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ORIGINAL ARTICLE

Carbon isotopic composition of cypress trees from South Florida and changing hydrologic conditions

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Abstract

$\delta^{13}\text{C}$ values were determined from cypress tree rings from two different study areas in South Florida. One site is located in the Southeastern Everglades Marsh, where pond cypress (*Taxodium ascendens*) was sampled from tree islands (annual tree rings from 1970 to 2000). Bald cypress (*Taxodium distichum*) trees were sampled at the other site, located along the Loxahatchee River in a coastal wetland (decadal tree rings from 1830 to 1990). The isotopic time series from both sites display different, location-specific information. The pond cypress isotopic time series has a positive correlation with the total amount of annual precipitation, while the bald cypress data from the Loxahatchee River study area had two different records dependent on the level of saltwater stress. In general, for terrestrial trees growing in a temperate environment, water stress causes an increase in water-use efficiency (WUE) resulting in a relative ^{13}C enrichment. Yet, trees growing in wetland settings in some cases do not respond in the same manner. We propose a conceptual model based on changes in carbon assimilation and isotopic fractionation as controlled by differences in stomatal resistance (water stress) and mesophyll resistance (biochemical and nutrient related) to explain the isotopic records from both sites. With further work and a longer time series, our approach may be tested, and used to reconstruct change in hydroperiods further back in time, and potentially provide a baseline for wetland restoration. © 2005 Elsevier GmbH. All rights reserved.

Keywords: Stable isotope biogeochemistry; Rainfall; Saltwater stress

Introduction

The isotopic investigations of plants, and moreover tree rings, have been used to understand a variety of

biogeochemically related processes, ranging from water stress, ecological site conditions, to nutrient variability (Anderson et al., 1998; Bert et al., 1997; Ewe and Sternberg, 2002; Leavitt and Long, 1988; Saurer et al., 1995b). Whatever the overall controlling factor affecting a tree-ring carbon isotopic record, two biochemical/physiological processes control the actual carbon isotopic ratio of a plant's organic matter: (1) the fractionation associated with stomatal diffusion between

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the plant and source CO_2 ; and (2) the fractionation associated with the biochemical fixation of CO_2 into the Calvin Cycle by Ribulose Bis-Phosphate Carboxylase (RuBisCo, associated here with mesophyll conductance). The relative contribution of these two conductances in determining assimilation will determine the isotopic fractionation during photosynthesis.

The investigation of plants growing in wetland settings poses important questions regarding how changing water levels affect different species. Presently, wetland ecosystems are under pressure throughout the world, and a great many of these have already been modified by human activity. One great example of human modification of the landscape can be observed in the South Florida Everglades, where water once flowed freely from the southern shore of Lake Okeechobee to Florida Bay and the Gulf of Mexico. Presently, this landscape is composed of a complex mixture of housing developments, agricultural zones, water conservation areas, and preserved areas bounded and connected by dikes, canals, and pumping structures (Fig. 1). The Everglades is the focus of an \$8 billion, federally funded, 50-year restoration project, whose goals include restor-

ing “natural” water flow through the system. Here, restoration efforts have to balance the water needs of the greater Everglades ecosystem and the locally developed agricultural and metropolitan areas. Miami-Dade County’s population is one of the fastest growing counties in the United States, with a 16.3% increase from 1990 to 2000 (US Census Bureau, 2003). The increasing future population in all counties boarding the wetland ecosystem in Florida will pose the biggest challenge to managers at the South Florida Water Management District (SFWMD). Most local communities do not realize that the same water in the Everglades serves in part as their water supply and reservoir (Walter et al., 2004).

In order to “restore” altered wetlands to their natural state and/or water levels, measures of past water depths and quality will be necessary where no historical documents/data exist. Presently, the United States Geological Survey (USGS), SFWMD, and the National Parks Service (NPS) maintain an extensive network of gauge stations throughout South Florida, but locally these stations typically have data only for the last 20–30 years (and more typically only 10 years).

Here we present the result of a carbon isotopic study of cypress trees from two different settings in South Florida (Fig. 1) and compare how the isotope chronologies at both sites are related to changing hydrologic conditions. These data may point the way toward an approach using the unique setting of these trees to record changes in water levels and or salinity stress.

Carbon isotopes in plants

Carbon isotope ratios in plants are regulated by processes associated with the photosynthetic fixation of CO_2 . This fixation and its associated processes results in the isotopic discrimination of carbon defined as

$$\Delta(\text{‰}) = \frac{(\delta_a - \delta_p)}{(1000 + \delta_p)} \times 1000, \quad (1)$$

which is approximately equal to the $\delta^{13}\text{C}$ value of the plant subtracted from that of atmospheric CO_2 . This fractionation is predominately controlled by two factors: (1) the fractionation by stomatal resistance, and (2) the biologic fractionation factor due to the isotopic discrimination of RuBisCo enzyme. The model of Francey and Farquhar (1982) is expressed as

$$\delta_p = \delta_a - a - (b - a)P_1/P_a, \quad (2)$$

where δ_p and δ_a are the $\delta^{13}\text{C}$ value of plant and atmospheric CO_2 , respectively, a is the diffusion fractionation across the boundary layer and the stomata ($\approx 4.4\text{‰}$), and b is the RuBisCo enzymatic biologic fractionation ($\approx 27.0\text{‰}$). P_1 and P_a are leaf internal and external partial pressures of CO_2 . Eq. (2) only holds true

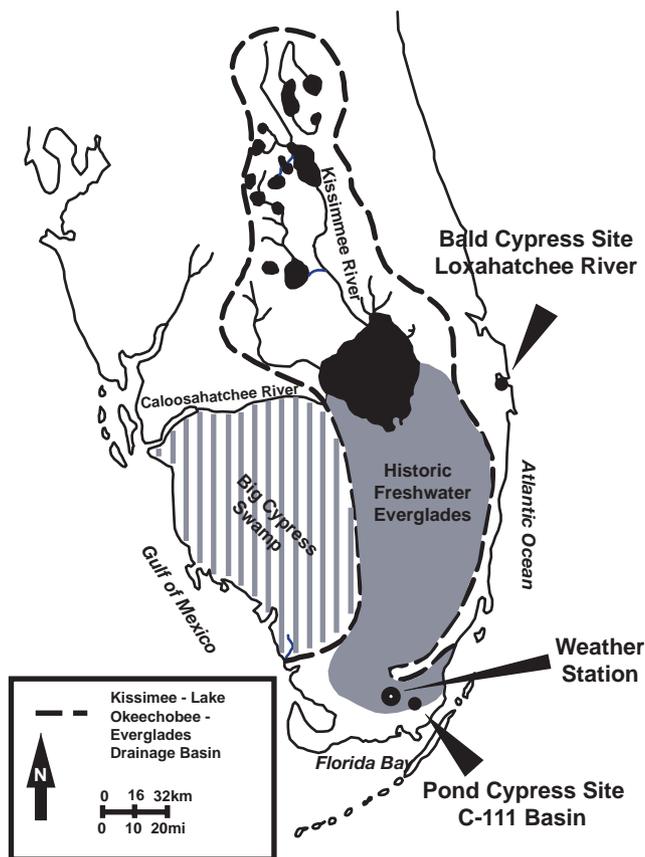


Fig. 1. Location of study sites, weather station at Royal Palm, ENP, and geographic extent of the historic Everglades and Big Cypress Swamp before human alteration and drainage (modified from Light and Dineen, 1994). Note that today the landscape has been highly modified, see text.

for bulk plant material, and since most stable isotopic analysis from plants are made from the cellulose fraction, it is important to consider the expression from White et al. (1993):

$$\delta_{\text{cellulose}} = \delta_p + \delta_{\text{cellulose-p}}, \quad (3)$$

where $\delta_{\text{cellulose-p}}$ is the difference between the bulk plant δ_p and the cellulose $\delta_{\text{cellulose}}$ values. The enzymatic and physical processes responsible for carbon fixation result in the plant's organic material being depleted in ^{13}C when compared to δ_a . As a result, most C_3 plants have δ_p values between -22% and -34% (Vogel, 1993).

Modifying Eq. (2), it can be seen that Δ is also related to the internal (P_i) and external (P_a) partial pressure of CO_2 :

$$\Delta = a + (b - a) \frac{P_i}{P_a}. \quad (4)$$

Although there may be several other factors associated with isotopic fractionation during photosynthesis including: respiration, liquid-phase diffusion, they are treated as a constant of 1% , and/or ignored (Bert et al., 1997). Assimilation, A , measured as CO_2 uptake is also related to P_i and P_a by Fick's law:

$$A = g_c(P_a - P_i), \quad (5)$$

where g_c is the stomatal and boundary layer conductance to CO_2 . Using the relationship that g_w , the leaf conductance to water vapor is 1.6 times g_c Eqs. (4) and (5) can be merged and solved for A/g_w , intrinsic water-use efficiency (iWUE) showing that iWUE is also a function of discrimination (Ehleringer et al., 1993):

$$\frac{A}{g_w} = \frac{b - \Delta}{b - a} \left(\frac{P_a}{1.6} \right). \quad (6)$$

Because the carbon isotopic signature in trees is controlled by gas transfer via the stomata (among other factors), any environmental changes affecting their functioning will affect P_i/P_a and subsequently the ^{13}C composition of the plant. Many studies have correlated $\delta^{13}\text{C}$ records from tree rings with annual meteorologic data showing a positive relationship with temperature and inverse relationships with precipitation amount and relative humidity (Anderson et al., 1998; Lipp et al., 1996a, b; Loader and Switsur, 1995; Robertson et al., 1997a, b; Saurer et al., 1995b; Switsur and Waterhouse, 1998). Other environmental perturbations such as air pollution (e.g. O_3) can drastically affect these records too by causing a relative enrichment of ^{13}C in plant organic matter as compared to non-stressed plants (Freyer, 1979; Saurer et al., 1995a). Pollutants such as SO_2 , O_3 , etc., can cause a reduction in stomatal apertures, limit the activity of RuBisCo, and/or cause tissue destruction (Saurer et al., 1995a). Salinity is another factor which can potentially affect $\delta^{13}\text{C}$ values of tree rings by affecting stomatal resistance (Lin and

Sternberg, 1992). Variations in the isotopic composition of source CO_2 can also lead to differences in the $\delta^{13}\text{C}$ values of plant material. For example, lower heights in the canopy of young trees restrict their access to the free atmosphere causing a "juvenile effect", because isotopically negative respired CO_2 from the soil is utilized for photosynthesis instead of the more isotopically enriched signal of the air reservoir above (Francey and Farquhar, 1982). Additionally, reduced light levels within the lower levels of a canopy can also cause a "juvenile effect" (Heaton, 1999).

Setting and methods

Two different studies were made in both pond and bald cypress trees from two locations in South Florida: (1) a southern location within the Everglades marsh, and (2) a northern location along the Loxahatchee River. Pond cypress trees were selected from tree islands south of the C-111 canal in the Panhandle area of Everglades National Park. The actual sampling site is immediately west of the park boundary in an area under the supervision of the SFWMD (Fig. 1). At the other more northern study area, bald cypress trees selected for study were located on the Loxahatchee River, along the Lower East Coast of Florida (northern Palm Beach and southern Martin Counties) and draining into the Jupiter Inlet (Fig. 1). In general, the climatological setting of South Florida is sub-Tropical, with pronounced dry (winter) and wet (summer) seasons. The wet season, as based on 50 years of rainfall data, occurs between April and October (Fig. 2).

Southern site – Pond Cypress Tree islands

Tree islands are found throughout the Everglades and are interspersed within short- and long-hydroperiod marshes. These islands are diverse, ranging from species-rich tropical hardwood hammocks, much like those found in terrestrial landscapes throughout south Florida, to cypress domes (Loveless, 1959). Tree islands of the southeastern Everglades have been classified as mixed swamp tree islands (Ross et al., 2000), red bay flat-tailed islands (Egler, 1952), and cocoplum islands (Craighead, 1971). Using the National Wetlands Inventory, these island types seem most closely related to mixed swamp forests in terms of hydroperiod (6–9 months) and pH (about neutral), but more similar to bay swamps in species composition, due to the many evergreens that occur there (although several deciduous species occur also, including cypress in some locations, such as our study site) (Cowardin et al., 1979). The development of these islands seems to be most aptly described as the colonization of species into areas of

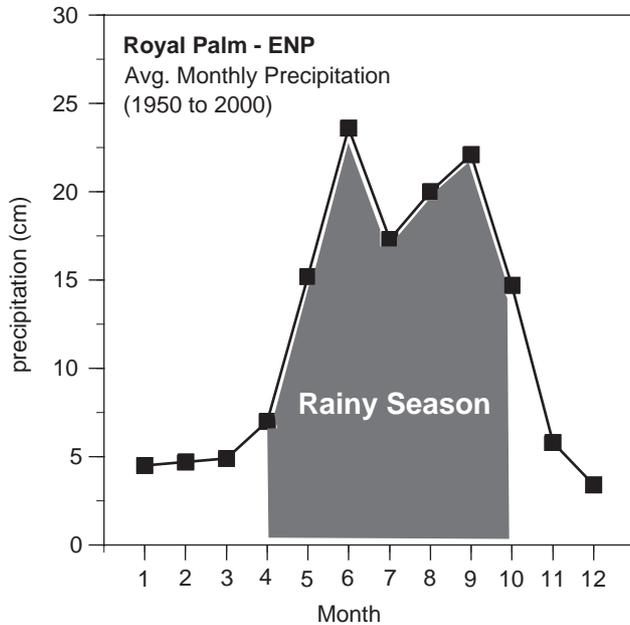


Fig. 2. Average monthly precipitation calculated from 1950 to 2000 from the weather station at Royal Palm, Everglades National Park. This station is adjacent to Taylor Slough. The gray high-lighted area indicates the rainy season.

built up organic matter caused by natural drainage patterns in the marsh (Loveless, 1959; Ross et al., 2000).

Pond cypress trees growing on the outermost portion of different individual tree islands were sampled with an increment borer (5 mm diameter). A total of four tree islands from the same immediate area were sampled with a similar hydrologic setting, one tree from each island. Each tree island (~0.20 ha in area) was located less than 150 m from one another. Care was taken to select trees with similar growth histories, chest height trunk circumference varied from 46 to 78 cm. Trees with circumferences >78 cm had “rotten” inner rings and were not selected for this study. Water levels in this area change from a depth of 0 cm in the dry season to 23 cm in the wet season within the island interiors, and 35 cm deep in the adjacent marsh (Gann, 2001).

Northern site – Bald Cypress

The Loxahatchee River is located along the Lower East Coast of Florida (northern Palm Beach and southern Martin Counties) and drains into the Jupiter inlet. The northwest fork of the river flows in a northerly direction passing through Jonathan Dickinson State Park (Martin County) where it begins to flow in a southeasterly direction towards the Intracoastal Waterway and on through the Jupiter Inlet (Palm Beach County). The northwest fork of the Loxahatchee River has undergone dramatic hydrological changes particularly from dredging of the Jupiter Inlet in 1947 and the

construction of the C-18 Canal in 1957–1958 (Zahina, 2004). The end result of these waterworks was the facilitation of upstream salt water migration during tidal flooding and a decrease of freshwater flow into the northwest fork (Zahina, 2004). These and previous anthropogenic effects have caused large mortality of cypress trees and the subsequent replacement by mangrove communities within the Jonathan Dickinson state park (Alexander and Crook, 1975). During the month of August 1991 we selected three cypress trees downstream from Kitching Creek, close to the Jonathan Dickinson State Park boat ramp which was approximately 9 km upstream from the Jupiter inlet, and three trees in the Trapper Nelson area of the park, approximately 17 km upstream from the Jupiter inlet. The boat ramp samples are located in an area showing salt water impact with several dead cypress trees whereas the Trapper Nelson samples showed little evidence of salt water intrusion. Trees were cored with a standard increment borer (Suunto, Forestry Supplies).

Sample processing

All tree rings were identified and dated using standard dendrochronological methods. The sampling approach is different between the two sites since these investigations were initiated at two different times and laboratories. For the southern tree island site (Everglades) with pond cypress, the last 30 years (1970–2000) of whole annual rings from all trees were separated and pooled together to represent the tree island stands, equal weights were used in order to balance the influence of each individual. Two individual trees had easily defined rings dating back only to the early 1970s, and the composite samples are missing years 1970–1974 from those two trees. The oldest pond cypress trees date back to the 1950s. Bald cypress rings from the northern site (Loxahatchee River) were grouped into 10-year segments from each individual tree sampled. Cellulose was processed from these samples after the whole wood samples were homogenized with either a Wiley mill or a modified coffee grinder. α cellulose was extracted from all samples using a method modified after Green (1963) for smaller (up to 80 mg) amounts of material.

Geochemical methods

All pond cypress isotopic analyses were measured at the Southeast Environmental Research Center Stable Isotope Laboratory using standard elemental analyzer isotope ratio mass spectrometer (EA-IRMS) procedures. The EA is used to combust organic material forming CO_2 , which was measured on a Finnigan MAT Delta C IRMS in a continuous flow mode. The samples' isotopic ratios are reported in the standard delta (δ) notation relative to international standard Vienna

Peedee Belemnite (VPDB) for carbon, where δ (‰) = $(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$. Analytical reproducibility of this method as based on sample replicates is better than $\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$. All bald cypress from the northern study site were processed and analyzed at the Laboratory of Stable Isotope Ecology in Tropical Ecosystems, Biology Department, University of Miami. Bald cypress samples were combusted in an off-line mode, where the cellulose is combusted to CO_2 in a 9 mm quartz tube in the presence of reduced Cu and CuO (Buchanan and Corcoran, 1959). Purified CO_2 samples were analyzed on a VG Prism (Micromass) IRMS via a dual inlet system at the University of Miami.

Results

Carbon isotopic results from both study areas show different trends (Figs. 3 and 4). Each data set has been

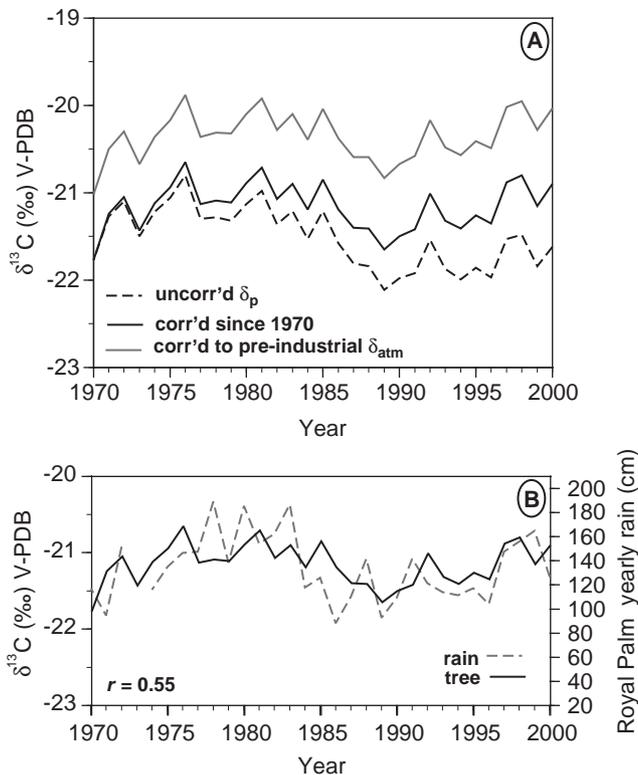


Fig. 3. $\delta^{13}\text{C}$ values of annual rings from Pond Cypress from tree islands in the C-111 basin from 1970 to 2000. (A) compares the raw, uncorrected data with different correction methods: the dark line is corrected to changes in atmospheric CO_2 $\delta^{13}\text{C}$ values since 1970, the first year in the times series, after Anderson et al. (1998), the gray line is corrected to pre-industrial CO_2 $\delta^{13}\text{C}$ values of McCarroll and Loader (2004). (B) Compares the corrected $\delta^{13}\text{C}$ values from (A) (solid black line) to total annual precipitation from Royal Palm climate station in ENP, with an $r = 0.55$ ($>99\%$ confidence level). Note, 1973 is not plotted with the precipitation data because 4 months of rainy season data were not reported/recorded.

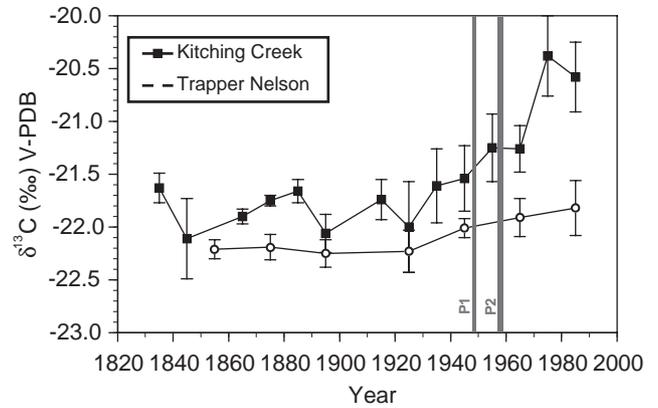


Fig. 4. A comparison between the $\delta^{13}\text{C}$ values of decadal ring groups from the Loxahatchee River study area. These values have been corrected to pre-industrial δ_{atm} values (after McCarroll and Loader, 2004). The Kitching Creek samples were collected from trees located close to the Jonathan Dickinson State Park boat ramp which was approximately 6 miles (9.7 km) upstream from the Jupiter inlet (open to the ocean). The Trapper Nelson site is further inland, approximately 11 miles (17.7 km) upstream from the Jupiter inlet. The error bars represent the standard error of the mean from the three individual trees measured. P1 and P2 are perturbations that might have affected the trees within the study area. P1 represents the timing of a major dredging effort of the Jupiter Inlet (1947), and P2 shows the timing of the construction of the C-18 Canal (1957–1958) (Zahina, 2004).

corrected for the change in δ_{atm} (atmospheric CO_2) since the period of industrialization caused by the use of fossil fuels. Fig. 3A shows two approaches for correcting the tree ring carbon isotope data from the tree island site. One approach corrects for changes in δ_{atm} since 1970 as based on a linear fit of atmospheric carbon isotope data from Francey et al. (1999) over the same time frame (Anderson et al., 1998), and the other uses the corrections to pre-industrial levels from McCarroll and Loader (2004). Both approaches are in excellent agreement, and linear correlation of the two correction factors gives a slope equal to 1, and $r^2 = 0.98$. In addition, Fig. 3B shows a comparison between the pond cypress $\delta^{13}\text{C}$ tree-ring record (corrected since 1970 for the change in δ_{atm}) with the total amount of precipitation recorded at the Royal Palm climate station (located within Everglades National Park, <15 km from the study area) from 1970 to 2000. The positive linear correlation between these two data sets has an $r = 0.55$ ($>99\%$ confidence level). The 1973 total precipitation data were not included in the plot and correlation because 4 months of rainy season data was missing from the climate record. The Royal Palm station does not record relative humidity, and all other climate data such as monthly temperature (min., avg. and max.) did not have a statistically significant relationship with the corrected $\delta^{13}\text{C}$ values from the tree rings (Fig. 3B).

Overall, the pond cypress trees 30-year record has both first- and second-order trends. The first-order changes in the corrected data (Fig. 3B) include an increasing isotopic enrichment to 1980, followed by a steady isotopic depletion to 1989, with a total change of 1.12‰, followed by a 0.85‰ enrichment trend from 1990 to 2000. The maximum $\delta^{13}\text{C}$ value occurred in 1976 (−20.65‰), while the minimum value occurred in 1970 (−21.77‰). Superimposed on the first-order changes are several second-order isotopic changes ranging from 3 to 4 year enrichment–depletion trends throughout the 30-year record.

In Fig. 4, the bald cypress $\delta^{13}\text{C}$ records from the two sites along the Loxahatchee River study are compared. The Kitching Creek site is the closest site to the marine influenced Jupiter Inlet (9 km distance), and showed evidence of saltwater intrusion. Whereas the Trapper Nelson site is located over 17 km from the inlet, and plants at this site displayed no signs of salt water intrusion. Each data point in Fig. 4 represents a 10-year sample of the rings from three different trees from each site (three from Trapper Nelson and three from Kitching Creek) (Fig. 4). The Kitching Creek site had the longest record dating from 1830 to 1990, while the Trapper Nelson site dates from 1850 to 1990. The first-order trend from the Kitching Creek site displays a depletion–enrichment trend over the complete record starting with a total 1.73‰ magnitude change. In contrast, the Trapper Nelson site displays only a minor depletion–enrichment trend with a total change of 0.29‰. The average $\delta^{13}\text{C}$ value for the Kitching Creek site is less depleted than the Trapper Nelson site, −21.53‰ vs. −22.09‰, respectively. The timing of two perturbations are noted as P1 and P2 in Fig. 4, where P1 represents the timing of dredging of the adjacent Jupiter Inlet and P2 shows the timing of the construction of the C-18 canal.

In order to evaluate whether any of the study areas trees' isotopic records were related to growth history, we compared indexed ring-width data with the isotopic data from each site. Both the pond cypress trees from the Everglades site and the bald cypress trees from the Kitching Creek site had a statistically significant relationship (Fig. 5), with a confidence interval higher than 95%. Fig. 5 displays the positive correlation between ring-width data and $\delta^{13}\text{C}$ values from the pond cypress trees, and a negative correlation between these parameters for the Kitching Creek site.

Discussion

The isotopic time series from both sites displays unique and different information. The pond cypress isotopic time series has a positive correlation with the total amount of annual precipitation (Fig. 3). While the

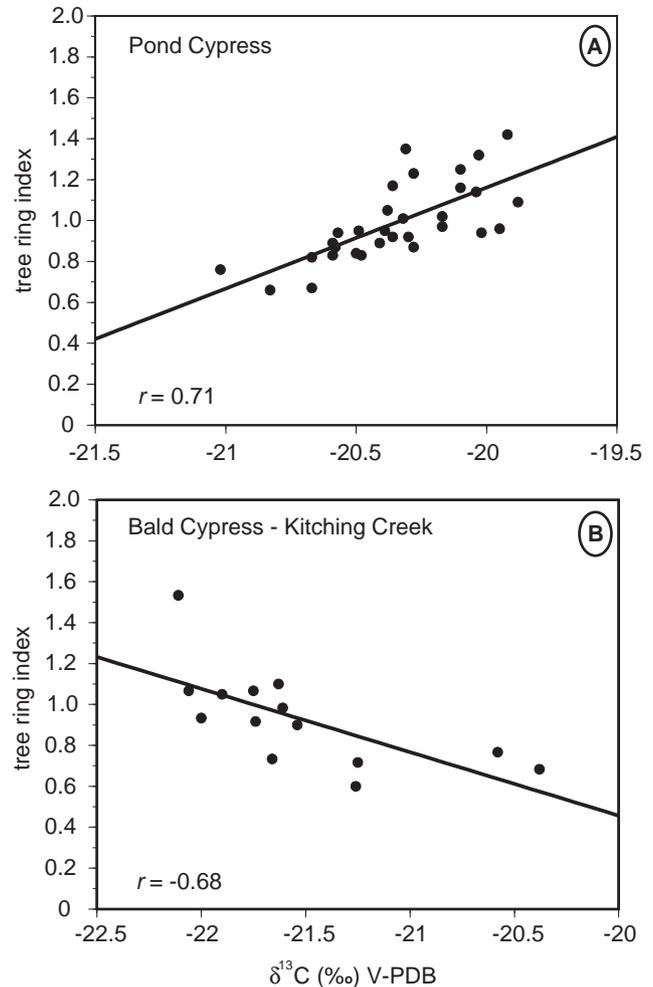


Fig. 5. A comparison between the cypress tree-ring width index and carbon isotope ratio. (A) Shows the positive correlation for the pond cypress trees from the tree island site. (B) Shows the negative correlation between the average decadal tree-ring index and carbon isotope values for the bald cypress trees at the Kitching Creek. Both relationships are above the 95% confidence level.

bald cypress data from the Loxahatchee River study area had two different records dependent on site location and level of saltwater stress (Fig. 4). With terrestrial trees growing in a temperate environment, water stress causes changes in water-use efficiency (WUE) and carbon assimilation that results in a relative isotopic enrichment (Ehleringer et al., 1993; Francey and Farquhar, 1982; Saurer et al., 1995b). Yet, trees growing in wetland settings may not respond in the same manner. Previous work in the Everglades has shown that during the wet season native plants respond to increased levels of precipitation by a reduction in stomatal conductance and/or an increase in assimilation (Ewe and Sternberg, 2002, 2003). Though controversial, it has been postulated that when water levels rise above the soil level causing anoxic conditions in the root zone,

water and nutrient uptake by the plant can be disrupted. Damage to roots from flooding can be from root hypoxia (Jackson and Drew, 1984), lowered root hydraulic conductivity (Davies and Flore, 1986; Else et al., 2001), increased abscisic acid concentrations (Kozłowski and Pallardy, 1984; Zhang and Davies, 1987), signaling from as yet undetermined chemical cues (Else et al., 1995), or accumulation of metabolic toxins from flooding (Jackson and Drew, 1984; Kozłowski, 1997). A possible effect of these changes in root function is a decrease in stomatal conductance (Ewe and Sternberg, 2002, 2003; Kozłowski and Pallardy, 1984; Naidoo, 1985a,b; Reid and Bradford, 1984), which would cause an overall decrease in transpiration and sap flow in the plant. If such a concept were to be true, the positive correlation between the pond cypress carbon isotopic data and rainfall would indicate water stress induced due to increasing water levels of the wet season. Ewe and Sternberg (2003) did show that several plants growing in the Everglades displayed relatively enriched $\delta^{13}\text{C}$ values from leaves that had grown in the wet season vs. the dry season, which was also accompanied by a reduction of stomatal conductance. However, in each plant where such a change was measured, assimilation rates were higher in the wet season, rather than the dry season. Therefore, any increase of water levels during the wet season that may have caused stress in the plant was overcome by other factors, such as changes in seasonal nutrient availability (Ewe and Sternberg, 2003). The pond cypress trees' $\delta^{13}\text{C}$ record from this work appears to be responding to changes in precipitation in a similar manner as the Everglades natives, with a positive correlation between the amount of precipitation and $\delta^{13}\text{C}$ values. Additionally, any water stress should result in a decrease in tree-ring width index, but the $\delta^{13}\text{C}$ values from pond cypress trees show a positive correlation with ring width (Fig. 5). Previous work by Stahle and Cleaveland (1992) on bald cypress in southeastern US (North Carolina, South Carolina, and Georgia) shows a positive correlation between spring rainfall and tree-ring width.

The bald cypress time series from both the Kitching Creek and Trapper Nelson sites show two different records. Between 1830 and 1930 both records display a similar trend, but after the 1940s the records diverge (Fig. 4). The Kitching Creek site has a positive enrichment trend from 1940 to 1990 of just over 1%. This site also showed signs of saltwater intrusion, and changes in local hydrology could have allowed for an increase of seawater to the area, whereas the Trapper Nelson site was unaffected, likely because of its further distance from the ocean inlet. The isotopic enrichment trend in the post-1940s record for the Kitching Creek trees is substantial considering the trees "overcame" the change in isotopic composition of the atmosphere since industrialization. Prior to the industrial revolution, ice

core records from Antarctica indicate the carbon isotopic composition of the atmosphere was about -6.4‰ (Francey et al., 1999; Friedli et al., 1986), and currently this value is near -8.0‰ . Note that the presented data are all corrected for changes in $\delta^{13}\text{C}$ value of the atmosphere back in time. The negative correlation between tree-ring width index of the Kitching Creek trees and $\delta^{13}\text{C}$ values indicate environmental stress is most likely causing the observed enrichment trend, and not an increase in assimilation.

In order to explain the observed data from the similar species with different site conditions we proposed a conceptual model in Fig. 6, based on Lambers et al. (1998):

$$A = \frac{P_a}{(1.6R_s + R_m)}, \quad (7)$$

where R_s is stomatal resistance to water (often related to water stress) and R_m is mesophyll resistance to CO_2 fixation (which is biochemical and nutrient related). Assuming that assimilation and P_a are constant, Eq. (8) can be rearranged to put R_m in terms of R_s by the following linear equation:

$$R_m = -1.6R_s + \frac{P_a}{A} \quad (8)$$

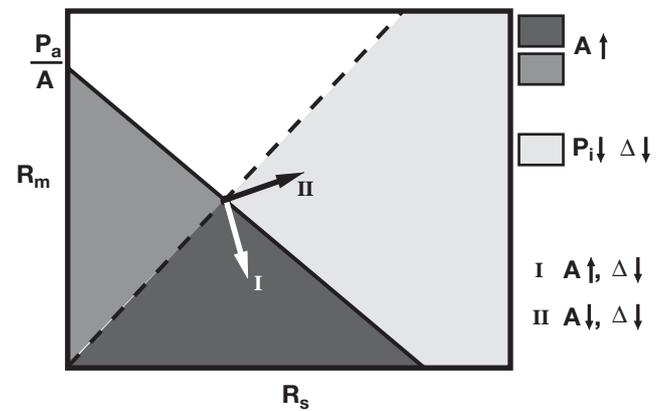


Fig. 6. Conceptual model and generalized plot of mesophyll resistance vs. stomatal resistance. Solid line represents the relationship between mesophyll resistance (R_m) versus stomatal resistance (R_s) such that assimilation remains constant (constant assimilation isocline). Shifts in R_m and R_s to values below this isocline (dark gray) will cause an increase in assimilation. Dashed line represents shifts in R_m and R_s such that P_i remains constant and discrimination does not change (constant P_i isocline). Shifts to the right of this isocline will cause P_i and discrimination (Δ) to decrease (light gray region). Scenario I represents our observations with the pond cypress sequence where we observed larger ring (presumably a higher assimilation) and decreased discrimination. Scenario II represents our observation with the Kitching Creek sequence where we observed smaller rings compared to the less stressed Trapper Nelson site (presumably because of lower assimilation) and decreased discrimination.

having the slope of -1.6 and the intercept of P_a/A . On the other hand since

$$A = \frac{P_a - P_i}{1.6 \times R_s} = \frac{P_i}{R_m}, \quad (9)$$

and if P_i (and therefore isotopic fractionation) is to remain constant with changes in stomatal resistance, then by rearranging Eq. (9) the relationship between R_m and R_s is given by the following equation:

$$R_m = \frac{1.6 \times P_i}{P_a - P_i} R_s. \quad (10)$$

Stomatal resistances that are compensated by an equivalent change in mesophyll resistance, satisfying the above two linear relationships, will have a particular photosynthetic assimilation and discrimination and lie at the intersection of the two lines described by the above equations (Fig. 6). Shifts in R_m and R_s to values below the constant assimilation isocline (dark gray, Fig. 6) will cause an increase in assimilation and shifts above it will cause a decrease in assimilation. Shifts in R_m and R_s to values on the right of the constant P_i isocline (light gray, Fig. 6) will cause a decrease in P_i and therefore in isotopic discrimination. Fig. 6 presents two examples of potential scenarios where changes in R_m and R_s are related to changes in assimilation. In scenario I, increased water levels lead to a decrease in mesophyll resistance to a greater extent than an increase in stomatal resistance, such that assimilation rates increase resulting in a lower P_i/P_a , less discrimination, and higher $\delta^{13}\text{C}$ values of plant organic matter, such as that observed in the pond cypress record. If tree-ring width is related to assimilation, then such a scenario can explain the positive correlation between ring width and $\delta^{13}\text{C}$ values for the pond cypress sample (Fig. 5). Previous work by Stuiver et al. (1984) has shown that sequoia and Douglas fir trees have a positive relationship between ring area and $\delta^{13}\text{C}$ values. In contrast, the Kitching Creek record could be explained by an increase in stomatal resistance (due to salinity) that is not compensated by an equivalent decrease in mesophyll resistance, and assimilation is decreased (Scenario II, Fig. 6). Nevertheless, one could still have a lower P_i/P_a leading to higher $\delta^{13}\text{C}$ values. This example would be more typical of a plant that is water stressed, with limited stomatal conductance. The decadal discrete sample resolution of the Trapper Nelson site is too coarse to show high-resolution changes in local climate, but indicates less saltwater stress than the Kitching Creek site.

Conclusion

As the original work of Saurer et al. (1995b) indicated, site conditions are very important in influen-

cing a certain tree's isotopic response to climate changes at a particular location. Each one of the records presented here has a different setting, and therefore the controls on the carbon isotopic composition of each time series are different. Wetlands are important components of many different landscapes, and especially in the Everglades setting of South Florida, where developing records of environmental change from these areas can help to establish baseline variability. The preliminary pond cypress record from the C-111 basin of Taylor slough shows that these trees may potentially be used to reconstruct changes in precipitation and potentially hydroperiod. Before this goal can be realized, better calibration data sets of climate parameters (rain fall, water level, relative humidity, etc) are needed. The bald cypress record from the Loxahatchee River shows how these trees may be used to understand the timing of hydrologic stress, such as potential saltwater effects, and perhaps intrusion into the coastal wetlands. With further work and longer time series, our approach may be further tested and used to reconstruct changes in hydroperiods farther back in time, and provide a baseline for wetland restoration.

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