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UTILIZATION OF FRESHWATER AND OCEAN WATER BY COASTAL PLANTS OF SOUTHERN FLORIDA[1]

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Abstract. The coastal vegetation of southern Florida is undergoing dramatic changes due to the instability of the ocean water–freshwater boundary. These vegetation changes will be determined by the response of each particular species to saline ocean water, particularly whether it can use ocean water or not. In this study, isotopic data were used to determine the relative usage of freshwater or ocean water by plants in the Florida keys.

The results indicate that, with some exceptions, plants toward the interior of the keys were using freshwater while those toward the edge were using ocean water. A plot of the hydrogen and oxygen isotopic composition of the plant water yielded a mixing line between typical freshwater values and those of ocean water. In general, the isotopic ratios of stem water for species found in hardwood hammocks were confined to the freshwater end of the line, followed by values of stem water from mangrove margin species. Species found in mangroves, however, had water with extremely variable isotopic ratios, ranging from values typical of ocean water to values typical of freshwater. This variability is consistent with the hypothesis that mangroves are fully capable of growing in freshwater, but are limited to saline habitats because of competitive exclusion by fast-growing glycophilic plants.

Key words: glycophilic; halophilic; hardwood hammock; isotope ratios; mangrove; plant water; salinity; stable isotopes.

INTRODUCTION

Southern Florida's unique coastal vegetation is characterized by the presence of several tropical species associated with mangroves and hardwood hammocks. This has not always been the case and dramatic vegetation changes have occurred in the last several thousand years (Alexander and Crook 1974, Cohen 1974). It is not unusual to find peat cores with a succession of mangrove peat (typically an ocean margin–dwelling plant community), followed by sawgrass peat (a freshwater community), followed by mangrove peat again (Cohen 1974). More recent effects have been evidenced by pine stumps (*Pinus elliottii*) in a thriving mangrove community (Alexander 1974). These vegetation changes are predominantly due to changes in the boundary between the freshwater table and ocean water. Southern Florida's unique physiography plays a crucial role in the instability of this freshwater–ocean water boundary. Southern Florida's bedrock is made of porous oolitic, bryozoan, or coralline limestone (Hoffmeister 1974). In conjunction with this porous substrate, southern Florida is characterized by a lack of topography, with the highest point (located in the Miami area) ≈18 m above sea level (Hoffmeister 1974). The porous substrate and relatively flat landscape make southern Florida's water table the shallowest in the continental United States and especially susceptible to periodic ocean water intrusion (Hoffmeister 1974). These intrusions can be caused by several factors such as an increase in ocean level caused by global climatic changes (Scholl et al. 1969), fluctuations in the freshwater table level caused by variation in the distribution and intensity of rainfall, or anthropogenic depletion of the freshwater table by well pumping and canal building. These changes in the boundary between freshwater and ocean water may have even more profound effects in the coastal vegetation of southern Florida's keys than on the mainland, since their freshwater supply occurs in smaller and more unstable freshwater tables called Ghyben-Hertzberg lenses (Cant and Weech 1986).

The vegetation changes in the coast of southern Florida are also determined by each species' particular physiological response to saline ocean water. There are several physiological adaptations that enable survival in saline ocean water. Among these, Scholander et al. (1962) recognized two major strategies: salt excluders such as *Rhizophora mangle* and salt excreters such as *Avicennia germinans*. An important test of physiological adaptation to saline ocean water is whether a plant

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uses ocean water in its transpiration stream. Certain species may exclude salt from their vascular system not only by ultrafiltration, but also by ceasing or diminishing transpiration when they are exposed to highly saline ocean water and resuming transpiration and photosynthesis when they are exposed to groundwaters with a lower salinity. Therefore, ocean water will not pass through the vascular tissue of these plants. Evidently these species will not survive prolonged periods of salinity. On the other hand, other species, such as *A. germinans,* continue and even increase transpiration when they are exposed to highly saline ocean water and may be true utilizers of saline ocean water (Hicks and Burns 1974). This is possible for *A. germinans* because it has the remarkable property of excreting salt through its leaf glands (Chapman 1944).

The purpose of this study was to determine the relative utilization of freshwater and ocean water by coastal plants in southern Florida's keys. This was accomplished by measuring the natural stable oxygen and hydrogen isotopic abundances of plant stem water for several species typical of the coastal vegetation. The estimation of freshwater and ocean water utilization by isotopic measurements is possible for two reasons. First, freshwater in southern Florida has different D/H and $^{18}O/^{16}O$ ratios than ocean water. Second, stem water has isotope ratios identical to the isotope ratio of the water available for root uptake (Gonfiantini et al. 1965, Wershaw et al. 1966, White et al. 1985). Thus the D/H and $^{18}O/^{16}O$ ratios of stem water will reflect the relative proportions of fresh- and ocean water taken up by the plant. The technique used here is the simplest possible to determine the utilization of freshwater or ocean water by plants. Salinity measurements within the plant could not be used, since some plants are able to accumulate salt even when they are exposed to freshwaters having low salinity (Teas 1979), or they may exclude salt when they are exposed to water with high salinity, as has been reported for *Rhizophora mangle* (Scholander et al. 1962). Salinity measurements of soil water are also not useful because some plants may exclude saline water by ceasing transpiration when salinity rises and resuming transpiration when that site becomes less saline.

BACKGROUND

A number of studies have been done on natural abundances of ^{13}C in plant biomass (Winter et al. 1983, Kalisz and Teeri 1986, Leavitt and Long 1986, and several others). Less familiar to plant physiologists and ecologists are studies of the natural abundance of deuterium and oxygen-18 in plant water and in plant biomass. The following roughly summarizes isotopic fractionations that occur during the global water cycle, also called the meteorological water cycle, during water uptake and eventual incorporation into plant biomass.

Both of the elements that compose water, hydrogen and oxygen, possess more than one stable isotope. In the case of oxygen, scientists are interested in the concentration of ^{18}O relative to the more abundant ^{16}O; ^{17}O is a third isotope of oxygen, but its amount is extremely low and is predictable by measuring ^{18}O. Hydrogen possesses two stable isotopes, protium ^{1}H and deuterium ^{2}H (D). The proportions of these isotopes are expressed in parts per thousand relative to the international standard known as SMOW (Standard Mean Ocean Water) by the following equation.

$$\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1]\cdot 1000\ (‰), \qquad (1)$$

in which R represents either the $^{18}O/^{16}O$ or the D/H ratio of the sample and standard respectively. As a result of differences in the vapor pressure of water containing the various isotopic species, D and ^{18}O are concentrated in the condensed phase. This difference can be described by the fractionation factor (α). Hence, for the equilibrium reaction

$$H_2O(\text{vapor}) \leftrightarrow H_2O(\text{liquid}), \qquad (2)$$

$$\alpha = R_{\text{liquid}}/R_{\text{vapor}}. \qquad (3)$$

At 25°C, α has a value of 1.0093 for oxygen and 1.076 for hydrogen. Hence, as a result of purely equilibrium effects, water vapor will be isotopically depleted in ^{18}O by 9.3‰ and in D by 76‰. Similarly precipitation condensing from this vapor will be enriched by the same amount and at least initially will have an isotopic composition for both hydrogen and oxygen similar to the original fluid. However, as the fluid is removed, the residual vapor becomes isotopically depleted, a process that can be described most simply by the Rayleigh distillation equation.

$$R = R_0\cdot\alpha\cdot F^{(\alpha-1)}, \qquad (4)$$

in which R is the isotopic ratio of the precipitation leaving the vapor, R_0 the isotopic ratio of the initial bulk vapor composition, F is the fraction of vapor remaining, and α is as defined above. The isotopic composition of precipitation condensing from this vapor therefore becomes progressively lighter and lighter. If the condensed phase is in isotopic equilibrium with the vapor, then the amount of D and of ^{18}O should be correlated. This correlation was termed by Craig (1961) as the meteoric water line (MWL) and is approximated by the following equation.

$$\delta D = 8\cdot\delta^{18}O + 10. \qquad (5)$$

However, as may be observed from this equation, the isotope ratios of the MWL do not pass through values of SMOW. This deviation from equilibrium behavior can be ascribed to kinetic effects, with the lighter isotopic species being preferentially removed from the liquid and vapor phases into undersaturated air. The net effective fractionation factor therefore is composed of the equilibrium fractionation factor (α) and a kinetic fractionation factor (Merlivat 1978).

The hydrogen and oxygen isotopic composition of rainfall worldwide has been studied in a program ini-

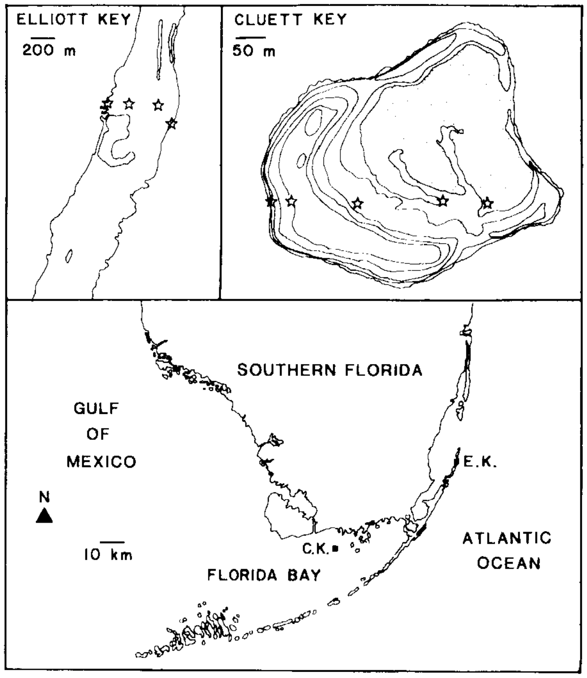

FIG. 1. Location of Cluett Key and Elliott Key in southern Florida and a detailed map of study sites. Isoclines are 10 cm in height for Cluett Key (Videlock 1983) and 1500 cm for Elliott Key. Also shown are specific sampling sites (☆) in both keys.

tiated by the IAEA (International Atomic Energy Agency). Although for southern Florida no direct measurements are available, the oxygen isotopic composition can be estimated using the compilation of IAEA data by Yurtsever and Gat (1981) as lying between −4 and −2‰ for $\delta^{18}O$ values and using the relationship in Craig (1961), −22 and −6‰ for δD values.

The isotopic composition of the groundwater in humid-climate zones, such as southern Florida, will integrate the local isotope ratios of the annual precipitation (Gat 1981). In the case of freshwater lenses in the Florida keys, the isotope ratios are probably determined by the isotope ratio of precipitation as well as of mixing between the lens and ocean water. Terrestrial plants utilize groundwater by root uptake. The absorption of water through the roots and conduction through the xylem occur without any preference for a particular isotope, and thus the isotope ratios of stem water will be the same as the isotope ratio of the groundwater available to the plant (Gonfiantini et al. 1966, Wershaw et al. 1966, White et al. 1985). With this in mind, isotopic analysis of stem water in coastal areas will give a good indication whether plants are utilizing freshwater with relatively low D/H and $^{18}O/^{16}O$ ratios, or ocean water with high D/H and $^{18}O/^{16}O$ ratios. Isotopic modifications during evapotranspiration in leaves and biochemical reactions during incorporation of hydrogen and oxygen into carbohydrates will occur (Epstein et al. 1976, DeNiro and Epstein 1979, Leaney et al. 1985, and several others), but they are not the focus of this paper.

MATERIALS AND METHODS

Plant stem water was sampled from sections of stems ≈50 cm away from transpiring leaf surfaces of several species growing in Cluett and Elliott keys (Fig. 1). These two keys were chosen for their contrasting developmental histories and composition of substrates. Samples were taken from Cluett Key on 8 May 1986. Cluett Key, formed during the past 5 000 yr as the sea level rose and flooded the Florida Bay, is a small round, carbonate mud island having an approximate diameter of 500 m, with the highest elevation of ≈½ m (Videlock 1983). In its interior it has a highly saline water basin (≈110 g/kg: Halley and Steinen 1979, Videlock 1983), which periodically becomes inundated with ocean water. Towards higher elevation Cluett Key's water lens has a lower salinity than ocean water (≈27 g/kg) and probably is partially composed of rain water (Halley and Steinen 1979). The predominant species found on Cluett Key were *Avicennia germinans*, *Batis maritima*, and *Salicornia virginica* in its outer edge and along the edges of the interior basin. Towards higher elevation, species such as *Borrichia frutescens*, *Sesuvium portulacastrum*, and *Lycium carolinianum* were observed followed by a dense population of bur grass (*Cenchrus* sp.).

The second site where plant stems were sampled was on Elliott Key. Samples were collected on 11 February 1986 and 15 August 1986. Elliott Key has a bedrock composed of Pleistocene coralline limestone. The highest elevation on the key is ≈1.5 m. Elliott Key is ≈13 km long and 700 m wide. The freshwater lens in Elliott Key extends from the surface to a depth of ≈1 m (S. V. Cofer-Shabica, *personal communication*). On its eastern ocean edge, within the high tidal zone, characteristic species found were *Laguncularia racemosa*, *B. maritima*, and *A. germinans*. *R. mangle* was not observed on this side of the island. West of this shore was an extensive hardwood hammock with typical species such as *Coccoloba diversifolia*, *Ficus aurea*, and several other tropical hardwood species. The west shore towards Biscayne Bay was characterized by a mangrove community with species such as *R. mangle*, *A. germinans*, and *La. racemosa* surrounded by a plant association typically found in sandy ridges at the margins of mangrove communities above mean high water level with typical species such as *Bo. frutescens*, *Se. portulacastrum*, *Thespesia populnea*, and several others (Lugo and Snedaker 1974).

Samples were taken from representative species of different plant associations found along a transect from the ocean towards the interior vegetation of the islands. Plant stems were immediately inserted in tubes sealed with a rubber stopper and taken to the laboratory for isotopic analysis. Samples were kept frozen until time for analysis. Water from stem samples was distilled

(Sternberg et al. 1986). For hydrogen isotope analysis of water samples, hydrogen was extracted by passing a small amount of the water through a hot uranium furnace (750°C) and collecting the hydrogen gas with a Toepler pump (Bigeleisen et al. 1952). Hydrogen samples were stored in glass ampules until mass spectrometer analysis.

Oxygen isotope ratios of water were determined by equilibrating a carbon dioxide aliquot of ≈ 300 μmol with 1 mL of water in a sealed container for a 48-h period and determining the oxygen isotope ratios of this equilibrated carbon dioxide. The oxygen isotope ratios of the water were then calculated by using the equilibrium fractionation factor of carbon dioxide and water and a mass balance equation (Epstein and Mayeda 1953).

Isotope ratios were measured using a Finnigan Mat 251 and expressed in δ values as defined previously. Conventional corrections were made for contribution of mass 46 from $^{13}C^{16}O^{17}O^{+}$, $^{12}C^{17}O^{17}O^{+}$, and of mass 3 for H_3^{+}. Data are reported relative to SMOW (Standard Mean Ocean Water) with a precision of ±2‰ for δD and ±0.2‰ for δ^{18}O values.

RESULTS AND DISCUSSION

Measurements of hydrogen and oxygen isotope ratios of tap water that came from the local Biscayne aquifer indicated significant deuterium and oxygen-18 depletion relative to ocean water and in the range predicted by Gat (1981; Table 1). In addition, measurement of the oxygen isotopic composition of rainwater averaged over the past 3 yr yielded a value of −2.75‰ (P. K. Swart, *personal observation*), clearly within the ranges predicted by Gat (1981). Our recent measurements of hydrogen isotope ratios of precipitation yield an average δD value of −11.3‰, a value very similar to that predicted by the meteoric water line (−12.0‰). Ocean water in some cases was isotopically enriched relative to previously reported values (Epstein and Mayeda 1953). This enrichment could have been caused by excessive evaporation in shallow bays and estuaries where these samples were taken. The variation in isotopic ratios of ocean water between different sites may have been due to differences in circulation of ocean water at the different bays and estuaries sampled here. For example, in Elliott Key, sea water from the Biscayne Bay (west side) was more enriched than sea water from the Atlantic Ocean (east side). This was because isotopic enrichment occurring in water from the Atlantic Ocean side was diluted by rapid mixing with oceanic water having δD and δ^{18}O values of 0. Mixing with oceanic water may occur at a slower rate in waters of the Biscayne Bay and at an even slower rate in Florida Bay where the Cluett Key samples were taken. The observed large isotopic differences between freshwater and ocean water affirm the feasibility of using isotopic techniques to trace relative ocean water and freshwater utilization by plants.

TABLE 1. Hydrogen and oxygen isotope ratios of tap water and ocean water collected at study sites in southern Florida.

	δD (‰)	δ^{18}O (‰)
Freshwater		
Tap water (Coral Gables)	−14	−2.1
Well water (Homestead)	−10	−1.5
Ocean water		
Elliott Key (west side)	+14	+1.7
Elliott Key (east side)	+7	+1.2
Cluett Key (sea water)	+19	+3.3
Cluett Key (saline pond)	+20	+3.7

The plant species sampled here were classified into three discrete vegetation types: mangrove, mangrove margin, and hardwood hammock (Table 2). Species found in the mangrove areas were typically *R. mangle, La. racemosa, A. germinans,* and *B. maritima*. In the mangrove margin, plant species were usually ground-hugging shrubs having succulent leaves. Typical species were *Bo. frutescens, Se. portulacastrum,* and *Suaeda linearis*. In the hardwood hammock community, which was found only on Elliott Key, typical species included *Psychotria nervosa, Swietenia mahogoni, Coccoloba diversifolia,* and several others. *Caesalpinia crista,* usually associated with sand dune vegetation, was also found abundantly in the hardwood hammocks. Water from plant species of the hardwood hammock was the most depleted in deuterium and oxygen-18 and had δD and δ^{18}O values within the range of values expected for precipitation in southern Florida's latitude (Table 2; Yurtsever and Gat 1981). Water from plants of the mangrove margin area had higher deuterium and oxygen content than water from plants in the hardwood hammock, indicating that these plants may be using a mixture of ocean water and freshwater. Surprisingly, mangrove species had stem water with isotopic values ranging from those typical of freshwater to values typical of those observed in ocean water.

As previously stated, each of the two islands studied here had a water lens with lower salinity than ocean water and that was presumably partially composed of rainwater having a lower deuterium and oxygen-18 abundance than ocean water. δD and δ^{18}O values of stem water in general followed the expected pattern. Plants growing towards the interior of the islands had lower isotope ratios, approaching values expected for freshwater (Fig. 2), and probably were utilizing water from the freshwater lens. The hydrogen isotope ratios of plant stem water were always lower than those of ocean water, even when the oxygen isotope ratios of plant stem water and ocean water were the same. This may have been caused by a small hydrogen isotope fractionation effect during water uptake, which would contradict previous reports on isotopic fractionation during water uptake by glycophilic plant species (Wershaw et al. 1966, White et al. 1985). Membrane-caused

TABLE 2. Hydrogen and oxygen isotope ratios of water extracted from plant stems, for plants growing in various communities in Elliott Key and Cluett Key in 1986.

Species	Site	Date	δD (‰)	δ^{18}O (‰)
Hardwood hammock				
Acrostichum aureum	E.K.	11 Feb	−9	−0.9
Caesalpinia crista	E.K.	11 Feb	−20	−2.8
Coccoloba diversifolia	E.K.	16 July	−19	−1.9
Ficus aurea	E.K.	16 July	−8	−0.9
Lysiloma bahamense	E.K.	16 July	−13	−1.5
Pithecellobium guadalupense	E.K.	16 July	−14	−1.6
	E.K.	16 July	−14	−2.1
Psychotria nervosa	E.K.	11 Feb	−9	−0.9
Swietenia mahagoni	E.K.	16 July	−12	−1.0
Mangrove margin				
Borrichia frutescens	E.K.	11 Feb	−1	+0.2
	C.K.	8 May	−3	+0.2
	C.K.	8 May	−4	+0.7
Thespesia populnea	E.K.	11 Feb	−5	−0.8
	C.K.	8 May	+5	+0.3
Lycium carolinianum	C.K.	8 May	−7	0
Suaeda linearis	C.K.	8 May	0	+1.1
Phyloxerus vermicularis	C.K.	8 May	+9	+2.6
Sesuvium portulacastrum	C.K.	8 May	+1	+0.7
Mangrove				
Avicennia germinans	C.K.	8 May	+11	+3.2
	C.K.	8 May	+6	+2.1
	E.K.	16 July	+2	+0.4
	E.K.	16 July	−5	−1.4
Batis maritima	E.K.	11 Feb	0	+1.0
	C.K.	8 May	+14	+3.7
	C.K.	8 May	+14	+3.0
	E.K.	16 July	+1	+0.6
Laguncularia racemosa	E.K.	11 Feb	−10	−0.2
	E.K.	16 July	−13	−1.4
	E.K.	16 July	−6	−0.2
Rhizophora mangle	E.K.	11 Feb	−13	−1.2
	C.K.	8 May	+9	+2.9
	E.K.	16 July	+3	+1.5
Salicornia virginica	C.K.	8 May	+10	+3.7

isotopic fractionation for three species of *Nautilus,* a marine organism living under a large saline gradient, has been previously reported (Crocker et al. 1985). For the halophilic plant species studied here, which may have a lower membrane conductivity (Field 1984), and a large saline gradient, isotopic fractionation is conceivable and should be the subject of further research.

In Elliott Key, it is interesting to note that a hardwood hammock species (*Pithecellobium guadalupense*) that grows only 1 m inland from the eastern shore and has its roots periodically flooded by ocean water still had δD and δ^{18}O values indicating freshwater usage (Fig. 2). *P. guadalupense* may exclude ocean water from its vascular system by ceasing transpiration and water uptake when it is exposed to ocean water, or it may tap into the freshwater lens with deeper roots. The mangrove species on the western shore of Elliott Key were also utilizing freshwater, even though their surface roots were exposed to ocean water, since the values observed for their stem water were similar to those observed for the hardwood hammock species located in the interior of the island (Fig. 2).

Isotopic values of stem water from plants sampled in Cluett Key followed a similar pattern: lower δD and δ^{18}O values towards the interior of the island and higher isotopic ratios towards the exterior of the island (Fig. 2). Water from species found in the mangrove area (*A. germinans, B. maritima,* and *S. virginica*) had δD and δ^{18}O values similiar to those observed for ocean water, while the mangrove margin species had lower δD and δ^{18}O values indicating some freshwater usage. Plant water from Cluett Key however never reached isotope ratios as low as those observed in Elliott Key. There may be several explanations for this. Cluett Key, being a smaller key, may have its freshwater lens mix with the isotopically enriched ocean water at a faster rate. Sea water from around Cluett Key had a higher δD and δ^{18}O value than sea water near Elliott Key. Thus, even if the mixing of freshwater and ocean water were equivalent to that observed in Elliott Key, the isotopic enrichment would be much greater than that of Elliott Key. Finally, Cluett Key being a muddy key, freshwater could become isotopically enriched by evaporation before it penetrates the soil and becomes

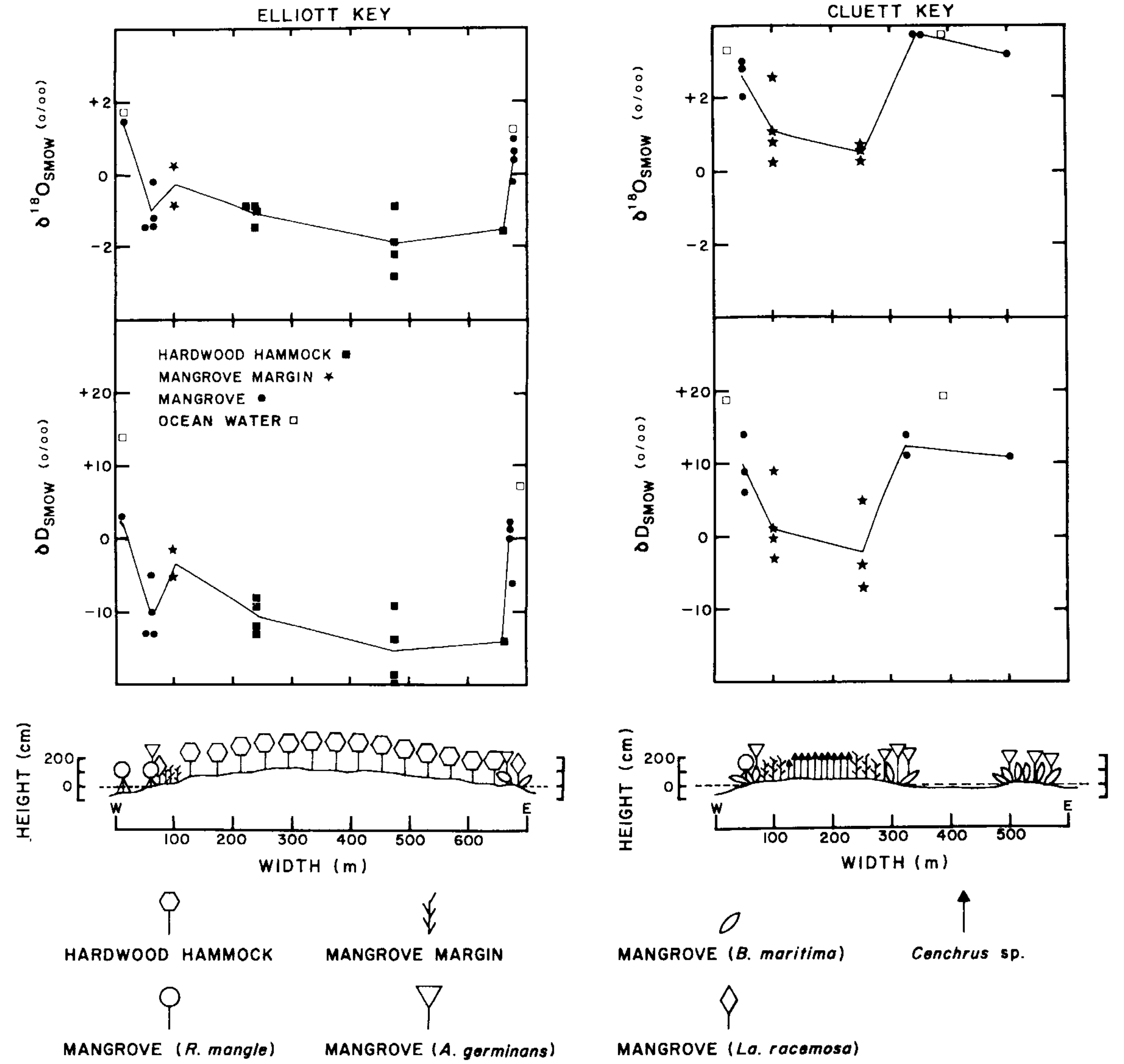

FIG. 2. δD and $\delta^{18}O$ values of ocean water and of stem water of plants along a transect through mangrove, mangrove margin, and hardwood hammock plant communities in Elliott Key and Cluett Key. For explanation of these measures of deuterium and oxygen-18 abundance, see Background.

incorporated in the freshwater lens. The answer to the following hypothesis can be acquired by sampling other mud keys, of different sizes, in the Florida bay. The first explanation, however, seems to be the most promising one since if either of the two latter explanations were correct no effects in the vegetation would be observed, i.e., the freshwater lens would have the same salinity as that of Elliott Key. Cluett Key, however, does not have a freshwater vegetation developed to the extent of that observed in Elliott Key and measurements indicate a substantial salinity in its lens (P. Swart and R. Steinen, *personal observation*).

The relationship between δD and $\delta^{18}O$ of plant stem water was highly significant ($r = 0.95$, $P \le .01$; Fig. 3). The meteoric water line shown in Fig. 3 represents the relationship between the oxygen and hydrogen isotope ratios of rainwater throughout the world as measured by Craig (1961). Hardwood hammock species were using water that had isotope ratios similar to values predicted by the meteoric water line, followed by water from plants growing in the mangrove margin. Mangrove species had plant water isotope values ranging from values typical of freshwater to values typical of those observed in ocean water during the sampling period. The highly significant regression line in Fig. 3 probably represents a freshwater–ocean water mixing line. Plants sampled here were thus utilizing various mixtures of freshwater and ocean water ranging from purely freshwater in hardwood hammock species to mangrove species using purely sea water. The large

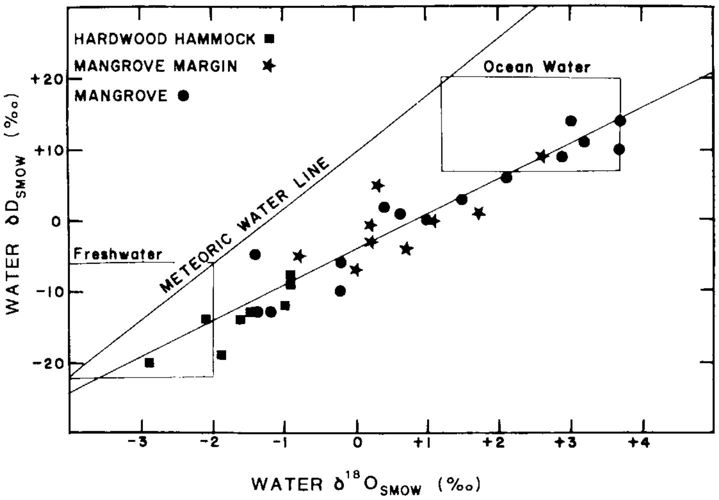

FIG. 3. δD vs. $\delta^{18}O$ values of plant stem water, the ranges of values of freshwater expected for southern Florida (Gat 1981), and range of values observed for ocean water in the vicinity of the study sites. Meteoric water line represents the relationship between δD and $\delta^{18}O$ values of precipitation throughout the world as observed by Craig (1961) and as predicted by the Rayleigh distillation equation. Measures of deuterium and oxygen-18 abundance explained in Background. Symbols for isotopic values of plant stem water as in Fig. 2.

variability of isotope ratios found in plant water from mangrove species such as *R. mangle, A. germinans,* and *La. racemosa* was consistent with speculations on the distribution and plasticity of the salt-tolerant physiological system. It has been demonstrated several times that mangrove species, particularly *R. mangle,* are fully capable of growing in freshwater (Cuong 1964, Teas 1979). The current hypothesis is that mangrove species are not found in areas of freshwater because of competitive exclusion by fast-growing freshwater plants (Teas 1979, Simberloff 1983). Measurements shown here indicate such a case. Mangrove species in Elliott Key were using freshwater where hardwood hammocks could not thrive, perhaps because periodic flooding by sea water at that site prevents hardwood hammock seedlings from germinating.

CONCLUSIONS

Our results show that isotopic measurements of plant stem water to determine relative ocean water and freshwater utilization by plants is feasible. There are several other coastal environments that may be analyzed by this technique including beach sand dune vegetation and coastal salt marshes. The measurements shown here indicate that species growing in the mangrove margin, characterized by succulent shrubs are probably using a 50:50 mixture of ocean and freshwater. Hardwood hammock species are fairly limited to intake of freshwater. Unlike hardwood hammock or mangrove margin species, however, mangrove species are utilizing water with a wide range of isotopic values ranging from those typical of the water utilized by hardwood hammock species probably being of a freshwater nature, to values typical of those observed for ocean water. This observation is consistent with the hypothesis that mangrove species are fully capable of growing on freshwaters, but are limited to ocean margins because of competitive exclusion.

Plant water from plants utilizing ocean water had an isotopic signature distinct from that of plants utilizing freshwater. These isotopic differences certainly will be recorded in the isotope ratios of cellulose-bound oxygen and hydrogen, if isotopic ratio modifications during evapotranspiration, photosynthesis, and cellulose synthesis remain constant. Since the oxygen and hydrogen isotope ratios of cellulose are ultimately dependent on leaf water available for photosynthesis (Epstein et al. 1977, DeNiro and Epstein 1979), there is a distinct possibility of using isotope techniques in relatively old wood from mangrove species capable of utilizing both freshwater and ocean water to determine historic climate and anthropogenic increases in ocean level and displacement of the freshwater table.

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