

Carbon Isotopic Compositions of Plants and Sediments of Tide Marshes in the San Francisco Estuary

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ABSTRACT

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Wetland sediments surrounding the San Francisco Bay Estuary contain a rich history of environmental change which can aid predictions of potential responses to future environmental change. Here we present results of a study of the stable carbon isotopic composition of modern surface sediments as they relate to the existing plant cover. The results indicate a strong correlation between the modern plant cover and the $\delta^{13}\text{C}$ value of underlying surface sediments (RMS = 1.331). Reasons for residual differences between predicted and observed isotopic values of the surface soils include intraspecific changes in $\delta^{13}\text{C}$ values of C3 plants, contributions to the carbon pool by algae, and effects of diagenesis on $\delta^{13}\text{C}$ value of plant matter. The goal of this research is to provide a basis for interpreting isotopic data obtained from sediment cores in terms of changes in vegetation resulting from changes in environmental conditions.

ADDITIONAL INDEX WORDS: *Carbon isotopes, environmental change, calibration study, climate change, tidal marshes, wetland sediments.*

INTRODUCTION

Stable carbon isotopes found in the organic material in paleosols and sediments have been used to reconstruct paleo-environmental conditions in a variety of settings (e.g., QUADE *et al.*, 1989; CERLING, 1992; CHMURA *et al.*, 1987). Changing stable carbon isotope ratios¹ reflect changes in the dominance of plant species, which in turn reflect changes in the physical conditions of the environment, including the climate. We present a study of the stable carbon isotopes from modern sediments from across several San Francisco Bay Estuary marshes, which span a gradient of salinity experienced in the Bay. The carbon isotopic compositions of modern surface sediments are compared with the plant species found in these marshes. This study demonstrates that marsh sediments on the surface derive their carbon isotopic composition (or $\delta^{13}\text{C}$ value) from the vascular plants present. Therefore this isotopic value, taken from sediment cores, can be used as a proxy tool for establishing past plant assemblages and in this way past climate conditions.

The San Francisco Bay Estuary is the largest estuary on the Pacific coast of North America and, like many other estuaries, it has been heavily impacted by anthropogenic activities and is now additionally threatened by climate change. Before European settlement, the Estuary (encompassing the

Sacramento-San Joaquin Delta, Suisun bay, San Pablo bay, the Central bay, and South San Francisco bay) was surrounded by approximately 800 km² of marshlands (ATWATER *et al.*, 1979). More than 85% of the original (i.e., pre-1850) marshes have been lost due to human activities, and today only an estimated 125 km² of marshland exist scattered around the Bay (DEDRICK, 1989; NICHOLS and WRIGHT, 1971). Some of this marshland post-dates hydraulic mining in the Sierra Nevada, which began after the 1849 California Gold Rush, and was banned in 1884. Hydraulic mining washed enormous amounts of sediments through the Bay Delta estuary system, creating upwards of 75 km² of new marshland after 1860 (see ATWATER *et al.*, 1979 for more on marsh creation before and after 1860).

The surviving intertidal marshlands surrounding the San Francisco Estuary have been the focus of environmental attention (e.g., CONOMOS, 1979; JOSSELYN, 1983; SAN FRANCISCO ESTUARY PROJECT, 1991). Wetlands filter toxins out of water supplies and are therefore protected by the Clean Water Act of 1973, requiring that any future loss of wetland acreage must be minimized and mitigated. Wetlands provide food and unique habitats for many indigenous and migratory animal species, including some which are rare and endangered. The intertidal marshlands are also of scientific interest (see for example, GOMAN, 1996; INGRAM *et al.*, 1996a and b) because the Estuary drains over 40% of the state of California. Thus the amount of fresh water passing through the estuary reflects the precipitation, and by association the climate, over this large region. The marshes are depositional

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¹ The stable carbon isotopic ratio of a sample is expressed as a $\delta^{13}\text{C}$ value, defined relative to a known standard Pee Dee Belemnite (PDB) (CRAIG, 1957) such that: $\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C}_{\text{std}} - ^{13}\text{C}/^{12}\text{C}_{\text{sample}})/^{13}\text{C}/^{12}\text{C}_{\text{std}} - 1] \times 1000$.

environments, with sediments containing a long record of environmental conditions, including changes in climate.

Our research primarily addresses this last point; however, we consider any progress made on elucidating past environmental conditions in the San Francisco Estuary marshes will also contribute to furthering the goals of environmental protection and restoration. State and local agencies charged with the long-term management of the Bay Estuary recognize the need for an informed evaluation of the environmental conditions existing before the 1800s and analysis of the resilience of wetlands when confronted by natural climate variations in the past (SUISUN ECOLOGICAL WORKGROUP, 1999). A rich history of past vegetation patterns is contained in the organic sediments of local marshes. These patterns reflect existing hydrologic conditions, as the distribution of marsh plants is largely determined by salinity and tidal flooding.

Past research has demonstrated that the $\delta^{13}\text{C}$ values of the remaining organic material in paleosols can be used as evidence for the replacement of C3 grasses by C4 grasses in semi-arid grassland regions and from these vegetation changes they inferred changes in climate patterns (see, e.g., QUADE *et al.*, 1989 and CERLING, 1992). Similarly, DELAUNE (1986) reconstructed the recent environmental history of a Louisiana salt marsh located in the Mississippi deltaic plain using the shifting isotopic ratios of the marsh sediments. The vegetation changes in this case were in response to the shifting position of the Mississippi river. Historical evidence supported his reconstructions. CHMURA *et al.* (1987) produced a mixing model to estimate the contribution of various plant species to the stable carbon isotopic value of sediments within several marshes in the Barataria Basin located in the Mississippi delta plain. This model was later used to predict sediment values for several typical coastal marshes (CHMURA and AHARON, 1995). They concluded that past estuarine facies may be reconstructed from the marsh sediments. In our calibration study, we used this mixing model to determine how well the $\delta^{13}\text{C}$ value of surface sediments in three marshes in the San Francisco Estuary along a salinity gradient reflected the existing plant species. Certain plant specific coefficients added to the mixing model improved the correspondence.

The intertidal marshes of San Francisco Bay Estuary contain plant taxa operating with the C3 photosynthetic pathway and taxa which operate with the C4 photosynthetic pathway. Species operating with the same biochemical pathways have similar $\delta^{13}\text{C}$ values, while significant isotopic differences exist between the two pathways. C3 plants return values of approximately -27‰ and C4 plants return significantly less negative values near -13‰ . C4 grasses evolved in semi-arid to arid environments. These plants use CO_2 more efficiently which increases their water efficiency as they have reduced stomatal conductance, an important adaptation in arid environments. In the case of tidal marshes, salty conditions are analogous to drought conditions. Only two C4 plant species are found in the San Francisco Estuary marshes and both species are adapted to high salinity environments. We also investigated the potential for intraspecific variability in the $\delta^{13}\text{C}$ values of certain C3 marsh plants.

This study can serve as a calibration for future work using

stable carbon isotope records to elucidate the paleo-ecological history of the Bay Estuary.

METHODS

Study Area

The San Francisco Estuary extends from the Golden Gate to the Sacramento-San Joaquin Delta, a distance of 80 kilometers. The Estuary experiences a wide range of salinity conditions, generally decreasing with distance from the Pacific Ocean. The tidal marshes surrounding the Estuary range from salt marshes at the western extreme of the Bay to increasingly brackish marshes eastward and finally freshwater marshes in the Delta (Figure 1). The research sites described here are located along a salinity gradient in the northern reach of San Francisco Bay Estuary. China Camp State Park lies furthest west, in San Pablo Bay (mean annual water salinity is ca. 25 ppt, SFEP, 1991), and is a fully tidal salt marsh. Benicia State Park, approximately 15 miles east of China Camp, is located in the Carquinez Strait (mean annual water salinity is ca. 15–17 ppt, SFEP, 1991), and is a tidal brackish marsh. Roe Island marsh is located in Suisun Bay, approximately 10 miles east of Benicia state park, and is the freshest of the three marsh sites (Figure 1).

The majority of vascular plant species found in tidal marshes use the C3 photosynthetic pathway. In the San Francisco Estuary, the two C4 species, *Distichlis spicata* and *Spartina foliosa*, are key indicators of certain environmental conditions. *D. spicata* ($\delta^{13}\text{C} = \text{ca. } -13.5\text{‰}$) is an upper marsh grass which tolerates highly salty conditions, typically greater than 30 ppt (see e.g., CUNEO, 1987), as well as some tidal flooding. While not the only species which can tolerate such conditions, the presence of this plant can be interpreted as evidence of high salinity. *S. foliosa* ($\delta^{13}\text{C} = \text{ca. } -12.6\text{‰}$) dominates the "low marsh" zone in San Francisco Estuary salt marshes and can tolerate high salt conditions as well as prolonged periods of deep inundation. *S. foliosa* is not dependent on high salinities and thrives in fresher conditions if no competition is present. In the San Francisco Bay Estuary, however, *S. foliosa* is excluded from the fresh water marshes by *Scirpus* spp., which are common to the brackish and fresh water marshes. Detection of *S. foliosa* can thus be interpreted as indicating the low marsh zone of tidal salt marshes.

Another common salt marsh plant, *Salicornia virginica*, uses the CAM photosynthetic pathway. The range of $\delta^{13}\text{C}$ values of CAM plants can lie between those of C3 and C4 plants, though in this study we found *S. virginica* returned no values higher than -25‰ . This species is common in San Francisco Estuary salt marshes and can often be found dominating the high marsh plant assemblage (JOSSELYN, 1983; CUNEO, 1987). *S. virginica* is intolerant of prolonged, deep inundation and cannot extend much into the lower marsh zone. The ecotone between high and low marsh is often marked by an abrupt transition between the high marsh dominated by *S. virginica* and the low marsh, populated almost exclusively by *S. foliosa* (MAHALL and PARK, 1976a,b,c).

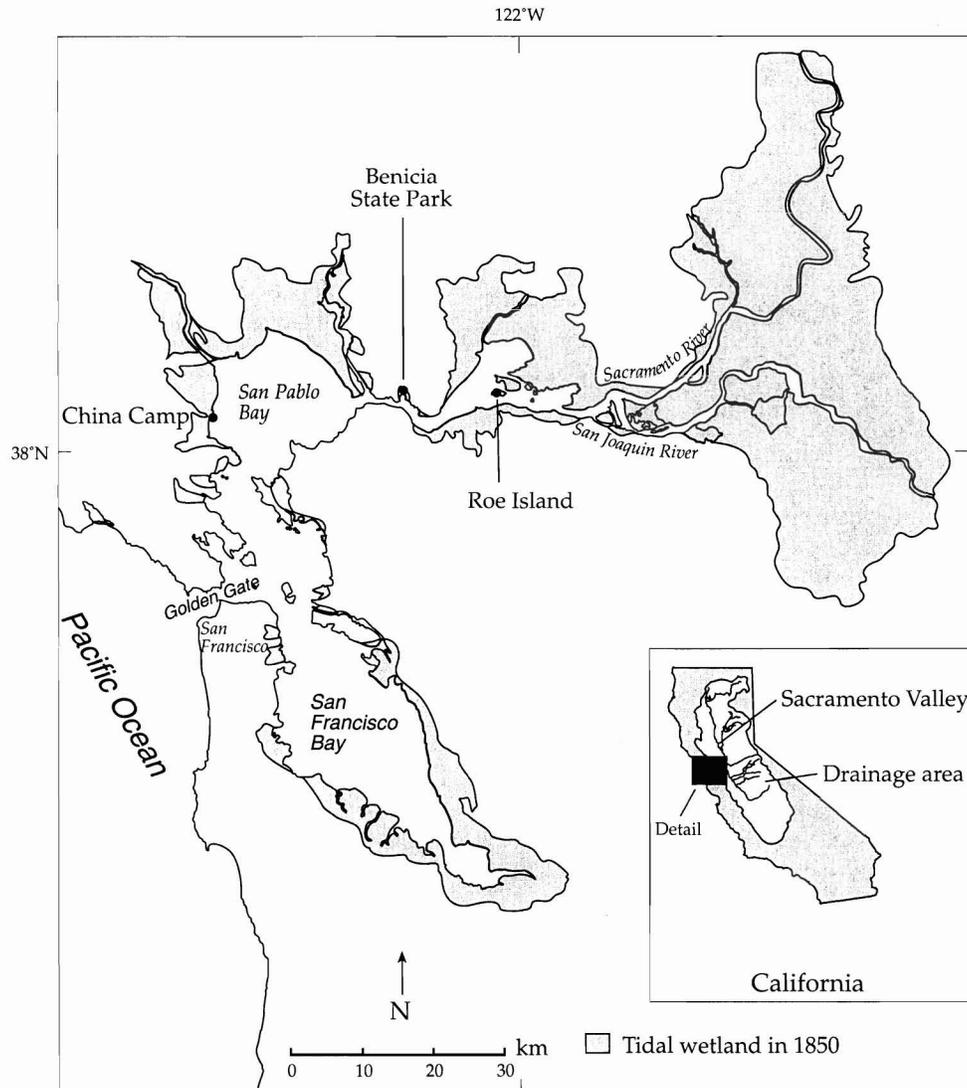


Figure 1. Location map of San Francisco Bay Estuary showing study sites.

Vegetational Analysis

A total of six transects (three for Benicia state park, two for China Camp and one for Roe Island) each 1 meter wide and of varying lengths were laid across the study sites in order to survey the plant cover and collect individual plant and sediment samples. The survey transects spanned the low and high marsh zones, and ran perpendicular to the shoreline. Two of the marshes, China Camp state park and Benicia state park, were surveyed during the Fall of 1997 and again in the Spring/early Summer of 1998. Roe Island marsh was surveyed once only, in the Fall of 1997.

Percent cover was determined on all transects at all sites. Percent cover includes estimates of the fraction of each plant taxon to the total vegetation and was assessed for each 1 m × 1 m plot. To avoid any inconsistencies, the same investigator conducted all cover estimates. The relatively large plot

size was used to ensure the best assessment of sources contributing to the organic matter of sediment samples collected from the center of each plot.

In addition to percent cover, above-ground biomass was also surveyed for two transects at Benicia state park and one transect at China Camp. Total biomass surveys were not used because they involve methods which are unacceptably destructive of the marsh surface, as 10 cm to 15 cm deep holes must be dug to include the root mass of the plants. Above-ground biomass was determined by cutting all live plants in 25 cm × 25 cm plots to the soil surface. The plants were returned to the laboratory, sorted by species, washed and weighed before and after drying in an oven at 100°C for 24 hours.

A total of 59 sediment samples were collected from all survey plots. Sediment samples were taken from the top 5 cm of

Table 1. $\delta^{13}\text{C}$ value (‰) of plants reused in this study.

Plant	(‰)	Notes
<i>Spartina foliosa</i>	-12.68	
<i>Salicornia virginica</i>	-27.21	mean value, n = 10
<i>Scirpus robustus</i>	-25.48	mean value, n = 21
<i>Scirpus californicus</i>	-27.55	mean value, n = 3
<i>Jaumea carnosa</i>	-27.23	
<i>Distichlis spicata</i>	-13.52	
<i>Typha latifolia</i>	-27.78	mean value, n = 8
Algae sp.	-22.06	
<i>Grindelia stricta</i>	-26.38	mean value, n = 27
<i>Frankenia grandifolia</i>	-30.16	
<i>Triglochin maritima</i>	-32.08	
<i>Cuscutta salina</i>	-29.78	
<i>Lepidium latifolium</i>	-26.58	
<i>Mesembryanthemum chilense</i>	-23.60	CHMURA and AHARON, 1995
<i>Juncus balticus</i>	-28.39	

soil, which was scraped from the surface from a spot near the center of each survey plot. The sediment samples were bagged, labeled and returned to the laboratory for isotopic analysis.

Salinity and Carbon Isotope Analyses

Plant and soil samples were collected from nine locations, including three sites at China Camp state park and six sites at Benicia state park. We collected a total of 68 individual plants from the following species: *Scirpus robustus*, *Scirpus californicus*, *Typha latifolium*, *Juncus balticus* and *Grindelia stricta*. For consistency, only the leaves of plants were used for this study. The plant material was prepared for isotopic analysis as described below, and the soil salinity was measured on the extract of soil samples collected using a YSI-30 salinity conductivity instrument. The soil extract was prepared following RHOADES (1982). A subsample of each sample was saturated and placed in a centrifuge for 10 minutes. The salinity of the solute was then measured. Another set of subsamples were weighed before and after air-drying for at least 3 days, and again after oven-drying for 24 hours at 100°C.

For carbon isotope analyses, whole plant samples were oven-dried for 24 hours at 100°C and allowed to cool in a desiccator in preparation for isotopic analysis. The plants were ground to a powder using a mortar and pestle. This powder was placed in a jar with 2 steel rods and rolled on a rolling mill for at least 24 hours to produce a fine powder to ensure sample homogeneity. Two to five mg samples were weighed out into small aluminum capsules and placed on the carousel of an automated 20/20 Europa mass spectrometer, located in the Environmental Science, Policy and Management department at the University of California, Berkeley. The capsules are dropped automatically into the mass spectrometer and combusted at approximately 1000°C. The CO_2 produced was purified through several traps and then introduced into a 20/20 Europa mass spectrometer. Stable isotopic measurements are calibrated against the standard NIST 1547 peach leaves. Precision for $\delta^{13}\text{C}$ on the machine used is

maintained at better than 0.1‰ standard deviation for 5 replicates.

Fifty-nine soil samples were wet sieved at 2 mm and 125 micron size fractions for carbon isotope analyses. The material caught in the 125 micron mesh represents decomposed plant matter mixed with mineral sediments. This fraction was then rinsed in a 0.1N HCl acid to remove carbonate material, and rinsed with distilled water. The residue was then placed in a 100°C oven for 24 hours, and allowed to cool in a desiccator for at least 1 hour. Samples were then crushed using a mortar and pestle and placed in a jar with 2 steel rods and rolled on a rolling mill for at least 24 hours to produce a homogenous powder. The sample size for soils ranged between 7 and 20 mg, depending on the mineral content of the soils (which was more than 98% in some cases). Powdered samples were introduced into the automated mass spectrometer and the carbon isotopic values measured as described above.

Stable carbon isotopic values are reported in the conventional delta notation in per mil (‰) relative to the PeeDee Belemnite standard (PDB) (CRAIG, 1957).

Data Analysis

The $\delta^{13}\text{C}$ values of different C3 plant species as related to salinity were subjected to both an F-test and the student's T-test at a significance level of $\alpha = 0.1$.

We used regression analysis to determine the relative accuracy of using plant cover to predict the $\delta^{13}\text{C}$ value of the surface sediments. Vascular plants contribute most significantly to the carbon content of marsh sediments and therefore are expected to account for the majority of the carbon isotopic value of the surface sediments. Establishing a direct correlation between the $\delta^{13}\text{C}$ value of surface sediments and the existing plant cover will provide a basis for interpreting changes in the $\delta^{13}\text{C}$ value of buried marsh sediments in terms of vegetation changes. It should be noted that *Mesembryanthemum chilense* and *Lepidium latifolium* are both alien species and therefore, while of increasing importance in modern marshes around the Estuary, are of little relevance in the paleo-ecology of the marshes.

For each sample, a predicted $\delta^{13}\text{C}$ value was calculated by multiplying the fraction of each species present by its $\delta^{13}\text{C}$ value.

$$\delta^{13}\text{C}_{\text{soil}} = \sum_{n=1} (\% \text{plant}_i \text{ cover}) (\text{plant}_i \delta^{13}\text{C}) / 100$$

Predicted $\delta^{13}\text{C}$ values for the soil were compared to observed values using regression analysis. To improve the results for the model 2 predictions over the null predictions, residual differences (the predicted $\delta^{13}\text{C}$ value minus the observed $\delta^{13}\text{C}$ value for each sample) were regressed against individual plants. This reflected how individual plants contributed to the differences between the observed $\delta^{13}\text{C}$ value of surface soils and the predicted value. Extrapolating the regression line in each species case to 1 (*i.e.*, when that species would comprise 100 percent of the plant cover) allowed us to determine a coefficient value to be incorporated in our second model.

Table 2. $\delta^{13}\text{C}$ value (‰) of selected C3 plant species under different salinity conditions.

	Soil salinity								
	China Camp 1	China Camp 2	China Camp 3	Benicia St. Pk. 1	Benicia St. Pk. 2	Benicia St. Pk. 3	Benicia St. Pk. 4	Benicia St. Pk. 5	Benicia St. Pk. 6
	55 ppt	35 ppt	40 ppt	8 ppt	19 ppt	16 ppt	5 ppt	4 ppt	1 ppt
<i>Scirpus californicus</i>	—	—	—	-27.98	-28.27	—	—	—	—
<i>Scirpus robustus</i>	-26.06*	-25.45*	—	—	—	-24.94	—	-25.45	—
<i>Grindelia stricta</i>	-25.85**	-26.52‡	—	—	-29.90	-26.58	—	—	—
<i>Typha latifolia</i>	-27.37†	—	-28.07	—	—	-26.56	—	—	—
<i>Juncus balticus</i>	—	—	-27.97	—	—	-28.06	—	—	-28.79
	—	—	—	-28.47	—	-27.88	—	—	-28.50
	—	—	—	-28.30	—	—	—	—	—

* Mean value, n = 9

** Mean value, n = 11

† Mean value, n = 7

‡ Mean value, n = 14

$$\delta^{13}\text{C}_{\text{soil}} = \sum_{n=1} (\% \text{plant}_i \text{ cover})(\text{plant}_i \delta^{13}\text{C} + \text{coeff}_i)/100$$

The predicted values and the observed values for each model were compared in two ways: first the Root Mean Square (RMS) value was calculated for each model as a measure of the average error of the prediction.² Then a standard linear regression was used to produce a slope and a y-intercept value of the best fit line for each model, and the R-squared value was calculated to describe the scatter of the data around the best fit line.

A reduced RMS value for the model, as well as a slope approaching 1, a y-intercept approaching zero and an R-squared value approaching 1 demonstrated improvement in the second model.

RESULTS

The $\delta^{13}\text{C}$ values for plants measured in this study are listed in Table 1. The $\delta^{13}\text{C}$ values represent the mean of three samples taken from each whole plant, unless otherwise noted. The $\delta^{13}\text{C}$ value used for *S. virginica* represents the mean of 10 whole plants, each with 3 samples, collected from four marshes surrounding the Bay.

² Because the slope of the zero error line on a graph comparing predicted and observed values is 1, the ratio of the shortest distance between any point on that graph and that line, and the vertical distance between the same point and line, is 1: $\sqrt{2}$; therefore the equation for RMS is: $\text{SQRT}\{\text{AVG}(\text{predicted } \delta^{13}\text{C}_i - \text{observed } \delta^{13}\text{C}_i)^2\}/\sqrt{2}$.

The $\delta^{13}\text{C}$ values of certain C3 plants are compared with salinity in Tables 2 and 3, and Figure 2. *Grindelia stricta* and *Scirpus robustus* displayed the greatest variability (overall standard deviations were 0.55 for *S. robustus* and 1.49 for *G. stricta*). However, for each of these species, student's T-tests were conducted on samples across different populations (we considered individuals growing at each site separate populations) which failed to support hypotheses of different means. One sample of *G. stricta* collected from Benicia state park returned a value which was outside the range of 2 standard deviations.

Observed soil $\delta^{13}\text{C}$ values were compared to the $\delta^{13}\text{C}$ values predicted directly from percent cover for each plant taxon multiplied by that plant's measured $\delta^{13}\text{C}$ value. The model prediction results are compared with the observed values from all study sites (Table 4). The model includes two sets of isotopic predictions—a null set and a modified model 2. The null predictions incorporated no coefficients to modify the contributions from the different plants. The regression analyses of these results demonstrate a general correlation between predicted and observed $\delta^{13}\text{C}$ values (Figure 3 and Table 5). Subsequent regressions of each plant taxon percent cover against the residual differences (predicted $\delta^{13}\text{C}$ value – observed $\delta^{13}\text{C}$) demonstrated that certain plants produced greater negative residuals as their fractional proportion increased in the percent cover, while others produced positive residuals (Figure 4). Coefficients were then determined for the individual plant species using these regressions. Results

Table 3. Statistical tests on mean $\delta^{13}\text{C}$ values (‰) for different populations of two C3 plants. Variances are also shown for each population.

	China Camp 1 55 ppt	Population Variance (s ²)	China Camp 2 35 ppt	Population Variance (s ²)	Student's T-test of Means	p-value
<i>Scirpus robustus</i>						
Mean	-26.06‰	0.32	-2.45‰	0.12	-2.74	>0.1
Sample size	n = 9		n = 9			
<i>Grindelia stricta</i>						
Mean	-25.85‰	2.24	-26.52‰	1.63	2.81	>0.1
Sample size	n = 11		n = 14			

Table 4. Predicting $\delta^{13}C$ values (‰) for modern sediments in marshes surrounding the San Francisco Bay Estuary using percent cover.

	Plants								
	Sp. foliosa	D. spicata	T. latifolia	Sa. virginica	Sc. robustus	Sc. californ.	L. latifol.	Algae spp.	T. marit.
	del ^{13}C (‰)								
	-12.68	-13.52	-27.78	-27.21	-25.48	-27.55	-26.58	-22.06	-32.08
Benicia State Park June 1998									
BSP 1				1.00					
BSP 2				0.90					
BSP 3			0.50	0.10	0.40				
BSP 4		0.80	0.05		0.10		0.05		
Benicia State Park Fall 1997									
BSP A		0.80		0.10	0.05				
BSP B	0.95					0.05			
BSP C	0.20	0.30		0.20	0.30				
BSP D			0.10	0.80	0.10				
BSP F					1.00				
BSP G			0.70			0.30			
BSP H	0.60		0.40						
BSP I	0.10		0.80			0.10			
BSP M		0.35		0.65					
BSP N	0.95		0.05						
BSP O	0.35		0.50	0.15					
BSP P	0.30		0.10			0.60			
BSP Qu			1.00						
BSP R		0.25		0.15	0.60				
Benicia State Park July 1998									
BSP 1	0.9							0.10	
BSP 2	0.45					0.55			
BSP 3	0.17		0.05		0.39	0.39			
BSP 4			0.40		0.4	0.20			
BSP 5			0.20	0.05	0.55				0.20
BSP 6		0.45			0.5				
BSP 7					0.1	0.25			
BSP 8		0.30		0.40					
China Camp State Pk Fall 1997									
CC 1								0.04	
CC 2									
CC 3				0.85			0.05		
CC 4				1.00					
CC 5				1.00					
CC 6				1.00					
CC 7				1.00					
CC 8				1.00					
CC 9				1.00					
CC 10				0.40					
CC 11				0.90					
CC 13									
China Camp State Pk June 1998									
CC 1		0.05		0.05	0.9				
CC 2		0.1		0.90					
CC 3				1.00					
CC 4		0.15		0.20					
CC 5		0.39		0.50	0.05	0.06			
CC 6				0.85	0.03			0.12	
CC 7				0.20	0.8				
CC 8		0.5		0.25	0.25				
Roe Island November 1997									
ROE 0				0.05			0.05		
ROE 30						0.60	0.35		
ROE 70		0.02		0.40	0.35	0.10			0.03
ROE 80		0.05		0.25	0.70				
ROE 90		0.20			0.80				
ROE 100		0.25		0.70	0.05				
ROE 110		0.45		0.50	0.05				
ROE 120					0.80		0.20		
ROE 130		0.75		0.03			0.02		0.05
ROE 140		1							
ROE 150		0.95							
ROE 160		0.6		0.37			0.03		
ROE 170		0.07		0.90					

Table 4. *Extended*

	Plants							Observed (‰)	Predictions	
	F. grand.	C. salina	J. balt.	J. carno.	G. stricta	M. chilén.	R. occid.		Null (‰)	Model (‰)
	del 13C (‰)									
	-30.16	-29.78	-28.39	-27.63	-26.38	-23.6	-27.01			
Benicia State Park June 1998										
BSP 1								-22.84	-27.21	-26.21
BSP 2		0.10						-27.74	-27.47	-26.57
BSP 3								-26.47	-26.80	-25.60
BSP 4								-17.27	-16.08	-17.56
Benicia State Park Fall 1997										
BSP A				0.05				-21.31	-16.19	-17.76
BSP B								-16.61	-13.42	-16.12
BSP C								-23.43	-19.68	-20.60
BSP D								-26.63	-27.10	-26.07
BSP F								-26.24	-25.48	-25.23
BSP G								-25.74	-27.71	-25.41
BSP H								-18.20	-18.72	-19.72
BSP I								-21.88	-26.25	-24.65
BSP M								-26.50	-22.42	-22.47
BSP N								-16.35	-13.44	-16.19
BSP O								-21.57	-22.41	-22.31
BSP P								-20.22	-23.11	-22.01
BSP Qu								-26.55	-27.78	-25.78
BSP R								-25.84	-22.75	-22.95
Benicia State Park July 1998										
BSP 1								-22.84	-13.62	-16.82
BSP 2								-20.52	-20.86	-20.56
BSP 3								-19.75	-24.23	-23.37
BSP 4								-24.45	-26.81	-25.31
BSP 5								-25.80	-27.35	-26.66
BSP 6				0.05				-24.20	-20.21	-21.06
BSP 7				0.65				-28.01	-27.40	-27.60
BSP 8				0.30				-24.41	-23.23	-23.88
China Camp State Pk Fall 1997										
CC 1			0.95					-26.24	-28.11	-26.89
CC 2			1					-25.22	-28.39	-26.89
CC 3	0.10							-26.51	-27.48	-26.43
CC 4								-26.90	-27.21	-26.21
CC 5								-26.27	-27.21	-26.21
CC 6								-26.58	-27.21	-26.21
CC 7								-26.80	-27.21	-26.21
CC 8								-25.87	-27.21	-26.21
CC 9								-25.55	-27.21	-26.21
CC 10					0.60			-26.45	-26.71	-26.31
CC 11					0.10			-25.52	-27.13	-26.23
CC 13	1.00							-27.77	-30.16	-28.16
China Camp State Pk June 1998										
CC 1								-23.18	-24.97	-24.79
CC 2								-26.25	-25.84	-25.14
CC 3								-25.44	-27.21	-26.21
CC 4				0.6	0.05			-25.51	-25.37	-26.37
CC 5								-25.17	-21.81	-21.89
CC 6								-24.18	-26.54	-26.28
CC 7								-24.72	-25.83	-25.43
CC 8								-24.46	-19.93	-20.62
Roe Island November 1997										
ROE 0						0.7	0.2	-27.97	-24.61	-24.56
ROE 30				0.05				-27.26	-27.21	-25.49
ROE 70		0.05		0.05				-26.77	-26.66	-25.97
ROE 80								-23.22	-25.32	-24.99
ROE 90								-19.48	-23.09	-23.29
ROE 100								-22.95	-23.70	-23.49
ROE 110								-20.47	-20.96	-21.35
ROE 120								-24.96	-25.70	-25.50
ROE 130			0.15					-21.31	-17.35	-18.57
ROE 140								-13.41	-13.52	-15.52
ROE 150				0.05				-15.15	-14.23	-16.20
ROE 160								-15.05	-18.98	-19.81
ROE 170			0.03					-22.17	-26.29	-25.48

from the null predictions were compared with predictions using the series of coefficients (Table 5) and demonstrated improvements in all criteria: RMS improved by 31%, R-squared by 6%, slope by 76% and Y-intercept by 86%.

Above-ground biomass measurements were obtained for 20 sample sites. Observed soil $\delta^{13}\text{C}$ values for those sites were compared directly to predicted values based on the fractions of above-ground biomass estimated for each plant taxon. We then applied the same set of coefficients to these predictions as were applied to improve the predictions based on percent cover. Statistical analyses of the results are shown in Table 6. While some improvement was seen in the R-squared value for above-ground biomass versus percent cover (33% improvement using the null prediction, 24% using model 2 prediction), all other criteria were improved using the percent cover estimates rather than above ground biomass estimates.

DISCUSSION

We have used a mixing model developed by CHMURA *et al.* (1987) and CHMURA and AHARON (1995) to assess how well the stable isotopic value of organic sediments reflect the plants present on the modern marsh surface. The model is used to "predict" sediment $\delta^{13}\text{C}$ values by pooling the carbon isotopic values of the existing plant cover. Our initial results were not as close as those reported by CHMURA *et al.* (1987). However, two out of the four marshes used in their study consisted only of C4 plants in near monospecific stands, producing predicted $\delta^{13}\text{C}$ values which varied from plot to plot by no more than 0.5‰. Another of their marshes consisted solely of C3 plants with one species, *Panicum hemitomon* (-25.2‰) dominating all plots in excess of 57%. Only their

intermediate brackish marsh was comparable in terms of plant diversity to the marsh sites used in this study. Estuary marshes with the diverse plant assemblages experienced in San Francisco Bay, particularly in the brackish zone, require more complex models to predict surface sediment $\delta^{13}\text{C}$ values.

We analyzed four models for predicting sediment $\delta^{13}\text{C}$ values: pooled isotopic values of plant species based on their percent cover (null prediction); the same values based on percent cover with the addition of plant-specific coefficients (prediction 2); pooled isotopic values of plant species based upon their relative above-ground biomass; and this biomass derived value with plant-specific coefficients. Several statistical measures were used to compare the models in this study, including RMS (root mean squares), R-squared value, and the slope and y-intercept of the best-fit line. The RMS best represents the distance of the data from the best-fit line. The perfect best-fit line would be one with a slope of 1 and a y-intercept of 0, demonstrating a one-to-one relationship between observed plant fraction values and soil $\delta^{13}\text{C}$ values. The model producing the best predictions (model 2) used percent cover values multiplied by each plant taxon's isotopic value plus a plant-specific coefficient (see Table 4). While the scatter of data points was not greatly improved with the model 2 prediction (R-squared went from 0.636 to 0.673), we consider the RMS value a better indicator of the predictive capability of our model and that number showed an overall improvement of 31% using the set of coefficients (RMS = 1.331). The slope was 0.943 and the intercept was (-0.878).

The coefficients used in the model 2 suggest that the C4 plants tend to be under-represented in the isotopic record. Model predictions of the surface sediment $\delta^{13}\text{C}$ required co-

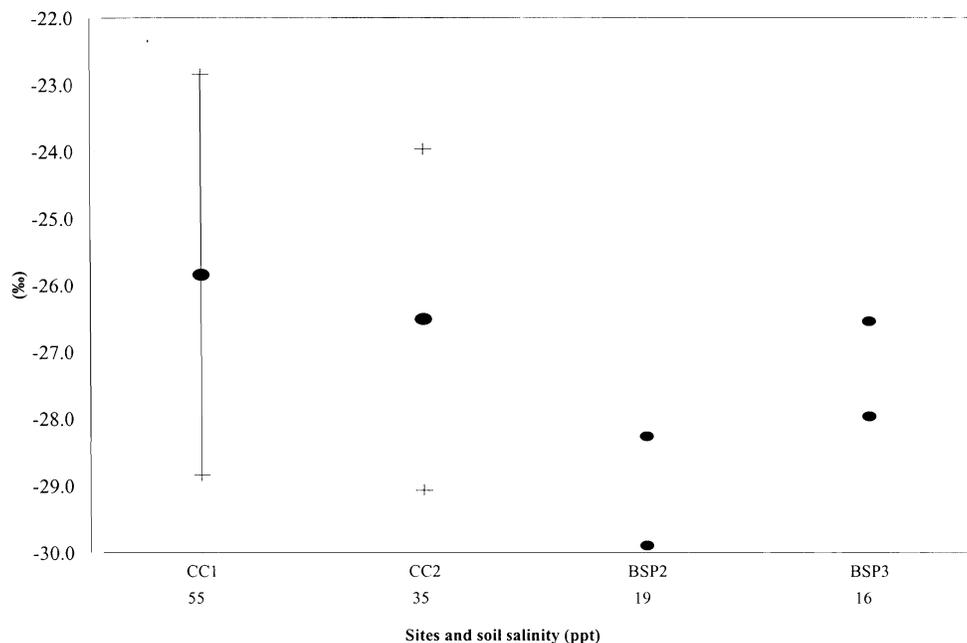


Figure 2. $\delta^{13}\text{C}$ values (on Y-axis) of the C3 plant *Grindelia stricta* under different soil salinity conditions (on X-axis). Sites CC1 (n=11) and CC2 (n=14) show the mean plus or minus 2 standard deviations (*i.e.*, 95% confidence interval). Sites BSP2 and BSP3 show individual samples (n=2).

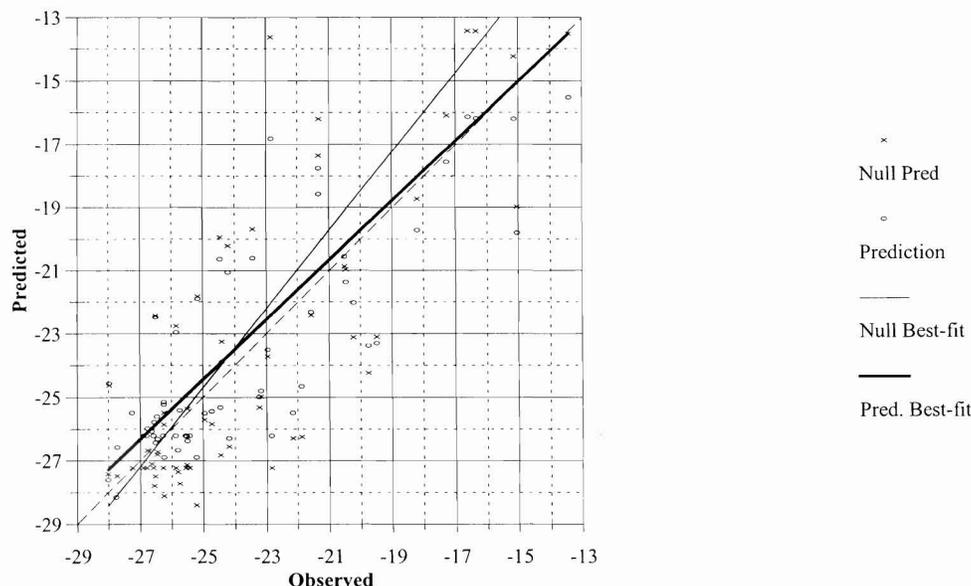


Figure 3. Observed $\delta^{13}\text{C}$ values (X-axis) in San Francisco Bay marsh soils are compared to two Predicted $\delta^{13}\text{C}$ values (Y-axis) estimated with the mixing model. The null prediction values are based on percent cover of plants multiplied by their $\delta^{13}\text{C}$ value; the model prediction 2 values include correction coefficients described in text. Stippled line represents ideal 1:1 fit line.

efficients of (-3) and (-2) for *S. foliosa* and *D. spicata*, respectively. Conversely, the carbon isotopic value of the C3 plant, *Scirpus californicus*, tended to be over-represented when present at a site, with a coefficient of $(+3)$. This implies that in sediment cores recovered from marsh sites with *S. californicus*, relatively subtle shifts in the $\delta^{13}\text{C}$ can indicate significant vegetational changes.

Data obtained from percent cover surveys was preferred over above-ground biomass surveys for the following reasons: 1) they are less destructive of wetland habitat; 2) sites can be resurveyed over time, and 3) the area included in percent cover studies is greater than that of biomass studies, and is therefore a better indicator of the surrounding plant cover. The last point is justified by the results of our linear regressions (see Table 6). In model iterations using both null predictions and applying the coefficients, the percent cover estimates produced better prediction results compared with above-ground biomass estimates for most criteria, with the noted exception of the R-squared value. One reason biomass estimates may fail to adequately predict soil $\delta^{13}\text{C}$ values may be that the plot size for the biomass survey must be fairly small. Our plots were 25 cm^2 , frequently the mix of plant taxa represented within that small plot was quite dissimilar to the larger plot area covered for percent cover estimates (1 m^2).

We consider that the larger plots better reflect the contributing sources of organic carbon to the soil.

There are three potential sources for the residual differences between measured soil carbon isotopic values and those predicted by our models. These include: 1) variability in $\delta^{13}\text{C}$ values among plants of the same species; 2) under-representation of algae (with $\delta^{13}\text{C}$ values which are intermediate between C3 plants and C4 plants) in percent cover estimates; 3) varying effects of diagenesis on plant $\delta^{13}\text{C}$ values. Each is discussed in more detail below. We do not consider allochthonous sedimentary material to be a significant source of residual differences as our measurements are limited to the coarse fraction ($>125\ \mu\text{m}$) of the soil samples.

Analyses of the carbon isotopic composition of certain C3 plants found in the San Francisco Bay Estuary revealed considerable intraspecific variability in the $\delta^{13}\text{C}$ values, particularly in the species *Grindelia stricta* and *Scirpus robustus*. The samples were collected from several locations of differing salinities, within the marshes at Benicia State Park and China Camp State Park (Table 2 and Figure 2). We considered each sample site a separate population for our statistical analyses. A student's T-test of the sample means from the different populations of *S. robustus*, China Camp site 1 (soil salinity = 55 ppt; $n = 9$) and site 2 (soil salinity = 35 ppt; n

Table 5. Statistical comparisons of results using null model and model 2 to predict soil $\delta^{13}\text{C}$ value (‰).

Model	RMS	R-squared	Slope of Line	Line Y-intercept	N
Null (without coefficients)	1.924	0.636	1.242	6.35	59
Model 2 (with coefficients)	1.331	0.673	0.943	-0.878	59
Improvement Model 2 vs. Null (%)	31	6	76	86	59

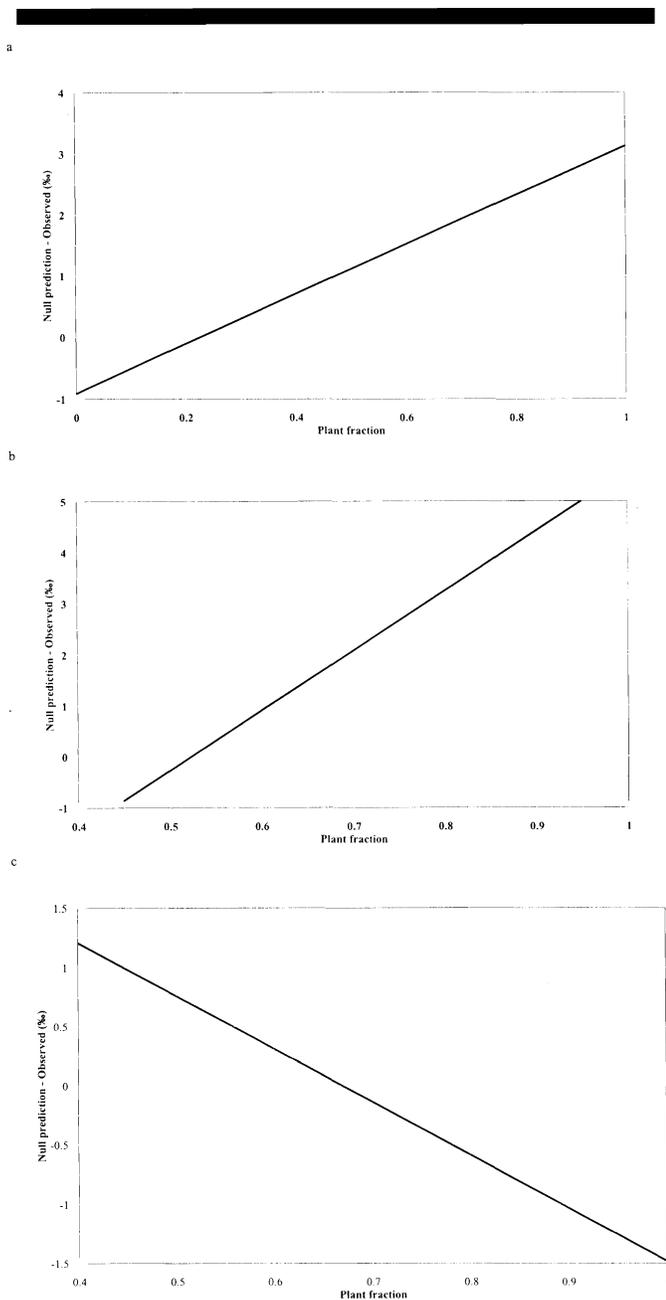


Figure 4. Residual differences for three marsh plant species. 4(a) *Distichlis spicata*, 4(b) *Spartina foliosa*, 4(c) *Salicornia virginica*. Residuals (Predicted - Observed) are regressed against plant fraction to indicate the influence these common species have on the sediment $\delta^{13}\text{C}$ value.

= 9) failed to support a significant difference between the means (significance level used was $\alpha = 0.1$). *G. stricta* had a greater variance than *S. robustus*, but a student's T-test of the populations from sites China Camp site 1 ($n = 11$) and site 2 ($n = 14$) also failed to support a difference in the means ($\alpha = 0.1$) (Table 3). One sample from Benicia state park site 2 (soil salinity = 19 ppt) had a $\delta^{13}\text{C}$ value of -29.90‰ , which was outside the range of 2 standard deviations of the China

Camp population means. The soil salinity at this site is only marginally different from site 3 (soil salinity = 16 ppt) and so the evidence does not support a causal link between salinity and $\delta^{13}\text{C}$ values.

Intraspecific variation in the $\delta^{13}\text{C}$ values for C3 plants may be related to isotopic fractionation caused by water availability (FARQUHAR *et al.*, 1989). The following equation describes carbon isotopic fractionation as follows.

$$\Delta = a + (b - a) \times p_i/p_a$$

where

- Δ = total fractionation (discrimination)
- a = fractionation due to diffusion in the air (4.4‰)
- b = net fractionation due to Rubisco (enzyme) carboxylation (ca. $20\text{--}30\text{‰}$)
- p_i = intercellular partial pressure of CO_2
- p_a = ambient partial pressure of CO_2

FARQUHAR *et al.* (1989) found in a series of experiments a positive relationship between the ratio p_i/p_a and total carbon isotopic fractionation. This ratio is largely determined by plant stomatal conductance, which is a function of environmental conditions (such as temperature and humidity). Our marsh sites encompass a range of hydrological conditions from those that are moist most of the time to sites which are infrequently wet. Slight differences in elevation or distance from the nearest channel can result in significant differences in moisture availability. While we found no evidence to support a relationship between salinity and the carbon isotopic composition of individual plants, water stress may still play a role in the variance we found in the $\delta^{13}\text{C}$ value of certain C3 species. Only one soil sample was collected from each location to determine salinity, but approximately 10 individual plants were collected from each site. As *G. stricta* is found along channel banks which can be steep, the individual plants may experience different hydrological conditions from each other depending on their relative elevations.

Similarly, nutrient supply could be an important factor in the isotopic variability within C3 species. In a study on the influence of nitrogen supply on the $\delta^{13}\text{C}$ value of C3, C4 and CAM plants, SCHMIDT *et al.* (1993) found that low nitrogen caused an increase in stomatal conductance in an annual C3 species, resulting in a more negative $\delta^{13}\text{C}$ value. In a controlled experiment, the plant, *Atriplex hortensis*, returned mean values of -26.09‰ in high nitrogen conditions, versus -27.82‰ under low nitrogen conditions (SCHMIDT *et al.*, 1993). More work would be required to determine the nutrient conditions experienced between and within our research sites, but it is possible that elevational differences may also affect the nitrogen availability for individual plants.

There is also carbon isotopic variability among individuals of certain plant taxa which are not C3. *Salicornia virginica* is the only common CAM plant found in the local brackish and salt marshes surrounding the San Francisco Estuary. Carbon isotopic measurements of 10 individual *S. virginica* plants from four different marshes range between -25.27‰ and -29.31‰ . The cause of this variability is that many plants operating with the CAM photosynthetic pathway are considered "facultative CAM". These plants are able to switch

Table 6. Statistical comparisons of results using above-ground biomass and percent cover to predict soil $\delta^{13}\text{C}$ value (‰).

Survey	RMS	R-squared	Slope of Line	Line Y-intercept	N
Null (without coefficients)					
Biomass	2.804	0.498	2.060	29.460	20
Percent cover	2.322	0.336	0.337	26.586	20
Improvement percent cover vs. biomass (%)	17	-33	37	10	
Model (with coefficients)					
Biomass	2.097	0.529	1.647	18.171	20
Percent cover	1.785	0.400	1.211	8.780	20
Improvement percent cover vs. biomass	15	-24	67	52	

between the more energy efficient C3 photosynthetic process and CAM as environmental conditions dictate. *S. virginica* found in the Estuary marshes experience a fairly wide range of salinity conditions and is capable of growing in salinities of 25‰ to 175‰ sea water (CUNEO, 1987). In a separate study we are testing the effects of salinity on the $\delta^{13}\text{C}$ value of *S. virginica*.

Another potential source of residual difference in our predicted and observed isotopic values for surface soils involves the contribution of algae to the total carbon of the surface sediments. Algae frequently forms mats growing on, or intertwined among, other vascular plants. The total input of algae to the surface carbon can be surprisingly high. ZEDLER (1980 and 1982) reported the production of algae in some Southern California marshes to be as much as 76% to 140% of the annual production of the local vascular plants. $\delta^{13}\text{C}$ values for algae tend to be intermediate between C3 and C4 plants (see CHMURA and AHARON, 1995; Table 2). The algae collected and measured from our surveys produced a value of -22.06‰. BIRD *et al.* (1995) describe a method for differentiating the marine and terrestrial constituents of estuarine sediments using specific n-alkanes of carbon using gas chromatography-mass spectrometer. However, CHMURA and AHARON (1995) considered the problem posed by algae greater for predicting modern soil isotopic values than for buried sediments. Algae is a major contributor of carbon to marsh food webs (SULLIVAN and MONCREIFF, 1990), and it decomposes rapidly and more completely than vascular plants. While surface sediments may reflect the influence of algal carbon, we assume the buried sediments have little or no algal carbon.

Finally, we consider the effects of diagenesis of marsh plants on soil $\delta^{13}\text{C}$. Several studies have looked at changes in plant $\delta^{13}\text{C}$ values as a result of diagenesis (BENNER *et al.*, 1987; DENIRO and HASTORF, 1985; EMBER *et al.*, 1987; FOGEL *et al.*, 1989). During diagenesis, the isotopically heavy fraction of the plant decomposes first, and the more refractory, isotopically lighter plant components are left behind. In particular, the most resistant compound, lignin, remains in the sediments and is generally depleted in $\delta^{13}\text{C}$ by 2 to 6‰. On marsh surfaces, initial decomposition appears to occur fairly rapidly (CHMURA *et al.*, 1987), resulting in an overall depletion of surface $\delta^{13}\text{C}$ by 1 to 4‰ (CHMURA and AHARON, 1995). After this initial depletion, though, there appears to be very little change in the isotopic value of buried sediments (FOGEL *et al.*, 1989; CHMURA and AHARON, 1995).

CONCLUSIONS

This study provides a calibration of modern marsh sediments and the plants occupying the present surface for 3 marshes along a transect of the San Francisco Bay Estuary. This is an important step toward utilizing stable carbon isotopes in marsh sediments as a proxy indicator of past plant assemblages. The sediments comprising the remaining marshes found in the Estuary contain a rich record of vegetation response to changes in paleo-environmental conditions in this region. Sensitive sites within the Bay Estuary include those in which changing salinity levels result in changing ratios of C3 to C4 plants; such changes would be reflected in shifts in the soil $\delta^{13}\text{C}$ values.

Stable carbon isotopes may be best used in combination with other established paleo-ecological proxy indicators, such as pollen. Weaknesses inherent in pollen analysis (such as limited ability to distinguish taxa below the family or genus level), can be addressed by using carbon isotopic compositions. For example, *D. spicata* (a C4 grass) is one of the key indicators of high marsh high salinity conditions, yet grass pollen cannot be identified below the family level. A shift in the isotopic ratio of sediments to less negative values, accompanied by the presence of grass pollen, would argue strongly for the presence of *D. spicata*, and thus for conditions found on the high marsh of a brackish to salt marsh. Using pollen analysis alone, the presence of grass pollen in the sediments cannot be interpreted unquestionably as evidence for *D. spicata*, as the pollen could be from other local C3 grasses, or even washed in from upstream of the marsh itself. Subtle changes in the $\delta^{13}\text{C}$ value of sediments, on the order of $\pm 4\text{‰}$ - 6‰ , likewise are difficult to interpret unless supporting pollen data are present.

This study will assist in justifying future work which uses stable carbon isotopes of marsh sediments to reconstruct past changes in plant assemblages related to environmental change. We see immediate benefits to future research from this study. Comparing isotopic record from several of our marshes with known salinity records in the Estuary for the last 1,000 - 2,000 years (see INGRAM *et al.*, 1996a and b), we can describe local vegetation responses to changes in the salinity of the Estuary, which is itself a reflection of climate as it is directly related to fresh water inflow. Building on that research, we can infer changes in estuarine salinity from the changes we find in the vegetation composition of marshes in

parts of the Estuary where the salinity history is incomplete, or to extend that history further back in time.

Future research sites will represent bimodal ecological situations, such that one physical parameter (e.g., salinity) has an overwhelming influence upon the plant assemblages found at the site. Our bimodal situations will include those in which presence or absence of C4 plant taxa can be detected in the sediment sample, and then interpreted in terms of either salinity or increased flood frequency. This research can help further our understanding of how the Estuary marshes have responded to past climate regimes, and how they might respond to future changes in climate as predicted due to the effects of global warming. This work should be of interest to both the scientific community and those involved in environmental policy decisions around the San Francisco Estuary.

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LITERATURE CITED

- ATWATER, B.F.; CONARD, J.N.; DOWDEN, C.W.; HEDEL, R.L.; MACDONALD, and SAVAGE, W., 1979. History, landforms and vegetation of the estuary's tidal marshes. In: CONOMOS, T.J., (ed.), San Francisco Bay: *The Urbanized Estuary*, San Francisco American Association for the Advancement of Science, Pacific Division, pp. 347-385.
- BENNER, R.; FOGEL, M.L.; SPRAGUE, E.K., and HODSON, R.E., 1987. Depletion of ^{13}C in lignin and its implications for stable carbon isotope studies. *Nature*, 329, 708-710.
- BIRD, M.I.; SUMMONS, R.E.; GAGAN, M.K.; ROKSANDIC, Z.; DOWLING, L.; HEAD, J.; FIFIELD, L.K.; CRESSWELL, R.G., and JOHNSON, D.P., 1995. Terrestrial vegetation change inferred from n-alkane $\delta^{13}\text{C}$ analysis in the marine environment. *Geochim. Cosmochim. Acta*, 59(13), 2853-2857.
- CERLING, T.E., 1992. Development of Grasslands and savannas in east Africa during the Neogene. *Global and Planetary Change*, 97(3), 241-247.
- CHMURA, G.L. and AHARON, P., 1995. Stable carbon isotope signatures of sedimentary carbon in coastal wetlands as indicators of salinity regime. *Journal of Coastal Research*, 11(1), 124-135.
- CHMURA, G.L.; AHARON, P.; SOCKI, R.A., and ABERNATHY, R., 1987. An inventory of ^{13}C abundances in coastal wetlands of Louisiana, USA: vegetation and sediments. *Oecologia* (Berlin), 74, 264-271.
- CONOMOS, T.J., (ed.) 1979. San Francisco Bay: The Urbanized Estuary. San Francisco: Pacific Division, American Association for the Advancement of Science.
- CRAIG, H., 1957. Isotopic standards for carbon and oxygen correction factors for mass-spectrometric analysis of carbon dioxide. *Geochim. Cosmochim. Acta*, 12, 133-149.
- CUNEO, K.L.C., 1987. San Francisco Bay salt marsh vegetation, geography and ecology: A baseline for use in impact assessment and restoration planning. Ph.D. dissertation, U.C. Berkeley.
- DEDRICK, 1989. San Francisco Bay marshland tidal acreages: recent and historic values. In: MAGOO, O.T., et al. (eds). *Proceedings of the sixth symposium on Coastal and Ocean Management*. Omni Hotel. Charleston, South Carolina, July 11-14, 1989. Volume 1, 383 pp.
- DELAUNE, R.D., 1986. The use of $\delta^{13}\text{C}$ signature of C3 and C4 plants in determining past depositional environments in rapidly accreting marshes of the Mississippi river deltaic plain, Louisiana, U.S.A. *Chemical Geology* 59: 315-320.
- DENIRO, M.J. and HASTORF, C.A., 1985. Alteration of $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ ratios of plant matter during the initial stages of diagenesis: Studies utilizing archaeological specimens from Peru. *Geochim. Cosmochim. Acta*, 49: 97-115.
- EMBER, L.M.; WILLIAMS, D.F., and MORRIS, J.T., 1987. Processes that influence carbon isotope variations in salt marsh sediments. *Marine Ecology Progress Series*, 36: 33-42.
- FARQUHAR, G.D.; HUBICK, K.T.; CONDON, A.G., and RICHARDS, R.A., 1989. Carbon isotope fractionation and water use efficiency. In: RUNDEL, P.W.; EHLERINGER, J.R., and NAGY, K.A. (eds). *Stable Isotopes in Ecological Research*. New York: Springer-Verlag, pp. 21-46.
- FOGEL, M.L.; SPRAGUE, E.K.; GIZE, A.P., and FREY, R.W., 1989. Diagenesis of organic matter in Georgia salt marshes. *Estuarine Coastal and Shelf Science*, 28: 211-230.
- GOMAN, M., 1996. A History of Holocene Environmental Change in the San Francisco Estuary. Ph.D. Dissertation. U.C. Berkeley.
- INGRAM, B.L.; INGLE, J.C., and CONRAD, M.E., 1996a. A 2000 year record of Sacramento-San Joaquin river inflow to San Francisco Bay estuary, California. *Geology* 24(4), 331-334.
- INGRAM, B.L.; INGLE, J.C., and CONRAD, M.E., 1996b. Stable isotope record of Late Holocene Paleosalinity and Paleo-discharge in San Francisco Bay, California, *Earth and Planetary Science Letters*, 141, 237-247.
- JOSSELYN, M., 1983. The Ecology of San Francisco Bay Tidal Marshes: A Community Profile. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, D.C. *FWS/OBS Report 83/82*, 102 p.
- MAHALL, B.E. and PARK, R.B., 1976a. The ecotone between *Spartina foliosa*, Trin. and *Salicornia virginica* L. in salt marshes in Northern San Francisco Bay: 1 Biomass and production. *Journal of Ecology*, 64, 421-433.
- MAHALL, B.E. and PARK, R.B., 1976b. The ecotone between *Spartina foliosa*, Trin. and *Salicornia virginica* L. in salt marshes in Northern San Francisco Bay: 2. Soil water and salinity. *Journal of Ecology*, 64, 793-809.
- MAHALL, B.E. and PARK, R.B., 1976c. The ecotone between *Spartina foliosa*, Trin. and *Salicornia virginica* L. in salt marshes in Northern San Francisco Bay: 3. Soil aeration and tidal immersion. *Journal of Ecology*, 64, 811-819.
- NICHOLS and WRIGHT, 1971. *Preliminary map of historic margins of marshlands, San Francisco Bay, California*. U.S. Geological Survey. Basic Data Contrib. 9. Menlo Park, California. 10 p. and map.
- QUADE, J.; CERLING, T.E., and BOWMAN, J.R., 1989. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature*, 342(6246), 163-166.
- RHOADES, J.D., 1982. Soluble salts, In: PAGE, A.L.; MILLER, R.H., and KEENEY, D.R., (eds). *Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties*. 2nd Edition. No. 9 in series Agronomy. Soil Science Society of America, 1982.
- SAN FRANCISCO ESTUARY PROJECT, 1991. Status and Trends Report on Wetlands and Related Habitats in the San Francisco Estuary.

- Public Report. Prepared by Association of Bay Area Governments, Oakland, California.
- SCHMIDT, G.; GEBAUER, G.; WIDMANN, K., and ZIEGLER, H., 1993. Influence of nitrogen supply and temperature on stable carbon isotope ratios in plants of different photosynthetic pathways (C3, C4, CAM). *Isotopenpraxis Environmental Health Studies*, 29, 9–13.
- SUISUN ECOLOGICAL WORKGROUP, 1999. Interagency Ecological Program, Draft Final Report.
- SULLIVAN, M.J. and MONCREIFF, C.A., 1990. Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. *Marine Ecology Progress Series*, 62, 149–159.
- ZEDLER, J.B., 1982. *The ecology of Southern California coastal salt marshes: A community profile*. U.S. Fish and Wildlife Service FWS/OBS-81/54.
- ZEDLER, J.B., 1980. Algal mat productivity: comparisons in a salt marsh. *Estuaries*, 3, 122–131.