolate annual the C-fixation the wetland from the leaf-to the wetland-scale.

2. Methods

2.1. Site description

The Mattabesett Wetland ($41^\circ 34'N$, $72^\circ 39'W$) is a 351-hectare tidal freshwater marsh (Fig. 1). The wetland is located at the confluence of the Coginchaug and the Mattabesett Rivers in Connecticut, 1.6 km upstream from the intersection with the Connecticut River (Metzler and Rosza, 1982). Semidiurnal tides extend throughout the area and the marsh experiences complete inundation during early spring because of snow melt- and rainfall-induced floods. Connecticut has a climate that is characterized by cold, wet winters and warm, humid summers. Temperatures vary by season, with a mean annual temperature of $8\text{--}10^\circ\text{C}$ and the average annual precipitation is 76–127 cm, based on data records for Bradley International Airport, Connecticut National Climate Data Center.

The Mattabesett wetland is a mature tidal freshwater marsh that has distinct zonation with vegetation typical of a high (less inundated) and low (almost constantly inundated) marsh. It hosts diverse group of annuals and perennials, including, broad leafed emergent macrophytes, annual and perennial sedges, grasses, and herbaceous annual plants. Plant species distributions in the wetland vary in accord with seasonal and local environmental variation. Six perennial plant species dominate the Mattabesett wetland including: *Acer saccharinum* L. (silver maple), *Acorus calamus* L. (sweet flag), *Zizania aquatica* L. (Wild Rice), *Peltandra virginica* (L.) Schott (arrow arum), *Pontederia cordata* L. (pickerelweed), and *Nuphar advena* L. (spatterdock). Spatterdock, seen early in the growing season, can be found in distinctively pure stands adjacent to open water, where they are often submerged during high tides, and arrow arum and pickerelweed grow during the spring into early summer and are most common in the low marsh (Odum et al., 1984a). Pickerelweed is distributed in more clumped patches compared to arrow arum, but both species are adapted to long periods of inundation (Odum et al., 1984a). Arrow arum, spatterdock, and pickerelweed were present throughout the 2015 growing season. Wild rice, a tall grass species that

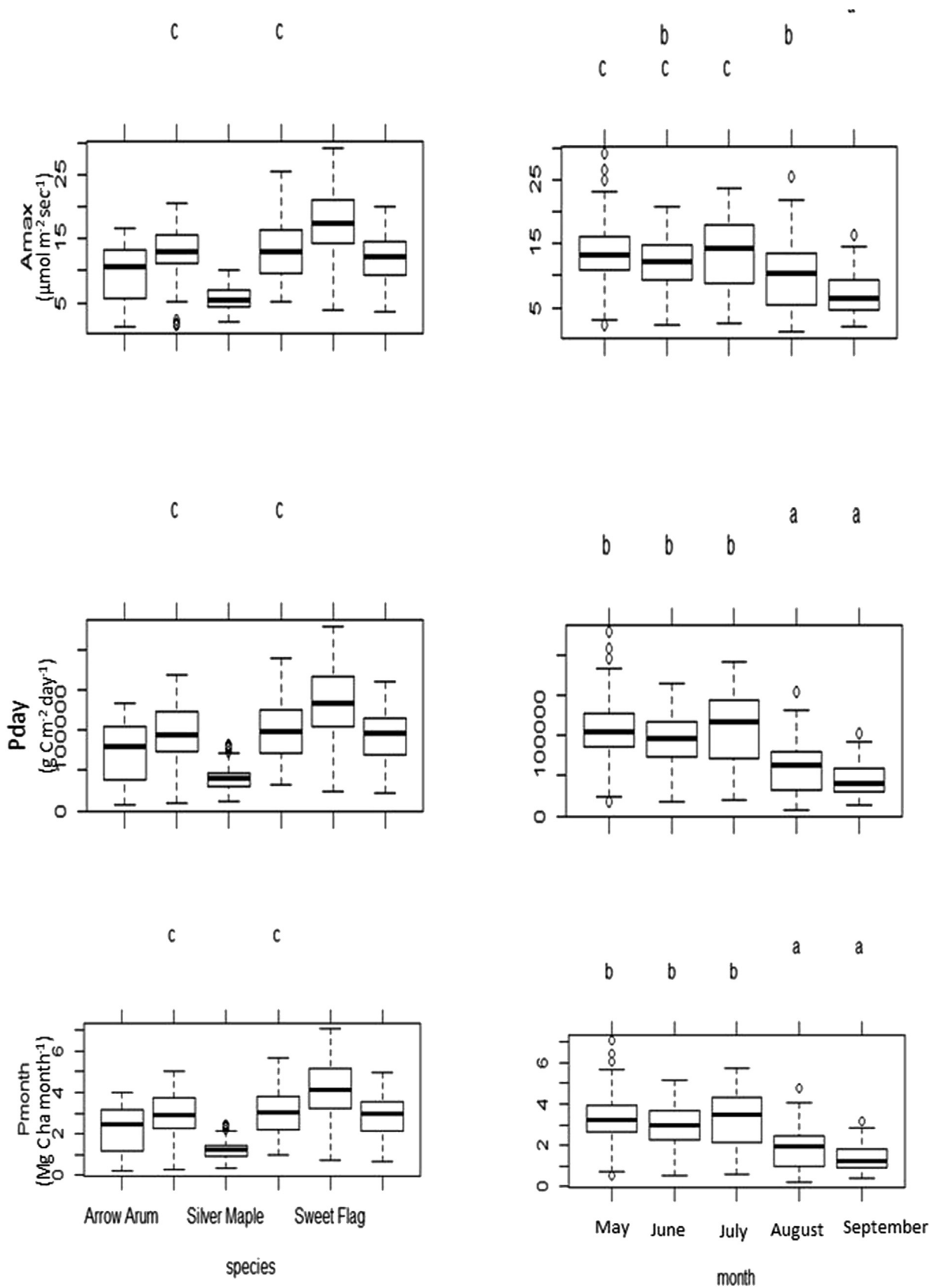


Fig. 2. Mean \pm S.E. A_{max} , P_{day} , and P_{month} by species and month. Significant pairwise differences are noted by letters. Species and months that do not share letters are significantly different at $P < 0.05$ according to Tukey's HSD tests.

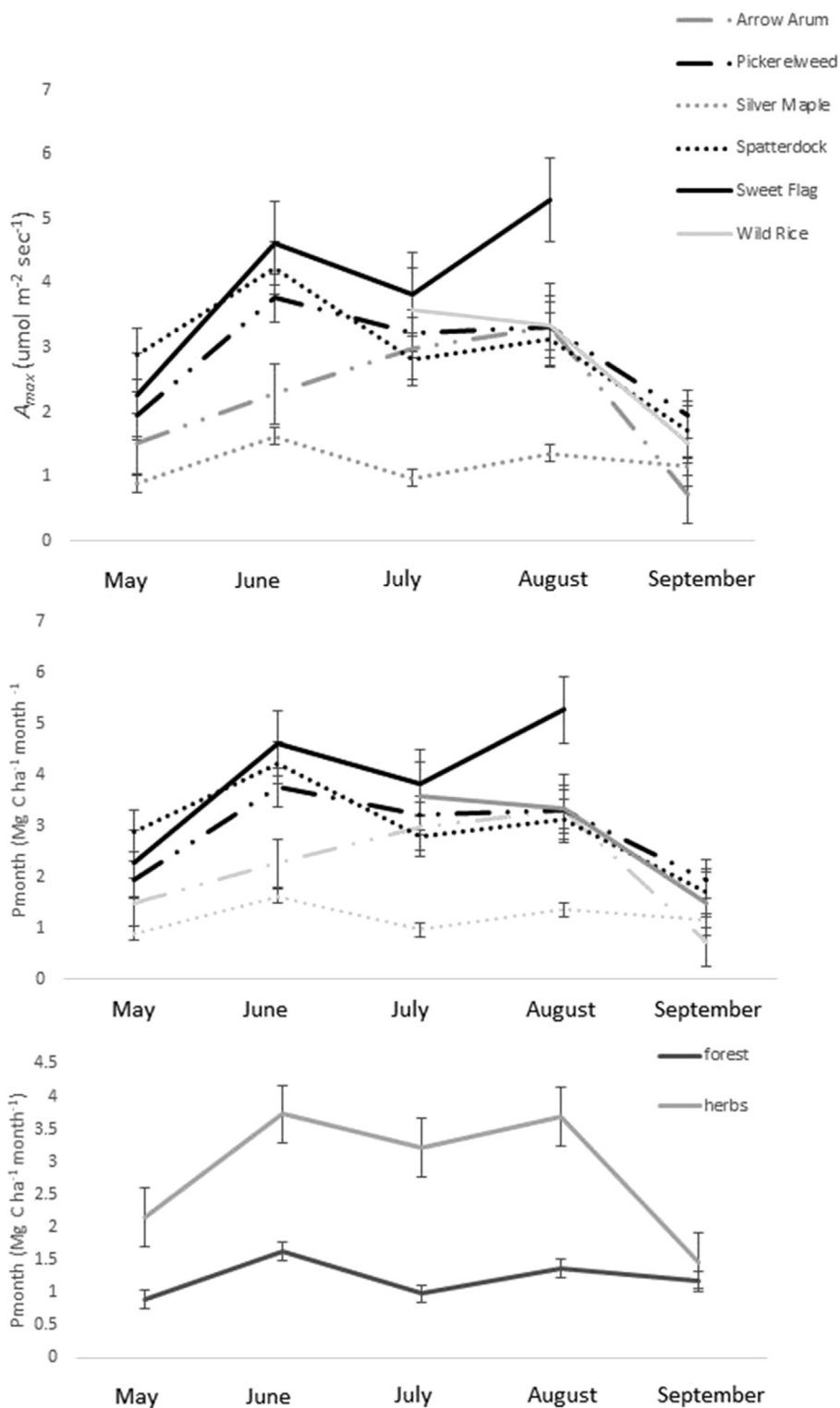


Fig. 3. Mean \pm S.E. A_{max} , P_{day} and P_{month} by species and vegetation cover-type by month.

can grow to be 1–4 meters tall, is widely distributed throughout the marsh, but this species is usually not noticeable until August or September because it is overtopped by other species before that time (Odum et al., 1984a). Sweet flag can be seen throughout the marsh starting in May and disappearing before the end of August, whereas silver maples are found on the fringes of the marsh year-round.

2.2. Photosynthesis measurements

All photosynthesis measurements were taken using a LI-COR 6400® (LI-COR, Inc., Lincoln, NE) portable infrared gas analyzer. Saturating light levels were determined for each species via light saturation curves (on three randomly-selected individuals per species) prior to taking field photosynthesis measurements (*A. saccharinum*, *A. calamus*, and *Z. aquatica* = $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, *P. virginica* and *N. advena* = $1200 \mu\text{mol}$

Table 1

ANOVA model (coefficients (estimate), and 95th percentile confidence intervals (CI) of the effects of species, month and their interaction on maximum daily photosynthetic rate (A_{max} ; $\mu\text{mol m}^{-2} \text{leaf sec}^{-1}$), daytime net carbon fixation, or photosynthetic production (P_{day} ; $\text{Mg C ha}^{-1} \text{day}^{-1}$), and total monthly carbon uptake (P_{month} ; $\text{Mg C ha}^{-1} \text{month}^{-1}$) Significant post-hoc pairwise differences among species and months for these variables are displayed in Fig. 2.

term	A_{max}			P_{day}			P_{month}		
	Estimate	CI	p	Estimate	CI	p	Estimate	CI	p
species									
(Intercept)	15539.91	5344.35–45185.83	<.001	Inf	Inf – Inf	<.001	9.45	7.19–12.43	<.001
Pickereelweed	24.27	5.19–113.59	<.001	Inf	Inf – Inf	<.001	1.98	1.33–2.94	<.001
Silver Maple	0.02	0.00–0.08	<.001	0	0.00–0.00	<.001	0.37	0.25–0.54	<.001
Spatterdock	43.82	9.69–198.28	<.001	Inf	Inf – Inf	<.001	2.24	1.52–3.30	<.001
Sweet Flag	2238.36	438.37–11429.33	<.001	Inf	Inf – Inf	<.001	6.21	4.09–9.44	<.001
Wild Rice	11.17	1.76–70.97	0.011	Inf	Inf – Inf	0.025	1.77	1.10–2.84	0.019
month									
(Intercept)	27.08	20.16–36.38	<.001	Inf	Inf – Inf	<.001	27.08	20.16–36.38	<.001
july	0.67	0.45–1.01	0.056	0	0.00 – Inf	0.059	0.67	0.45–1.01	0.056
june	1.01	0.68–1.50	0.964	Inf	0.00 – Inf	0.559	1.01	0.68–1.50	0.964
may	0.25	0.16–0.38	<.001	0	0.00–0.00	<.001	0.25	0.16–0.38	<.001
september	0.15	0.10–0.23	<.001	0	0.00–0.00	<.001	0.15	0.10–0.23	<.001
interactions									
monthjuly:speciesPickereelweed	1.26	0.53–2.98	0.605	Inf	0.00 – Inf	0.604	1.26	0.53–2.98	0.605
monthjune:speciesPickereelweed	4.41	1.94–10.05	<.001	Inf	Inf – Inf	<.001	4.41	1.94–10.05	<.001
monthmay:speciesPickereelweed	1.54	0.63–3.80	0.347	Inf	0.00 – Inf	0.348	1.54	0.63–3.80	0.347
monthseptember:speciesPickereelweed	3.38	1.37–8.32	0.009	Inf	Inf – Inf	0.009	3.38	1.37–8.32	0.009
monthjuly:speciesSilver Maple	0.95	0.40–2.25	0.91	0	0.00 – Inf	0.914	0.95	0.40–2.25	0.91
monthjune:speciesSilver Maple	3.72	1.63–8.46	0.002	Inf	Inf – Inf	0.002	3.72	1.63–8.46	0.002
monthmay:speciesSilver Maple	3.85	1.56–9.47	0.004	Inf	Inf – Inf	0.004	3.85	1.56–9.47	0.004
monthseptember:speciesSilver Maple	10.86	4.41–26.74	<.001	Inf	Inf – Inf	<.001	10.86	4.41–26.74	<.001
monthjuly:speciesSpatterdock	1.02	0.45–2.32	0.966	2E+258	0.00 – Inf	0.965	1.02	0.45–2.32	0.966
monthjune:speciesSpatterdock	8.63	3.79–19.65	<.001	Inf	Inf – Inf	<.001	8.63	3.79–19.65	<.001
monthmay:speciesSpatterdock	4.87	1.98–11.99	<.001	Inf	Inf – Inf	<.001	4.87	1.98–11.99	<.001
monthseptember:speciesSpatterdock	3.18	1.29–7.83	0.012	Inf	Inf – Inf	0.013	3.18	1.29–7.83	0.012
monthjuly:speciesSweet Flag	0.33	0.14–0.78	0.013	0	0.00–0.00	0.013	0.33	0.14–0.78	0.013
monthjune:speciesSweet Flag	1.47	0.65–3.35	0.356	Inf	0.00 – Inf	0.27	1.47	0.65–3.35	0.356
monthmay:speciesSweet Flag	0.3	0.12–0.75	0.01	0	0.00–0.00	0.011	0.3	0.12–0.75	0.01
monthjuly:speciesWild Rice	1.78	0.75–4.22	0.192	Inf	0.00 – Inf	0.185	1.78	0.75–4.22	0.192
monthseptember:speciesWild Rice	2.11	0.86–5.21	0.104	Inf	0.00 – Inf	0.106	2.11	0.86–5.21	0.104
Observations	305			305			305		

PAR $\text{m}^{-2} \text{s}^{-1}$, and $P. cordata = 800 \mu\text{mol m}^{-2} \text{s}^{-1}$). For the six different species, maximum photosynthesis at saturating light intensity (A_{max}) was measured on healthy, mature, and fully-expanded leaves following Sutton-Grier and Megonigal (2011). A_{max} was measured on a single leaf from each of 10–15 individual plants for each of the six species, on the 15th of each month throughout the growing season (May–September 2015) Healthy individuals of each species were randomly selected from within homogeneous and monospecific stands of vegetation throughout the wetland. Photosynthesis measurements were taken between 8:00 AM and 12:00 PM during the peak of photosynthetic activity and leaves were patted dry with paper towels prior to taking measurements. We dug up all emergent aquatic plant specimens, leaving the roots intact, and we immediately placed them in buckets of water prior to taking measurements. This was done because it was impossible to take photosynthesis measurements on the plants in-situ because they were growing in standing water and had wet leaves. We transported individuals to nearby areas of exposed bare wetland soil where the Licor was stationed on a large piece of plywood to prevent it from sinking into the sediment. A_{max} was measured immediately upon digging up each plant in an effort to minimize changes in leaf structure and physiology as result of harvesting. A_{max} , stomatal conductance, transpiration, and intracellular CO_2 concentrations were recorded for each plant. The leaf chamber CO_2 concentrations were matched to the reference chamber prior to each A_{max} measurement. The CO_2 concentration of the chamber was kept at a constant $400 \mu\text{mol CO}_2 \text{mol}^{-1}$ using a CO_2 mixing chamber, the flow was maintained at $500 \mu\text{mol s}^{-1}$, and the relative humidity varied throughout the growing season between 37–68%. The leaves of all species filled the entire 2×3 cm chamber head, so leaf area corrections were not necessary.

2.3. Net plant photosynthetic production

Daytime net carbon fixation, or photosynthetic production (P_{day}), was estimated for each plant species following Clough et al. (1997) using leaf area index (LAI) and A_{max} data. Field A_{max} values for each individual plant in each sampling interval were used to calculate species-specific P_{day} for each day, each month, and over the entire growing season, from May through September. We calculated daytime net carbon fixation as $P_{day} = 0.0432 * d * L * A$, where P_{day} = daytime net carbon fixation in $\text{g C m}^{-2} \text{ha}^{-1} \text{day}^{-1}$, d was daylength in hours (h), L was LAI for the month corresponding to the field sampling interval, A , was the average rate of net photosynthesis for the whole canopy ($\mu\text{mol CO}_2, \text{m}^{-2} \text{leaf s}^{-1}$) and the coefficient, 0.0432, converted A , from units of $\mu\text{mol CO}_2, \text{m}^{-2} \text{leaf s}^{-1}$ to units of $\text{g C m}^{-2} \text{leaf h}^{-1}$. We assumed that active photosynthesis occurred between the hours of 8:00 am and 12:00 pm, based on our field observations of stomatal conductance initiation and cessation over the mornings of our instantaneous A_{max} measurements. Thus, we used 4 hours (h) as a conservative estimate of the duration of diurnal photosynthetic production. Monthly composite LAI data were obtained from 500-m resolution monthly MODIS (Moderate Resolution Imaging Spectroradiometer) fPAR/LAI data for each month of the 2015 growing season (<https://lpdaac.usgs.gov/>). LAI data were separated by forested and emergent aquatic vegetation cover types within the Mattabesett wetland. Geospatial forest and emergent aquatic vegetation coverages for the Mattabesett were obtained from the National Wetlands inventory, US Fish and Wildlife Service, (<https://www.fws.gov/wetlands/data/google-earth.html>) and used for total annual wetland carbon fixation rate estimates. For each monthly LAI composite, we calculated a zonal LAI mean of the forest and emergent vegetation pixels within the Mattabesett,

separately, using zonal statistics in the spatial analyst toolbox in ArcMap (ESRI, 2017). The mean values among all pixels in the emergent and forest wetland cover types were used as the L term in the calculation of P_{day} for herbaceous and forest vegetation types separately.

Total and species-specific monthly net carbon fixation rates (P_{month}) were calculated in $\text{Mg C ha}^{-1} \text{ month}^{-1}$ by species and by vegetation type by multiplying the P_{day} values for each specimen by the number of days in each month of the growing season. Total annual net carbon fixation rates (P_{ann}) were then calculated for each species, vegetation type, and for the entire wetland by adding the P_{month} values for each month over the growing season. Only those species that were present at each sampling interval were used in this calculation (i.e. wild rice was not included in months prior to August, and sweet flag was absent in September). Finally, we calculated the total net annual carbon fixation for the aerial coverage of each vegetation type and over the entire wetland over one year by multiplying P_{ann} by the area of forest (127.3 ha), emergent aquatic vegetation (147.2 ha), and the entire vegetated portion of the wetland (274.5 ha), which were derived from the National Wetlands Inventory data for the Mattabesett wetland.

2.4. Statistical analysis

Species-specific differences in A_{max} , P_{day} and P_{month} were evaluated using by one-way analysis of variance (ANOVA); post-hoc comparisons were calculated with Tukey's Honest Significant Differences (HSD). All statistical analyses were performed with R statistical software, version 3.2.3 and the multcomp package for post-hoc pairwise comparisons (R Development Core Team, 2017).

3. Results

3.1. Wetland plant photosynthetic rates

A_{max} varied significantly by species ($F = 45.49$, $P < 0.0001$), month ($F = 15.329$, $P < 0.0001$), and for the interaction term between species and month ($F = 27.67$, $P < 0.0001$) (Figs. 2 and 3, Table 1). Sweet flag had the highest mean photosynthetic rate ($17.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), followed by spatterdock ($13.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), pickerelweed ($12.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), wild rice ($12.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), arrow arum ($9.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and silver maple ($5.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), respectively. Daily and monthly carbon fixation rate patterns mirrored those of the A_{max} values.

Individual species' C-assimilation rates also differed significantly over the growing season ($P < 0.05$, Fig. 3). Photosynthetic rates were significantly higher in July and August than other months for all species but spatterdock ($P < 0.05$). Silver maple had significantly lower photosynthetic rates than the herbaceous species over all months of the growing season except September ($4.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $6.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $4.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and $5.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively) when arrow arum dropped lower than silver maple ($3.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ vs. $5.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively). Sweet flag had the highest mean A_{max} and P_{month} values in June, July, and August, whereas spatterdock and pickerelweed had the highest rates for May and September, respectively (Fig. 3).

Total monthly carbon uptake (P_{month}) was significantly higher for herbaceous vegetation relative to forest ($P < 0.0001$) for all months except September (Fig. 4, Table 2). Mean P_{month} was 1.9 Mg C ha^{-1} for May, 3.3 Mg C ha^{-1} in June, 2.9 Mg C ha^{-1} in July, 3.3 Mg C ha^{-1} in August, and 1.4 Mg C ha^{-1} in September with an overall average of 2.7 Mg C ha^{-1} across the growing season for all species. The total annual above-ground C-sequestration of the 274-ha wetland was 2868.9 Mg C , with herbaceous vegetation sequestering 2099.2 Mg C and forest sequestering 769.7 Mg C over 147.2 and 127.3 ha of wetland area, respectively.

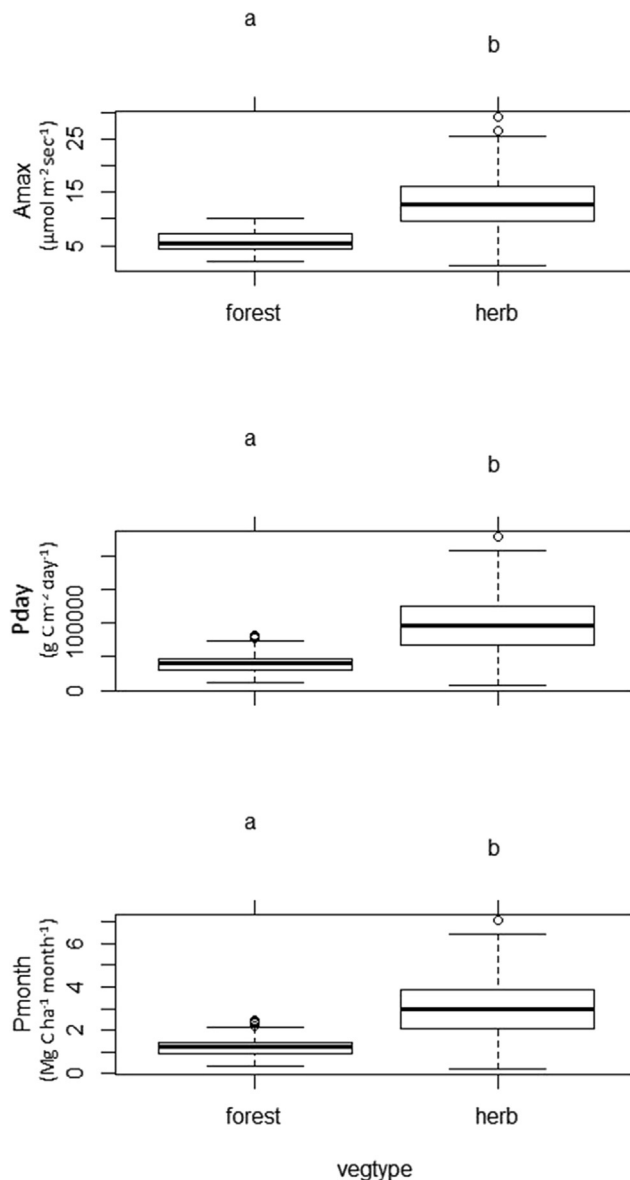


Fig. 4. Mean \pm S.E. A_{max} , P_{day} , and P_{month} of herbaceous versus forest vegetation. Vegetation types that do not share letters are significantly different at $P < 0.05$ according to Tukey's HSD tests.

4. Discussion

The results of this study demonstrate the C-fixation capacity of wetland vegetation, and our numbers compare well with C-fixation rates of other wetland species elsewhere (e.g., Dai and Wiegert, 1996; Clough et al., 1997). Our use of fine-scale field data and freely-available imagery over the entire growing season provides an estimate of growing-season biomass C-fixation potential for a temperate freshwater wetland. Such methods are important for informing wetland carbon cycle science, especially since most current wetland carbon research focuses on long-term sedimentary organic carbon stocks and accretion rates, but not on the C-fixation of the living biomass within the wetlands themselves.

The annual C-sequestration rates of the vegetation in the Mattabesett wetland are within the range of other coarser-resolution satellite-derived net primary productivity (NPP) estimates for the study area (i.e. MODIS NPP, <https://lpdaac.usgs.gov/>), which averaged $9.1 \pm 0.25 \text{ g C m}^{-2} \text{ day}^{-1}$ for our field-based estimates compared to a mean seasonal NPP of

Table 2

ANOVA model (coefficients (estimate), and 95th percentile confidence intervals (CI) of the effects of vegetation type (forest or herbaceous), month and their interaction on A_{max} ($\mu\text{mol m}^{-2}$ leaf sec^{-1}), P_{day} ($\text{Mg C ha}^{-1} \text{ day}^{-1}$) and P_{month} ($\text{Mg C ha}^{-1} \text{ day}^{-1}$). Significant post-hoc pairwise differences among species and months for these variables are displayed in Fig. 3.

	A_{max}			P_{day}			P_{month}		
	Estimate	CI	p	Estimate	CI	p	Estimate	CI	p
(Intercept)	3.91	2.20–6.94	<.001	Inf	Inf – Inf	<.001	3.91	2.20–6.94	<.001
vegtypeherb	10.21	5.44–19.16	<.001	Inf	Inf – Inf	<.001	10.21	5.44–19.16	<.001
month									
monthjuly	0.68	0.30–1.53	0.35	0	0.00 – Inf	0.356	0.68	0.30–1.53	0.35
monthjune	1.3	0.62–2.74	0.486	Inf	0.00 – Inf	0.406	1.3	0.62–2.74	0.486
monthmay	0.62	0.28–1.41	0.257	0	0.00 – Inf	0.262	0.62	0.28–1.41	0.257
monthseptember	0.84	0.36–1.93	0.677	0	0.00 – Inf	0.681	0.84	0.36–1.93	0.677
vegtypeherb:monthjuly	0.93	0.38–2.25	0.874	0	0.00 – Inf	0.878	0.93	0.38–2.25	0.874
vegtypeherb:monthjune	0.8	0.35–1.82	0.596	0	0.00 – Inf	0.72	0.8	0.35–1.82	0.596
vegtypeherb:monthmay	0.35	0.14–0.85	0.022	0	0.00–0.00	0.024	0.35	0.14–0.85	0.022
vegtypeherb:monthseptember	0.13	0.05–0.32	<.001	0	0.00–0.00	<.001	0.13	0.05–0.32	<.001
Observations	305			305			305		

$6.25 \pm .14 \text{ g C m}^{-2} \text{ day}^{-1}$ for 2015 MODIS imagery covering the Mat-tabesett wetland. These results highlight the utility of the fine-scale productivity estimates calculated herein, and they also suggest that the satellite-derived data products may underestimate freshwater tidal wetland NPP. This is particularly important given that most satellite-derived NPP data products are restricted to greater than 500 m^2 spatial resolution, and may include mixed pixels including other non-wetland land cover types. We acknowledge that a portion of this wetland C-sequestration may be offset by wetland respiration and CH_4 emissions. Long-term eddy covariance, soil/root respiration, and CH_4 emissions measurements would likely also inform the source-sink nature of freshwater wetland metabolism. We also note that only a small fraction of the carbon that is stored in the plant biomass will be subsequently trapped in the soil sediments over long time-scales due to export of plant materials out of the wetland and decomposition (Middelburg et al., 1997; Mcleod et al., 2011), however some of the above-ground plant material will likely be incorporated into below-ground sedimentary organic carbon stocks for long-term organic carbon storage.

Freshwater tidal wetlands comprise highly diverse plant communities (Odum et al., 1984a, 1984b; Odum, 1988). Wetland vegetation varied in its maximum carbon sequestration rate both by species and by growing season month, although herbaceous emergent vegetation displayed higher C-sequestration capacity of relative to wetland fringe forest throughout the entire growing season. This demonstrates the greater instantaneous C-sequestration capacity of herbaceous vegetation relative to nearby terrestrial vegetation types, although, their uptake could be offset by the higher lability of the carbon compounds in their plant structures (Odum and Heywood, 1978). At the same time, all of the herbaceous species in the study had root systems that were directly anchored within the sediments and translocation of photosynthate into the sediments through root exudation likely supplied direct inputs of organic carbon into the sediments where they could be stored over the long-term in the sedimentary carbon pools. In contrast, since silver maple is a woody plant, the species itself likely comprises a longer-term C-sink than the other four herbaceous species due to greater C-storage in woody plant tissues over the short term (Mcleod et al., 2011). However, upon tree death, rapid reemission of CO_2 into the atmosphere during woody plant decomposition relative to the slow underwater decomposition of herbaceous plant matter as it incorporates into sediments is a well-known explanation for the high and long-term C-capture of wetlands worldwide (Mcleod et al., 2011; Siikamäki et al., 2013). Thus, the high instantaneous C-fixation rate of herbaceous emergent wetland vegetation relative to terrestrial forests may partially explain why wetlands represent one of the largest C sinks in the world.

Our data highlight the importance of examining the fine-scale spatiotemporal and compartmental variation in wetland carbon cycling

in tidal freshwater wetlands. While much emphasis has been placed on quantifying long-term sedimentary organic C stocks in wetlands, annual wetland productivity is also an important component of wetland C-cycling as photosynthesis represents the major C input to these systems. Quantifying wetland carbon-fixation can inform policy makers about the importance of wetlands and their need for preservation (Hewson et al., 2013; Hiraishi et al., 2014), although additional wetland respiration studies would add to our knowledge of C flux in freshwater tidal wetlands. Our results emphasize that, in addition to the contribution of the below-ground C-holding capacity of freshwater tidal wetlands, photosynthesis provides the primary inputs into the organic C cycle. Wetland plants will continue to be important components of the global C-budget under climatic change, although higher temperatures may also increase CH_4 emissions in wetlands (Whiting and Chanton, 2001), and influence their C sink-source dynamics. Nonetheless, freshwater wetlands are important C sinks that are major players in buffering the effects of climate change (Chmura et al., 2003; Choi and Wang, 2004; Duarte et al., 2005; Chmura, 2013; Howard et al., 2014; Marín-Muñiz et al., 2014). Such wetland ecosystems are important for the national greenhouse gas inventory because coastal wetlands represent significantly larger C-sinks than interior wetlands (Lu et al., 2017), although their location near the coast also makes them vulnerable to a variety of anthropogenic stressors (Duarte et al., 2005; Mitsch et al., 2013). Therefore, intensive management is required to conserve and protect these coastal ecosystems to preserve the long-term security of these carbon sinks.

5. Conclusions

The method employed herein has the potential for application elsewhere in temperate wetlands with similar plant species composition to quantify biomass C-sequestration rates using the photosynthesis data presented herein and ancillary imagery from other freshwater wetlands in the northeastern United States. Moreover, the methods employed in this study provide a model for future work at other sites where landscape-scale wetland C-fixation could be estimated using species-specific data. Such an approach could even provide regional-scale estimates of C-fixation for facilitating calculations of C-cycling to achieve Tier II and Tier III IPCC carbon accounting goals. Our approach provides a relatively simple technique that can be used by managers and policy makers in other coastal ecosystems to monitor carbon pools and cycling. Preservation of coastal blue carbon sinks and their carbon pools is important as wetlands continue to be lost at an alarming rate worldwide. Understanding their potential for ameliorating and buffering the effects of climate change is of paramount importance as the Earth continues to experience the effects of continued warming.

Declarations

Author contribution statement

Poulos, H. Milligan, G. Gilmore, M. Berlyn, G. Milligan, J. Chernoff, B: Conceived and designed the analysis; Performed the experiments; Analyzed and interpreted the data; Contributed analysis tools or data; Wrote the paper.

Funding statement

This work was supported by Wesleyan University College of the Environment and a grant from The Nature Conservancy.

Competing interest statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper

References

- Adam, E., Mutanga, O., Rugege, D., 2009. Multispectral and hyperspectral remote sensing for identification and mapping of wetland vegetation: a review. *Wetl. Ecol. Manag.* 18, 281–296.
- Adhikari, S., Bajracharya, R.M., Sitaula, B.K., 2009. A review of carbon dynamics and sequestration in wetlands. *J. Wetl. Ecol.* 2, 42–46.
- Bernal, B., Mitsch, W.J., 2008. A comparison of soil carbon pools and profiles in wetlands in Costa Rica and Ohio. *Ecol. Eng.* 34, 311–323.
- Bernal, B., Mitsch, W.J., 2012. Comparing carbon sequestration in temperate freshwater wetland communities. *Glob. Chang. Biol.* 18, 1636–1647.
- Bridgman, S.D., Megonigal, J.P., Keller, J.K., Bliss, N.B., Trettin, C., 2006. The carbon balance of North American wetlands. *Wetlands* 26, 889–916.
- Chmura, G.L., 2013. What do we need to assess the sustainability of the tidal salt marsh carbon sink? *Ocean Coast Manag.* 83, 25–31.
- Chmura, G.L., Anisfeld, S.C., Cahoon, D.R., Lynch, J.C., 2003. Global carbon sequestration in tidal, saline wetland soils. *Glob. Biogeochem. Cycles* 17, 1111.
- Chmura, G.L., Short, F., Torio, D., Arroyo-Mora, P., Fajardo, P., Hadtvany, M., van Ardenne, L., 2016. North America's Blue Carbon: Assessing Seagrass, Salt Marsh, and Mangrove Distribution and Carbon Sinks. Commission for Environmental Cooperation, Montreal, Canada.
- Choi, Y., Wang, Y., 2004. Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. *Glob. Biogeochem. Cycles* 18.
- Clough, B., Ong, J., Gong, W., 1997. Estimating leaf area index and photosynthetic production in canopies of the mangrove *Rhizophora apiculata*. *Mar. Ecol. Prog. Ser.* 285–292.
- Dai, T., Wiegert, R.G., 1996. Estimation of the primary productivity of *Spartina alterniflora* using a canopy model. *Ecography* 19, 410–423.
- Duarte, C.M., Middelburg, J.J., Caraco, N., 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2, 1–8.
- ESRI, 2017. ArcGIS Release 10.5.1. Environmental Systems Research Institute, Redlands, CA.
- Grimsditch, G., Alder, J., Nakamura, T., Kenchington, R., Tamelander, J., 2013. The blue carbon special edition—Introduction and overview. *Ocean Coast Manag.* 83, 1–4.
- Hewson, J., Steininger, M., Pasmajoglou, S., 2013. REDD+ Measurement, Reporting and Verification (MRV) Manual: USAID-Supported Forest Carbon, Markets and Communities Program. USAID, Washington, DC. http://www.fcmglobal.org/documents/mrvmanual/MRV_Manual.pdf.
- Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Jamsranjav, B., Fukuda, M., Troxler, T., 2014. 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands.
- Howard, J., Hoyt, S., Inensee, K., Pidgeon, E., Telszewski, M., 2014. Coastal Blue Carbon: Methods for Assessing Carbon Stocks and Emissions Factors in Mangroves, Tidal Salt Marshes, and Seagrass Meadows. International Oceanographic Commission of UNESCO, International Union for Conservation of Nature, Conservation International.
- Junk, W.J., 2002. Long-term environmental trends and the future of tropical wetlands. *Environ. Conserv.* 29, 414–435.
- Kayranli, B., Scholz, M., Mustafa, A., Hedmark, Å., 2010. Carbon storage and fluxes within freshwater wetlands: a critical review. *Wetlands* 30, 111–124.
- Lal, R., 1997. Land use and soil management effects on soil organic matter dynamics on Alfisols in Western Nigeria. *Soil Proc. Carbon Cycle* 11, 109.
- Lal, R., 2008. Carbon sequestration. *Phil. Trans. Biol. Sci.* 363, 815–830.
- Lavery, P.S., Mateo, M.-Á., Serrano, O., Rozaimi, M., 2013. Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS One* 8, e73748.
- Lu, W., Xiao, J., Liu, F., Zhang, Y., Liu, C., Lin, G., 2017. Contrasting ecosystem CO₂ fluxes of inland and coastal wetlands: a meta-analysis of eddy covariance data. *Glob. Chang. Biol.* 23, 1180–1198.
- Marín-Muñiz, J.L., Hernández, M.E., Moreno-Casasola, P., 2014. Comparing soil carbon sequestration in coastal freshwater wetlands with various geomorphic features and plant communities in Veracruz, Mexico. *Plant Soil* 378, 189–203.
- Matthews, E., Fung, I., 1987. Methane emission from natural wetlands: global distribution, area, and environmental characteristics of sources. *Glob. Biogeochem. Cycles* 1, 61–86.
- Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* 9, 552–560.
- Megonigal, J.P., Neubauer, S.C., 2009. Biogeochemistry of Tidal Freshwater Wetlands. Coastal Wetlands: an Integrated Ecosystem Approach. Elsevier, Amsterdam, pp. 535–562.
- Metzler, K., Rosza, R., 1982. Vegetation of fresh and brackish tidal marshes in Connecticut. *Newsl. Conn. Bot. Soc.* 10, 1–3.
- Middelburg, J., Nieuwenhuize, J., Lubberts, R., Van de Plassche, O., 1997. Organic carbon isotope systematics of coastal marshes. *Estuar. Coast Shelf Sci.* 45, 681–687.
- Mitra, S., Wassmann, R., Vlek, P.L., 2005. An appraisal of global wetland area and its organic carbon stock. *Curr. Sci.* 88, 25.
- Mitsch, W.J., Bernal, B., Nahlik, A.M., Mander, Ü., Zhang, L., Anderson, C.J., Jørgensen, S.E., Brix, H., 2013. Wetlands, carbon, and climate change. *Landscape Ecol.* 28, 583–597.
- Mitsch, W.J., Gosselink, J.G., 2000. The value of wetlands: importance of scale and landscape setting. *Ecol. Econ.* 35, 25–33.
- Mitsch, W.J., Gosselink, J.G., 2007. Wetlands, fourth ed. J. Wiley & Sons, Inc.
- Odum, W.E., 1988. Comparative ecology of tidal freshwater and salt marshes. *Annu. Rev. Ecol. Systemat.* 147–176.
- Odum, W.E., Heywood, M.A., 1978. Decomposition of Intertidal Freshwater Marsh Plants. *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York, pp. 89–97.
- Odum, W.E., Smith III, T.J., Hoover, J.K., McIvor, C.C., 1984a. Ecology of Tidal Freshwater Marshes of the United States East Coast: A Community Profile. Virginia Univ., Dept. of Environmental Sciences, Charlottesville (USA).
- Odum, W.E., Smith, T., Hoover, J.K., McIvor, C.C., 1984b. The ecology of tidal freshwater marshes of the United States east coast: a community profile. *Citeseer*.
- Pant, H.K., Rechcigl, J.E., Adjei, M.B., 2003. Carbon sequestration in wetlands: concept and estimation. *Food Agric. Environ.* 1, 308–313.
- Pasternack, G., 2009. Hydrogeomorphology and sedimentation in tidal freshwater wetlands. *Tidal Freshw. Wetl.* 31–40.
- R Development Core Team, 2017. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Samaritani, E., Siegenthaler, A., Yli-Petäys, M., Buttler, A., Christin, P.A., Mitchell, E.A., 2011. Seasonal net ecosystem carbon exchange of a regenerating cutaway bog: how long does it take to restore the C-sequestration function? *Restor. Ecol.* 19, 480–489.
- Siikamäki, J., Sanchirico, J.N., Jardine, S., McLaughlin, D., Morris, D., 2013. Blue carbon: coastal ecosystems, their carbon storage, and potential for reducing emissions. *Environment* 55, 14–29.
- Sutton-Grier, A.E., Megonigal, J.P., 2011. Plant species traits regulate methane production in freshwater wetland soils. *Soil Biol. Biochem.* 43, 413–420.
- Thomas, S., 2014. Blue carbon: knowledge gaps, critical issues, and novel approaches. *Ecol. Econ.* 107, 22–38.
- Weston, N.B., Neubauer, S.C., Velinsky, D.J., Vile, M.A., 2014. Net ecosystem carbon exchange and the greenhouse gas balance of tidal marshes along an estuarine salinity gradient. *Biogeochemistry* 120, 163–189.
- Whiting, G.J., Chanton, J.P., 2001. Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. *Tellus B* 53, 521–528.
- Wu, F.Y., Chung, A.K.C., Tam, N.F.Y., Wong, M.H., 2012. Root exudates of wetland plant influenced by nutrient status and types of plant cultivation. *Int. J. Phytoremediation* 14, 543–553.
- Zedler, J.B., Kercher, S., 2005. Wetland resources: status, trends, ecosystem services, and restorability. *Annu. Rev. Environ. Resour.* 30, 39–74.