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Radiocarbon isotopic evidence for assimilation of atmospheric CO₂ by the seagrass *Zostera marina*

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Abstract

Submerged aquatic vegetation assimilates dissolved inorganic carbon (DIC) in the water column as a carbon source across its thin cuticle layer. However, it is expected that marine macrophytes also use atmospheric CO₂ when exposed to the air during low tide, although assimilation of atmospheric CO₂ has never been quantitatively evaluated. Using the radiocarbon isotopic signatures ($\Delta^{14}\text{C}$) of the seagrass *Zostera marina* and DIC, we show quantitatively that *Z. marina* takes up and assimilates atmospheric modern CO₂ in a shallow coastal ecosystem. The $\Delta^{14}\text{C}$ values of the seagrass (−36 to −8‰) were significantly higher than those of aquatic DIC (−45 to −18‰), indicating that the seagrass uses a ¹⁴C-rich carbon source (atmospheric CO₂, +17‰). A carbon-source mixing model indicated that the seagrass assimilated ~46% (mean: 22%) of its inorganic carbon as atmospheric CO₂. CO₂ exchange between the air and the seagrass may be enhanced by the presence of a very thin water film over the air-exposed leaves during low tide. Our radiocarbon isotope analysis, showing assimilation of atmospheric modern CO₂ as an inorganic carbon source, offers better understanding of the role of seagrass meadows in coastal carbon dynamics.

1 Introduction

Submerged aquatic vegetation assimilates dissolved inorganic carbon (DIC) from the water column as a carbon source. Seagrasses take up DIC across their thin cuticle layer (Hemminga and Duarte, 2000), as their leaves lack stomata despite their being angiosperms (Larkum and Den Hartog, 1989). An alternative carbon source, atmospheric CO₂ (C_{air}), cannot directly reach seagrasses when they are completely submerged; however, seagrasses can take up C_{air} when their leaves are exposed to air during low tide (Leuschner and Rees, 1993; Clavier et al., 2011; Jiang et al., 2014). Seagrasses rely largely on aqueous CO₂ [CO₂(aq)] as a DIC source in nature (Beer and Koch, 1996). As CO₂(aq) is in limited supply under normal seawater conditions,

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comprising only 1 % (roughly 10–15 $\mu\text{mol L}^{-1}$) of the DIC pool, photosynthesis in sea-grasses is frequently limited by carbon availability under high light conditions (Zimmerman et al., 1995; Invers et al., 2001; Campbell and Fourqurean, 2013). Moreover, the diffusion rate of CO₂(aq) in water is much slower than that in the air. Air-exposed aquatic macrophytes have a thin layer of water between the air and their leaves, which promotes the uptake of C_{air} (Ji and Tanaka, 2002). Previous studies (Clavier et al., 2011; Cooper and McRoy, 1988; Raven et al., 2002) have shown the possibility of C_{air} uptake by seagrasses, using evidence from the stable carbon isotope ($\delta^{13}\text{C}$) in sea-grasses and the two carbon sources (DIC and C_{air}). However, the ^{13}C method has considerable uncertainty because the $\delta^{13}\text{C}$ values of seagrasses are also determined by other factors in addition to the source of carbon, such as the form of DIC [CO₂(aq) or HCO₃⁻] and the primary production rate.

The natural abundance of radiocarbon (^{14}C) has recently been used to assess food web structures (Ishikawa et al., 2014) and the origin and components of organic-matter pools (Goñi et al., 2013), as carbon sources have specific ^{14}C concentrations ($\Delta^{14}\text{C}$). The $\Delta^{14}\text{C}$ values of inorganic carbon also have specific values depending on the source, such as DIC and C_{air}. As any effects from isotopic fractionation are eliminated in calculating $\Delta^{14}\text{C}$, the $\Delta^{14}\text{C}$ values of seagrasses are determined only by the two inorganic carbon sources. Furthermore, $\Delta^{14}\text{C}$ values represent carbon turnover times in ecosystems. The age of DIC is generally older than that of atmospheric CO₂ because of the long residence time in the ocean.

This study is the first to show quantitative evidence of the assimilation of modern C_{air} by the seagrass, *Zostera marina*, by analyzing the $\Delta^{14}\text{C}$ values of the seagrass and two carbon sources.

2 Material and methods

2.1 Field surveys

Field surveys were conducted during the growing season of *Z. marina* (May and July 2014) in Furen Lagoon, Japan (43°19'46.5" N, 145°15'27.8" E). Furen Lagoon is brackish (salinity: ~ 30), and covered by large seagrass meadows (67% of the total area) dominated by *Z. marina*. Surface water samples (depth: 0.1 m) for DIC in the water column were collected from a research vessel along the salinity gradient at 7 stations in the lagoon. At each station, the salinity of the surface water was recorded using a conductivity-temperature sensor (COMPACT-CT; JFE Advantech, Nishinomiya, Japan). The samples for isotopic analysis of DIC were dispensed into 500 mL screw-cap glass culture bottles, which were poisoned with mercuric chloride (400 µL per bottle) to prevent changes in DIC due to biological activity. Seagrass (*Z. marina*) leaves were collected at 4 stations along the salinity gradient. The stations were located at subtidal zones (mean water depth: 0.83–1.12 m). The aboveground biomass of the seagrass ranged from 400 to 4300 g wet-weight m⁻². Each sample included 3–4 shoots. To estimate the $\Delta^{14}\text{C}$ of C_{air} , leaves of a terrestrial plant (*Phragmites australis*) were collected near the lagoon. The plant samples were freeze-dried, and subsamples were homogenized. To remove carbonate, the samples were acidified with 1 N HCl and dried again.

2.2 Carbon isotope analysis

We determined the stable carbon isotope ratio ($\delta^{13}\text{C}$) and radiocarbon concentration ($\Delta^{14}\text{C}$) of plant leaves and DIC samples. The $\delta^{13}\text{C}$ of plant leaves was measured with an isotope-ratio mass spectrometer (Delta Plus Advantage; Thermo Electron, Bremen, Germany) coupled with an elemental analyzer (Flash EA 1112; Thermo Electron). The $\delta^{13}\text{C}$ values were reported relative to Vienna Pee Dee Belemnite. Data were corrected using an internal standard (L-histidine ($\delta^{13}\text{C} = -10.19\text{‰}$); SI Science Co., Ltd,

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Saitama, Japan). The analytical precision was within 0.2‰. Prior to $\Delta^{14}\text{C}$ measurements, samples were subjected to graphite purification using the following method. Samples for $\Delta^{14}\text{C}$ and $\delta^{13}\text{C}$ analysis of DIC were acidified ($\text{pH} < 2$) with H_3PO_4 and sparged using ultra-high purity mixed N_2/H_2 gas. The powdered samples for $\Delta^{14}\text{C}$ analysis of plant leaves were combusted by either (1) a Euro EA3000 elemental analyzer (EuroVector, Milan, Italy), or (2) a Flash 2000 elemental analyzer (Thermo Fisher Scientific Inc., Waltham, USA). For each process, the CO_2 evolved was collected cryogenically and purified in a vacuum line. The purified CO_2 was then reduced to graphite using hydrogen and an iron catalyst at 650°C for 10 h. The ^{13}C and ^{14}C concentrations were measured using an accelerator mass spectrometer (AMS). The AMS results are reported as $\Delta^{14}\text{C}$ (‰) values (Stuiver and Polach, 1977) as follows:

$$\Delta^{14}\text{C}(\text{‰}) = \delta^{14}\text{C} - 2(\delta^{13}\text{C} + 25)(1 + \delta^{14}\text{C}/1000). \quad (1)$$

The $\Delta^{14}\text{C}$ values were corrected by the radioactive decay of an international standard (oxalic acid) since AD 1950 (Stuiver and Polach, 1977). The analytical precision of the AMS was within 0.7‰ for $\delta^{13}\text{C}$ of DIC and 3‰ for $\Delta^{14}\text{C}$.

2.3 Data analysis

A general linear model (GLM) was used to examine the difference between the $\Delta^{14}\text{C}$ values of the seagrass leaves and those of DIC. We selected salinity, type (seagrass leaves vs. DIC), and their interaction (salinity \times type) as the explanatory variables (Table 1). Akaike's Information Criterion (AIC) was used to select the most parsimonious model.

The relative contribution of C_{air} to assimilated seagrass carbon was calculated by a two-carbon-source mixing model using the $\Delta^{14}\text{C}$ values of DIC ($\Delta^{14}\text{C}_{\text{DIC}}$), C_{air} ($\Delta^{14}\text{C}_{\text{air}}$), and the seagrass ($\Delta^{14}\text{C}_{\text{seagrass}}$) as follows:

$$C_{\text{air}} \text{ contribution} = (\Delta^{14}\text{C}_{\text{seagrass}} - \Delta^{14}\text{C}_{\text{DIC}}) / (\Delta^{14}\text{C}_{\text{air}} - \Delta^{14}\text{C}_{\text{DIC}}) \times 100. \quad (2)$$

$\Delta^{14}\text{C}_{\text{DIC}}$ was calculated from the best GLM (Table 1). $\Delta^{14}\text{C}_{\text{air}}$ was estimated from the $\Delta^{14}\text{C}$ value of the sampled terrestrial plant ($\Delta^{14}\text{C} = +17.2\text{‰}$).

3 Results and discussion

Our radiocarbon isotopic analysis is the first to show quantitatively that the seagrass *Z. marina* uses C_{air} in the shallow lagoon (Fig. 1a and Table 1). The GLM strongly highlighted the effect of salinity on the $\Delta^{14}\text{C}$ of DIC and the seagrass (Table 1; GLM, $p < 0.001$). These results indicate that the changes in the $\Delta^{14}\text{C}$ of DIC are regulated mostly by mixing between high- $\Delta^{14}\text{C}$ river water and low- $\Delta^{14}\text{C}$ seawater, and that the seagrass use aquatic DIC as a main carbon source, as expected from previous studies (Hemminga and Duarte, 2000; Invers et al., 2001; Campbell and Fourqurean, 2013). However, the model also reinforced our observations that the $\Delta^{14}\text{C}$ of the seagrass was higher than that of DIC (Fig. 1a and Table 1; GLM, $p < 0.001$). This shows that the seagrass assimilates ^{14}C -rich C_{air} ($\Delta^{14}\text{C}$ around 17‰). The two-carbon-source mixing model indicated that the seagrass assimilated $\sim 46\%$ of its inorganic carbon as C_{air} ; the contribution was $25 \pm 14\%$ (mean \pm SD) in the low-salinity zone (12–15) and $18 \pm 12\%$ in the high-salinity zone (25–29) (Fig. 1b). As mean water depth (difference is about 0.3 m) and shoot length (K. Watanabe, unpublished data) are comparable among the sampling sites, we cannot examine the relationship between the contribution of C_{air} and exposure time to the air; however, the exposure time could mediate the assimilation of C_{air} (Clavier et al., 2011).

As the $\Delta^{14}\text{C}$ of DIC was significantly lower than that of C_{air} , the contribution of C_{air} can be determined (Fig. 1a). This radiocarbon isotopic approach would be useful in high latitude of Pacific Ocean, where ^{14}C -depleted surface seawater ($\Delta^{14}\text{C} < 0\text{‰}$) is distributed (Talley, 2007). In contrast, the $\Delta^{14}\text{C}$ of DIC in surface seawater is generally higher than that of C_{air} in other regions of Pacific Ocean because of bomb-derived ^{14}C

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(Talley, 2007). Nevertheless, the $\Delta^{14}\text{C}$ approach would have a potential to apply to other regions, using the $\Delta^{14}\text{C}$ gradient.

Our $\Delta^{14}\text{C}$ analysis considerably improves the limitations and uncertainties of conventional methods such as that using only $\delta^{13}\text{C}$ (Clavier et al., 2011; Cooper and McRoy, 1988; Raven et al., 2002). In particular, the use of $\Delta^{14}\text{C}$ has the advantage of avoiding effects of isotopic fractionation. The use of $\delta^{13}\text{C}$ does not and therefore generates large uncertainties. The $\delta^{13}\text{C}$ of the seagrass were low ($-14.0 \pm 1.9\text{‰}$) in the low-salinity zone (12–15) and high ($-9.2 \pm 0.7\text{‰}$) in the high-salinity zone (25–29) (Fig. 1c). As the $\delta^{13}\text{C}$ of HCO_3^- (0‰) is isotopically distinct from both $\text{CO}_2(\text{aq})$ (-9‰) and C_{air} (-8‰), seagrasses with the different degrees of HCO_3^- use have various isotopic signatures (Campbell and Fourqurean, 2009; Raven et al., 2002). The high $\delta^{13}\text{C}$ ($> -10\text{‰}$) in the high-salinity zone shows that the seagrass use HCO_3^- as carbon source because ^{13}C -depleted organic plant compounds are produced via the photosynthetic processes (the diffusion of inorganic carbon source and the carboxylase activity of Rubisco; Raven et al., 2002). In contrast, the low $\delta^{13}\text{C}$ ($< -10\text{‰}$) in the low-salinity zone could be partly explained by the contribution of atmospheric ^{13}C -depleted CO_2 . However, it is difficult to distinguish the contribution of C_{air} from that of $\text{CO}_2(\text{aq})$.

The seagrass assimilated C_{air} when its leaves were exposed to air during low tide (Fig. 2a and b). CO_2 exchange between the air and water would occur at the very thin film of water on the air-exposed seagrass leaves (Fig. 2c), likely enhancing the passive uptake of C_{air} by diffusion.

The net ecosystem production of seagrass meadows is a key factor determining whether they are sinks or sources of C_{air} (Maher and Eyre, 2012; Tokoro et al., 2014; Watanabe and Kuwae, 2015). Previously, however, such an exchange of CO_2 has been thought to occur only via the air–water interface with subsequent exchange with seagrasses as DIC. This study is the first to quantify the assimilation of modern C_{air} by the seagrass using radiocarbon isotope analysis. Moreover, our radiocarbon isotopic approach has a poteantial for application to other photoautotrophs living near the air–water interface, such as intertidal macroalgae and amphibious macrophytes. However,

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the relative contribution of the gas exchange via the air–seagrass water-film to the total exchange is still unknown. To understand the role of seagrass meadows in the global carbon cycle, it will be necessary in future studies to precisely measure both air–water and air–seagrass water-film CO₂ exchanges.

5 *Author contributions.* K. Watanabe and T. Kuwae designated the work; K. Watanabe carried out the field surveys and analyzed the data; and K. Watanabe and T. Kuwae wrote the manuscript.

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Table 1. Coefficients (median \pm standard error) and significance levels for the general linear models (GLMs) examined.

Variables	Best model (AIC = 292.61)		Full model (AIC = 294.30)	
	Coefficients	<i>p</i>	Coefficients	<i>p</i>
Salinity	-1.68 ± 0.13	< 0.001	-1.76 ± 0.19	< 0.001
Type (seagrass)	9.74 ± 2.10	< 0.001	7.26 ± 5.12	n.s.
Salinity \times type (Intercept)	2.80 ± 2.72	n.s.	0.14 ± 0.26	n.s.
	3.97 ± 3.52	n.s.		

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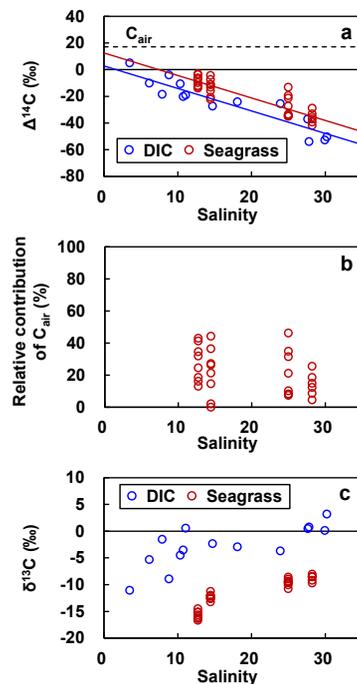


Figure 1. (a) Spatial distribution of the $\Delta^{14}\text{C}$ values of dissolved inorganic carbon (DIC) (blue open circles) and the seagrass (red open circles) along the salinity gradient in Furen Lagoon, Japan. Blue and red solid lines represent the best fitting model of all of the general linear models (GLMs) examined for DIC and the seagrass, respectively. The dashed line indicates the $\Delta^{14}\text{C}$ of atmospheric CO₂ (C_{air}). (b) Spatial distribution of the relative contribution of C_{air} to total inorganic carbon assimilated by the seagrass along the salinity gradient, as calculated by the two-carbon-source mixing model. (c) Spatial distribution of the $\delta^{13}\text{C}$ values of dissolved inorganic carbon (DIC) (blue open circles) and the seagrass (red open circles) along the salinity gradient.

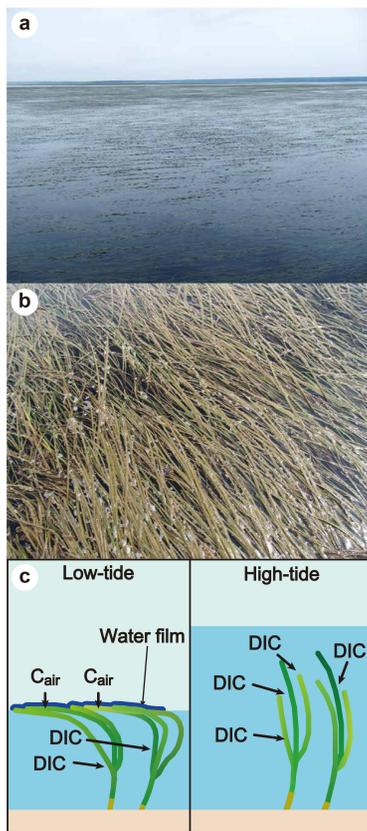
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Figure 2. (a) Distant view and (b) close-up view of the seagrass leaves exposed to the air during low tide in Furen Lagoon, Japan. (c) Conceptual diagram of the uptake of atmospheric CO₂ (C_{air}) across the surface-water film on the seagrass leaves during low tide (left), and the uptake of DIC during high tide (right).

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