A multiproxy peat record of Holocene mangrove palaeoecology from Twin Cays, Belize

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Abstract: The extent and function of coastal mangrove ecosystems are likely to be influenced by future changes in sea level. Multiple proxies of past mangrove ecosystems preserved in a 780 cm long peat core (TCC2) taken from Twin Cays, Belize, record palaeoecological changes since ~8000 cal. yr BP. The proxies included pollen and the stable-isotope (C, N and O) compositions of mangrove leaf fragments. *Rhizophora mangle* (red mangrove) has been dominant at this site on Twin Cays for over ~8000 years. Variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ suggest past changes in stand structure between dwarf, transition and tall *R. mangle* through the Holocene. Marked changes in the $\delta^{18}\text{O}$ (up to ~4‰) of mangrove leaf fragments throughout TCC2 most likely record variations in the proportion of seawater versus precipitation taken up by past mangroves, reflecting the degree of inundation of the site with seawater resulting from changes in the rate of Holocene sea-level rise. Notably, a decline in peat accumulation rate at ~7200 cal. yr BP correlates with a decrease in the rate of rise in sea level. This was not accompanied by a marked change in the pollen assemblages. However, changes in assemblage composition began to occur ~6300 cal. yr BP, with an increase in *Myrsine*-type and *Avicennia germinans* (black mangrove) pollen. An increase in the $\delta^{18}\text{O}$ between 6100 and 5300 cal. yr BP, which correlates with other records from Central America, indicates a significant increase in the rate of rise in sea level.

Key words: Palaeoecology, mangroves, Holocene, stable isotopes, pollen, oxygen, carbon, nitrogen, Belize.

Introduction

Mangrove ecosystems perform significant roles in global carbon cycling (Chmura *et al.*, 2003; Dittmar *et al.*, 2006) and in protecting tropical and subtropical coastlines from disturbances such as tsunamis (Kathiresan and Rajendran, 2005; Danielsen *et al.*, 2005). The extent and function of mangrove ecosystems present along tropical coastlines are likely to be significantly influenced by fluctuations in sea level (Blasco, 1984; Woodroffe, 1995b; Ellison and Farnsworth, 1997; Swarzbach, 1999). These can be short-term (episodic) changes,

such as flooding associated with tsunamis (Kathiresan and Rajendran, 2005; Danielsen *et al.*, 2005) and hurricanes, or longer-term changes associated with fluctuations in sea level resulting from global environmental changes, such as arctic warming (Arctic Monitoring and Assessment Programme (AMAP) *et al.*, 2004). Although episodic changes can be studied by examining recent past events (eg, Danielsen *et al.*, 2005; Maa *et al.*, 2006; Piou *et al.*, 2006) and by conducting laboratory or manipulative field-based experiments (eg, Ellison and Farnsworth, 1997), it is more difficult to examine mangrove responses to more gradual or longer-term changes in sea level. This challenge is compounded by potential spatial variability (eg, local habitat versus regional ecosystem).

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Documented changes in sea level of the Caribbean region during the Holocene (Blanchon and Shaw, 1995; Toscano and Macintyre, 2003; Gischler and Hudson, 2004; Blanchon, 2005; Gischler, 2006) show that the rate of rise in sea level was greatest prior to ~7000 calendar years before present (cal. yr BP) and then diminished after this time. 'Stepped' increases in the rate of rise in sea level may also have occurred during the Holocene (Blanchon and Shaw, 1995; Blanchon, 2005). Some records from Central and South America have been interpreted as evidence of falling sea level during this period (Jacob and Hallmark, 1996; Wooller *et al.*, 2004a; Angulo *et al.*, 2006). However, a comprehensive review of evidence from the Brazilian coast shows that although the rate of rise in sea level during the Holocene may have slowed at times, it is unlikely that sea level substantially dropped (Angulo *et al.*, 2006).

Studies of Holocene palaeoenvironments of Belize and other parts of Central America have largely focused on mainland sites (Leyden, 1987; Alcalaherrera *et al.*, 1994; Hodell *et al.*, 1995; Jacob and Hallmark, 1996; Whitmore *et al.*, 1996; Curtis *et al.*, 1998). Findings from these studies have been related to Mayan population dynamics (eg, Jacob and Hallmark, 1996; Islebe *et al.*, 1996; Curtis *et al.*, 1998) and changes in sea level (eg, Alcalaherrera *et al.*, 1994; Hodell *et al.*, 1995; Jacob and Hallmark, 1996). In some instances, sea-level variability has indirectly complicated limnological interpretations at mainland sites by influencing the levels of phreatic aquifers (eg, Alcalaherrera *et al.*, 1994; Hodell *et al.*, 1995; Jacob and Hallmark, 1996). For instance, the relative rise in Holocene sea level seems to have been the main control on mainland lagoonal stratigraphy in lowland northern Belize (Alcalaherrera *et al.*, 1994). Despite the relevance of coastal ecosystems to the Mayan civilization in Belize (McKillop, 2002, 2005), few studies of mangrove palaeoecology (eg, McKee and Faulkner, 2000a; Wooller *et al.*, 2004a) have been conducted along the coasts of Belize.

We discuss pollen and stable isotope (C, N and O) data from a 780 cm peat core (TCC2) from Twin Cays in the light of evidence from a previous Twin Cays core (TCC1) (Wooller *et al.*, 2004a), Holocene changes in sea level (Blanchon and Shaw, 1995; Toscano and Macintyre, 2003; Gischler and Hudson, 2004; Blanchon, 2005; Gischler, 2006) and Central American palaeoenvironmental changes. Pollen and stable carbon and nitrogen isotope analyses of mangrove peat cores are useful to track past changes in mangrove floral composition (Behling and da Costa, 2001; Behling *et al.*, 2001; Wooller *et al.*, 2004a), stand structure and nutrient limitation (Wooller *et al.*, 2003b, 2004a). In addition to these analyses, we investigate the analyses of two novel proxies: stable-oxygen-isotope composition of mangrove leaf fragments and relative peat hardness (penetrometer analyses).

The $\delta^{18}\text{O}$ of organic matter in plant leaves is primarily influenced by the $\delta^{18}\text{O}$ of the water available to a plant, in addition to some physiological mechanisms (eg, evapotranspiration) and environmental conditions (eg, humidity and temperature) (Sauer *et al.*, 2001; McCarroll and Loader, 2004). A number of studies have been devoted to understanding the relationship between the $\delta^{18}\text{O}$ of source water in mangrove habitats and the $\delta^{18}\text{O}$ of mangroves (Sternberg and Swart, 1987; Lin and Sternberg, 1993, 1994; Verheyden *et al.*, 2004). These studies have included investigations of the relationship between the $\delta^{18}\text{O}$ of source water and the $\delta^{18}\text{O}$ of stem water, in addition to the relationship between source water and organically bound oxygen (ie, cellulose) in mangrove species (eg, *Avicennia germinans* and *Rhizophora mangle*). Mangroves in southern Florida growing in close proximity to ocean water had stem water with a $\delta^{18}\text{O}$ that reflected that of the ocean water, while those less frequently inundated with ocean water had relatively lower $\delta^{18}\text{O}$ values indicating that they were using proportionally more rainwater (Sternberg and Swart, 1987). Ishshalomgordon *et al.*, (1992) subsequently grew groups of

mangroves that were supplied with water with the same $\delta^{18}\text{O}$ value and a range of different salinities. They found no significant difference in the $\delta^{18}\text{O}$ of leaves from trees grown at different salinities; the $\delta^{18}\text{O}$ of the leaf organic matter reflected the $\delta^{18}\text{O}$ of the source water. They concluded that the $\delta^{18}\text{O}$ values of cellulose in *R. mangle* leaves are a faithful recorder of the $\delta^{18}\text{O}$ changes in water associated with sea water intrusion and therefore rates of change in sea level. Since mangroves seem to depend on water in the surface layers of the substrates in which they grow as their primary water source, and there is no fractionation in oxygen isotopes during water uptake by mangrove roots (Lin and Sternberg, 1994), it seems plausible that the $\delta^{18}\text{O}$ of mangrove subfossils (ie, leaf fragments and tree rings) could be an effective indicator of the $\delta^{18}\text{O}$ of past surface waters, as previously suggested by Ishshalomgordon *et al.* (1992) and Sternberg and Swart (1987).

Although the difference in $\delta^{18}\text{O}$ between ocean water and precipitation in the tropics is not as large as it is at high latitudes (Bowen *et al.*, 2005), rainfall in the tropics tends to have more-negative $\delta^{18}\text{O}$ values (<0‰) relative to standard mean ocean water (0‰) (Benway and Mix, 2004; Bowen *et al.*, 2005; Curtis *et al.*, 1998). These isotopic differences can be reflected in the $\delta^{18}\text{O}$ of mangroves depending on the relative proportions of ocean water versus rainfall (Ishshalomgordon *et al.*, 1992). There are also no reasons to suspect significant changes in the past water source and history of water-vapour transport in Central America during the early Holocene relative to today (Curtis *et al.*, 1998).

Although mangroves can exist in saline environments, they can also exist in fresh water as facultative halophytes (Sternberg and Swart, 1987). We acknowledge that interpreting $\delta^{18}\text{O}$ analyses of plant organic matter can be challenging when considered in isolation (McCarroll and Loader, 2004), so we conducted these analyses within a multiproxy approach (McCarroll and Loader, 2004). An initial examination of the past $\delta^{18}\text{O}$ of mangrove leaf fragments is thus presented in the light of the other palaeoecological proxies. In this context, we also present a measure of the relative hardness and softness of the peat, acquired with a penetrometer. Mangrove peat can present a notoriously subtle stratigraphy, with very little variation in colour and minor variation in texture. The penetrometer data is a means of measuring peat hardness that might allow future correlation between independent cores from the region.

Study site

Twin Cays is composed of two islands, the west and east island, located ~12 km from the mainland of Belize, at 16°50'N, 88°06'W (Feller, 2002; McKee *et al.*, 2002; Wooller *et al.*, 2004a) (Figure 1). The two islands combined measure approximately 1.4 km long and 1.1 km wide (Woodroffe, 1995a) with an area of ~92 ha (Koltes *et al.*, 1998). There are currently three species of mangrove trees present on Twin Cays: *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* [L.] Stearn. (black mangrove) and *Laguncularia racemosa* [L.] Gaertn. f. (white mangrove) (Koltes *et al.*, 1998; McKee *et al.*, 2002). *R. mangle* is the dominant species on the island today (Koltes *et al.*, 1998; Feller, 2002; Wooller *et al.*, 2004a). This plant is present in a variety of heights ranging from dwarf (<1.5 m high) to tall (>1.5 m high) growth forms (Feller, 1995; Woodroffe, 1995a; Koltes *et al.*, 1998; McKee *et al.*, 2002; Lovelock *et al.*, 2006). The dwarf and tall forms are the same species, but the dwarf form is primarily phosphorus-limited and the tall form is primarily nitrogen-limited (Feller, 1995; Woodroffe, 1995a; Cameron and Palmer, 1995; Koltes *et al.*, 1998; McKee *et al.*, 2002; Lovelock *et al.*, 2006). Trees of intermediate height (~2–4 m tall) are limited by both nitrogen and phosphorus (Feller, 1995; McKee *et al.*, 2002). This distribution in growth forms is apparent on many coastal islands in Belize (Woodroffe, 1995a).

Figure 1 Location of core TCC2 (and TCC1) from Twin Cays, Belize (large-scale map adapted from Smithsonian Caribbean Coral Reef Ecosystems map)

Dwarf *R. mangle* are generally found near the island's interior, in ponds and basins partially closed off from tidal input (Woodroffe, 1995a). The tall form (usually 5–6 m tall on Twin Cays) generally surrounds the edge of the island and the banks of the channel separating the two islands, growing in areas more frequently inundated with seawater (Garcia and Holtermann, 1998; Koltes *et al.*, 1998; McKee *et al.*, 2002; Lovelock *et al.*, 2006). Tall and dwarf growth forms of *R. mangle* have indistinguishable pollen but can possess different stable carbon and nitrogen isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) (Wooller *et al.*, 2003b, 2004a). Although decomposition of *R. mangle* leaves alters the original isotopic signatures, leaves from tall *R. mangle* trees generally exhibit $\delta^{13}\text{C}$ values less than -27‰ , while $\delta^{13}\text{C}$ of dwarf trees ranges from -24‰ to -26‰ . The $\delta^{15}\text{N}$ values of tall trees generally range from -2.8‰ to $+3.2\text{‰}$, whereas dwarf trees are characterized by $\delta^{15}\text{N}$ values of $<-3\text{‰}$ (Wooller *et al.*, 2003b). These isotopic signatures are altered very little through the process of leaf senescence (Wooller *et al.*, 2003b).

A. germinans are usually found inland of tall *R. mangle* and in regions less frequently inundated with seawater (Wooller *et al.*, 2003b). Of the species found on Twin Cays, *A. germinans* is tolerant of high salt concentrations and survives in areas ranging from 38–65 parts per thousand (ppt) (Woodroffe, 1995a; Garcia and Holtermann, 1998; McKee and Faulkner, 2000b; Sobrado and Ewe, 2006). In addition to these four tree species, herbs, grasses and ferns are also present (Woodroffe, 1995a). Unvegetated flats, which are dry or shallow at low tide, characterize some areas in the interior of Twin Cays, and many are surrounded by dwarf *R. mangle* (Koltes *et al.*, 1998; Woodroffe, 1995a).

A peat core, TCC2, was taken from an area in the interior of the west island of Twin Cays, where standing water and dwarf

R. mangle were present (Figure 1). A previous core, TCC1, has a basal age of ~ 8300 cal. yr BP and shows significant palaeoecological changes, including a period dominated by *Myrsine* sp. pollen (Wooller *et al.*, 2004a). By developing a palaeoenvironmental reconstruction for Twin Cays, we aim to provide an improved assessment of local habitat variability in mangrove ecosystems during the Holocene.

Methods

Field work

A 780 cm core (TCC2) of continuous peat was taken from the west island of Twin Cays, Belize (Figure 1) following the protocol described by Wooller *et al.* (2004a) using a Russian peat corer. Most of TCC2 (0–715 cm) is composed of mangrove peat, which contains *R. mangle* leaf fragments, roots and organic material. The bottom 65 cm (715–780 cm) is a grey mud lacking macrofossils. The cores are currently stored ($\sim 4^\circ\text{C}$) at the Water and Environmental Research Center (WERC) at the University of Alaska Fairbanks.

Radiocarbon dating, peat accumulation and penetrometer analysis

R. mangle leaf fragments were picked from TCC2 in order to obtain seven accelerator mass spectrometry (AMS) radiocarbon dates. Once separated from the mangrove peat, the leaf fragments were washed with deionized water. Leaf fragments were sparse at 45 cm depth, so 1 cm³ of bulk peat was dated instead. The samples were freeze dried and stored in glass vials. The glass vials had previously been heated to 300°C in a muffle furnace to remove any organic contaminants. A sample from the outer layer of wood from a large (~ 75 cm diameter) stump of a dead *A. germinans* that was present at the coring site was also sent for AMS dating. The samples were sent to the National Ocean Sciences Accelerator Mass Spectrometry Facility at Woods Hole Oceanographic Institution in Massachusetts for ^{14}C AMS dating. Radiocarbon dates were converted to cal. yr BP using Calib 5.0.2. (Stuiver *et al.*, 1998) (<http://calib.qub.ac.uk/calib/>, last accessed 13 September 2007). Peat accumulation rates (cm/yr) were calculated for each of the core sections between radiocarbon dates, assuming constant accumulation between dated horizons.

The relative hardness of the TCC2 peat was assessed with a hand-held penetrometer (ELE International pocket penetrometer 29-3729 with adapter foot). The penetrometer was fitted with the 2 cm diameter flat foot, which is used for relatively soft material such as peat. While the peat core was held in its plastic core liner, the penetrometer was pushed into the peat at 3 cm intervals until the core surface was level with the top of the penetrometer foot. The reading of the gauge was then recorded. Two measurements were taken side by side at each depth, and the mean of the two measurements was calculated. A five point, weighted, running mean was calculated from these data.

Pollen analyses

Palynological processing and identification methods for TCC2 replicate methods for TCC1 (Wooller *et al.*, 2004a). Approximately 1 cm³ (~ 1 g to 2 g) samples were taken at 10 cm intervals between 0 cm and 780 cm. A tablet of exotic *Lycopodium* spores was added to each sample prior to acetolysis in order to determine the pollen concentration (grains/cm³). Clay-sized particles were removed from the basal silt samples (710–780 cm) with a 7–10 μm Nitex cloth sieve. The samples were mounted in glycerin jelly.

Whenever possible, a minimum of 300 grains were counted and identified for each sample. However, this was not always possible owing to low pollen concentrations. In such cases, a minimum of

Figure 2 (a) Peat-accumulation rates between radiocarbon dates and (b) relative hardness and softness of peat (penetrometer increments) from TCC2

100 grains were identified and counted. Relative abundances are expressed as a percentage of the pollen sum. The pollen sum did not include foraminifera test linings, diatoms and fungal spores, which are recorded as the total number observed. Unidentified taxa represent a maximum 3% of the pollen sum. The pollen diagram was generated using TILIA (Grimm, 1987) and was zoned using CONISS in this program. All of the data from core TCC2 are reported relative to the pollen zones (see Figure 3).

Carbon, nitrogen and oxygen stable isotope analyses of leaf fragments

Mangrove leaf fragments were collected at 5 cm intervals throughout most of TCC2 (0–605 cm). The number and approximate proportions (length and width in mm) of fragments from each sample were recorded to give an approximation of leaf-fragment abundance (leaf-fragment area, cm²) present at each sample depth (Wooller *et al.*, 2004a). Since the fragments were sparse below ~580 cm, the sampling frequency decreased. From 605–730 cm, samples were taken at 10 cm intervals. There were no leaves below 730 cm. Leaf fragments were rinsed with deionized water and freeze-dried prior to isotopic analysis.

In addition to the stable isotopes processed on *R. mangle* leaf fragments, five bulk (Total Organic Matter) sediment samples from the base of TCC2 were analysed. Bulk sediment samples taken from 710, 720, 740, 750 and 760 cm were acid-fumed to remove carbonate and freeze dried. Once dry, 0.30–0.50 mg of each sample was weighed and placed in a 3.75 mm tin cup and crimped shut.

Acetanilide (C₈H₉NO) was used as a standard to determine the analytical precision for $\delta^{13}\text{C}$ (0.2‰), $\delta^{15}\text{N}$ (0.3‰), %C (6%) and %N (1%). An Elemental Analyser (EA) fitted to a stable-isotope ratio mass spectrometer (IRMS) (Ce Instruments, NA 2500 Series EA attached to a Finnigan MAT, Delta^{plus}XL) was used to produce $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Stable-isotope ratios (C and N) are reported relative to Vienna Pee Dee Belemnite (VPDB) and air using standard delta notation. A five-point weighted running mean was calculated for the isotope data.

The $\delta^{18}\text{O}$ of leaf fragments from TCC2 was analysed using the protocol and instrumentation described by Wooller *et al.* (2004b). The data are expressed relative to Vienna Standard Mean Ocean Water (VSMOW). Benzoic acid (C₇H₆O₂) was used to determine analytical precisions associated with $\delta^{18}\text{O}$ and %O analysis for each run, which were 0.4‰ and 2%, respectively.

Table 1 List of AMS radiocarbon dates (analysed at National Ocean Sciences Accelerator Mass Spectrometry Facility, NOSAMS) for core TCC2 from Twin Cays Belize using handpicked fragments of mangrove leaves (LF) or whole wood from a dead black mangrove (BMW)

NOSAMS accession number	Material dated	Depth (cm)	¹⁴ C yr BP	Age error	Calibrated age yr BP	Calibrated age range yr BP (1 sigma)
OS-57502	BMW	n.a.	205	30	168	150–186
OS-42359	Peat	45	240	35	230	151–312
OS-54559	LF	150	2880	65	3014	2889–3139
OS-54558	LF	226	4650	70	3744	3644–3845
OS-40701	LF	295	5190	40	5950	5911–5988
OS-40700	LF	425	6090	40	6900	6810–6999
OS-40699	LF	465	6320	35	7240	7163–7306
OS-40698	LF	620	6610	45	7500	7434–7561
OS-40697	LF	712	7040	45	7860	7792–7932

n.a., not applicable.

Figure 3 (a) Summary pollen diagram showing vegetation groups and pollen concentrations of the TCC2 core from Twin Cays, Belize. (b) Percentage pollen diagram of the most frequent pollen and spore taxa of the TCC2 core

Results

Core description and radiocarbon dates for core TCC2

TCC2 was almost entirely composed of peat (Figure 2), with the exception of a small section (~780–710 cm) composed of a fine grey mud that was harder than the peat (Figure 2b). During coring, a relatively hard layer of peat was encountered at ~400 cm overlying a softer layer of peat. These field observations are confirmed by the penetrometer data (Figure 2b), which show the peat below ~450 cm to be relatively soft compared with the peat between ~450 cm and ~320 cm. Another hard layer is evident at ~100 cm. The transition from relatively soft peat to harder peat at ~450 cm correlates with a marked change in peat accumulation rates at site TCC2 (Figure 2). Below ~460 cm the peat accumulation rate ranged from ~0.3 to 0.6 cm/yr. Above ~460 cm the peat accumulation rate is consistently < ~0.3 cm/yr.

Eight radiocarbon dates were obtained from TCC2 (Table 1) at 45, 150, 226, 295, 425, 465, 620 and 712 cm. The radiocarbon dates presented herein have been converted to cal. yr BP (Table 1), and interpolation between these dates assumes constant accumulation rates between radiocarbon dates. Interpolated dates have been calculated for the boundaries between pollen zones at 200, 345 and 720 cm. An additional radiocarbon date of 168 cal. yr BP was obtained from the outer layer of a dead *A. germinans* mangrove stump at the site (Table 1).

The basal age of TCC2 is ~8100 cal. yr BP (extrapolated). The peat between 780 cm and 720 cm (pollen zone TCC2-I) accumulated between ~8100 and ~7900 cal. yr BP (Figure 2a). Peat between 720 cm and 345 cm (pollen zone TCC2-II) accumulated between ~7900 and ~6300 cal. yr BP, and peat in pollen zone TCC2-III (345 cm to 200 cm) accumulated between ~6300 and ~3500 cal. yr BP. The peat from 200 cm to the surface (pollen zone TCC2-IV) accumulated over ~3500 cal. years.

Description of the pollen diagram from core TCC2

Throughout most of TCC2, *R. mangle* pollen dominates the assemblages (Figure 3a, b). This is partially due to the fact that *R. mangle* produces greater amounts of pollen compared with *A. germinans* and *L. racemosa* (Behling *et al.*, 2001). Within pollen zone TCC2-I, pollen concentrations and accumulation rates reach peak values (Figure 3b) and remain relatively high between 600 and 550 cm, the interval with the highest peat accumulation rates (Figure 2). Pollen concentrations and accumulation rates are relatively uniform during pollen zone TCC2-III, but decrease markedly at the start of pollen zone TCC2-IV.

Pollen zone TCC2-I

The period represented by pollen zone TCC2-I is characterized by high amounts of *R. mangle* (56–98%) (Figure 3a). At ~750 cm there is a marked increase in other trees and shrubs (including *Pinus*). This is followed by a marked increase in *L. racemosa*-type pollen (up to 70%).

Pollen zone TCC2-II

Pollen zone TCC2-II is characterized by high percentages of mangrove pollen (~80–100%) (Figure 3b), which is dominated by *R. mangle*. Relatively low (<20%) percentages of pollen from other trees and shrubs, including *Myrsine*-type and *Pinus*, are also evident throughout the zone. The distinguishing feature of this zone is the marked increase in the number of micro-foraminifera (Figure 3b) and fungal spores (Figure 3a) at ~450 cm, preceded by an increase in the abundance of *A. germinans* pollen at ~500 cm. The zone ends with a marked decrease in *R. mangle* pollen and an increase in *Myrsine*-type pollen.

Pollen zone TCC2-III

The base of zone TCC2-III is distinguished by a spike (>70%) in the abundance of *Myrsine*-type pollen. Above ~330 cm the percentage

Figure 4 (a) Estimate of leaf-fragment area, (b) the stable nitrogen-, (c) carbon- and (d) oxygen-isotope composition of leaf fragments from core TCC2

of *Myrsine*-type pollen generally increases from ~5% to ~30% at the end of the zone. Large amounts of *R. mangle* pollen (22–89%) are present throughout. This zone contains low to moderate amounts of *A. germinans* (up to 7%), *L. racemosa* (up to 5%) and grass (up to 13%) pollen. Fungal spores are rare, and the number of micro-foraminifera test linings varies from 1 to 15.

Pollen zone TCC2-IV

Pollen assemblages between 200 cm and 0 cm contain high percentages of *R. mangle* pollen (41–75%) and moderate amounts of forest taxa (5–32% *Pinus*). Minor pollen types include *Myrsine*-type (0–41%), *A. germinans* (0–12%), *L. racemosa* (0–2%), Poaceae (0–16%) and Asteraceae (0–2%). Fungal spores and micro-foraminifera are present in low numbers throughout the zone.

Leaf fragments from TCC2

Although leaf fragments were not present in the mud samples examined from pollen zone TCC2-I, leaf fragments are present in the overlying peat (Figure 4). Several peaks in leaf area are evident in pollen zone TCC2-II, with the two highest evident at ~530 cm and ~350 cm. Very few fragments were found in pollen zone TCC2-III. The highest total leaf area was found in pollen zone TCC2-IV.

Stable carbon, nitrogen and oxygen isotope data from the analysis of leaf fragments

Although there is no significant correlation between the stable isotope data, it is noted that low $\delta^{13}\text{C}$ are typically associated with relatively high values of $\delta^{18}\text{O}$ (Figure 4). Bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from zone TCC2-I ranged from –26.3‰ to –26.8‰ and 6.2‰ to 7.7‰, respectively. The leaf fragments from pollen zone TCC2-II reveal decreasing values of $\delta^{15}\text{N}$, from ~1.5‰ at the start of the zone to ~–3‰ at ~670 cm. Above 670 cm, $\delta^{15}\text{N}$ increases to a peak value of ~3‰ at ~550 cm. Between ~550 cm and ~450 cm $\delta^{15}\text{N}$ values range between –3‰ and 1.5‰. From ~450 cm to the end of the zone, the $\delta^{15}\text{N}$ values increase from –3‰ to 3.5‰. $\delta^{13}\text{C}$ values reveal an overall decrease from –24‰, near the base of the zone, to a minimum value of –28‰ at ~450 cm. Between ~550 cm and 500 cm values increase to ~–24‰. At ~450 cm $\delta^{13}\text{C}$ values increase abruptly to ~–21‰, followed by a slight decrease to ~–25‰ at the top of the zone. $\delta^{18}\text{O}$ values peak twice during this zone, once near the base of the zone (~650 cm) and again between ~550 and 450 cm. A marked decrease in $\delta^{18}\text{O}$ occurs at ~450 cm, with values as low as 17‰. $\delta^{18}\text{O}$ values then remain relatively stable (~18‰) for the duration of the zone.

A sharp decrease in $\delta^{15}\text{N}$ from ~3‰ to ~–2‰ occurs at the start of pollen zone TCC2-III, after which $\delta^{15}\text{N}$ values generally increase to ~1‰ at the top of the zone. $\delta^{13}\text{C}$ values also increase overall throughout the zone from a low of ~28‰ at the base of the zone to ~25‰ at the top. $\delta^{18}\text{O}$ increases from a low value of ~17‰ at the base of the zone to 20‰ at ~300 cm, after which values generally decrease to ~17‰ at the top of the zone.

$\delta^{15}\text{N}$ values decrease from ~2‰ at the base of pollen zone TCC2-IV to ~–2‰ at 160 cm, with two slight peaks (up to 2‰) at ~130 cm and at ~10 cm. $\delta^{13}\text{C}$ values decrease slightly from ~–24‰ at the base of the zone to ~–26.5‰ at ~150 cm, then increase to ~–23‰ at 30 cm. $\delta^{18}\text{O}$ values increase from ~17‰ at the base of the zone to a maximum value of ~21‰, at ~150 cm. Two lesser peaks occur at 120 cm and ~50 cm, followed by an abrupt decrease in $\delta^{18}\text{O}$ to a minimum value of 16‰ at ~100 cm.

Discussion and interpretation

Zone TCC2-I (8100 to 7900 cal. yr BP)

Mangroves established at the site of TCC2 on a mud-covered limestone platform ~8100 cal. yr BP, coincident with development

of mangroves at other locations on the island (eg, Wooller *et al.*, 2004a). The initial mangrove stand was composed of *L. racemosa*, *R. mangle* and *A. germinans*. Since both *A. germinans* and *L. racemosa* are relatively low pollen producers (Behling *et al.*, 2001), the very presence of their pollen indicates that they probably comprised a substantial proportion of the local vegetation.

Since our chronology is primarily based on radiocarbon analyses of leaf fragments, we have avoided some of the problems associated with dating mangrove peat samples (see Gischler and Hudson, 2004; Gischler, 2006). For instance, when analyses are conducted on bulk peat the date of the sample can be complicated by the penetration of younger roots into older peat. We acknowledge that dating material, such as leaves, from mangrove peat does not avoid some of the variability associated with slight differences in substrate elevation between different mangrove habitats. However, these elevation differences are relatively small in Belize, even if peat is encountered from *A. germinans*, which usually grows at slightly higher elevations (see discussions in Blanchon and Shaw, 1995; Toscano and Macintyre, 2003; Gischler and Hudson, 2004; Blanchon, 2005; Gischler, 2006). Differences in elevation do not pose a problem, because the primary goal of our study is to date changes in the core, not to use the dates to estimate the relative height of sea level.

The relatively high bulk $\delta^{15}\text{N}$ values of the mud from the base of the core (older than 7900 cal. yr BP) suggest that this site may have received deposits of bird guano. High $\delta^{15}\text{N}$ values have previously been observed in all aspects (eg, peat and mangrove trees) of Man of War Cay, a mangrove island near Twin Cays (Wooller *et al.*, 2003a). Man of War Cay hosts a large number of marine birds (eg, frigate birds) that contribute large amounts of nitrogen-rich bird droppings to the sediment. A similar environment may have prevailed during the early formation of Twin Cays.

In Belize the highest diversities of foraminifera have been found in well-circulated areas of normal and constant marine salinities (Gischler *et al.*, 2003). The duration and frequency of subaerial exposure have been shown to be the most important factors influencing the abundance foraminifera associated with some mangrove habitats (Woodroffe *et al.*, 2005). Thus, multiple lines of evidence, including $\delta^{15}\text{N}$ values, mixed mangrove stands and relatively high number of micro-foraminifera, suggest that this site, currently located in the centre of the western island of Twin Cays, was a transitional mangrove habitat during zone TCC2-I. The presence of Arecaceae, the Palm family, can also be attributed to a transitional mangrove habitat (Torrescano and Islebe, 2006). A lithology of this type is consistent with the sequence that occurred during the flooding of the platform in Belize during the early part of the Holocene (Halley *et al.*, 1997).

Zone TCC2-II (7900 to 6300 cal. yr BP)

The base of pollen zone TCC2-II, at 7900 cal. yr BP, is distinguished by a change in sediment composition from grey mud to the pure mangrove peat typical of the rest of the core. This transition coincides with the first appearance of mangrove leaf fragments. The entire zone, from the base to the top at 6300 cal. yr BP, is dominated by pollen of *R. mangle*, with minor contributions from other mangrove species.

Myrsine-type pollen is present in small amounts. Whereas plants that produce this pollen type are not known to be present on the island today, species of *Myrsine* are found on the mainland (Balick *et al.*, 2001). Some producers of *Myrsine*-type pollen are documented disturbance indicators (*Ardisia escallonioides* and *Myrsine coriacea*) (Pascarella, 1998). High concentrations of *Myrsine*-type pollen are also recorded at intervals in core TCC1 (Wooller *et al.*, 2004a). However, the relatively low concentrations present throughout zone TCC2-II are consistent with regional transport, possibly from the mainland. This is likely also the case for pollen of *Pinus* and Poaceae.

A 'stepped' increase (Blanchon, 2005) in the rate of rise in sea level in the Caribbean is recorded between ~8500 cal. yr BP and ~7500 cal. yr BP, although the temporal resolution of this event is relatively coarse. After 7700 cal. yr BP, the rate of rise in sea level apparently decreased from ~5.2 mm/yr to ~1.5 mm/yr (Toscano and Macintyre, 2003). Sea-level curves presented by Gischler and Hudson (2004) and Gischler (2006) indicate that the decrease in the rate of sea-level rise occurs after ~7000 cal. yr BP. This decrease in the rate of sea-level rise correlates with a decrease in peat-accumulation rates, which likely occurred as mangroves at the site adjusted to the decelerating rate of sea-level rise. Correlation between these events supports the interpretation that the change in peat accumulation rate resulted from sea-level changes, rather than a catastrophic die-off of mangroves, which can cause peat collapse (eg, Cahoon *et al.*, 2003). Although the pollen data imply that species composition remained relatively constant during this time, peat accumulation rates, peat hardness and stable isotope data record some marked ecological changes. After ~7200 cal. yr BP peat-accumulation rates decreased significantly.

Relatively sharp isotopic changes recorded at ~7200 cal. yr BP on Twin Cays imply that the *R. mangle* habitat became less regularly inundated with seawater. This is evident from the abrupt increase in $\delta^{13}\text{C}$ and concurrent decrease in $\delta^{15}\text{N}$ to minimum (<3‰) values between 7200 and 6300 cal. yr BP. High $\delta^{13}\text{C}$ and low $\delta^{15}\text{N}$ values are typical of dwarf *R. mangle* found in the interior of the modern island. Tidal delivery replenishes phosphorus in the sediment but toward the interior tidal influx is limited, creating less nutrient exchange (Feller, 1995). Today the majority (but not all) of the dwarf trees are found towards the interior areas of Twin Cays. Decreasing $\delta^{18}\text{O}$ values support reconstruction of a site at TCC2 less inundated with seawater after 7200 cal. yr BP. Whereas the $\delta^{18}\text{O}$ of lacustrine proxies are interpreted on the basis of evaporation to precipitation ratios (eg, Curtis *et al.*, 1996, 1998), our data are more liable to be a reflection of changes in the proportions of precipitation versus seawater, because mangroves derive their water from varying proportions of these two end members (Ishshalomgordon *et al.*, 1992). Although variations in the $\delta^{18}\text{O}$ of plants can be challenging to interpret (McCarroll and Loader, 2004), decreasing $\delta^{18}\text{O}$ values after ~7200 cal. yr BP in TCC2 are consistent with mangroves deriving a greater proportion of water from tropical precipitation, which is liable to have a more negative $\delta^{18}\text{O}$ (eg, <−4‰) relative to ocean water (standard mean ocean water = 0‰) (eg, Benway and Mix, 2004). Detailed studies of the controls of $\delta^{18}\text{O}$ in modern mangrove habitats have shown that mangrove organic matter is likely a reliable record of the $\delta^{18}\text{O}$ of source water and the proportion of seawater versus rainwater (Sternberg and Swart, 1987; Lin and Sternberg, 1993, 1994; Verheyden *et al.*, 2004). Our own modern precipitation $\delta^{18}\text{O}$ data (N. Monacci and M.J. Wooller, unpublished data, 2007) supports this finding. In addition, we have found that the difference (~26‰) between the $\delta^{18}\text{O}$ of modern mangrove leaves in Belize and the $\delta^{18}\text{O}$ of water in the substrates of mangroves habitats is consistent with the fractionation associated with carbohydrate synthesis by plants (reviewed by McCarroll and Loader, 2004) and cellulose synthesis in *R. mangle* leaves (Ishshalomgordon *et al.*, 1992). We therefore consider that the most logical interpretation of the marked decrease in the $\delta^{18}\text{O}$ at ~7200 cal. yr BP is a decrease in the proportion of seawater inundating site TCC2. Although a similar shift could be produced by increasing the proportion of rainfall relative to seawater at the site, the former interpretation is more likely given the correlation between the timing of the $\delta^{18}\text{O}$ decrease (~7200 cal. yr BP) with the documented decrease in the rate of sea-level rise (ie, Gischler, 2006).

Analyses of coral skeletons from the Belize reef complex have revealed seasonal variations in $\delta^{18}\text{O}$ (Gischler and Oschmann, 2005). Although changes in water temperature were taken into

account, Gischler and Oschmann (2005) partially attribute these alterations in the $\delta^{18}\text{O}$ of the water surrounding the coral. They note that high temperatures coincide with high seasonal rainfall, lowering the $\delta^{18}\text{O}$ in the coral. Corals from the Belize reef complex also show a marked decrease in $\delta^{18}\text{O}$ (up to ~2‰) after ~6990 yr BP (Gischler and Oschmann, 2005).

Zone TCC2-III (6300 to 3500 cal. yr BP)

The transition to pollen zone TCC2-III at ~6300 cal. yr BP is associated with a series of habitat changes. At the base of the zone the abundance of *Myrsine*-type pollen peaks abruptly before declining to background levels. From 6300 to 3500 cal. yr BP the $\delta^{13}\text{C}$ of the mangrove leaves decreased and the $\delta^{18}\text{O}$ increased, implying greater inundation with ocean water. This interpretation is consistent with slight increase in the number of micro-foraminifera at ~4700 cal. yr BP and with evidence for a stepped increase in the rate of rise in sea level at this time (Blanchon, 2005). A major flooding event between ~6400 and ~5500 cal. yr BP at Cobweb Swamp on the Belize mainland was associated with rising sea level (Jacob and Hallmark, 1996), and a high stand in sea level occurred along the eastern Brazilian coast between ~5800 and 5000 cal. yr BP (Angulo *et al.*, 2006). Flooding of the Rio Honde and increases in mangrove habitat area in southeastern Mexico after ~4600 cal. yr BP have also been attributed to a rise in sea level (Torrescano and Islebe, 2006).

After ~5800 cal. yr BP the percentage of the *Myrsine*-type pollen in TCC2 again increases. A secondary peak at ~3600 cal. yr BP is coeval with very high concentrations of *Myrsine*-type pollen in core TCC1 (Wooller *et al.*, 2004a). Although percentages of *Myrsine*-type pollen remain relatively high between 4500 and 3500 cal. yr BP at the site of TCC2, we do not see the very high concentrations evident between 4280 and 4040 cal. yr BP in TCC1. It seems likely that a plant producing *Myrsine*-type pollen was local to Twin Cays during this time period, when the island supported a heterogeneous patchwork of habitats. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data imply that the *R. mangle* at the site of core TCC2 were of a transitional type, while the pollen data indicate that they were interspersed with *A. germinans* and *L. racemosa*.

Zone TCC2-IV (3500 cal. yr BP to present)

The base of pollen zone TCC2-IV records a significant increase in the percentage of pollen from *Pinus* and Poaceae. The low pollen concentrations imply that these types, which are known to be transported over long distances, are most likely from the mainland. Although the increase in pine and grass pollen could be associated with a change in the prevailing wind direction, the abundance of *Pinus* on Twin Cays is a likely a direct result of increased amounts of *Pinus* on mainland Belize. The ~3500 cal. yr BP increase is coeval with an increase in *Pinus* pollen in core TCC1 (Wooller *et al.*, 2004a) and at various sites on the mainland (Leyden, 1987; Islebe *et al.*, 1996; Curtis *et al.*, 1998; Wahl *et al.*, 2006). Regional climatic changes (warmer and wetter) caused a change in mainland vegetation from savanna to forest ~4000 cal. yr BP (Markgraf, 1993; Leyden, 2002). Drier conditions followed (Curtis *et al.*, 1996), and an interval of peak aridity 1300 and 1100 cal. yr BP has been related to the collapse of the Classic Maya civilization (Hodell *et al.*, 1995). After 3500 cal. yr BP, the TCC2 site is dominated by *R. mangle* and, according to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data, these trees were of a transitional type. A marked increase in the $\delta^{18}\text{O}$ to the maximum core values ~2500 cal. yr BP is associated with a decrease in the $\delta^{13}\text{C}$. These changes imply that the site was more frequently inundated with seawater, and the stand structure of *R. mangle* changed from transitional to tall. This hypothesis is supported by sea-level reconstructions that suggest that the rate of rise in sea level slowed (from 1.5 mm/yr to 0.9 mm/yr) after ~2000 cal. yr BP (Toscano and Macintyre, 2003). An

increase in inundation by seawater may account for the rise in some lake levels on the Belize mainland after 3400 cal. yr BP through raising of phreatic aquifers (Alcalaherrera *et al.*, 1994). A subsequent peak in the *Myrsine*-type pollen at ~1000 cal. yr BP on Twin Cays, which has previously been associated with a decrease in seawater inundation (Wooller *et al.*, 2004a), is associated with a marked decrease in $\delta^{18}\text{O}$, indicating that more pore water was derived from precipitation. This increase in *Myrsine*-type pollen is also associated with a relatively hard portion of the peat core and a subsequent increase in the percentage of *A. germinans* pollen, indicative of development of a mixed stand of *R. mangle* and *A. germinans*. Although this is not consistent with the vegetation of the modern site (ie, an interior pond dominated by *R. mangle*), inspection of the pond revealed a number of very large (up to ~1 m diameter) submerged *A. germinans* stumps, with the outer portion of one of the larger stumps producing a radiocarbon date of 168 cal. yr BP (Table 1). Evidence for maximum middle to late Holocene aridity on the mainland is derived from $\delta^{18}\text{O}$ analyses of inorganic biological fractions (eg, ostracods and gastropods) in lakes of Central and South America (eg, Hodell *et al.*, 1991; Curtis *et al.*, 1996, 1998; Whitmore *et al.*, 1996). The isotopic and palynological changes we document at the site of TCC2 ~1000 cal. yr BP record a change in the mangrove ecosystems off of the coast of Belize, raising the possibility that changes in sea level may have played a key role in late-Holocene palaeoenvironmental changes of Central America.

Our data provide evidence of changes in the composition and physiology of mangrove habitats on Twin Cays throughout the middle to late Holocene. Two new proxies were included in our multiproxy analysis of mangrove peat cores: $\delta^{18}\text{O}$ analyses of leaf fragments and penetrometer measurements of the relative hardness of the peat. As with the application of any novel proxies of past environments, there is the need for further investigations. For instance the $\delta^{18}\text{O}$ data are generated from the analysis of total organic oxygen retained in the leaf fragments. We acknowledge that some of the variation in our data may represent diagenetic alteration of the organic composition of the leaves over time. Studies of the stable-isotope composition of organic material preserved in deposits sometimes resort to the analysis of recalcitrant single compounds or groups of compounds (eg, Ficken *et al.*, 2000) to reduce the possible noise associated with diagenesis. In terms of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of leaf fragments, we set up a series of taphonomic experiments to assess the degree to which the isotopic signatures are likely to be altered over time (Wooller *et al.*, 2003b). These experiments showed that despite various taphonomic processes that take place prior to a mangrove leaf being preserved in peat, including leaf senescence, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ could still distinguish leaves from tall versus dwarf *R. mangle*. The analyses were performed only after it had been established that variation was preserved in bulk isotope measurements of leaf fragments from peat cores (Wooller *et al.*, 2003b). We provide evidence that the bulk $\delta^{18}\text{O}$ of leaf fragments in peat cores varies over time, sometimes in accordance with other proxies. We now see merit in performing a study of the $\delta^{18}\text{O}$ of leaf fragments during taphonomic processes (ie, senescence), similar to that of Wooller *et al.* (2003b).

We also see merit in further assessments of the physical characteristics of peat cores. The penetrometer data has illustrated marked shifts between hard and soft peat that cannot be ascribed to burial and compaction (ie, softer peat at the bottom of the core and harder peat at the surface). Despite the fact that some sections of the TCC2 penetrometer data are exceedingly variable, some portions of the core are consistently harder. A similar trend is also evident in the core TCC1 from Twin Cays. Thus, penetrometer analyses are a potential correlation tool.

Rates of rise in sea level are known to have varied during the Holocene, with an overall deceleration towards the present day.

During the early Holocene, when the rate of rise in sea level was still relatively high (~5 mm/yr), peat-accumulation rates were highest. Calculations of peat-accumulation rates for the deeper part of our core TCC2 may even be considerable underestimations, since the base of the core may have undergone the most compaction.

We find both similarities and dissimilarities between the two cores from Twin Cays (TCC1, Wooller *et al.*, 2004a; and TCC2, this study). Many features of the data from site TCC2 are consistent with the previous findings from site TCC1. We have noted very similar trends in the penetrometer data from both cores (TCC2 Figure 2b and TCC1 M.J. Wooller, unpublished data, 2007). We also note marked decreases in sedimentation rate at ~7000 cal. yr BP in both cores. In terms of the pollen, we note that both sites were covered by *R. mangle* throughout the majority of the Holocene. High percentages of *R. mangle* dominate the pollen assemblages from both TCC1 and TCC2 during the period from ~8000 cal. yr BP to ~5000 cal. yr BP. Although both sites show a marked single peak in the percentage of *Myrsine*-type pollen during this period, these peaks do not correlate. However, a marked increase in the percentage of *Myrsine*-type pollen from ~4300 cal. yr BP until ~3800 cal. yr BP in core TCC2 correlates with the previously published (Wooller *et al.*, 2004b) high concentrations of this pollen type documented in core TCC1. Since the percentages and concentrations of this pollen type in core TCC2 do not approach the high levels previously shown in core TCC1 during this time period, it seems that this feature of the pollen assemblages was locally restricted to site TCC1 at Twin Cays. This interval is also represented by a notable absence or reduction in the leaf fragment area and an increase in the percentage of *A. germinans* pollen in both cores. In addition, both cores show a marked increase in the percentage of pollen from *Pinus* and other shrubs and trees after ~4000 cal. yr BP, which has previously been interpreted as changes in the proportion of pollen derived from the mainland (Wooller *et al.*, 2004b). Both pollen diagrams show a decrease followed by an increase in the percentage of *Pinus* pollen between ~2000 and 1000 cal. yr BP. Broad changes (ie, weighted running means) in the stable isotopic trends (TCC2 Figure 4 and TCC1 based on published isotope data in Wooller *et al.*, 2004b) also show similarities, most notably a marked decrease in $\delta^{13}\text{C}$ from ~7600 to ~7000 cal. yr BP. Further synthesis of the patterns will be possible once similar multiproxy records have been established from other sites in Belize (eg, Drowned Cays, N. Monacci and M.J. Wooller, unpublished data, 2007).

Conclusions

Our data have implications for predicting how mangrove ecosystems may respond to future changes in sea level. A range of scenarios and rates of rise in sea level are predicted for the next ~100 years (AMAP *et al.*, 2004). Mangroves at Twin Cays were able to maintain a mangrove habitat despite changing Holocene sea levels; these data suggest that frequent inundations with seawater stimulate higher rates of peat accumulation in mangrove habitats. This likely 'releases' mangroves from the nutrient limitation that dwarf mangroves experience in the interior of mangrove cays in Belize (Feller, 1995; Lovelock *et al.*, 2006). However, some sea-level scenarios predict higher rates of rise in the future than those evident in the Caribbean during the Holocene (ie, >5 mm/yr) (AMAP *et al.*, 2004). It is not possible to say at what point mangroves on cays such as Twin Cays may be unable to maintain a sufficient peat-accumulation rate to keep up with these higher rates of rise in sea level. It seems that past decreases in the rate of rise in sea level, or possible decreases in sea level, coincide with some of the most marked Holocene changes in mangrove habitats

located on Twin Cays. These changes include a decrease in peat accumulation, an increase in peat hardness and, in some instances, species-composition changes and changes in the stand structure of the dominant modern mangrove (*R. mangle*). The ecological 'options' for mangrove ecosystems along barrier islands, on atolls and on cays, are more limited compared with mangroves on the mainland, which have the additional option of migrating inland in response to marine transgressions. During the earlier part of the Holocene, mangroves at site TCC2 were able to keep pace with a relatively rapid rise in sea level. Our data also imply that the mangroves were able to take advantage of varying proportions of precipitation versus seawater during the Holocene, which likely came about as the rate of sea-level rise changed.

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