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C_4 Plant Productivity and Climate-CO_2 Variations in South-Central Texas during the Late Quaternary

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A continuous record of organic carbon $\delta^{13}C$ from a buried soil sequence in south-central Texas demonstrates: 1) strong coupling between marine and adjacent continental ecosystems in the late Pleistocene as a result of glacial meltwater entering the Gulf of Mexico and 2) ecosystem decoupling in the Holocene associated with a reduction of meltwater and a shift in global circulation patterns. In the late Pleistocene, reduction in C_4 plant productivity correlates with two well-documented glacial meltwater pulses (~15,000 and 12,000 ^{14}C yr B.P.), indicating a cooler-than-present adjacent continental environment. Increased C_4 production between 11,000 and 10,000 ^{14}C yr B.P. suggests that the Younger Dryas was a warm interval responding to the diversion of glacial meltwater away from the Mississippi River. With waning meltwater flow, C_4 productivity generally increased throughout the Holocene, culminating in peak warm intervals at ~5000 and 2000 ^{14}C yr B.P. Shifts in the abundances of C_3–C_4 plants through the late Quaternary show no correlation to ecophysiological responses to atmospheric CO_2 concentration.

Key Words: **stable isotopes; C_4 plants; buried soil; glacial meltwater; atmospheric CO_2.**

INTRODUCTION

Differences in quantum yield between C_3 and C_4 species are temperature-dependent and result in strong positive correlations between temperature and the relative productivity of C_4 species (Terri and Stowe, 1976; Boutton *et al.*, 1980; Epstein *et al.*, 1997; Ehleringer *et al.*, 1997; Collatz *et al.*, 1998). These Quantum yield differences also depend on atmospheric CO_2 concentration (pCO_2), which favor C_3 species at higher pCO_2 (Ehleringer *et al.*, 1997; Collatz *et al.*, 1998). Hence, reconstruction of relative C_3–C_4 productivity through time, as identified from shifts in $\delta^{13}C$ values, should enhance understanding of long-term vegetation dynamics in response to past changes in climate and the gas composition of the atmosphere (Cerling *et al.*, 1989; Boutton, 1996; Balesdent and Mariotti, 1996). Because there is little change in the $\delta^{13}C$ of plant tissue as it decomposes and becomes incorporated into the soil organic carbon pool (Melillo *et al.*, 1989; Boutton *et al.*, 1998), the $\delta^{13}C$ of paleosol organic carbon provides a record of the relative productivity of C_3 and C_4 plants that can persist unmodified for millions of years (Cerling *et al.*, 1989).

The purpose of this study is to examine variations in relative C_3–C_4 productivity in south-central Texas of the southern Great Plains during the late Quaternary and to relate those variations to known changes in climate and pCO_2. To accomplish this, we developed a high-resolution paleoenvironmental record based on $\delta^{13}C$ of organic carbon from a continuous alluvial buried soil sequence that spans the past 15,000 ^{14}C yr.

STUDY AREA

The study site (29.5°N, 98.5°W, 160 m elevation) consists of an alluvial buried soil sequence from the Medina River valley in south-central Texas (Fig. 1). The area is in the Southern Great Plains-Gulf Coastal Plain ecotone, located approximately

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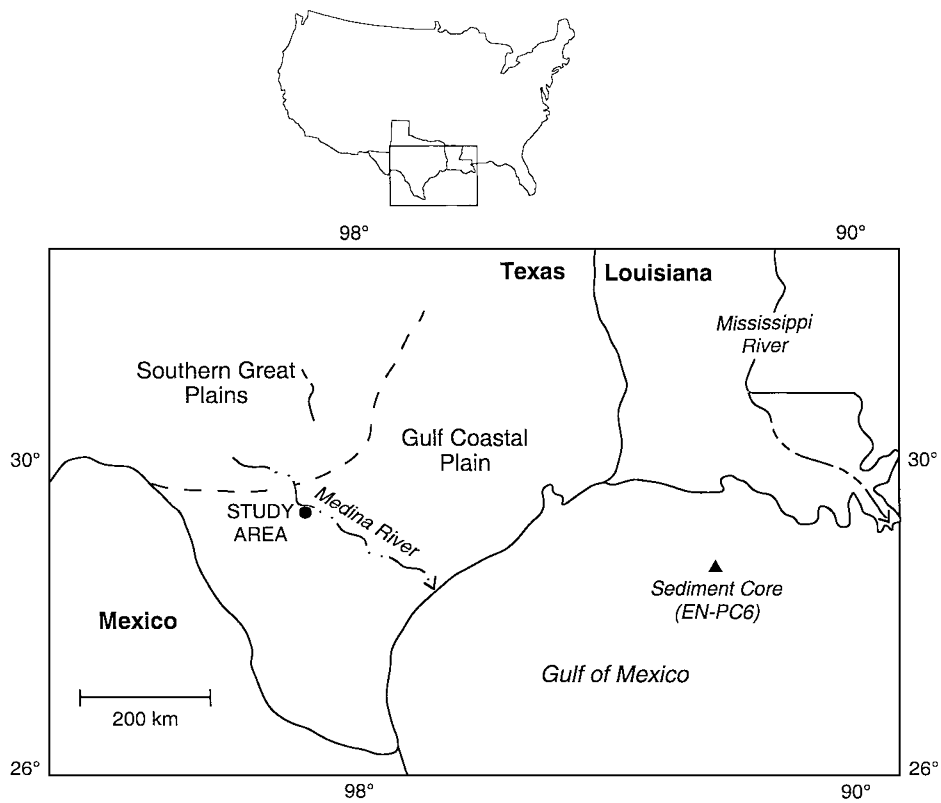

FIG. 1. Location map of the Medina River study area, 15 km south of San Antonio, Texas, showing ecological zones and the location of the Gulf of Mexico sediment core EN-PC6 (Leventer, 1982).

220 km from the Gulf of Mexico (Fig. 1). The modern climate is humid subtropical and influenced strongly by warm, moist air from the Gulf of Mexico, with occasional intrusions of Pacific and polar fronts (Bomar, 1983). Mean annual precipitation and temperature are 75 cm and 21°C, respectively. Modern vegetation is subtropical savanna consisting of a matrix of mid- and tall-grasses with the C_4 photosynthetic pathway and woody plants (*Prosopis glandulosa*, *Juniperus* spp.) of variable density with the C_3 pathway.

The Medina River drainage basin begins approximately 100 km northwest of the study area and covers mainly Cretaceous limestones and marls (Barnes, 1983). Based on field observations, most soils on the uplands are Mollisols and shallow Inceptisols, whereas soils of the floodplains are primarily Mollisols, Inceptisols, and Entisols. Our study focused on the Applewhite terrace adjacent to the Medina River floodplain. Six buried soils and a surface soil were recognized in the nearly 20 m of late Quaternary alluvium (Thoms and Mandel, 1992) (Fig. 2). Stratigraphic relations at the study site show that during the late Quaternary the Medina River never migrated into the vicinity of the Applewhite terrace (Thoms and Mandel, 1992). Consequently, these soils formed in sediments deposited in a slowly aggrading floodbasin setting that contains no erosional unconformities. All buried soils formed from carbonate-rich alluvium with textures consisting mainly of silty clay loam, loam, clay loam, and sandy clay loam. The buried soils have weakly expressed A-Bw and A-Bk horizons (Haplustepts, Ustifluvents) that formed during a few hundred years of pedogenesis prior to burial (Fig. 2). The exception is the Leon Creek paleosol (Haplustoll) that formed during 1000 to 1500 to ^{14}C yr of quasi-landscape stability.

Organic carbon concentrations range from 1.2% to 0.1% throughout the buried soil sequence and systematically decrease with depth in each soil. The organic carbon component is dominantly pedogenic. However, the BC and C horizons in the lower solum may contain a partial detrital organic carbon fraction. The Medina River drainage basin encompasses a relatively uniform ecosystem such that any detrital organic carbon transported into the alluvium is largely derived from eroded upland soils that formed in equilibrium with the same climate as the Medina River alluvial soils. Thus, the pedogenic and detrital organic components should provide a similar record of the paleovegetation.

The calcium carbonate content of detrital alluvium, derived from surrounding Cretaceous bedrock, ranged from approximately 20% to 55% with minor redistribution into secondary carbonate forms. The absence of redoximorphic features indicative of wetness in the buried soil sequence reduces the possibility that riparian vegetation was a factor during landscape evolution.

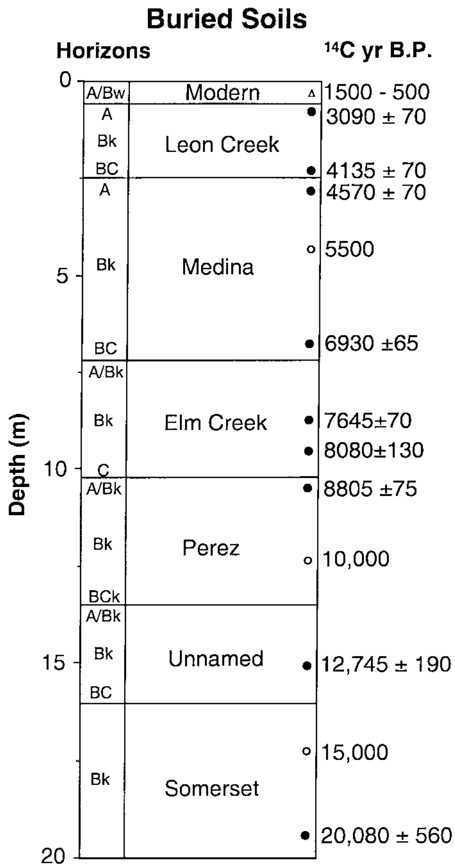

FIG. 2. Continuous stratigraphic column of buried soils from Applewhite terrace alluvium in the study area. Solid circles represent radiocarbon ages, hollow circles are interpolated ages based on rates of deposition, and the hollow triangle is an estimated age based on time-diagnostic artifacts (see Table 1).

METHODS

Fifty-one samples were collected by horizon for carbon isotopic analysis from a vertical column extending continuously through the alluvial buried soil sequence. Carbonate carbon was removed from the samples and $\delta^{13}C_{\text{V-PDB}}$ of bulk soil organic carbon determined in duplicate by methods described previously (Midwood and Boutton, 1998). δ^{13}C values are expressed relative to the V-PDB standard by calibration through NBS-19 (Coplen, 1996). Precision (± 1 SD) is ± 0.2‰ for all analyses.

The relative proportion of buried soil organic carbon derived from C_4 plant sources was estimated from the mass balance equation

$$\delta^{13}C_{soil} = (\delta^{13}C_{C_4})(x) + (\delta^{13}C_{C_3})(1-x),$$

where $\delta^{13}C_{soil}$ is the δ^{13}C of paleosol organic carbon, $\delta^{13}C_{C_4}$ is the average δ^{13}C of C_4 plants (-13 per mil), $\delta^{13}C_{C_3}$ is the average δ^{13}C of C_3 plants (-27 per mil), x is the relative proportion of carbon from C_4 plant sources, and $1 - x$ is the relative proportion of carbon from C_3 plant sources. The proportion of carbon derived from C_3 and C_4 plants should be regarded as estimates because (1) $\delta^{13}C$ values of C_3 and C_4 end members are not known precisely and vary slightly in response to environmental and genetic variation (Farquhar *et al.*, 1989); (2) the δ^{13}C of atmospheric CO_2 has varied ($\sim$1‰) over the past 15,000 ^{14}C yr (Indermuhle *et al.*, 1999); (3) differential decomposition and/or preservation of isotopically distinct plant biochemical fractions (Benner *et al.*, 1987) could potentially influence δ^{13}C of soil organic carbon; and (4) microbial respiration may increase δ^{13}C of residual soil organic carbon by 1‰ (Nadelhoffer and Fry, 1988). Collectively, these potential sources of error are small, and δ^{13}C values of soil organic carbon appear to faithfully record the relative carbon inputs of C_3 and C_4 plants in both modern (Melillo *et al.*, 1989; Boutton, 1996; Boutton *et al.*, 1998; Balesdent and Mariotti, 1996) and ancient (Cerling *et al.*, 1989) soils.

A chronology for the buried soil sequence was established using nine radiocarbon ages and time-diagnostic prehistoric artifacts (Table 1). δ^{13}C values were correlated with specific points in time by assuming constant rates of deposition between successive radiocarbon ages. This approach is reasonable given that (1) the radiocarbon ages were primarily from charcoal; (2) the samples were obtained from a continuum of floodbasin sediments without intervening erosional unconformities; (3) and episodes of pedogenesis were relatively brief.

SOIL C_4 BIOMASS PRODUCTION AND LATE QUATERNARY CLIMATES

δ^{13}C values of soil organic carbon ranged from -25.1‰ to -16.7‰ during the last 15,000 ^{14}C yr (Fig. 3), indicating that plant communities at this site varied from strongly C_3-dominated to strongly C_4-dominated. At present, C_4 species of the North American Great Plains are almost exclusively warm-season grasses of tropical and subtropical origin, with few C_4 dicot species and no C_4 woody plants (Paruelo and Lauenroth, 1996;

TABLE 1
Radiocarbon Ages from Buried Soils in the Medina River Valley Study Area

Buried Soil[a]	^{14}C yr B.P.[b]	Cal yr B.P.[b]	Lab No.	Dated material
Leon Creek	3090 ± 70	3370–3212	Beta 36702	charcoal-hearth
Leon Creek	4135 ± 70	4824–4529	Beta 43330	charcoal-treeburn
Medina	4570 ± 70	5321–5057	Beta 38700	charcoal-treeburn
Medina	6930 ± 65	7779–7644	Beta 47525	charcoal-hearth
Elm Creek	7645 ± 70	8424–8360	Beta 47529	charcoal-hearth
Perez	8080 ± 130	9204–8676	Beta 44386	charcoal-hearth
Perez	8805 ± 75	9906–9653	Beta 47527	charcoal-hearth
PS7	12,745 ± 190	15,360–14,686	Beta 47528	charcoal-dispersed
Somerset	20,080 ± 560	—	Beta 47563	humate-bulk soil

[a] See Figure 2 for stratigraphic relations.

[b] Radiocarbon ages (^{14}C yr B.P.) and calendar years (cal yr B.P.) are expressed in years before A.D. 1950. ^{14}C ages were converted to calibrated yr by CALIB (Stuiver and Reimer, 1993) after correcting for variations in δ^{13}C. The age range represents the 95% confidence interval based on the 1-σ error limits of the ^{14}C age. For details of other ^{14}C ages from the area, see Thoms and Mandel (1992).

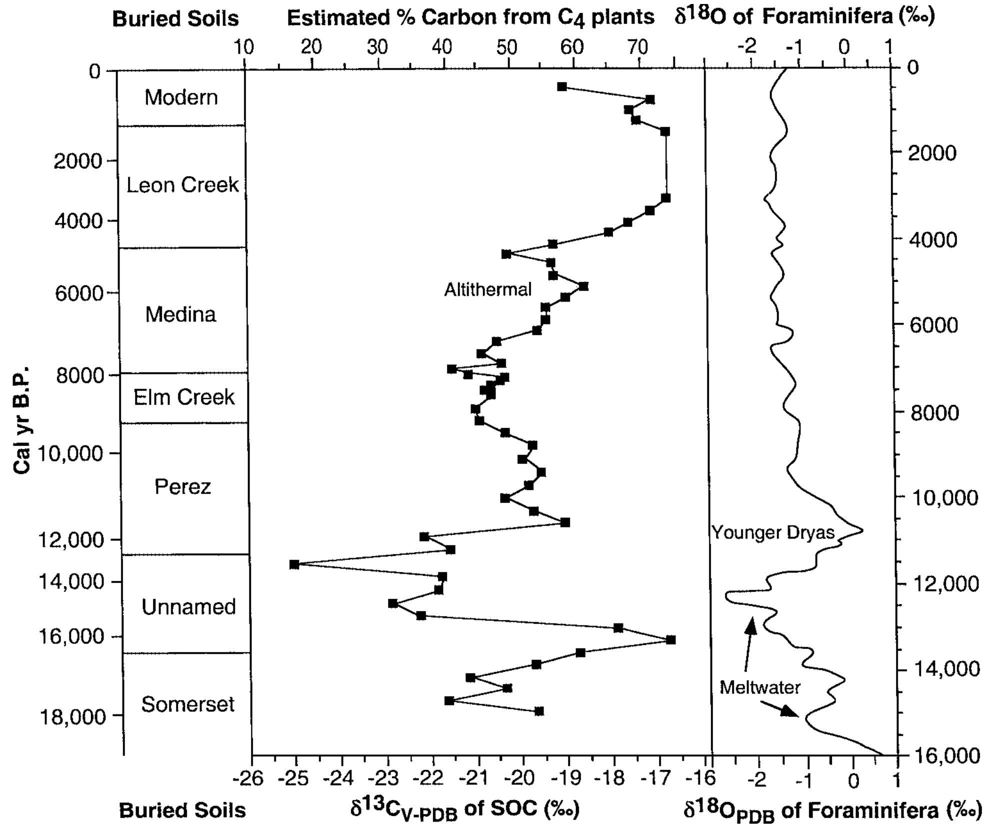

FIG. 3. $\delta^{13}C_{V\text{-}PDB}$ values of soil organic carbon (SOC) in the Medina River buried soil sequence. Values are shown with respect to buried soil, calendar years (left axis), radiocarbon years (right axis), and $\delta^{18}O_{PDB}$ values of foraminifera in the Gulf of Mexico (values from Leventer *et al.*, 1982, for core EN32-PC6 [see Fig. 1], with chronology modified by Flower and Kennett, 1990). The proportion of organic carbon derived from C_4 plant production (top axis) was estimated by mass balance calculations.

Ehleringer *et al.*, 1997). The C_4 plant biomass typically comprises more than 30% of soil organic carbon thoughout the buried soil sequence (Fig. 3). Because C_4 grasses are relatively shade-intolerant (Ehleringer *et al.*, 1997; Collatz *et al.*, 1998), the study area probably was grassland or open savanna, a conclusion that is consistent with late Quaternary pollen records from the southern Great Plains (Hall and Valastro, 1995). The strong dependence of C_4 grasses on growing season soil moisture (Paruelo and Lauenroth, 1996; Ehleringer *et al.*, 1997; Collatz *et al.*, 1998) further implies that a significant proportion of annual precipitation occurred during or just prior to the warmest portions of the growing season at this site. The C_3 component of the vegetation in the study area is more difficult to define, but it could potentially consist of cool-season grasses, herbaceous dicots, and/or trees and shrubs.

From 15,000 to 10,000 ^{14}C yr B.P., $\delta^{13}C$ values of soil organic carbon show large and rapid fluctuations as summer solar insolation began to increase following the last glacial maximum (COHMAP, 1988) (Fig. 3). Distinct periods of low relative C_4 productivity occurred between 15,500 and 14,000 ^{14}C yr B.P. and between 13,000 and 11,000 yr ^{14}C B.P., which correlates strongly with two well-documented episodes of glacial meltwater flux from the Laurentide ice sheet into the Gulf of Mexico via the Mississippi River. These meltwater spikes were recorded as negative $\delta^{18}O$ anomalies (Fig. 3) in foraminifera from Gulf sediments (Leventer *et al.*, 1982; Spero and Williams, 1990; Kennett *et al.*, 1985), as changes in seawater salinity (Leventer *et al.*, 1982; Kennett *et al.*, 1985; Spero and Williams, 1990), as sediment pulses into the Gulf from continental erosion (Brown and Kennett, 1998), and for the second spike as a significant rise in sea level (Fairbanks, 1989). It appears that cold water inputs into the Gulf of Mexico resulted in cooler climatic conditions in the adjacent terrestrial environment, thereby reducing the relative productivity of C_4 grasses during meltwater episodes. This probably also decreased the land–sea temperature differential and the summer monsoonal rainfall.

The $\delta^{13}C$ values of buried soil organic carbon between 15,500 and 14,000 ^{14}C yr B.P. correlate with isotopic values from an alluvial deposit dating to 15,000 ^{14}C yr B.P. in central Texas (Nordt *et al.*, 1994). Noble gas concentrations in groundwater (Stute *et al.*, 1992) from south Texas and fossil pollen from east-central Texas (Bryant and Holloway, 1985; Bousman, 1998) substantiate these results and suggest that temperatures were as much as 5°C cooler than present.

Between the two late Pleistocene meltwater pulses, soil $\delta^{13}C$ peaked at −16.8‰ approximately 13,500 ^{14}C yr B.P., showing that relative C_4 productivity was higher than present. In addition, $\delta^{18}O$ and $\delta^{13}C$ of lacustrine $CaCO_3$ at a site in north-central Texas were more enriched at this time (Humprhey and Ferring, 1994), implying warmer temperatures and significant C_4 productivity.

Between 13,000 to 11,000 ^{14}C yr B.P., relative C_4 productivity decreased significantly, reflecting the arrival of cooler conditions in response to the second and largest meltwater pulse into the Gulf of Mexico (Leventer *et al.*, 1982; Spero and Williams, 1990). Regional continental records based on pollen frequencies (Bryant and Holloway, 1985; Bousman, 1998), $\delta^{18}O$ of lacustrine $CaCO_3$ (Humphrey and Ferring, 1994), and fossil vertebrate remains (Toomey *et al.*, 1993) indicate that between 13,000 and 11,000 ^{14}C yr B.P., temperatures were cooler and drier than the present. In addition, general circulation models suggest that mean annual temperatures in the adjacent Gulf Coastal Plain region were at least 2°C cooler and precipitation slightly lower than present as a consequence of reduced water temperatures in the Gulf of Mexico (Overpeck *et al.*, 1989; Maasch and Oglesby, 1990).

Between 11,000 and 10,000 ^{14}C yr B.P., $\delta^{13}C$ values of soil organic carbon increased, indicating another increase in relative C_4 productivity. This increase corresponds precisely with a significant reduction in meltwater flow into the Gulf of Mexico (Broeker *et al.*, 1989; Spero and Williams, 1990; Teller, 1990) and perhaps to increased summer monsoonal precipitation and temperatures (COHMAP, 1988). During this time, retreat of the Laurentide ice sheet exposed the St. Lawrence River drainage, diverting meltwater into the North Atlantic rather than the Gulf of Mexico. $\delta^{18}O$ and $\delta^{13}C$ values of pedogenic $CaCO_3$ indicate higher temperatures and high relative C_4 productivity in north-central Texas (Humphrey and Ferring, 1994), whereas fossil vertebrates (Toomey *et al.*, 1993) and fossil pollen (Bryant and Holloway, 1985; Bousman, 1998) indicate higher precipitation in central Texas. Further, Holliday (2000) documents high C_4 plant production and temperatures between 11,000 and 10,000 ^{14}C B.P. on the southern Great Plains that correlates with episodic drought as indicated by the emergence of upland eolian deposits. All evidence points to increasing temperatures in the region between 11,000 and 10,000 ^{14}C B.P., and regardless of the periodicity of drought, summer rains were sufficient for the flourishing of C_4 plants. Cool and dry conditions normally associated with the Younger Dryas (∼12,500–11,500 cal yr B.P. and ∼11,000–10,000 ^{14}C yr B.P.) in northerly latitudes were clearly absent in the Gulf of Mexico and adjacent terrestrial environment.

Between 10,000 and 9000 ^{14}C yr B.P., $\delta^{13}C$ values of soil organic carbon decreased only slightly, indicating similar C_4 production and climate as during the Younger Dryas. At 10,000 yr B.P., several studies suggest that cold glacial meltwater was routed back to the Mississippi River and Gulf of Mexico in response to the last advance of the Laurentide ice sheet (Broeker *et al.*, 1989; Flower and Kennett, 1990; Spero and Williams, 1990; Teller, 1990). New evidence indicates that glacial meltwater was routed to the Arctic Ocean after the Younger Dryas, never to return to the Gulf of Mexico (Smith and Fisher, 1993; Marchitto and Wei, 1995). Our isotopic data supports the latter interpretation in that we show no negative $\delta^{13}C$ anomalies indicative of cool conditions between 10,000 and 9000 ^{14}C yr B.P.

Soil organic carbon $\delta^{13}C$ values decreased appreciably at 7000 ^{14}C yr B.P., evidence for a cooling trend. The interval from 8000 to 7000 ^{14}C yr B.P. (9000–8000 cal yr B.P.) has recently been recognized as the most prominent and globally widespread cold period to have occurred in the past 10,000 ^{14}C yr (Hu *et al.*, 1999; Barber *et al.*, 1999). This event may have been caused by changes in atmospheric and oceanic circulation resulting from the final breakup of the Laurentide ice sheet and to the subsequent drainage of large glacial lakes into the North Atlantic. This interval also corresponds to the termination of the last global sea-level rise documented in the western Atlantic (Fairbanks, 1989).

$\delta^{13}C$ values of soil organic carbon increased again at 5000 ^{14}C yr B.P., indicating more relative C_4 productivity compared to the early Holocene. This warm, dry interval correlates with the well-known Altithermal of the North American Great Plains and is also recorded in the isotopic composition of organic and inorganic carbon (Dorale *et al.*, 1992; Kelly *et al.*, 1993; Humphrey and Ferring, 1994; Boutton *et al.*, 1994; Nordt *et al.*, 1994; Fredlund and Tieszen, 1997; Baker *et al.*, 1998), in fossil pollen frequencies (Winkler *et al.*, 1986; Bousman, 1998), in faunal reconstructions (Toomey *et al.*, 1993), in increased eolian activity (Holliday, 1995; Forman *et al.*, 1995), and in alluvial stratigraphic sequences (Mandel, 1995). Global circulation models indicate that at this time, regional temperatures were approximately 2°C warmer than present because of waning monsoonal summer precipitation and an increase in dry, westerly airflow (COHMAP, 1988).

For a brief time after 5000 ^{14}C yr B.P., $\delta^{13}C$ values sharply decreased, indicating reduced relative C_4 productivity and temperatures compared to the Altithermal. $\delta^{13}C$ values then increased between 3000 to 1500 ^{14}C yr B.P., pointing to another period of high relative C_4 productivity and temperature. Other $\delta^{13}C$ records based on buried soils in north-central (Humphrey and Ferring, 1994) and central (Nordt *et al.*, 1994; Boutton *et al.*, 1994) Texas suggest a relatively cool interval between approximately 4000 to 2500 ^{14}C yr B.P., followed by a warm interval with high relative C_4 productivity from gpproximately 2500 to 1000 ^{14}C yr B.P. The occurrence of a cool interval in our study area immediately following the Altithermal is supported by fossil pollen data showing an increase in tree cover beginning at 5000 ^{14}C yr B.P. and continuing to at least 3000 ^{14}C yr B.P. (Bousman, 1998). The reasons for isotopic changes indicative of warmer conditions in the late Holocene may be related to eastward shifts of the Bermuda High in the Atlantic Ocean, consequently reducing the flow of warm, moist Gulf air into the region (Forman *et al.*, 1995).

Decreasing $\delta^{13}C$ values during formation of the surface soil suggest that the climate was becoming slightly cooler between

1500 and 500 ^{14}C yr B.P., although conditions were still relatively warm. Even though minor historic disturbance of the surface soil may have occurred, the near-surface $\delta^{13}C$ value is almost identical to values recorded during soil formation just prior to historic times in a central Texas locality (Nordt *et al.*, 1994).

C_4 PLANTS AND ATMOSPHERIC CO_2

The increase in pCO_2 from 235 to 285 ppmV that occurred during the past 15,000 ^{14}C yr (Indermuhle *et al.*, 1999) may have increased both the productivity and water-use efficiency of C_3 plants by 25–50% (Polley *et al.*, 1993). This potential improvement in C_3 plant carbon and water relations has led to the suggestion that C_3 species may have become more competitive relative to C_4 species during the Holocene (Ehleringer *et al.*, 1997; Collatz *et al.*, 1998). Indeed, C_4-to-C_3 vegetation shifts near the Pleistocene–Holocene boundary have been documented in desert grassland in southwestern North America (Cole and Monger, 1994; Liu *et al.*, 1996). Results from our study and others throughout the North American Great Plains indicate that relative productivity of C_3 plants in this region generally decreased while that of C_4 plants increased during the past 15,000 ^{14}C yr. Furthermore, recent field studies show that relative C_3–C_4 productivity in native tallgrass prairie in Kansas remained unchanged following exposure to approximately 700 ppmV CO_2 for 8 years (Owensby *et al.*, 1999). Collectively, these studies suggest that variations in pCO_2 over the range from 235 to 700 ppmV exert little control over relative C_3–C_4 productivity in the North American Great Plains.

CONCLUSIONS

Based on relative C_4 plant productivity from a late Quaternary buried soil sequence in south-central Texas, we demonstrate strong coupling between glacial meltwater pulses and adjacent continental climates in the late Pleistocene and a decoupling in the Holocene as glacial meltwater inputs subsided. The Younger Dryas is recorded as a time of increasing C_4 plant production and temperature with enhanced summer monsoonal rainfall. Two periods of enhanced warming occurred in the Holocene as interpreted from increased C_4 plant production. In general, C_4 plant productivity increased during the Holocene, even in association with rising atmospheric CO_2.

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