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# Vegetation persistence and carbon storage: implications for environmental water management for *Phragmites australis*

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## Abstract

Environmental water allocations are used to improve the ecological health of wetlands. There is now increasing demand for allocations to improve ecosystem productivity and respiration, and enhance carbon sequestration. Despite global recognition of wetlands as carbon sinks, information regarding carbon dynamics is lacking. This is the first study estimating carbon sequestration for semiarid *Phragmites australis* reedbeds. The study combined aboveground biomass assessments with stable isotope analyses of soils and modeling of biomass using Normalized Digital Vegetation Index (NDVI) to investigate the capacity of environmental water allocations to improve carbon storage. The study considered relationships between soil organic carbon (SOC), carbon sources, and reedbed persistence in the Macquarie Marshes, a regulated semiarid floodplain of the Murray-Darling Basin, Australia. SOC storage levels to 1 m soil depth were higher in persistent reedbeds (167 Mg ha<sup>-1</sup>) than ephemeral reedbeds (116-138 Mg ha<sup>-1</sup>). In situ *P. australis* was the predominant source of surface SOC at persistent reedbeds; mixed sources of surface SOC were proposed for ephemeral reedbeds. <sup>13</sup>C enrichment with increasing soil depth occurred in persistent and ephemeral reedbeds and may not relate to flow characteristics. Despite high SOC at persistent reedbeds, differences in the rate of accretion contributed to significantly higher rates of carbon sequestration at ephemeral reedbeds (approximately 554 and 465 g m<sup>-2</sup> yr<sup>-1</sup>) compared to persistent reedbeds (5.17 g m<sup>-2</sup> yr<sup>-1</sup>). However, under current water regimes, rapid accretion at ephemeral reedbeds cannot be maintained. Effective management of persistent *P. australis* reedbeds may enhance carbon sequestration in the Macquarie Marshes and floodplain wetlands more generally.

## Disciplines

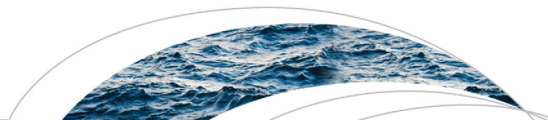
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### RESEARCH ARTICLE

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# Vegetation persistence and carbon storage: Implications for environmental water management for *Phragmites australis*

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#### Key Points:

- Identified relationships between biomass, soil carbon, and reedbed persistence
- Environmental water may enhance biomass and soil carbon of reedbeds
- Reedbed persistence may enhance carbon sequestration benefits

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**Abstract** Environmental water allocations are used to improve the ecological health of wetlands. There is now increasing demand for allocations to improve ecosystem productivity and respiration, and enhance carbon sequestration. Despite global recognition of wetlands as carbon sinks, information regarding carbon dynamics is lacking. This is the first study estimating carbon sequestration for semiarid *Phragmites australis* reedbeds. The study combined aboveground biomass assessments with stable isotope analyses of soils and modeling of biomass using Normalized Digital Vegetation Index (NDVI) to investigate the capacity of environmental water allocations to improve carbon storage. The study considered relationships between soil organic carbon (SOC), carbon sources, and reedbed persistence in the Macquarie Marshes, a regulated semi-arid floodplain of the Murray-Darling Basin, Australia. SOC storage levels to 1 m soil depth were higher in persistent reedbeds (167 Mg ha<sup>-1</sup>) than ephemeral reedbeds (116–138 Mg ha<sup>-1</sup>). In situ *P. australis* was the predominant source of surface SOC at persistent reedbeds; mixed sources of surface SOC were proposed for ephemeral reedbeds. <sup>13</sup>C enrichment with increasing soil depth occurred in persistent and ephemeral reedbeds and may not relate to flow characteristics. Despite high SOC at persistent reedbeds, differences in the rate of accretion contributed to significantly higher rates of carbon sequestration at ephemeral reedbeds (approximately 554 and 465 g m<sup>-2</sup> yr<sup>-1</sup>) compared to persistent reedbeds (5.17 g m<sup>-2</sup> yr<sup>-1</sup>). However, under current water regimes, rapid accretion at ephemeral reedbeds cannot be maintained. Effective management of persistent *P. australis* reedbeds may enhance carbon sequestration in the Macquarie Marshes and floodplain wetlands more generally.

## 1. Introduction

Wetlands perform a suite of vital ecosystem services that contribute to human societies around the world, including flood mitigation; sediment, nutrient, and pollutant retention; water storage; groundwater recharge; and carbon sequestration are typically areas of high habitat heterogeneity, rich in biodiversity and biological activity [Costanza *et al.*, 1998; Finlayson *et al.*, 1999; Kingsford and Thomas, 2004]. However, these valuable resources are globally threatened; global reductions in wetland extent as a result of human activity are estimated at 50% [Zedler and Kercher, 2005] and drainage for agricultural purposes has been considered as the major cause of this loss, especially in floodplain wetlands [Tockner and Stanford, 2002].

Reductions in wetland extent have been documented for the Murray-Darling Basin (MDB) [Kingsford, 2000a,b], one of the largest inland drainage basins in Australia, which drains an area of approximately 1,061,000 km<sup>2</sup> of prime agricultural land [Rogers and Ralph, 2011a]. Significant water resource development and construction of water storages have occurred over the past century, the bulk of which occurred between the mid-1950s and 1990 [Rogers and Ralph, 2011b]. The ensuing change to hydrological regimes in the MDB is mirrored globally for low-land rivers and associated floodplain wetlands that have undergone significant water resource development [Zedler and Kercher, 2005]. In the MDB, water resource development and land use changes have affected the ecology and hydrology of floodplain wetlands and led to the development of criteria for delivering water from dams in the upper catchment, known as “environmental water,” to meet environmental objectives, such as improving the success of waterbird breeding events [see, e.g., DECCW, 2010].

Altered rainfall and increased air temperatures in association with global climate change and climate variability are also influencing the hydrology and ecology of wetlands, particularly those that are dependent

upon freshwater flows [Rogers and Ralph, 2011a]. Projections of the combined impacts of water resource development, climate variability, and climate change indicate a 12% decrease in available surface water by 2030 across the MDB [CSIRO, 2008], although there is considerable variability in the nature of this decrease within the subregions of the MDB. Despite the difficulty in projecting water availability, it is evident that the combined effects of water resource development, climate change, and climate variability will create increasing demand for environmental water to meet multiple environmental objectives.

As a consequence of the need to mitigate climate change, there is increasing global interest in the capacity of wetlands to sequester carbon from the atmosphere [Bridgham *et al.*, 2006; Chmura *et al.*, 2003; Kayranli *et al.*, 2010; Mitsch *et al.*, 2013]. High productivity of biota, inundation, and associated lower decomposition of organic matter has facilitated significant carbon storage in wetland soils. Anaerobic soil conditions slow the rate of decomposition of soil organic matter (SOM) such that the rate of carbon fixation, indicated by primary productivity, and continual addition of new SOM exceeds the rate of decomposition of SOM resulting in a net gain in carbon storage within the soil. The effectiveness of wetlands at storing carbon is attested by the proportion of carbon storage within wetland soils, which is estimated to range from 20 to 30% of the global soil carbon reservoir [Mitsch *et al.*, 2013], compared to the distribution of wetlands on the Earth's surface, estimated at 5–8% [Mitsch and Gosselink, 2007]. However, the emergence of carbon trading markets and incentives has increased scrutiny of the capacity of wetlands to sequester carbon, particularly as decomposition of SOM can occur through aerobic and anaerobic processes; resulting in the release of carbon dioxide and methane to the atmosphere by ebullition or diffusion. Methane has higher radiative efficiency than carbon dioxide [Brix *et al.*, 2001] and the IPCC advocate a global warming potential over a 100 year period ( $GWP_{100}$ ) of 34 when accounting for carbon-climate feedbacks [Myhre *et al.*, 2013]. Due to their higher radiative efficiency, these methane emissions are drawing the most scrutiny, with wetlands estimated to emit 20–25% of current global methane emissions.

Identification of the environmental conditions that enhance carbon sequestration is also a key issue. Floodplain wetlands by virtue of the variable nature of water flows typically do not exhibit persistent saturated conditions. With the exception of permanent wetland areas, floodplain wetland soils undergo periods of wetting and drying, whereby pathways to SOM decomposition shift between anaerobic decomposition and aerobic decomposition. Seasonality in ecosystem respiration is commonly correlated with temperature flux whereby elevated temperatures may enhance productivity resulting in the production of more organic matter that is more rapidly decomposed by the warmer conditions [Kayranli *et al.*, 2010]. Similarly, seasonality in ecosystem respiration may correlate with water availability, a factor that is yet to be fully explored for floodplain wetlands. In an ephemeral wetland in southeastern Australia, Boon *et al.* [1997] demonstrated that during interflood periods, soils may become increasingly aerobic, thereby facilitating the decomposition of SOM and conversion to carbon dioxide. During flood conditions, the dominant process of SOM decomposition reverts to methanogenesis. This behavior has been confirmed for a seasonal wetland in the wet-dry tropics of northern Australia [Beringer *et al.*, 2013].

The vigor of vegetative response to inundation is commonly used as an indicator of the success of environmental watering actions [Rogers *et al.*, 2013]. Enhancing productivity of wetlands for carbon sequestration benefits, or minimizing emissions, is therefore a potential objective of environmental water management. In this study, we explore the links between maximum aboveground biomass, as a surrogate for productivity, and belowground carbon storage for a floodplain wetland in the Murray-Darling Basin of southeast Australia. We initially considered our first hypothesis that vegetation persistence (i.e., persistent coverage) will increase aboveground carbon storage (hypothesis 1). While we did not specifically measure hydrological parameters or the contribution of water availability to plant productivity, this research hypothesis is built upon existing relationships between water regimes and vegetation distribution and condition at the Macquarie Marshes [OEH, 2012], which supports our assumption that vegetation persistence was related to higher frequency of inundation.

On the basis of this assumption, our second hypothesis was that soil organic carbon storage was enhanced when vegetation growth was persistent and had higher inundation frequency (hypothesis 2). The mechanisms that may enhance carbon storage in persistent wetland vegetation include greater contributions from aboveground biomass, and slower decomposition of organic material due to the higher frequency of inundation and associated soil saturation; exploring the variable contribution of these mechanisms to soil organic carbon storage was not differentiated in this study.

We did, however, seek evidence that carbon storage was related to vegetation persistence using stable isotope analysis and specifically considered two hypotheses. First, the stable carbon isotope signature of soil organic carbon where vegetation was persistent corresponded to the isotopic signature of living organic material of the persistent vegetation (hypothesis 3); and second, the stable carbon isotope signature of soil organic matter where vegetation was less persistent did not correspond to the isotopic signature of living organic material of the ephemeral vegetation (hypothesis 4). While stable carbon isotope analysis does not provide definitive evidence of carbon provenance [Cloern *et al.*, 2002], it remains a useful technique for exploring broad changes in carbon sources, such as plants with C<sub>3</sub>, C<sub>4</sub>, or CAM photosynthetic pathways [Farquhar *et al.*, 1989; O'Leary, 1988].

We focused our study on *Phragmites australis* reedbeds in the Macquarie Marshes, NSW, Australia, as these reedbeds exhibited varying degrees of persistence, which was strongly correlated to hydrological conditions, and acted as a proxy for different approaches to environmental water management. These different approaches to environmental water management may include varying the frequency, volume, or timing of the delivery of environmental water. We complemented aboveground measures of biomass with belowground measures of carbon storage and carbon sources using stable isotope analysis; estimates of aboveground biomass were used to calibrate Normalized Difference Vegetation Index (NDVI) that was applied to Landsat imagery to estimate the total biomass for the *P. australis* reedbeds at the study site.

## 2. Methods

### 2.1. Study Area

The Macquarie Marshes is located within the lower Macquarie catchment of the Murray-Darling Basin, NSW, Australia (30°45'S, 147°33'E, Figure 1) in a semiarid climatic zone (Koppen classification BSh) with an average annual rainfall of approximately 448 mm [BOM, 2015] (rainfall gauge 051042). They consist of a complex network of wetlands, including channels and flood-outs, swamps, lagoons, and floodplain wetlands (Figure 1). The extent of the Macquarie Marshes is variable, consisting of permanent and ephemeral wetlands of approximately 150,000 ha in size during larger floods [OEH, 2012]. The Macquarie Marshes is a dynamic landscape [Ralph and Hesse, 2010; Yonge and Hesse, 2009] with an extensive history of fluvial change driven by climate and the variable hydrology of the Macquarie River over a variety of time scales. The Macquarie Marshes is estimated to have formed between 6000 and 8000 years ago [Yonge and Hesse, 2009]; formation and abandonment of channels and marshes have occurred over time scales of less than 100 years to over several thousand years [OEH, 2012]. The most significant changes post-European settlement are associated with river regulation following the completion of Burrendong Dam in 1967 in the upper catchment of the Macquarie River, which facilitated large-scale irrigation [OEH, 2012].

As a consequence of this evolution and hydrological flows, the Macquarie Marshes is regarded as being amongst the most biologically diverse wetland systems in the Murray-Darling Basin, and supports some of the largest waterbird breeding events in Australia [Kingsford and Auld, 2005; OEH, 2012]. This biological diversity is confirmed by the listing of the Macquarie Marshes as a wetland of international significance under the International Convention on Wetlands (Ramsar Treaty). Currently, three portions of land are designated as Ramsar reserves; the Southern and Northern Nature Reserves and U-Block. This study focusses on wetlands in the Southern Nature Reserve which is managed by the NSW National Parks and Wildlife Service.

This study focused on *P. australis* reedbeds due to their high abundance, ecological significance, wide distribution, and persistence throughout the Macquarie Marshes [Bowen and Simpson, 2010; OEH, 2012; Wen *et al.*, 2012]. Study sites were selected on the basis of the occurrence of contiguous reedbed dominated communities, and transects were located where hydrological flow is currently regular and persistent (transect AB), seasonal (transect CD), or ephemeral (transect EF). The flow regime of the Macquarie Marshes is complex and characterized by frequent small to medium flows and less frequent large floods prior to regulation, and constant low flows and infrequent large floods after regulation in 1967 [OEH, 2012]. The prevailing hydrological conditions under which SOC accumulated covers both of these periods is difficult to describe, and would be highly variable between transects. As a consequence, hydrological flow was not controlled over the course of the study and the conditions under which SOC accumulated are largely inferred on the basis of the current flow regime, pattern of vegetation distribution, and geomorphology. Transect AB was located at lower Monkeygar Creek in Willancorah Swamp; and transects CD and EF were

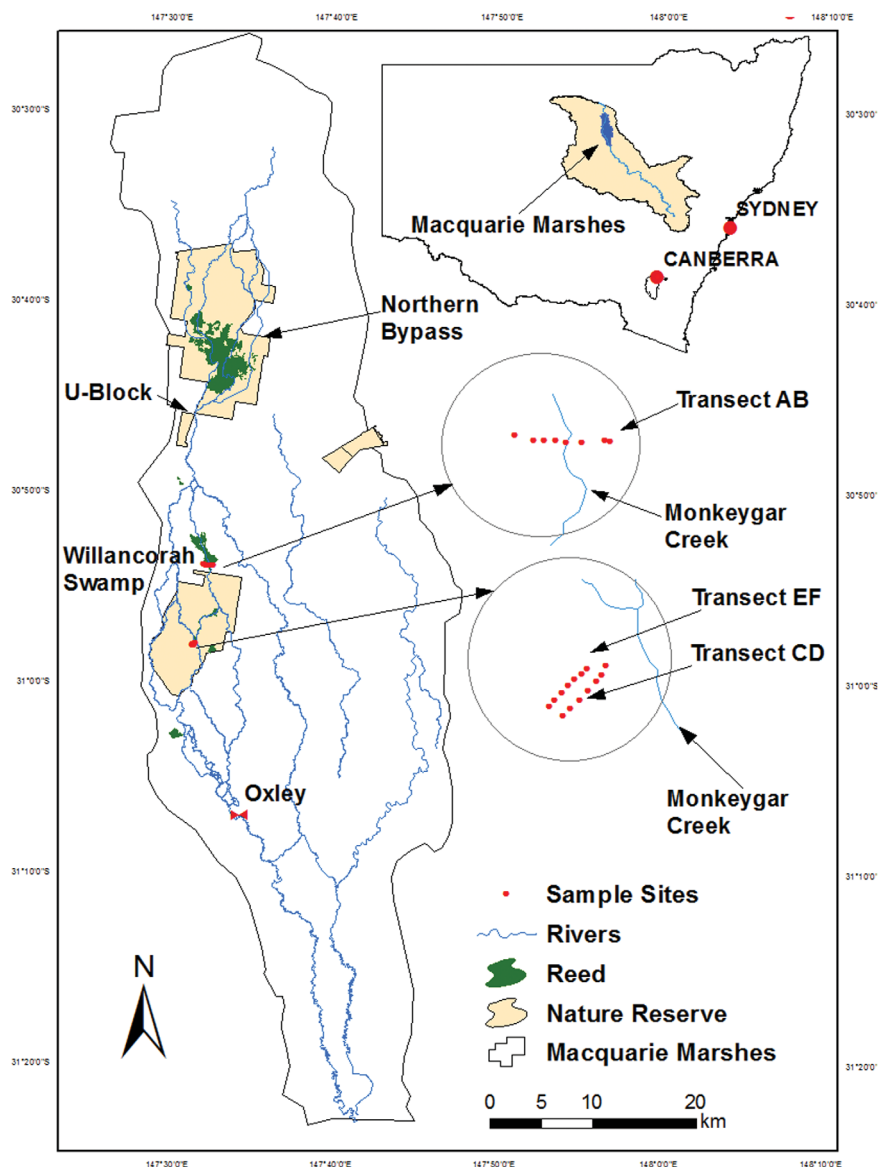


Figure 1. Location of Macquarie Marshes, *Phragmites australis* reedbeds, and sampling sites.

located in the Southern Nature Reserve (SNR) within the Macquarie Marshes (Figure 1). Two separate reedbed communities were chosen for sampling (transects AB and CD); an additional study site was located in the SNR where the culms of an ephemeral reedbed were evident, but there was no evidence of living biomass (transect EF); each study site represented varying degrees of inundation and reedbed persistence [Bowen and Simpson, 2010].

The northernmost site (transect AB) was located at the intersection of lower Monkeygar Creek and Gibson’s Way, just north of the SNR (Figure 1). At this site, Monkeygar Creek flows into the southern end of Willancorah Swamp, breaking down into a wide and shallow anastomosing channel. Willancorah Swamp is characterized by extensive and persistent reedbeds of *Phragmites australis*. These reedbeds have persisted through droughts, including the drought from 2003 to 2008 [Bowen and Simpson, 2010]. This area is regularly inundated; the persistence of water is evident by the presence of the perennial grass *Typha orientalis* and *T. domingensis* [DECCW, 2010; OEH, 2012]. Sediment and vegetation samples were collected across the channel at transect AB, starting from the east edge of the channel (A) and working westward to the opposite edge of the channel (B). Eight cores were extracted along transect AB to estimate SOC.

The southernmost sites (transects CD and EF) were located within the SNR, where the Northern Bypass Channel branches from Monkeygar Creek (Figure 1). The reedbeds in the SNR rely on overbank flow from Monkeygar Creek; hence, they are less persistent than the reedbeds at Willancorah Swamp; this is demonstrated by vast decreases in reedbed extent between 1991 and 2008 [Bowen and Simpson, 2010]. Reedbeds at transect CD, located adjacent to Monkeygar Creek and the Northern Bypass Channel, exhibited poor condition at the time of sampling; the history of inundation at the study site indicates that they were inundated by overbank flow from the flooding events of 2010–2011 and 2011–2012 [OEH, 2012]. Transect EF was parallel to transect CD and was positioned further from the Northern Bypass Channel amongst sparse dead stands of *P. australis*. Seven cores were extracted along transect CD and EF to estimate SOC. Vegetation samples were only collected at transect CD as the ephemeral reedbeds were not present at transect EF at the time of sampling.

## 2.2. Vegetation Persistence and Aboveground Carbon Storage

To determine the contribution of vegetation persistence to aboveground carbon storage (i.e., hypothesis 1), we used the primarily nondestructive sampling techniques of Thursby *et al.* [2002] to determine the aboveground biomass of reedbeds at the study sites. This method, which establishes strong relationships between stem heights of *Phragmites australis* and biomass, was selected as destructive methods were not suitable due to the volume of the standing biomass of the *Phragmites* reedbeds at the Macquarie Marshes and the status as a protected habitat within the Macquarie Marshes Nature Reserve and as part of the Ramsar wetland. This sampling technique comprised two phases, a calibration (destructive) phase and an application (nondestructive) phase. In the calibration phase, an allometric relationship between mass and height was established; in the application phase, height and density measurements were obtained and applied to the allometric relationship. Unique allometric relationships were established between *P. australis* mass and height for transect AB and transect CD to account for structural differences between the persistent and ephemeral reedbed communities. These are the first published allometric equations for Australian freshwater *P. australis* wetlands.

In the calibration phase, 50–100 *P. australis* shoots, covering a range of heights, were collected along each transect. The height of shoots was recorded (to the nearest 5 mm) and shoots were labeled before being dried. Shoots were dried at 60°C for 48 h until a constant weight was reached (to the nearest 0.1 g) and their mass was recorded. The ratio of the height and dry mass, known as dry mass ratio, was determined for each shoot.

The mean and standard deviation of values for height, dry mass, and dry mass ratio were determined for each transect and their distribution was tested for normality. All statistical analyses were carried out using a significance level of 0.05 using JMP 11.0 statistical software, and analysis of variance was used to identify statistical differences between transects AB and CD, with transect as the effect variable and measured variables of shoot height, dry mass of shoots, and dry mass ratio as dependent variables. The mass of individual shoots was plotted against their height for each transect and a power curve “line of best fit” was applied to the data points. A predictive equation, identified here as the *height to mass conversion equation*, was generated which described the relationship between height and mass.

In addition, five quadrats (0.5 m × 0.5 m) were randomly chosen along each transect, covering a range of heights. At each quadrat, the heights of the five tallest shoots were measured; the shoot density of the quadrat was recorded and all shoots from the quadrat were collected, bagged, dried to constant weight, and weighed. The mean and standard deviation of values for height of five tallest shoots and quadrat density were determined for each transect and their distribution tested for normality. Analysis of variance was used to identify statistical differences between transects AB and CD (effect variable) for the measured dependent variables of height and density.

The average height of the five tallest shoots from each quadrat was compared against the height and mass predictive equation to derive a mass. The derived mass was multiplied by the shoot density, which gave an estimate of the mass of plant material in each quadrat. These mass measurements were overestimates, given that the average heights of the tallest five shoots were used. To correct these overestimates, the measured mass of the quadrats was plotted against the predicted overestimated mass derived from the five tallest shoots for both transects AB and CD; an exponential linear “line of best fit” was applied to data points which described the relationship between the mass of quadrats in each transect derived from the

five tallest shoots and the measured mass of the quadrats from each transect. A predictive equation was generated for each transect, identified here as the *correction equation*, and used to estimate the mass of quadrats based on the mass of the five tallest shoots.

In the application phase, four quadrats (0.5 m × 0.5 m) were randomly chosen within a 2 m radius from cores located in transects AB and CD (Figure 1). A total of 32 quadrats were sampled on transect AB (8 core locations × 4 quadrats) and 28 quadrats were sampled on transect CD (7 core locations × 4 quadrats). The height of the five tallest shoots and the shoot density were recorded for each quadrat. The average height of the five tallest shoots from each quadrat was applied to the *height to mass conversion equation* to determine the average shoot mass; this mass was multiplied by the shoot density of the corresponding quadrat to yield an overestimated quadrat mass. To determine the corrected mass for each quadrat, the *correction equation* was applied to the overestimated mass values. The mean and standard deviation of quadrat biomass were determined for each transect and their distribution tested for normality. Analysis of variance was used to identify statistical differences between the dependent variable of reedbed biomass for transects AB and CD.

Carbon accumulation in *P. australis* biomass exhibits little variability between leaves, stems, panicles, and roots, with the ratio of carbon mass to dry biomass reported to range between 0.41 and 0.45 [Soetaert et al., 2004]. We used a conversion factor of  $0.43 \pm 0.02$  on estimates of aboveground biomass to estimate aboveground carbon accumulation in *P. australis* reedbeds at transects.

To test whether vegetation persistence will increase aboveground carbon storage (i.e., hypothesis 1), analysis of variance was used to identify statistical differences between carbon storage for quadrats at transects AB and CD.

To explore aboveground biomass dynamics, NDVI was used as it is a dimensionless radiometric measure that serves as an indicator for the relative abundance and productivity of vegetation [Wen et al., 2012]. NDVI is calculated as the difference between near-infrared and red reflectance values, normalized over the sum of the two values [Wilkie and Finn, 1996]. This study used data from Landsat 7 ETM+, which has a spatial resolution of 30 m for the required color bands, to calculate NDVI values for the study area. We downloaded 14 high-quality (i.e., cloud less than 5%) satellite images spanning from August 2012 to May 2013 from USGS (<http://glovis.usgs.gov/>). After converting the images to reflectance, we computed NDVI values for each date. To account for the spatial heterogeneity, we extracted the NDVI values from nine grids centered at each sampling site, and used the mean NDVI to fit the relationship between NDVI data and aboveground biomass measured for the site. Using R version 3.1.1, we fitted a total of 14 logistic regression models and the one with lowest AIC (Akaike information criterion) [Akaike, 1974] was then used to calculate a raster data set, with NDVI as the input (x) values and aboveground biomass as the output (y) values.

Total aboveground biomass of reedbeds in 2013 was parameterized using the mapping of reedbed extent in 2013, documented by Bowen and Fontaine [2014]. To identify temporal dynamics in aboveground biomass, the established relationship between NDVI and aboveground biomass was also applied to NDVI data in 1991 using the mapping of reedbed extent in 1991 [Wilson et al., 1993] to parameterize the biomass estimates; and 2008 using the mapping of reedbed extent in 2008 [Bowen and Simpson, 2010] to parameterize the biomass estimates.

The annual productivity of aboveground biomass of *P. australis* is reported to correlate with the maximum standing crop of aboveground biomass [Brix et al., 2001; Westlake, 1982]. Brix et al. [2001] estimated that belowground production of *P. australis* is of similar magnitude to aboveground production; while aboveground production is reportedly 3–15% higher than the maximum aboveground biomass [Westlake, 1982]. On the basis of the relationships established between aboveground productivity, aboveground biomass, and belowground productivity by Brix et al. [2001] and Westlake [1982], we used estimates of maximum aboveground biomass for each reedbed to estimate total aboveground productivity according to the following conversion:

$$P \approx (2.18 \pm 0.12) \times B$$

where

$P \approx$  annual production (g m<sup>-2</sup> yr<sup>-1</sup>);

$B \approx$  maximum above-ground biomass (g m<sup>-2</sup>).



### 2.3. Vegetation Persistence and Belowground Soil Organic Carbon Storage and Sources

To determine whether soil organic carbon varied with vegetation persistence (i.e., hypothesis 2), belowground soil carbon was analyzed for cores collected along transects. Samples from these cores were also processed for stable carbon isotope analysis to identify relationships between carbon provenance and vegetation persistence (i.e., hypothesis 3 and 4). While there is not a standard soil depth for determining carbon storage, cores of up to 1 m length have been used to measure soil organic carbon [Badiou *et al.*, 2011; Saintilan *et al.*, 2013]. It was assumed that the bulk of carbon degradation has occurred above 1 m soil depth and that surface SOC and the mineralization of SOC will be adequately characterized in the upper 1 m [Brady and Weil, 1996]; for terrestrial soils, carbon storage is typically reported for the upper 0.3–1.0 m [Harper and Tibbett, 2013]. We extracted cores from transects using a Wacker vibracorer, with care taken to minimize compaction and disturbance of the soil profile. Eight cores were extracted at 100 m intervals along transect AB to cover the extent and variation in water depth within the channel. Seven cores each were extracted at 50 m intervals along transects CD and EF in the SNR in order to cover the variation along the channel. From each core, four subsamples were taken at 0–10, 20–30, 50–60, and 80–90 cm. Some soil cores experienced compaction below 80 cm, in which case, substitute samples were collected higher in the core (70–80 cm). Samples were bagged and labeled, and kept in cold storage at 3–5°C until further analysis.

The bulk density of soil samples was determined by oven drying the samples at 60°C until constant weight. Bulk density ( $\text{g cm}^{-3}$ ) was estimated as the ratio between dry mass (g) and wet sample volume ( $\text{cm}^3$ ). Large soil aggregates were broken down by hand within each sample bag in order to aid drying.

Dried sediment core samples were subsampled using coning and quartering to avoid systematic error within samples [Tan, 1996]. Subsamples for each core were taken from quartered samples and ground to a fine powder ( $<250 \mu\text{m}$ ) using a Retsch vibrator mill. A pilot comparison of samples undergoing acid wash treatment to remove carbonates and controls using a matched pairs analysis yielded no significant difference in %C ( $p = 0.40$ ,  $t$  ratio =  $-0.87$ ) and  $\delta^{13}\text{C}$  ( $p = 0.31$ ,  $t$  ratio =  $-1.1$ ); a finding which reflected a previous analysis of soils from the Macquarie Marshes by Mazumder *et al.* [2010]. Subsamples did not undergo further acid treatment, hence analyses of soil carbon are representative of total carbon and carbonates were presumed to be negligible. Seven samples of living root, shoot, and leaf material from *P. australis* in the core wetland area of the Macquarie Marshes were also prepared for isotope analysis by drying and grinding.

Powdered and homogenized sediment and reference plant samples were loaded into tin capsules and were analyzed with a continuous flow isotope ratio mass spectrometer (CF-IRMS), model Delta V Plus (Thermo Scientific Corporation, USA), interfaced with an elemental analyzer (Thermo Fisher Flash 2000 HT EA, Thermo Electron Corporation, USA) at the Australian Nuclear Science and Technology Organization (ANSTO) in Lucas Heights, NSW, Australia. The data reported relative to IAEA secondary standards that have been certified relative to VPDB for carbon. The data were normalized with a two-point calibration, using standards that bracket the analyzed samples. Two quality control references, Elem Micro B2042 for % C and IAEA USGS-40 for  $^{13}\text{C}$ , were included in each run of analysis using standard reference materials. The results are accurate to 1% of the actual value for % C and  $\pm 0.3\text{‰}$  for  $\delta^{13}\text{C}$  value. Carbon isotope ratios are reported as  $\delta^{13}\text{C}$  values, which were calculated as:

$$\delta^{13}\text{C} = \frac{(R_{\text{sample}} - R_{\text{reference}})}{R_{\text{reference}}}$$

where

$$R = \frac{^{13}\text{C}}{^{12}\text{C}}$$

Data were collated to determine the mean and standard deviation for bulk density, soil percentage carbon, carbon density, and  $\delta^{13}\text{C}$  value at various depths. All statistical analyses were carried out using a significance level of 0.05 using JMP 11.0 statistical software, and the data were tested for normality. As some data were not normally distributed, generalized linear models were used to identify statistical differences in the dependent variables of bulk density, soil percentage carbon, carbon density, and  $\delta^{13}\text{C}$  between the effects of transect and soil depths. Where statistical differences were identified, post hoc Tukeys HSD was performed to establish where the differences within an effect exist.

**Table 1.** Mean (Standard Deviation) of Reedbed Characteristics in the Calibration and Application Phases of Biomass Reedbed Estimation, and *p* Value (*f* Ratio) for Tests of Statistical Differences in Values Between Transects AB and CD for Each Variable in the Calibration and Application Phases

Phase	Variables	Mean (SD) for Transects		<i>p</i> Value ( <i>f</i> Ratio)
		AB	CD	
Calibration	Shoot heights (m)	2.4 (0.4)	2.8 (0.5)	0.047* (2.8)
	Shoot dry mass (g)	22 (12)	26 (11)	0.0010* (16)
	Shoot dry mass ratio (g m <sup>-1</sup> )	8.9 (3.8)	9.0 (2.8)	0.82 (0.054)
	Tallest five shoots height (m)	2.7 (0.40)	2.8 (0.7)	0.87 (0.027)
	Density (shoots/quadrat)	48 (32)	80 (30)	0.10 (3.3)
	Tallest five shoots dry mass ratio (g m <sup>-1</sup> )	4.8 (0.8)	3.5 (1.3)	0.057 (4.6)
	Tallest five shoot heights (m)	2.8 (0.3)	2.8 (0.5)	0.86 (0.031)
Application	Density (shoots/quadrat)	62 (24)	72 (32)	0.18 (1.9)
	Biomass (g m <sup>-2</sup> )	3300 (780)	2800 (720)	<0.001* (3.6)

\*Significant *p* values.

Carbon density data for each transect were plotted against soil depth and nonlinear regression analyses were used to detect differences in carbon storage with soil depth and between transects. We assumed that recalcitrant carbon would always be present in soils at depth (i.e., carbon storage > 0) and developed an exponential model expression using a three parameter fit with an asymptote approaching zero. The modeled expression was integrated at various depths between 0 and 100 cm to determine carbon storage per hectare for each core location. Analysis of variance was used to establish whether soil organic carbon storage was different between transects representing varying degrees of vegetation persistence (i.e., hypothesis 2).

To establish a relationship between vegetation persistence and soil organic carbon source, matched pairs *t* tests analyses were used to identify statistical differences between  $\delta^{13}\text{C}$  values of SOC and living root, shoot, and leaf material (i.e., hypothesis 3 and 4).

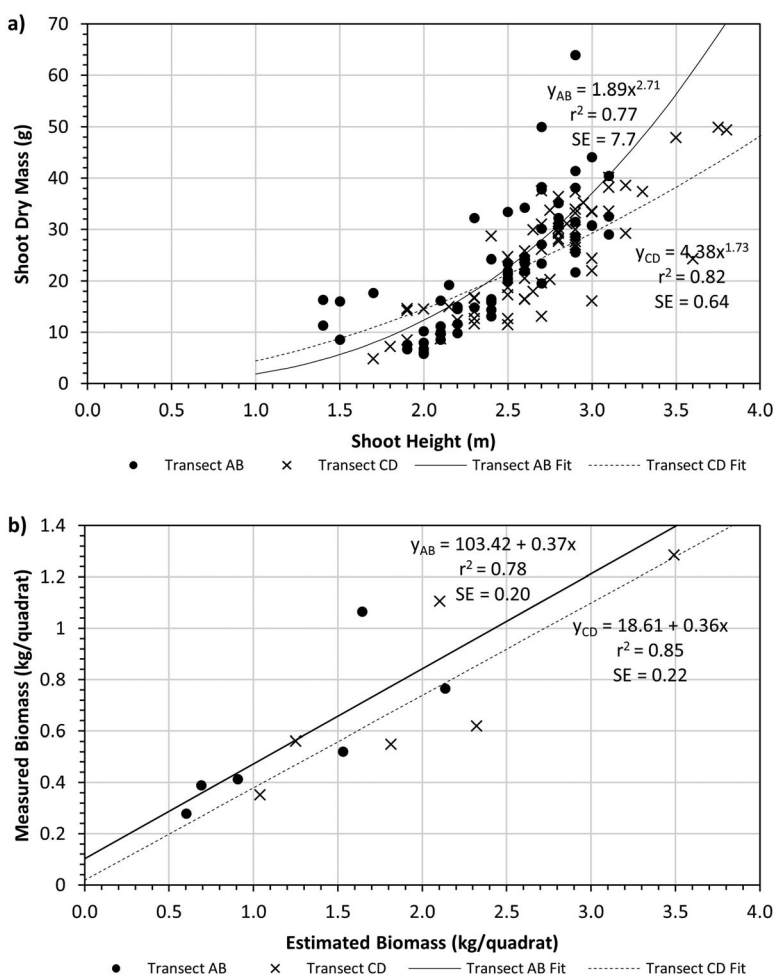
### 3. Results

#### 3.1. Vegetation Persistence and Aboveground Biomass and Carbon Storage

Individual shoots collected in the calibration phase of biomass estimates were significantly taller along transect CD compared to those from transect AB ( $p = 0.047$ , Table 1). While there was a significant amount of mass per shoot lost during drying for both transect AB ( $p < 0.0001$ ) and CD ( $p < 0.0001$ ); there was no significant difference in the dry mass between the shoots collected along transects AB and CD ( $p = 0.094$ , Table 1). Despite similarities in the dry mass of shoots along transects AB and CD, differences in reed heights resulted in considerably different *height to mass conversion equations* being developed for transects AB and CD (Figure 2a).

The height of the tallest five shoots in quadrats along transects AB and CD were not significantly different ( $p = 0.87$ , Table 1). The mean density of shoots within quadrats was markedly greater for quadrats along transect CD than AB (Table 1), but this observation was not statistically significant ( $p = 0.10$ ). In contrast, the calculated dry mass ratio for the five tallest shoots was greater for quadrats along transect AB than CD, and this also was not a statistically significant observation ( $p = 0.057$ ). The ensuing relationship between the measured biomass and estimated biomass with correction equations for transects AB and CD is illustrated in Figure 2b.

Differences in dry mass ratio for the five tallest shoots resulted in height to mass conversion equations and correction equations that differed between transects. These values yielded significantly different biomass estimates for both transects AB and CD ( $p < 0.0001$ , Table 1 and Figure 3), and reflect the contrast in reedbed morphology between transects AB and CD, such as smaller stem diameter at transect CD and greater stem density at transect AB. Estimates of aboveground biomass ranged from  $1955 \pm 620$  to  $4504 \pm 876$  g m<sup>-2</sup> and were reasonably consistent between transects AB and CD (see supporting information Table 1 for quadrat biomass estimates). Consequently, estimates of total biomass productivity, based on a conversion factor of  $2.2 \pm 0.12$ , and biomass carbon accumulation, based on a conversion factor of  $0.43 \pm 0.01$ , reflected the differences in biomass between transects AB and CD (Table 2 and Figure 3). Aboveground carbon storage was enhanced at transects AB where vegetation was persistent compared to



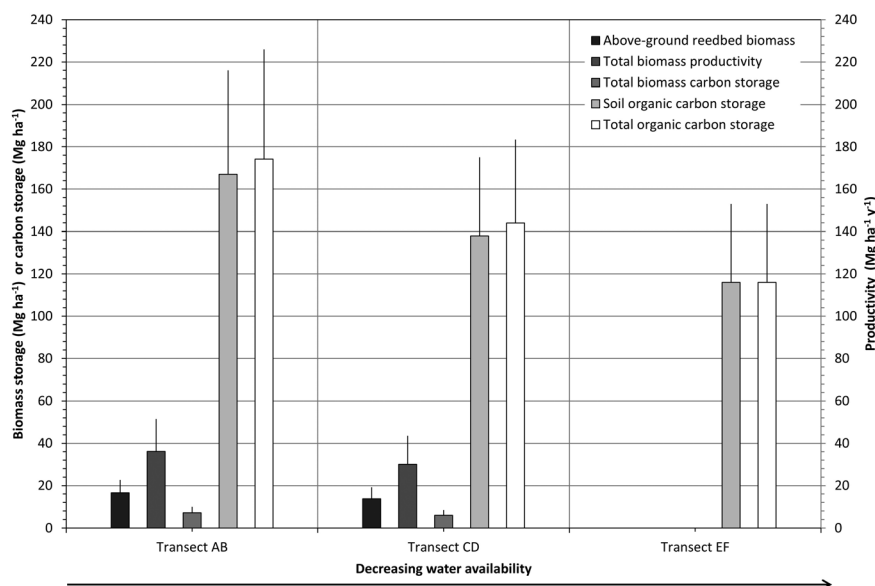
**Figure 2.** Relationship between (a) *Phragmites australis* shoot height and shoot dry mass for 50–100 individual shoots samples along transects AB and CD; and (b) relationship between measured and estimated biomass of *Phragmites australis* from quadrats along transects AB and CD. Allometric equations for height to mass conversion, and correction equations were developed for each transect.

transect CD ( $p < 0.0001$ ), thereby confirming hypothesis 1. Without applying the biomass conversion equation, we found that aboveground biomass was over estimated by 150–170%, and total organic carbon in biomass and soil was overestimated by approximately  $10 \text{ Mg ha}^{-1}$  for both transects AB and CD.

A mean NDVI value was derived from the 15 NDVI pixels that corresponded to each core location; though two core location points (AB 6 and EF 1) were excluded as outliers as they had low NDVI and high biomass values. A highly correlated relationship was established between aboveground biomass and NDVI data from 23 March 2013 ( $r^2 = 0.91$ , Figure 4). A new raster layer of aboveground biomass was derived by applying this relationship to the NDVI data set; a total of 115,000 Mg of aboveground biomass was estimated for the 4900 ha of reedbed throughout the Macquarie Marshes in 2013, equating to approximately  $24 \text{ Mg ha}^{-1}$ . Estimates of aboveground biomass varied between years and corresponded to flow at the Oxley gauge and reedbed extents estimated for 1991 [Wilson et al., 1993], 2008 [Bowen and Simpson, 2010], and 2013 [Bowen and Fontaine, 2014] (Table 3).

### 3.2. Vegetation Persistence and Soil Organic Carbon Storage

Soil bulk density increased significantly with soil depth at all transects (Tables 2 and 4: Model A  $p < 0.0001$ ) and there was no statistical difference between transects (Table 4: Model A  $p = 0.86$ ). Decreases in % C and C density with soil depth corresponded to the pattern of increase in soil bulk density. The most pronounced decrease of % C and C density with soil depth occurred between 0–10 and 20–30 cm for all transects and



**Figure 3.** Biomass, biomass productivity, biomass carbon storage, soil organic carbon storage, and total organic carbon storage, and decreasing water availability, represented by using transects AB, CD, and EF as surrogates for water availability.

these variables were found to vary significantly with depth (Table 4: Model B  $p < 0.0001$  and Model C  $p < 0.0001$ ). However, C density did not vary significantly between transects (Table 4: Model C  $p = 0.066$ ).

Modeled soil carbon storage over the full sediment profile (0–100 cm) for each core location is provided in supporting information Table 2. Modeled soil carbon storage varied significantly with transect location ( $p = 0.0022$ ,  $F = 8.637$ ) and correlated with the decline in aboveground biomass and persistence of reedbeds between transects (i.e., transect AB < CD < EF), thereby confirming hypothesis 2 that soil organic carbon storage was enhanced when vegetation was persistent.

### 3.3. Vegetation Persistence and Soil Organic Carbon Sources

The enrichment of  $^{13}\text{C}$  with soil depth was evident for all cores and all transects ( $p < 0.0001$ ), and there was no significant difference in  $\delta^{13}\text{C}$  between transects (Table 4: Model D  $p = 0.12$ ), however enrichment appeared to be less pronounced at transect CD (Table 2 and Figure 5).

Living shoot, leaf, and root material of *P. australis* had  $\delta^{13}\text{C}$  values of  $-28.2 \pm 0.7$  ( $n = 7$ ),  $-28.0 \pm 0.7$  ( $n = 7$ ), and  $-27.6 \pm 0.7$  ( $n = 7$ ), respectively. Our analyses indicated that  $\delta^{13}\text{C}$  values of upper-profile soil samples from transect AB (0–10 and 20–30 cm) (Table 2) was similar to the  $\delta^{13}\text{C}$  values for living *P. australis* material, suggesting the persistent vegetation was the primary soil organic carbon sources for the upper portion of the soil profile. This was identified despite marked  $^{13}\text{C}$  enrichment at 20–30 cm at core location 1. Significant differences in  $\delta^{13}\text{C}$  values between soil samples from transect AB and *P. australis* materials were only detected below 30 cm (50–60 and 80–90 cm) (Table 5), thereby partly confirming hypothesis 3. Significant differences in  $\delta^{13}\text{C}$  values were detected between reference *P. australis* materials and all soil samples from transects CD and EF, with the exception of root material and soil from transect EF at 0–10 cm depth (Table 5), confirming hypothesis 4 that stable carbon isotopic signatures where vegetation was less persistent did not correspond to the isotopic signatures of the living organic material of the ephemeral vegetation.

## 4. Discussion

### 4.1. Vegetation Persistence and Aboveground Carbon Storage

Our study utilized three sites representing three states of semipermanent reedbed condition along an inundation gradient. Transect AB represents a site of regular (near annual) inundation; by contrast, transects CD and EF occur higher on the floodplain and are inundated less frequently. While transects CD and EF had been inundated in the wetter than average 2010–2011 and 2011–2012 seasons, the site is less frequently

**Table 2.** Mean (Standard Deviation) Values for Bulk Density, Soil Percentage Carbon, Carbon Density, and  $\delta^{13}\text{C}$  at Various Soil Depths for Cores Extracted From Transects AB, CD, and EF

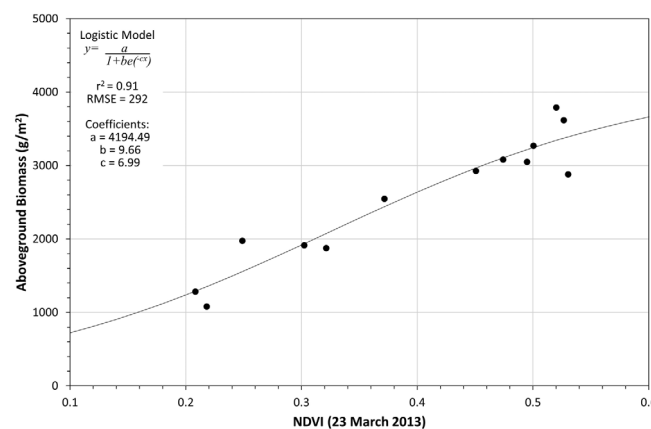
Aboveground Variables	Transect AB			Transect CD			Transect EF <sup>a</sup>							
	Biomass (g m <sup>-2</sup> )	Carbon Storage (g m <sup>-2</sup> )	Productivity (g m <sup>-2</sup> yr <sup>-1</sup> )	Biomass (g m <sup>-2</sup> )	Carbon Storage (g m <sup>-2</sup> )	Productivity (g m <sup>-2</sup> yr <sup>-1</sup> )	Bulk Density (g cm <sup>-3</sup> )	C Content (%C)	C Density (g cm <sup>-3</sup> )	$\delta^{13}\text{C}$ (‰)	Bulk Density (g cm <sup>-3</sup> )	C Content (%C)	C Density (g cm <sup>-3</sup> )	$\delta^{13}\text{C}$ (‰)
Estimated value	3320 ± 777	1430 ± 2633	7305 ± 399	2760 ± 721	1190 ± 28	6075 ± 331								
Soil Depth (cm)														
0–10	0.81 (0.39)	4.4 (2.0)	0.030 (0.0050)	-26.6 (1.37)	1.13 (0.40)	2.9 (1.0)	0.028 (0.089)	-24.7 (1.64)	1.07 (0.29)	2.9 (1.1)	0.030 (0.011)	-24.2 (1.15)		
20–30	1.30 (0.15)	1.7 (1.1)	0.021 (0.012)	-23.2 (4.32)	1.31 (0.29)	1.4 (0.20)	0.017 (0.0094)	-24.5 (1.04)	1.33 (0.27)	0.90 (0.20)	0.012 (0.0036)	-22.8 (3.15)		
50–60	1.53 (0.10)	1.0 (0.50)	0.015 (0.0060)	-18.5 (5.25)	1.48 (0.25)	0.60 (0.30)	0.098 (0.0061)	-23 (2.41)	1.57 (0.13)	0.60 (0.30)	0.0087 (0.0033)	-19.7 (3.95)		
80–90	1.62 (0.30)	0.60 (0.10)	0.0090 (0.0030)	-17.3 (5.65)	1.49 (0.20)	0.60 (0.20)	0.0088 (0.0019)	-19.4 (4.02)	1.47 (0.29)	0.40 (0.10)	0.0062 (0.0016)	-18.0 (2.52)		
Soil carbon storage prediction expression (g cm <sup>-3</sup> )	$y = 0.0020 + 0.030e^{-0.017x}$ $r^2 = 0.52$ ; SSE = 0.0015			$y = 0.0076 + 0.025e^{-0.040x}$ $r^2 = 0.57$ ; SSE = 0.0013			$y = 0.0070 + 0.034e^{-0.073x}$ $r^2 = 0.74$ ; SSE = 0.0009							
Estimated soil carbon storage (Mg ha <sup>-1</sup> ) (0–100 cm)	170 ± 49			140 ± 37			120 ± 37							

<sup>a</sup>Aboveground biomass, carbon storage, and productivity have been omitted for transect EF as the ephemeral reedbeds were not present at the time of sampling and there was not aboveground material to sample.

inundated than AB, and had not been inundated in the 12 months prior to this survey. *P. australis* within transect EF had died back to culms. Variable vegetation persistence between all transects, which is mediated by variation in inundation frequency throughout the floodplain, was found to have an effect on shoot height, dry mass, biomass, and aboveground carbon storage, and hypothesis 1 was accepted.

Our estimates of aboveground biomass for *P. australis* are amongst the first for Australian freshwater reedswamps. We found our allometric equations, developed using the methods of Thursby et al. [2002], provided a robust estimate of biomass; though different equations were generated for the different condition classes of transects AB and CD. Our sampling was timed to coincide with peak aboveground biomass in the region

(mid-Autumn) [Hocking, 1989]. The estimates of aboveground biomass in this study are not as high as nutrient enriched marshes in Australia (9890 g m<sup>-2</sup> from a nutrient enriched swamp on Mirrool Creek in the Murray-Darling Basin: Hocking [1989]) or Europe (4933 g m<sup>-2</sup> for eutrophic ponds in the Czech Republic: Vymazal and Kröpfelová [2005]). However, they are higher than brackish *P. australis* marshes in the northern USA (310 g m<sup>-2</sup> for a saltmarsh on Rhode Island, USA: Thursby et al. [2002]) and Australia (788 g m<sup>-2</sup> for a flow through constructed wetland in South Australia: Adcock and Ganf [1994]).



**Figure 4.** Correlation between NDVI and aboveground biomass of *Phragmites australis* using a logistic model.

**Table 3.** NDVI-Derived Estimates of Aboveground Biomass for the *P. australis* Reedbeds at the Macquarie Marshes<sup>a</sup>

Year	Biomass (Mg)	Flow (GL)	Area (ha)	Standardized Biomass (Mg ha <sup>-1</sup> )
1991	109,000	721	4780	22.8
2008	56,000	92.6	2300	24.3
2013	115,000	510	4900	23.5

<sup>a</sup>These estimates correspond to flow at the Oxley gauge (gauge number 421,022) and the estimated area of reedbeds in 1991 [Wilson et al., 1993], 2008 [Bowen and Simpson, 2010], and 2013 [Bowen and Fontaine, 2014].

Spot measurements of aboveground biomass are likely to be less useful than assessments of the relationship between biomass and water regime. To this end, we sought to use our plot data to calibrate NDVI-derived estimates of biomass that could be applied over the broader spatial and temporal scales for which water and wetland assets are managed. Our model provided an accurate estimate of observed biomass. To demonstrate the utility of the approach, we

estimated biomass for the entire Southern Nature Reserve of the Macquarie Marshes using the 1991 mapped reedbed extent of Wilson et al. [1993] to parameterize estimates for 1991, the 2008 mapped reedbed extent of Bowen and Simpson [2010] to parameterize estimates for 2008, and the 2013 mapped reedbed extent of Bowen and Fontaine [2014] to parameterize estimates for 2013. This time period encompassed significant changes in the distribution and condition of the reedbeds, including the isolation of the southern Macquarie Marshes floodplain from overbank flows [Ralph et al., 2011], one of the longest and most severe droughts on record (2000–2007) corresponding to prolonged El Niño-related drought, and a series of years with higher than average rainfall and extensive inundation associated with the La Niña phase of the El Niño Southern Oscillation. The extent of semipermanent reedbed declined by 2480 ha between 1991 [Wilson et al., 1993] and 2008 [Bowen and Simpson, 2010]. Our NDVI model suggests aboveground *P. australis* biomass declines of approximately 53,000 Mg over the same period (Table 3) or a loss of approximately 22,800 Mg of carbon from the aboveground carbon storage of the Southern Nature Reserve. Subsequent increases in flow and reedbed extent in 2013 resulted in restoration of biomass and aboveground carbon store of reedbeds to levels similar to 1991 (Table 3).

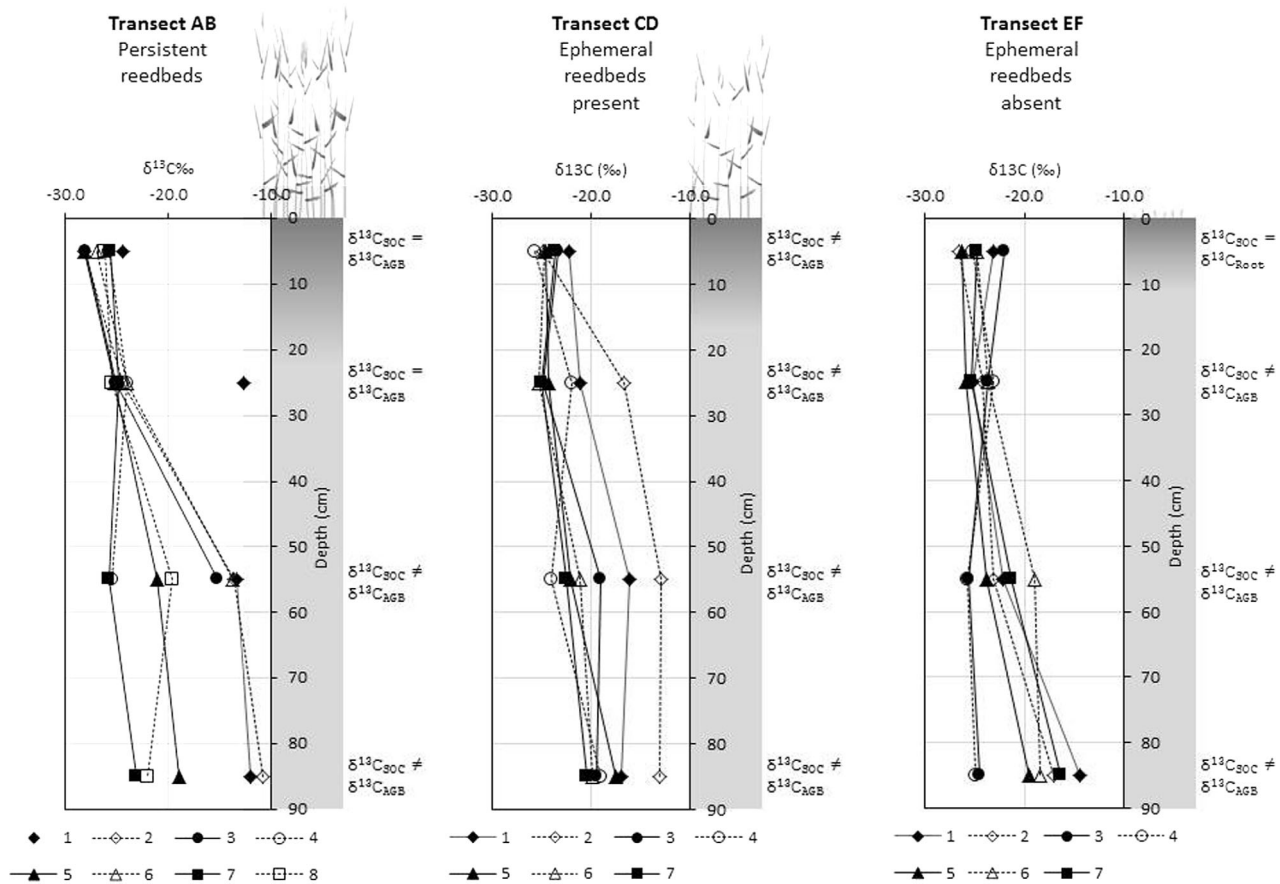
#### 4.2. Vegetation Persistence on Belowground Carbon Storage

While the aboveground biomass of *P. australis* is large, more than 90% of carbon stored in the Macquarie Marshes reedbeds is belowground. Our wetter site at transect AB sustained a slightly higher belowground carbon storage than the drier transects CD and EF. Page and Dalal [2011], in the review of wetland carbon stocks in Australia, found that SOC in the upper 1 m of freshwater wetland soils ranged between 144 and 240 Mg ha<sup>-1</sup> and proposed that 240 Mg ha<sup>-1</sup> was a “reasonable” SOC for the upper 1 m of freshwater wetlands soils. The SOC storage for freshwater systems lags behind their coastal equivalents that are dominated by mangrove and saltmarsh, where SOC reportedly ranges between 25 and 881 Mg ha<sup>-1</sup> [Howe et al., 2009; Page and Dalal, 2011; Saintilan et al., 2013]. For saline coastal wetlands, aerobic oxidation of organic carbon is limited by anaerobic conditions; however, unlike many freshwater wetlands, saline conditions may further limit aerobic and anaerobic oxidation, thereby reducing both carbon dioxide and methane emissions and slowing carbon decomposition [Kristensen et al., 2008; Magenheimer et al., 1996; Nyman and DeLaune, 1991]. However, despite carbon storage generally being lower for freshwater wetlands, our reported carbon

**Table 4.** Results From Generalized Linear Models for Differences Between Bulk Density, % C, Carbon Bulk Density, and δ<sup>13</sup>C, Between Transects (AB, CD, and EF), and at Various Soil Depths (0–10, 20–30, 50–60, 80–90 (or 70–80) cm)

Model	Variables			GLM Model		Significance: <i>p</i> Values ( <i>f</i> Ratios)			
	Dependent	Effect 1	Effect 2	Distribution	Link	Whole Model	Effect 1	Effect 2	Interaction
A	Bulk density	Soil depth	Transect	Normal	Identity	<0.0001* (5.6)	<0.0001* (18)	0.86 (0.15)	0.44 (0.98)
B	% C	Soil depth	Transect	Exponential	Reciprocal	<0.0001* (47)	<0.0001* (41)	0.45 (1.6)	0.95 (1.6)
C	C density	Soil depth	Transect	Normal	Identity	<0.0001* (11)	<0.0001* (38)	0.066 (2.8)	0.74 (0.58)
D	δ <sup>13</sup> C	Soil depth	Transect	Normal	Identity	<0.0001* (5.9)	<0.0001* (18)	0.12 (2.2)	0.30 (1.2)

\*Significant *p* values.



**Figure 5.** Changes in  $\delta^{13}C$  with depth in replicate sediment cores extracted from transect AB where reedbeds are persistent, transect CD where reedbeds are ephemeral, and present at the time of sampling, and transect EF where reedbeds are ephemeral and absent at the time of sampling. AGB, aboveground biomass; SOC, soil organic carbon.

storage correlates with freshwater wetlands carbon storage reported for Northern Territory [Fogarty, 1980] (cited in Page and Dalal [2011]).

We did not detect a significant difference in soil carbon density between transects, though analyses of soil carbon density that accounted for variability over the soil profile were significant, and modeled soil carbon storage over the full sediment profile (0–100 cm) for each core location did vary significantly between transects. These differences were primarily driven by differences in carbon density at transect AB where water supply was consistent and reedbeds were persistent, and transect EF where *P. australis* reedbeds were ephemeral and absent at the time of sampling, and corresponded to the trend in decreasing water

**Table 5.** Matched Pairs *t* Test Probability (*t* Ratio) Values for Tests of Differences Between  $\delta^{13}C$  Values of Living Leaf, Shoot, and Root of *P. australis* Plant Material and  $\delta^{13}C$  Values of Soil Samples Collected From Different Transects (AB, CD, and EF) and at Various Depths

Soil Depth (cm)	Transect AB			Transect CD			Transect EF		
	Leaf	Shoot	Root	Leaf	Shoot	Root	Leaf	Shoot	Root
0–10	0.26	0.220	0.53	0.0009*	0.0066*	0.0069*	0.028*	0.044*	0.062
	1.3	1.5	0.68	8.7	5.2	5.1	3.4	2.90	2.6
20–30	0.061	0.072	0.094	0.014*	0.015*	0.022*	0.014*	0.015*	0.025*
	2.6	2.4	2.2	4.2	4.1	3.6	4.2	4.1	3.5
50–60	0.0097*	0.014*	0.016*	0.0076*	0.011*	0.013*	0.0007*	0.0027*	0.0040*
	4.7	4.1	4.1	5.0	4.5	4.3	9.4	6.7	6.0
80–90	0.01*	0.014*	0.016*	0.0005*	0.0006*	0.0008*	0.011*	0.013*	0.017*
	4.6	4.2	4.0	10	9.9	9.2	4.4	4.2	3.9

\*Significant differences between SOC  $\delta^{13}C$  and  $\delta^{13}C$  values of living shoot ( $-28.2 \pm 0.7$ ,  $n = 7$ ), leaf ( $-28.0 \pm 0.7$ ,  $n = 7$ ), and root ( $-27.6 \pm 0.7$ ,  $n = 7$ ) material from *P. australis* sampled from the Macquarie Marshes.

availability (Figure 3). This trend also corresponded with observations of decreasing biomass between transects and estimates of productivity for each transect location (Figure 3), and hypothesis 2 was accepted.

#### 4.3. Vegetation Persistence and Soil Organic Carbon Sources

Similarities in  $\delta^{13}\text{C}$  values detected between upper-profile soil at transect AB and *P. australis* living material indicates that the standing biomass, not carbon from other sources such as carbon delivered by hydrological flows, was the primary source of surface carbon at transect AB. However, this trend was not consistent over the full soil profile. Hence, we have concluded that standing biomass has contributed to carbon in the upper portion of the soil profile and accepted hypothesis 3.

With the exception of root living biomass at transect EF, significant differences were detected between  $\delta^{13}\text{C}$  values of surface soil samples at transects CD and EF and the  $\delta^{13}\text{C}$  values for living *P. australis* root, shoot, and leaf material. We therefore partly accepted hypothesis 4 that SOC stable isotope signature did not correspond to the isotopic signature of living organic material where *P. australis* was ephemeral. *P. australis* roots can remain viable for 3–6 years [Haslam, 1969] and may explain the absence of a significant difference between the carbon isotopic signature of the living root material and SOC in the upper 10 cm of the soil profile at transect EF. Significant differences in SOC and living plant material at transects CD and EF may be explained by mixed sources of soil carbon at sites where reedbeds are less persistent, and where allochthonous inputs, perhaps from itinerant vegetation or hydrological flows, are higher [Ralph et al., 2011]. Preferential decomposition of labile SOM under enhanced aerobic soil conditions is reported to result in greater preservation of resistant components that are more depleted in  $^{13}\text{C}$ , such as cellulose, lipid, and lignin and the loss of  $^{13}\text{C}$  enriched components such as proteins, carbohydrates, and leaves [Benner et al., 1987]; however, this is contrary to our observations of  $^{13}\text{C}$  enrichment of surface soil samples at transects CD and EF where aerobic soil conditions are prevailing. We have applied these hypotheses to our data set under the assumption that living *P. australis* exhibits a distinct isotopic signature that can be used to fingerprint carbon sources. While studies have shown that there may be some variation in isotopic composition of plants over spatial and temporal scales [Cloern et al., 2002], we found very little variability in leaf, root, and shoot  $\delta^{13}\text{C}$  values of *P. australis* at the Macquarie Marshes (Table 4). Shoot  $\delta^{13}\text{C}$  values are reported to exhibit greater variability in relation to salinity and our observed values corresponded with other  $\delta^{13}\text{C}$  values from nonsaline wetlands [Choi et al., 2005]. Hence, mixing of carbon sources from *P. australis* and other plant species at transects CD and EF appears to be the more likely explanation. The differences in  $\delta^{13}\text{C}$  values between surface soil samples at persistent reedbeds and ephemeral reedbeds corresponds to reported differences in  $\delta^{13}\text{C}$  values for dissolved organic carbon of water samples for study sites with increasing inter-flood interval [Sives, 2011].

All cores, including those derived from the persistent reedbeds at transect AB, showed a trend of enrichment in  $^{13}\text{C}$  with soil depth, of an average  $\delta^{13}\text{C}$  value of 7.6‰ and up to 17.3‰ (transect AB: core 2). This trend of enrichment in  $^{13}\text{C}$  with soil depth confounds vegetation reconstructions and is consistent with observations from a range of environments [Wang et al., 2008], including saline wetlands [Saintilan et al., 2013] and terrestrial forests [Boström et al., 2007], though is rarely this pronounced. We propose four hypotheses to explain this trend in the Macquarie Marshes:

1. Boström et al. [2007] propose that up to 1.5‰ decrease in  $\delta^{13}\text{C}$  value may be attributed to decreases in atmospheric  $^{13}\text{C}$  since the beginning of the eighteenth century due to industrialization and associated burning of fossil fuels, also known as the “Seuss effect.” However, the degree of  $^{13}\text{C}$  enrichment in this case is greater than can be attributed to the Seuss effect alone, particularly in sections of cores more than a century old. Similarly  $^{13}\text{C}$  enrichment has been demonstrated in 100 year old archived soil material from the Russian steppe [Torn et al., 2002].
2. *P. australis* organic material is enriched in  $^{13}\text{C}$  as it decomposes [V.-Balogh, 2006]; perhaps influenced by preferential use of lighter carbon sources in metabolic reactions of decomposer microbes [Dümig et al., 2013]; differential loss of components of organic matter by microbial decomposers (e.g., lipids, lignin, protein) with different  $\delta^{13}\text{C}$  values [Benner et al., 1987; Hobbie and Werner, 2004]; or increase in microbial components in residual SOM [Boström et al., 2007].
3. Incorporation of alternative sources of autochthonous carbon. Water couch (*Paspalum distichum*) is a widely distributed  $\text{C}_4$  grass found in the southern Macquarie Marshes, and is enriched in  $^{13}\text{C}$  compared



to the dominant  $C_3$  plants including *P. australis* and *Eucalyptus camaldulensis*. The distribution of *P. distichum* varies with hydrological conditions and grazing intensity, and appears to have contracted in recent years within the Southern Nature Reserve [Bowen and Simpson, 2010].

4. Incorporation of alternative sources of allochthonous carbon. The proportion of river-borne carbon might be expected to change over time, particularly as wetlands infill and inundation frequency and duration is lessened. Sediment organic matter is an important alternative source of carbon and is generally enriched in the lower Macquarie with respect to the  $C_3$  plant signature (D. Mazumder, unpublished data).

It is apparent that mechanisms causing enrichment of  $^{13}C$  with soil depth occur in all transects despite differences in flow characteristics, rates of anaerobic and aerobic decomposition, and rates of soil organic carbon accumulation. Further analyses of  $^{13}C$  enrichment under differing hydrological conditions may provide insight into microbial processes that facilitate carbon decomposition and mineralization.

#### 4.4. Carbon Sequestration and Implications for Environmental Water Management

The core locations used by Ralph *et al.* [2011] correspond to the transects used in this study, with accretion at transect AB likely to be in the order of 0.3–0.4 mm yr<sup>-1</sup> over the past 5000 years and 4–5 mm yr<sup>-1</sup> at transects CD and EF over the past 150 years. Accordingly, using conservative estimates of accretion of 0.3 mm yr<sup>-1</sup> at transect AB and 4 mm yr<sup>-1</sup> at transects CD and EF; we estimate that the carbon sequestration potential at the Southern Nature Reserve (transect CD  $\approx$  554 g m<sup>-2</sup> yr<sup>-1</sup>; transect EF  $\approx$  465 g m<sup>-2</sup> yr<sup>-1</sup>) is 2 orders of magnitude greater than the permanent marsh area (transect AB  $\approx$  5.17 g m<sup>-2</sup> yr<sup>-1</sup>), by virtue of the rapid accretion occurring at this site over the past 200 years. Bernal and Mitsch [2012] documented temperate freshwater carbon sequestration rates ranging between 25 g m<sup>-2</sup> yr<sup>-1</sup> for peat swamps in Georgia [Craft *et al.*, 2008] to 504 g m<sup>-2</sup> yr<sup>-1</sup> for *P. australis* swamps in Denmark [Brix *et al.*, 2001]. This is the first study estimating rates of carbon sequestration for semiarid *P. australis* reedbeds. While the rate of sequestration is comparable to temperate swamps, it is apparent that productivity lags behind the more productive temperate counterparts in Europe [Brix *et al.*, 2001].

The rapid rate of accretion documented by Ralph *et al.* [2011] in the Southern Nature Reserve is not likely to be sustainable, with overbank flows now limited to occurring only in association with large flood events. As a consequence of the changes in water regime, the health and productivity of reedbeds at the Southern Nature Reserve are documented to be in decline between 1991 [Wilson *et al.*, 1993] and 2008 [Bowen and Simpson, 2010]. This is further confirmed in this study by differences in NDVI-derived productivity between transects positioned in the persistent reedbeds and the Southern Nature Reserve. The resulting outcome of reduced frequency of overbank flooding is likely to be a decline in the capacity of *P. australis* to allocate carbon to biomass; and increasingly aerobic conditions which would facilitate aerobic decomposition of organic material. Kobayashi *et al.* [2008] demonstrated that floodplain sediments in the Macquarie Marshes release nutrients and carbon to overlying floodwaters following exposure of sediment under dry antecedent conditions. In this study, we found that carbon allocation to biomass and soils corresponds to the persistence of reedbeds, which subsequently corresponds to inundation frequency of *P. australis* reedbeds.

Page and Dalal [2011] estimate that an average of 25% organic carbon in the upper 1 m of drained Australian wetland soils may be lost in the first 50 years following drainage. Comparison of the carbon storage of transect AB, where flows have been persistent, and transects CD and EF, where channels have been abandoned over the past 100 years and flows have become increasingly ephemeral since regulation, approximate this average rate of decline in carbon storage in the upper 1 m from drained soils.

This study suggests that the maintenance of persistent reedbeds by regular inundation is a means of promoting carbon sequestration. Equally, alterations to flooding regime that lead to the dieback of reedbeds and the drying of soils have the potential to cause considerable losses of carbon to the atmosphere. The management of river hydrology, being an activity of government, is a means by which these carbon fluxes to the atmosphere can be manipulated. Further quantification of gas flux and transfers between soil and water is required to fully articulate a carbon budget relating to phases of wet and dry conditions within the reedbeds of the Macquarie Marshes. The technique developed in this paper of combining the biomass assessment methods of Thursby *et al.* [2002] with NDVI modeling provides an effective means of assessing changes in aboveground carbon storage associated with flows that could have broader application in environmental water monitoring and evaluation.

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