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Vegetation succession and carbon sequestration in a coastal wetland in northwest Florida: Evidence from carbon isotopes

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Abstract. Measurements of stable carbon isotopic ratios as well as carbon (C), nitrogen (N), and phosphorus (P) contents in soils and plants were made along a chronovegetation sequence stretching from high marsh to low marsh in a coastal wetland in northwest Florida. The wetland is dominated by *Juncus roemerianus* , which is a C3 plant and has an average $\delta^{13}C$ of −27‰. Lesser amounts of other species, including C4 plants, are also present in the area. The $\delta^{13}C$ values of soil organic matter from low and middle marshes range from −24 to −27‰, which are consistent with the current plant community. However, the $\delta^{13}C$ values of soil organic matter from high marsh show significant variations, from −23‰ in the surface soil to −17‰ at depth. This large C isotopic variation within soil profiles indicates a shift in local vegetation, from a C4-dominated community to the current C3 plant-dominated marsh, as a result of landward expansion of the wetland due to sea level rise. Radiocarbon dates on soil organic matter indicate that this ecological change occurred in the past hundred years or so as a result of sea level rise presumably due to global warming. Soil organic carbon inventory was $\sim 29 \pm 3.6$ kg m^{-2} in low marsh (the oldest part of the wetland), 15 ± 3.6 kg m^{-2} in middle marsh, and 13 ± 6.0 kg m^{-2} in high marsh (the youngest and most inland part of the wetland). N and P inventories are also higher in low marsh than in high marsh and seem to correlate directly with aboveground productivity in the marshes. The much higher C storage in low marsh than in high marsh indicates that carbon sequestration increased significantly as coastal wetland evolves from high marsh (initial stage) to low marsh (steady state). This has important implications to the global C cycle. As sea level rises owing to global warming, coastal wetlands are expected to expand landward in many areas where topography is gentle, which would provide a significant sink for atmospheric carbon dioxide.

1. Introduction

Coastal wetlands form chains of marshes and swamps along most of the world's coasts and provide enormous benefits to wildlife, human economy, and environment [*Titus*, 1991]. Studies have shown that coastal wetlands have very high primary productivity [*Bouwman*, 1990; *Coultas*, 1996; *Hsieh*, 1996] and contain ~10% of the total soil carbon [*Armentano*, 1980; *Schlesinger*, 1977, 1995]. Unlike most upland soils, coastal wetlands can continuously sequester carbon through plant production and burial process associated with sea level rise. Although it has been recognized that tidal coastal wetlands respond to sea level rise by expanding landward, accreting vertically, and, on some coasts, by expanding seaward as well, how these changes affect carbon sequestration in coastal wetlands has received little attention.

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Coastal wetlands along the gulf coast of Florida are typically composed of four vegetation zones: low marsh, middle marsh, salt barren, and high marsh (Figure 1). A salt barren is a zone separating high marsh from middle marsh. Salt barrens are sandy, hypersaline environments that support sparse vegetation. The marshes are dominated by black needlerush (*Juncus roemerianus*), with lesser amounts of cordgrass (*Spartina alterniflora*) in low marsh and middle marsh and salt meadow cordgrass (*Spartina Patens*) in the transition zone between high marsh and upland forest. There are also several other species of grasses and a few succulent plants (e.g., *Salicornia bigelovii*, *Salicornia virginica*, *Batis maritima*, and *Distichlis spicata*) in salt barren and high marsh [*Montague and Odum*, 1997]. Low marsh and middle marsh are within the regularly flooded zone that is inundated twice daily by tidal water, and high marsh is in the irregularly flooded zone where inundation is less frequent [*Kurz and Wagner*, 1957; *Montague and Wiegert*, 1990].

The natural difference in stable carbon isotopic ratios of different plants provides an opportunity to study the vegetation succession in coastal wetlands [*Chmura et al.*, 1987; *Craft et al.*, 1988; *DeLaune*, 1986] and has the potential to provide valuable evidence

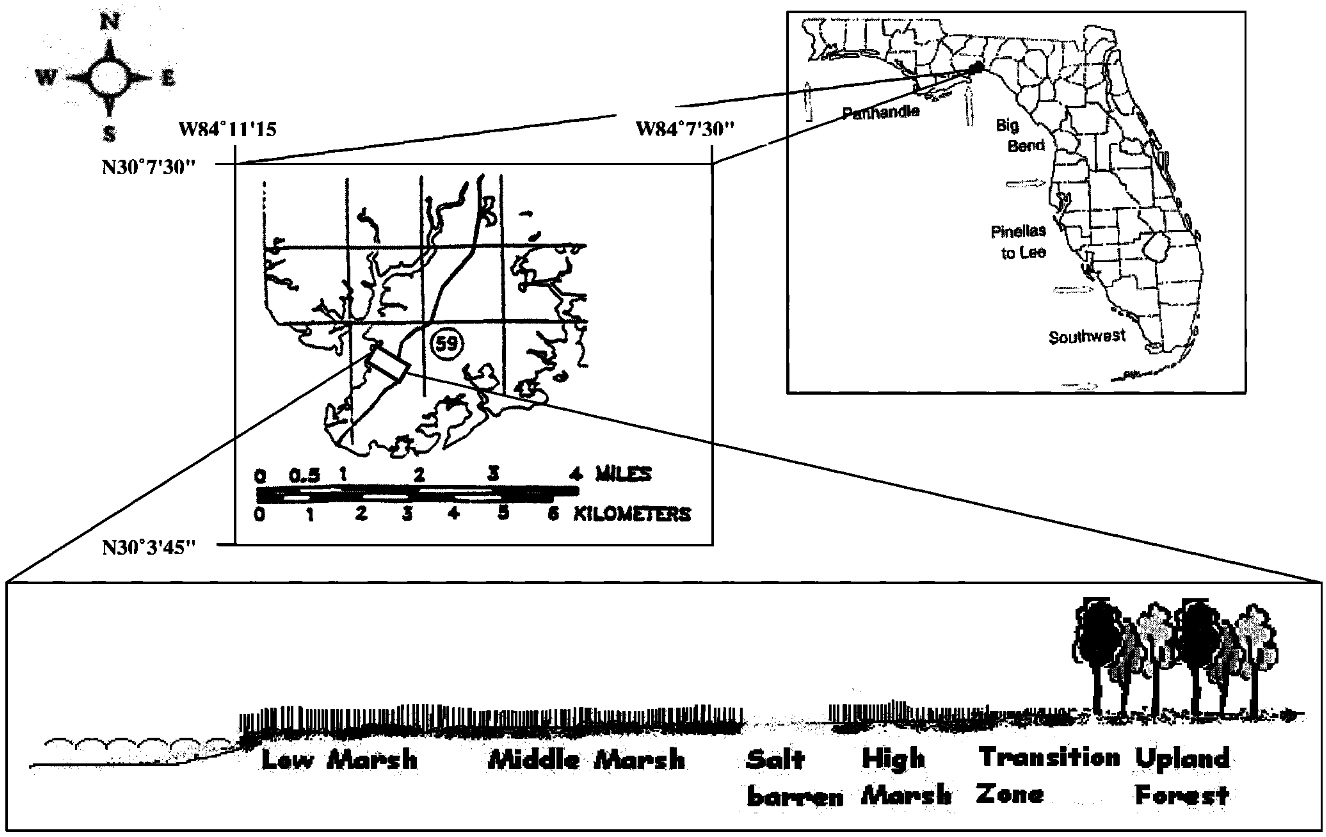

Figure 1. A map showing the study area in the St. Marks Wildlife Refuge (Wakulla County, Florida) and schematic cross-section diagram (not to scale) showing the vegetation zones (i.e., low marsh, middle marsh, salt barren, high marsh, and transition zone) in the area.

of sea level fluctuations [*Chmura and Aharon*, 1995; *DeLaune*, 1986]. Plants are depleted in the heavy C isotope ^{13}C relative to the atmospheric CO_2 owing to both enzymatic and physical processes that discriminate against the heavier isotope in favor of the lighter one during photosynthesis [*Lajtha and Michener*, 1994]. Terrestrial plants can be divided into three groups according to their photosynthetic pathways: C3, C4, and crassulacean acid metabolism (CAM) plants [*O'Leary*, 1981, 1988]. C3 plants use the Calvin cycle (C3 photosynthetic pathway) and include all trees, most shrubs, herbs, and forbs, and cool season grasses and sedges. C4 plants use the Hatch-Slack cycle (C4 photosynthetic pathway) and are mostly warm season grasses and sedges; CAM plants use the crassulacean acid metabolism photosynthetic pathways and include succulents. During photosynthesis, C3 plants discriminate against $^{13}CO_2$ to a greater extent than do C4 plants [*Deines*, 1980; *O'Leary*, 1981; *Vogel*, 1980]. As a result of this fractionation, plants with C4 photosynthetic pathways have $\delta^{13}C$ values between -9 and -17‰, with an average of -13‰, whereas C3 plants have $\delta^{13}C$ values ranging from -23 to -34‰, with an average of -27‰ [*Deines*, 1980]. The large ($\sim$14‰) difference in $\delta^{13}C$ values between C3 and C4 plants can be used to quantify the proportion of C3 and C4 species contributing to a mixture of plant material [*Cerling*, 1984; *Cerling et al.*, 1988; *Cerling and Hay*, 1986; *Cerling et al.*, 1989; *Dzurec et al.*, 1985; *Gulliet et al.*, 1988; *Schwartz et al.*, 1986; *Volkoff and Cerri*, 1986]. Because soil organic matter has a stable carbon isotopic composition comparable to that of the source plant material [*Dzurec et al.* , 1985; *Gulliet et al.*, 1988; *Schwartz et al.*, 1986], changes in C3 and C4 vegetation types will affect the $\delta^{13}C$ values of the soil organic matter. Therefore it is possible to detect changes in the relative proportion of C3 and C4 plants in the past by measuring the carbon isotopic compositions of the current plant community and soil organic matter [*Balesdent et al.*, 1987; *O'Brien and Stout*, 1978; *Wang et al.*, 1993].

Studies in coastal marshes of eastern North America and southern California [*Chmura and Aharon*, 1995] and in Louisiana on the northern coast of the Gulf of Mexico [*Chmura et al.*, 1987; *DeLaune*, 1986] have shown that the stable carbon isotopic ratios of sedimentary organic matter provide reliable evidence of the salinity regime of marsh deposits in those regions. Although the Gulf of Florida estuary supports different plant species from those found on the Atlantic coast and Louisiana coast, the transition in plant communities are similar in terms of C3 and C4 compositions. Therefore a change in dominance of C3 or C4 vegetation resulting from changes in salinity regime should also be detectable in the stable carbon isotopic record in the marsh.

The sea level along the Florida Gulf coast has been rising at a rate of $\sim$17–24 cm per century, which is higher than the global average rate of 12 cm per century [*Penland and Ramsey*, 1990]. The rate of sea level rise has apparently accelerated considerably in the last century, presumably due to the global warming [*Leatherman et al.*, 2000; *Penland and Ramsey*, 1990; *Varekamp and Thomas*, 1998]. As sea level rises, the marsh areas expand landward in areas with low topography, causing ecological changes in the marsh, such as the conversion of high marsh to low marsh. This type of change has been documented in New England tidal marshes over the past decades through peat core analysis [*Warren and Niering*, 1993]. Similar changes in wetland plant communities could be occurring along other coasts, and these changes could have important consequences

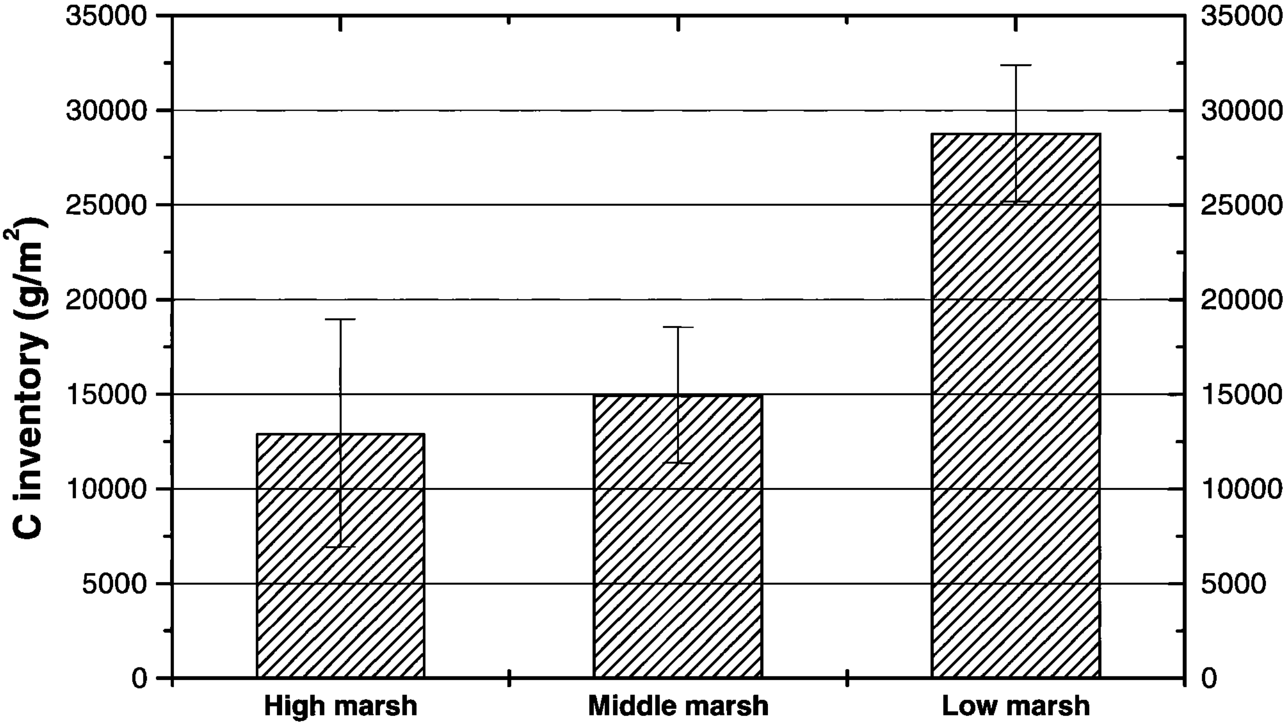

Figure 2. Total carbon inventories (0–86.4 cm) in St. Marks wetland soils.

for the global C cycle, wildlife habitat and other functions of coastal wetlands.

In this study, we analyzed the carbon isotopic composition of plant and soil samples collected along a transect stretching from low marsh to high marsh in a coastal wetland in northwest Florida. In addition, we measured the carbon (C), nitrogen (N), and phosphorus (P) contents of these samples. Low marsh, middle marsh, and high marsh soils form a chronovegetation sequence with low marsh being the oldest and high marsh being the youngest (and most inland). The objective of this study is to examine the

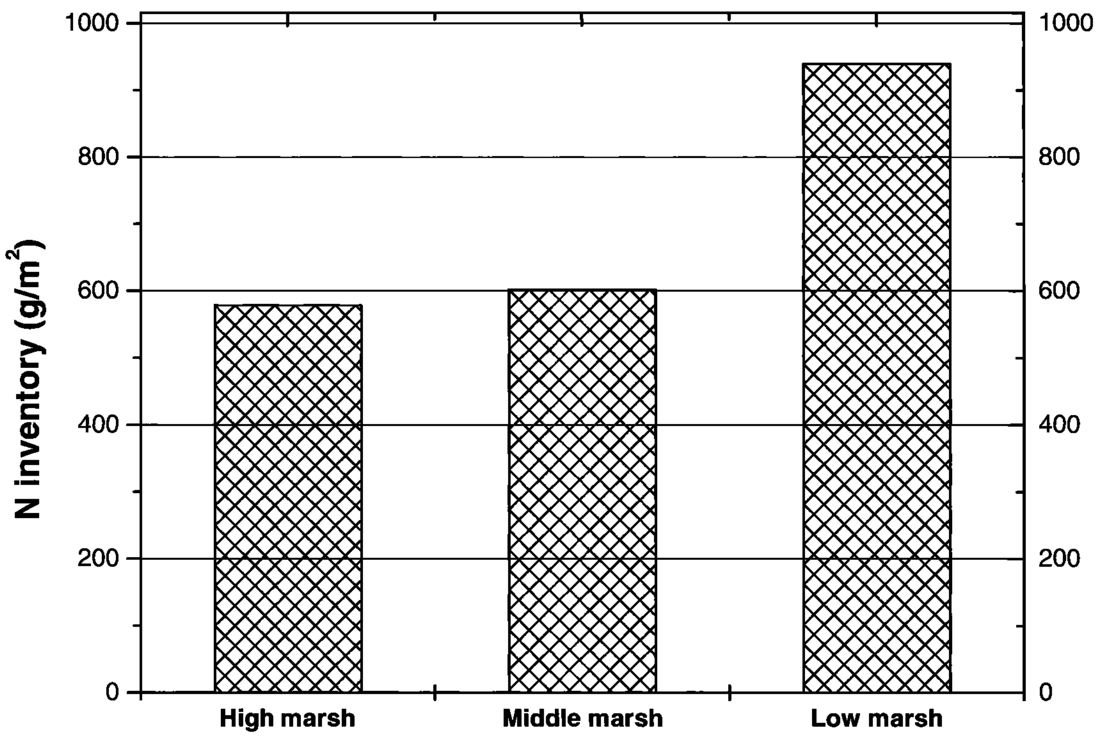

Figure 3. Total nitrogen inventories (0–50 cm) in St. Marks wetland soils.

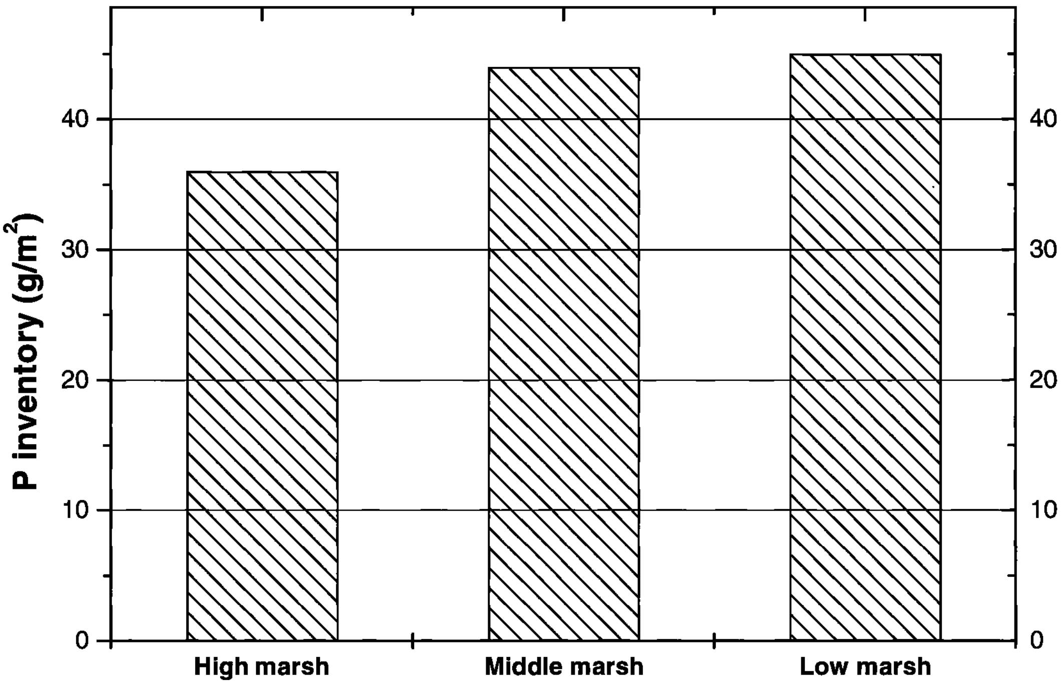

Figure 4. Total phosphorus inventories (0–50 cm) in St. Marks wetland soils.

effects of sea level rise on vegetation succession and carbon sequestration in this coastal wetland.

2. Field and Laboratory Methods

2.1. Study Area and Sample Collection

The coastal marshes in the St. Marks National Wildlife Refuge in Wakulla County of Florida are the focus of this study. Wakulla County is situated in the Big Bend area of the Florida panhandle. The study area is located at 30°05′N, 84°10′W and is bounded on the south by the Gulf of Mexico (Figure 1). This study area has a very low sedimentary supply [*Tanner*, 1960; *Tanner and Demirpolat*, 1989] because of the flat topographical feature, low tidal energy, and lack of large rivers. The mean annual precipitation in the area is ~134 cm, and the mean annual temperature range is from 26.1° to 15.9°C [*Coultas*, 1996].

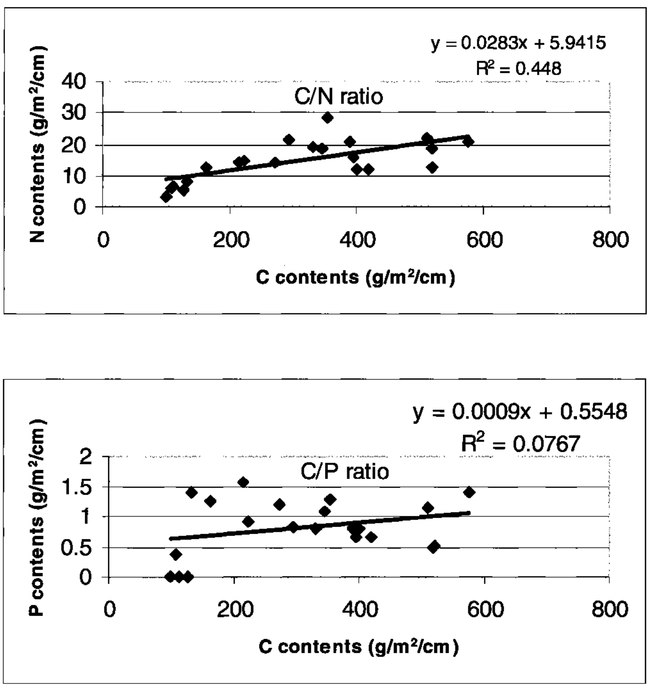

Figure 5. C/N and C/P ratios in St. Marks soils, showing a positive correlation between C and N but no correlation between C and P.

The marshes in the study area have very high aboveground net primary production ranging from 1000 to 4000 g C m^{-2} yr^{-1}, which is significantly higher than the adjacent upland forests, which are estimated at 200–1000 g C m^{-2} yr^{-1} [*Hsieh*, 1996; *Kruczynski et al.*, 1978]. The soils in the study area are essentially peat (i.e., rich in organic matter) and have loamy sandy texture overlying limestone at the depth of 90–120 cm. Soil cores were collected in 7.2 cm diameter PVC tubes with sharpened edges, which minimized compaction. Compaction was estimated by inspecting the surface of the soil inside and outside of the core. Any core with compaction >1 cm was excluded from analysis. We collected 13 cores from high marsh, middle marsh, and low marsh for measurements of C, N, and P contents and C isotopic composition. Various plant samples were also collected from low, middle, and high marsh area for C isotopic analyses.

2.2. Sample Preparation and Analyses

Soil samples were weighed before and after being dried at 60°C for 4 days. The weight difference between wet and dry samples was used for determining the water content and the bulk density of the soils. Dried soil samples were handpicked of visible living roots and leaves, and the rest of materials were ground to pass through 2 mm sieve. The ground sample was treated with 10% HCl for 3 hours to dissolve inorganic carbonate in the sample, washed with distilled water five times via centrifugation, and then freeze-dried. After being freeze-dried, soil samples were ground again to a very fine powder. Plant samples were dried at 60°C and were ground in a grinder. The ground plant samples were also treated with acid to remove inorganic carbonate. Soil and plant samples were combusted to produce CO_2 with CuO, Cu, and silver foil in a

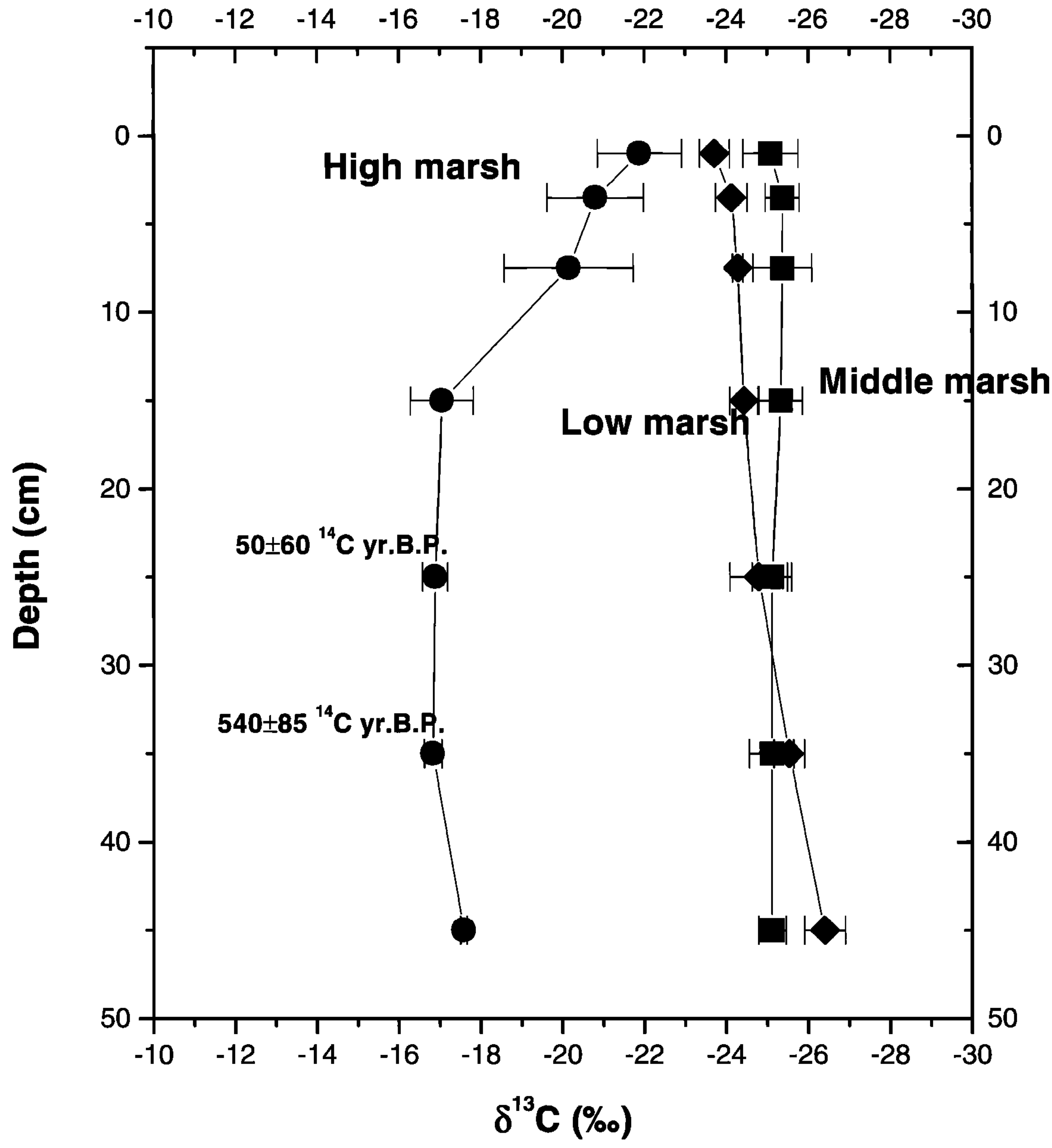

Figure 6. Stable carbon isotopic composition and radiocarbon dates of soil organic matter in a coastal wetland in northwest Florida (St. Marks, Wakulla County).

vycor tube under vacuum at 875°C for 2 hours. The CO_2 was then purified cryogenically for stable and radiocarbon analyses. The stable isotope ratio of the purified CO_2 was measured on a stable isotope ratio mass spectrometer at the Florida State University. For radiocarbon measurements the purified CO_2 was reduced to graphite, and its radiocarbon content was determined on an accelerator mass spectrometer in the radiocarbon laboratory at the University of Arizona. The stable carbon isotope data are reported in the standard delta notation with reference to the international Pee dee belemnite (PDB) standard as

$$\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{PDB} - 1]1000.$$

Radiocarbon data are reported as radiocarbon years before present (B.P.). Weight percentage C content was determined from CO_2 yield on a manometer. Weight percentage N was analyzed on an auto elemental analyzer (Flow solution 3000, Persporp Analytical, Inc.). P content was determined using Kjeldahl digestion method [*Sparks et al.*, 1996]. Inventories for carbon, nitrogen, and phosphorus were calculated from weight percent content of each element and soil bulk density. Analytical precision for $\delta^{13}C$ and ^{14}C analyses was ±0.1‰ and ±0.7 pm C, respectively.

3. Results and Discussion

3.1. Carbon and Nutrient Contents in Soils

There are large differences in soil carbon content between different vegetation zones. As shown in Figure 2, soil carbon content is highest in low marsh (the oldest part of the wetland) and lowest in high marsh. This indicates that carbon is being sequestrated into soils as coastal wetlands move landward, providing a sink for atmospheric CO_2. Previous studies have shown that 30–100 kg m^{-2} soil organic carbon (SOC) have been accumulated in coastal wetland area which is 10 times that of the adjacent upland forest soils [*Coultas*, 1996]. In this study, the total soil organic carbon inventory was found to be ~29 ± 3.6 kg m^{-2} in low marsh, 15 ± 3.6 kg m^{-2} in middle marsh, and 13 ± 6.0 kg m^{-2} in high marsh. The increased accumulation of SOC is the result of reduced decomposition and increased primary production. The productivity in the study area increases from 243 g m^{-2} yr^{-1} in high marsh, to 595 g m^{-2} yr^{-1} in middle marsh and to 949 g m^{-2} yr^{-1} in the low marsh [*Kruczynski et al.*, 1978]. Soil N and P contents also show an increasing trend from high marsh to low marsh (Figures 3 and 4). This change in soil nutrients along the chronovegetation sequence may explain the differences in productivity in the marshes. Soil C content seems to be positively correlated with the N content, but there is no correlation between soil C and P (Figure 5).

As sea level rises, part of low marsh may be lost due to inundation, if accretion rate cannot keep up with the rate of sea level rise. The fate of the soil organic carbon associated with the lost low marsh is not clear at this point and warrants further study. Also, the CO_2 sequestration effect of a salt marsh on global warming may be offset by the production of CH_4. However, salt marsh has not been a significant source for CH_4 owing to sulfate reduction [*Stumm and Morgan*, 1981].

Besides soil nutrient content, salinity may also be an important factor for the decreasing productivity landward. Low marsh and middle marsh area have a more or less constant salinity (20–25‰). However, the salinity in the high marsh fluctuates much more significantly (15–35‰). This means that extreme fluctuations in salinity maybe more harmful for the growth of *Juncus roemerianus* [*Coultas*, 1996; *Kruczynski et al.*, 1978].

3.2. Carbon Isotopic Composition of Vegetation and Soil

The $\delta^{13}C$ values of soil organic matter from low marsh and middle marsh show little variation (<3‰) with depth (Figure 6) and are consistent with the current C3 plant-dominant community (Figure 7). However, there is a larger shift in the $\delta^{13}C$ values of organic matter within peat profiles in high marsh, from −22‰ at the surface to about −17‰ at depth (Figure 6). This larger $\delta^{13}C$ shift in the high marsh profiles is not likely caused by changes in

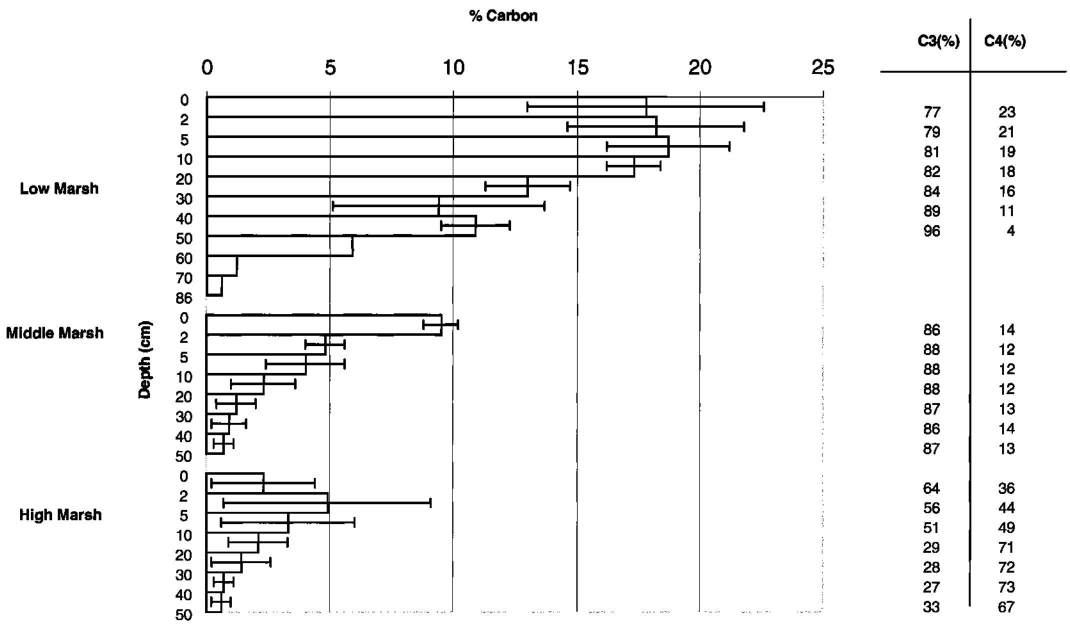

Figure 7. Carbon content (%) and the relative contribution of different photosynthetic-type plants (C3 versus C4) to soil organic matter in St. Marks wetland soils. The relative contribution of C3 and C4 plants to soil organic matter was estimated from mass balance relationship (i.e., $\delta^{13}C_{SOM} = \delta^{13}C_{C3\ plant}(1 - X) + \delta^{13}C_{C4\ plant}X$, where X is the fraction of organic matter derived from C4 plants and $\delta^{13}C_{C3\ plant}$ and $\delta^{13}C_{C4\ plant}$ are average $\delta^{13}C$ values of C3 and C4 plants, respectively, in the study area).

Table 1. Stable Carbon Isotopic Composition of Wetland Plants in St. Marks Area (Wakulla County, Florida)

Plants	$\delta^{13}C$, ‰	Vegetation Type
Salicornia bigelovii (annual glasswort)	−28.3	C3
Salicornia virginica (perennial glasswort)	−28.6	C3
Batis maritima (saltwort)	−25.4	C3
Distichlis spicata (saltgrass)	−14.0	C4
Juncus roemerianus (black needlerush)	−27.0	C3
Spartina alterniflora (smooth cordgrass)	−13.0	C4
Spartina patens (salt meadow cordgrass)	−13.2	C4

the $\delta^{13}C$ values of atmospheric CO_2 [*Friedli et al.*, 1986; *Leuenberger et al.*, 1992] nor can it be explained isotopic fractionation associated with microbial decomposition of organic matter [*Boutton*, 1996; *Dzurec et al.*, 1985; *Gulliet et al.*, 1988; *Schwartz et al.*, 1986]. Although some studies show that organic matter from mineral soils tends to be enriched in ^{13}C by 1−3‰ with age and increasing depth, owing to preferential utilization of ^{12}C by microbes during decomposition [*Goh et al.*, 1976, 1977; *Kaplan and Rittenberg*, 1964; *O'Brien and Stout*, 1978; *Rosenfeld and Silverman*, 1959; *Schleser and Bertram*, 1981; *Schleser and Pohling*, 1980; *Stout et al.*, 1981; *Stout and Rafter*, 1978; *Stout et al.*, 1975; *Troughton et al.*, 1974], other studies suggest little or no isotope fractionation in soils where decomposition is restricted and undecomposed plants accumulate, such as in peats and New Zealand Agathis soils [*Craft et al.*, 1988; *Stout et al.*, 1981; *Stout et al.*, 1975]. In general, stable carbon isotopic composition of soil organic matter is comparable to that of the source plant material, and the isotopic fraction during decomposition is <3‰ [*Boutton*, 1996; *Dzurec et al.*, 1985; *Gulliet et al.*, 1988; *Schwartz et al.*, 1986]. Therefore the large C isotopic shift (6−7‰) observed in high marsh profiles indicates a change in local vegetation from a C4-dominated community to a C3-dominated marsh.

The coastal wetlands in north Florida are currently dominated by *Juncus roemeritus*, which is a C3 plant. However, a few other species, including *Spartina alterniflora* (cordgrass), *Distichlis spicata* (saltgrass), and *Spartina Patens* (salt meadow cordgrass), are also present in the marshes (Table 1). *Spartina alterniflora*, *Distichlis spicata*, and *Spartina patens* are all C4 plants and have $\delta^{13}C$ values of −13 to −14‰. A higher proportion of these C4 species in the local community would shift the $\delta^{13}C$ of soil organic matter (SOM) to less negative values. In the study area, *Spartina alterniflora* occurs along the edges of tidal creeks in low marsh and middle marsh and is not found in high marsh. In other words, *Spartina alterniflora* does not appear until the area has evolved into middle and low marshes. *Distichlis spicata* is only found in salt barren and high marsh as a minor component. On the other hand, *Spartina patens* (salt meadow cordgrass), the predominant species in the transition zone between high marsh and the upland forest, is a C4 plant and has an average $\delta^{13}C$ value of −13.2‰ (Table 1). Considering the recent history of sea level change [*Leatherman et al.*, 2000; *Penland and Ramsey*, 1990; *Varekamp and Thomas*, 1998], the organic matter with less negative $\delta^{13}C$ values in the high marsh profiles is most likely derived from *Spartina patens* as a result of landward expansion of coastal wetland due to sea level rise. Because of the rising sea level, forest retreated and gave way to salt-tolerant *Spartina patens*, which was then replaced by *Juncus roemeritus* as salinity increased further (Figure 1). As *Spartina patens* was replaced by *Juncus roemeritus*, the dominant marsh plant, $\delta^{13}C$ of soil organic matter shifted to more negative values. The vegetation distribution observed in the area may be controlled by the competition advantage (i.e., production efficiency) and salt tolerance of different species [*Clewell*, 1996]. The stable carbon isotopic signatures of soil organic matter in the high marsh reflect the history of vegetation shift from *Spartina patens* to *Juncus roemerianus* and therefore the rate of the salt marsh development.

Radiocarbon dates of bulk peat from high marsh soils (Figure 6) indicate that this change in dominance from *Spartina patens* to *Juncus roemeritus* in the current high marsh area occurred quite recently (within the past hundred years or so), probably as a result of accelerated sea level rise over the last century [*Leatherman et al.*, 2000; *Penland and Ramsey*, 1990; *Varekamp and Thomas*, 1998]. This ecological change has been gradual and continuous, perhaps to the present date. The exact timing of this ecological shift cannot be determined accurately with radiocarbon dating because radiocarbon dates of soil organic matter are generally much younger than the age of a soil (i.e., the time when soil formation began) owing to continuous input of "new" carbon into the soil through both aboveground and belowground plant production [*Wang et al.*, 1996]. However, this is less of a problem in organic soils or peats than in upland soils. In peats, soil organic matter is accreting vertically and "contamination" by new carbon is greatly reduced once the organic matter is buried below the active root zone owing to accretion. Therefore radiocarbon dating of peats can provide valuable estimates of the rate and timing of peat accumulation [*Glaser*, 1992; *Gorham*, 1991; *McDowell et al.*, 1969; *Schell*, 1983]. The discrepancy of radiocarbon dates from the timing of the peat deposition depends on the amount of time that the peat layer resided in the active root zone before being buried by newly accreted peat layer and is reduced when accretion rates are high.

4. Conclusions

Global warming is expected to cause sea level rise. As sea level rises, coastal wetlands expand landward in areas where topography is gentle, forming high marsh, middle marsh, and low marsh, which represent different stages of coastal wetland formation. Soil carbon content is highest in low marsh (the oldest part of the coastal wetland) and lowest in high marsh (the youngest and most inland part of the coastal wetland). This indicates that carbon is being sequestrated into soils as coastal wetland evolves from high marsh to low marsh. Total soil carbon inventory in upper 86 cm of the soil in our study area is $\sim$29 ± 3.6 kg m^{-2} in low marsh, $\sim$15 ± 3.6 kg m^{-2} in middle marsh, and $\sim$13±6.0 kg m^{-2} in high marsh. These estimated carbon storages in coastal marshes are much higher than those of the adjacent upland forests (5−10 kg m^{-2} SOC). This implies that coastal wetlands can potentially be a significant sink for atmospheric CO_2 (a major greenhouse gas) as they expand landward and replace the upland forests.

The stable carbon isotopic composition of soil organic matter in low marsh and middle marsh in our study area is consistent with the current plant community, which is dominated by *Juncus roemeritus*. However, the $\delta^{13}C$ of soil organic matter in high marsh increased significantly with depth. This large C isotopic shift indicates a recent change in local vegetation from a C4-dominated community (*Spartina patens*) to the current C3-dominated (*Juncus roemeritus*) marsh. This change in vegetation recorded in the high marsh soils is most likely the result of landward expansion of the coastal wetland due to accelerated sea level rise in the past centuries. If sea level continues to rise, forest will move farther inland and give way to salt marshes.

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