Grassland expansion as an instrument of hydrologic change in Neogene western North America

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A B S T R A C T

The evapotranspiration (ET) flux accounts for approximately two thirds of terrestrial precipitation worldwide, and in grassland regions ET is equivalent in magnitude to precipitation. Regional contributions to the terrestrial hydrologic budget, however, have been far from constant in the past as distribution of vegetation changed dramatically. The rise of grass-dominated ecosystems is one of the most profound paleoecological changes in the Cenozoic. Why then, would grassland expansion not feature prominently in the record of Neogene hydrologic change? Despite numerous stable isotope paleoenvironmental studies in Neogene North America, the contributions of land cover change have been largely ignored. We present a compilation of 16 oxygen isotope studies of pedogenic carbonate and smectite from western North America, including 4 new records. Nearly all records from California, the Basin and Range, the Rocky Mountains and the Great Plains show increases in $\delta^{18}O$ on the order of 2–6‰. In order to assess the role of ET in the hydrologic cycle, we developed an isotopic water vapor transport model wherein we manipulated ET parameters along a specified air mass trajectory. Grasslands lead to $\delta^{18}O$ of precipitation ($\delta^{18}O_p$) values that are up to 5‰ greater than broadleaf and needleleaf vegetation at inland study sites. These results demonstrate that changes in vegetation played a critical role in establishing the modern hydrologic regime in western North America. We suggest that this isotopic increase is due to three primary reasons: 1) Increased evaporation and transpiration fluxes in grassland regions affect water balance, 2) Shallower rooting depths of grasses lead to the transpiration of soil water enriched in ^{18}O due to evaporation, and 3) Grasslands transpire ^{18}O-rich waters during a shorter, more punctuated growing season. We argue that the observed isotope signals are indicative of a feedback mechanism wherein grasslands not only respond to regional and global climatic trends, but also act as a driver of hydrologic change. By enhancing seasonality and aridity, grasslands transmit hydrologic disturbances downstream, engineering climatic conditions favorable for their expansion.

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1. Introduction

The expansion of grass-dominated ecosystems is one of the most prominent ecological changes of the Late Cenozoic. Paleobotanical, paleofaunal and stable isotope studies have documented the rapid rise of C_4 grasslands at the expense of forests in the Middle to Late Miocene (Axelrod, 1985; Cerling et al., 1993; Latorre et al., 1997; Jacobs et al., 1999). These studies have interpreted this ecological change as a result of global cooling and aridification driven by decreasing atmospheric pCO_2 (Cerling et al., 1993; Jacobs et al., 1999; Fox and Koch, 2003). Recent alkenone-based pCO_2 estimates, however, show that carbon dioxide concentrations in the atmosphere were constant through the Miocene (Pagani et al., 2009) whereas terrestrial proxies permit a 200–300 ppm increase during the Middle Miocene (Beerling and Royer, 2011). Pagani et al. (2009) proposed a negative feedback in which photorespiration reduces terrestrial plant productivity, thereby reducing silicate chemical weathering associated with the biosphere and buffering atmospheric pCO_2. Recent studies have not found pCO_2 decrease a necessary step to C_4 grassland dominance and instead support rise of strong seasonality patterns, leading to the rise of a fire climate advantageous to grasslands (Keeley and Rundel, 2005; Beerling and Osborne, 2006; Staver et al., 2011; Hirota et al., 2011).

Interactions between grasslands and the hydrologic cycle have profound implications for the evolution of the Earth's climate system. The C_4 photosynthetic pathway decreases carbon loss to photorespiration by internally concentrating CO_2 and fixing carbon in the bundle sheath as well as mesophyll cells. This mechanism allows C_4 plants to reduce stomatal opening, leading to increased

water use efficiency associated with evapotranspiration. As a result, C_4 plants have an evolutionary advantage over C_3 vegetation in seasonal, warm, arid and low-pCO$_2$ environments (Ehleringer et al., 1997; Jacobs et al., 1999). The distribution, diversity and evolution of such plants is therefore coupled to the climate system.

Grassland expansion has been proposed as a driver of global-scale paleoenvironmental change via its roles in carbon storage, phosphorus and nitrogen fixation, albedo change, dehumidification, adaptability to wildfire, and herbivore coevolution (Retallack, 2001). In fulfilling these roles, the rapid expansion of C_4 vegetation is intimately linked to the establishment of the modern rainout, vapor recycling and seasonality patterns in Neogene western North America (Jacobs et al., 1999). Stable isotope studies that evaluate paleoelevation, paleoclimate, and paleoecology in western North America have largely disregarded grasslands as a major driver of hydrologic change, however. Most lacustrine, pedogenic and authigenic oxygen isotope records from western North America are consistent with an increase in δ^{18}O of surface waters from the Middle Miocene to the Quaternary. These increases in δ^{18}O have been interpreted as a result of a reduction of surface elevation of the Sierra Nevada and Basin and Range (Poage and Chamberlain, 2002; Horton et al., 2004; Crowley et al., 2008; Mulch et al., 2008) or deeper northward penetration of the North American Monsoon (NAM) as a result of downdrop of the Basin and Range (Horton and Chamberlain, 2006). Moreover, while carbon isotopes of paleosols in western North America feature prominently in paleoecological reconstructions, corresponding oxygen isotope records have been underutilized. Such studies have typically offered short interpretations of oxygen isotope shifts due to changes in regional temperature, moisture source, precipitation amount, or evaporative ^{18}O enrichment (Quade et al., 1994; Fox and Koch, 2004). As oxygen and hydrogen isotope compositions of precipitation (δ^{18}O$_p$, δD$_p$) are intimately linked to the hydrologic cycle, ecological changes must produce corresponding changes in δ^{18}O$_p$ and δD$_p$ on a continental scale.

Here, we test a mechanism in which grasslands act as a biological force that drives Neogene hydrologic change in western North America. First, we provide Neogene stable isotope data from pedogenic carbonate in several basins of western North America (Fish Lake Valley, NV, Ibapah Badlands, UT, North and Middle Parks Basins, CO, and a composite section in Nebraska) spanning the Neogene. In order to eliminate potential reduction of surface elevation in the Basin and Range and other topographic effects as a possible explanation (Horton and Chamberlain, 2006), we include samples from outside the Basin and Range province such as Nebraska and Colorado. Second, we combine these new stable isotope data with published work to produce a spatially extensive compilation of the δ^{18}O of Neogene precipitation (Fig. 1). Finally, we develop an isotopic vapor transport model to determine how the expansion of grasslands would have changed δ^{18}O$_p$. Nearly all of the basins we studied underwent ~2–6‰ increases in δ^{18}O during the Neogene. Our conceptual model demonstrates that grassland expansion can account for a substantial portion of the observed changes in δ^{18}O$_p$ and further suggests that grassland expansion played a major role in Neogene hydrologic change in western North America.

2. Stable isotope records of paleoenvironmental change

2.1. Stable isotope methods

In 2009 and 2010, we collected samples of pedogenic carbonate in western North America. Fifty-five carbonate samples were prepared by manually drilling a powder from the sample. Weighed aliquots of the sample powder were loaded into sealed Exetainer vials and flush filled with helium gas. Using a Thermo
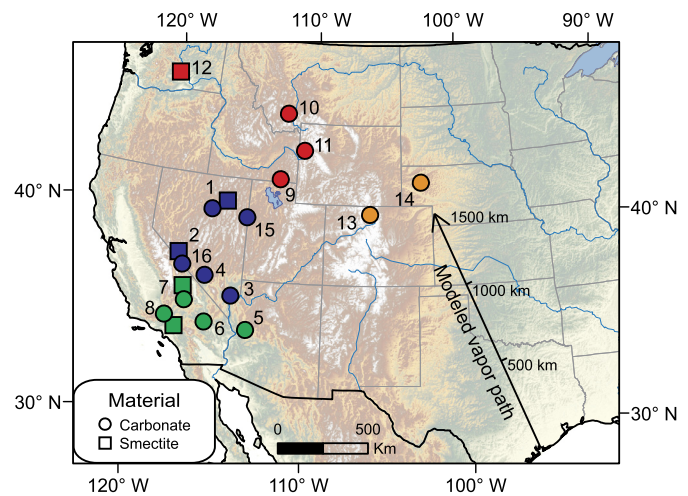
Fig. 1. Index map of stable isotope studies included in this compilation. The transect used in our simulations of moisture transport is included for reference. The full list of studies is included in Supplemental Table 2. Red: Pacific Northwest; Blue: Basin and Range; Green: South and West of Basin and Range; Orange: Great Plains and Rocky Mountains.

Finnigan GasBench, the carbonate component of the sample was reacted with phosphoric acid at 72 °C, then introduced into a Thermo Finnigan Delta^{plus} XL mass spectrometer and measured under continuous flow conditions in the Stable Isotope Biogeochemistry Laboratory at Stanford University. Repeated analyses of carbonate standards have shown the precision of this method to be <0.2‰ for both δ^{18}O and δ^{13}C. Finally, we incorporated 12 additional published δ^{18}O records from sedimentary basins covering a spatially and temporally extensive portion of Neogene western North America.

2.2. Results of isotope studies

We collected stable isotope data from four basins in western North America: 1) the Miocene Troublesome, North Park and Browns Park Formations in Middle and North Park Basins, CO (Beekly, 1915; Montagne and Barnes, 1957; Izett, 1968; Izett and Barclay, 1973; Montagne, 1991); 2) the Miocene Arikaree and Hemingford groups, the Pliocene Ogallala group, and several ashes from major Pliocene and Pleistocene eruptions in western Nebraska (Swineford et al., 1955; Stout et al., 1971; Boellstorff, 1976; Swinehart et al., 1985; Diffendal, 1995); 3) the Middle to Late Miocene Salt Lake Formation in the Ibapah Badlands, UT (Heylmun, 1965; Perkins et al., 1998; Smith and Nash, 1976); and 4) Miocene, Pliocene and Pleistocene sediments in Willow Wash, Cave Spring Wash, and Horse Thief Canyon in Fish Lake Valley, NV (Reheis and Sawyer, 1997; Reheis and Block, 2007).

The δ^{18}O values of pedogenic carbonate from all records increase from the Middle Miocene to the Quaternary (Fig. 2, Supplemental Table 1). In western Nebraska, δ^{18}O values increase by approximately 6‰ from ~9 to 1 Ma. In northern Colorado, δ^{18}O increases by 1–2‰ from 17 to 8 Ma. Sections from the Ibapah Badlands (UT) and Fish Lake Valley (NV) show similar changes: δ^{18}O values of carbonates increase by ~3‰ from 12 to 9 Ma in the Ibapah Badlands and by approximately 3‰ over the last 8 Ma in Fish Lake Valley. The δ^{13}C values of carbonates in each of the four basins shows no significant trends (Fig. 2, Supplemental Table 1). In northern Colorado, δ^{13}C values center around −6‰ with a positive excursion at approximately 16 Ma. In Nebraska, δ^{13}C values cluster around −7‰. In the Ibapah Badlands and Fish Lake Valley, δ^{13}C values decrease with age, in the opposite manner as δ^{18}O.
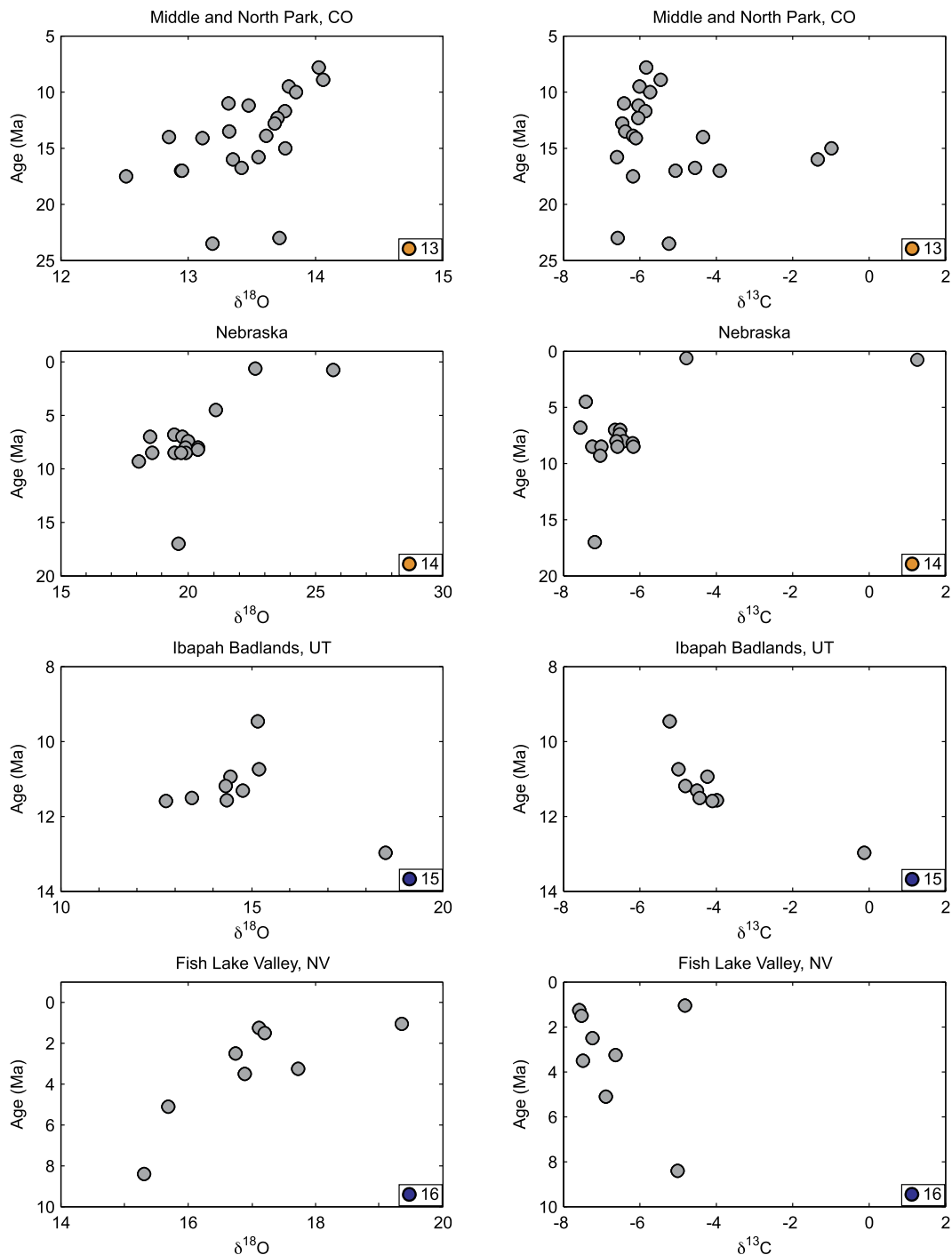
Fig. 2. Pedogenic carbonate isotope records of this study. Insets indicate location as shown on index map.

2.3. Compilation of isotope records

In order to document the broader context of Neogene hydrologic change, we combined our new data with published records to produce a spatially and temporally extensive compilation (Supplemental Table 2). Nearly all isotope records increase in $\delta^{18}O$ since the Middle Miocene (Supplemental Fig. 1). In the Rocky Mountains near Jackson, Wyoming, the $\delta^{18}O$ of paleosol carbonate increases by 9‰ between 14 and 4 Ma (Chamberlain et al., 2012). In the Basin and Range of Nevada and California all records show increasing $\delta^{18}O$ with decreasing age. Specifically, in the Elko Basin (NV), $\delta^{18}O$ of paleosol carbonate increases by 4‰ between 13 and 2 Ma (Horton et al., 2004). Similarly, $\delta^{18}O$ values of paleosol carbonate

and smectite from weathered ashes increase by 7‰ in Death Valley (CA) from 23 to 5 Ma, by 3–6‰ in the El Paso Basin (CA) from 13 to 7 Ma, by 5‰ in Lake Mead (NV) from 8 to 5 Ma, by 1–2‰ in the Rainbow Basin (CA) from 20 to 2 Ma and by 4‰ in western Arizona from 12 to 2 Ma (Poage and Chamberlain, 2002; Horton and Chamberlain, 2006). In the interior of the western Basin and Range, smectite and carbonate increase by 1 to 5‰ from 12 to 2 Ma (Poage and Chamberlain, 2002).

The area immediately east of the Cascades is one notable exception to this increasing trend in $\delta^{18}O$ since the Miocene. In eastern Oregon and Washington, the $\delta^{18}O$ values of equid teeth and smectite decrease by 3 to 5‰ since the Middle Miocene (Kohn et al., 2002; Takeuchi and Larson, 2005; Takeuchi et al., 2010). Similarly,
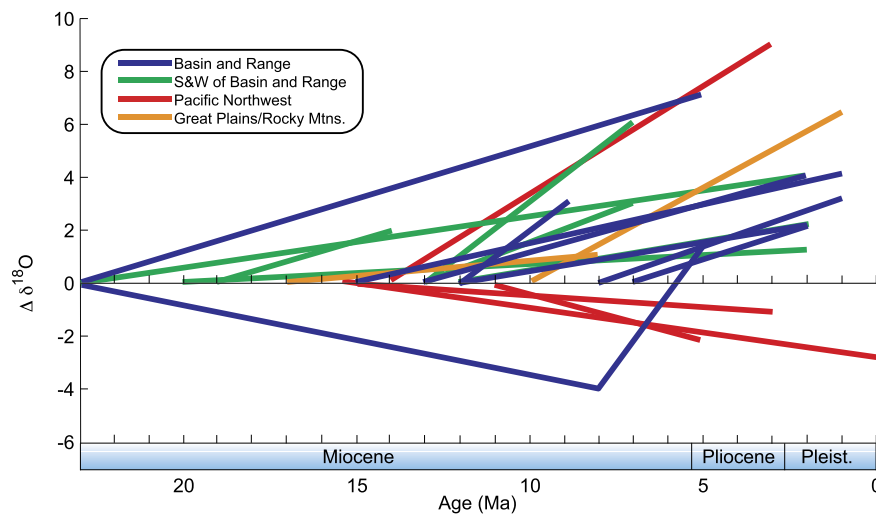
Fig. 3. Plot of change in $\delta^{18}O$ in published and new Neogene sedimentary basins. All records outside the Pacific Northwest increase in $\delta^{18}O$ during the Neogene.

$\delta^{18}O$ values of paleosol carbonate decrease by 2‰ in the Bannock Basin (ID) from 11 to 5 Ma and by 1‰ in the Sage Creek Basin (MT) from 15 to 3 Ma (Chamberlain et al., 2012). These decreases in $\delta^{18}O$ most likely result from progressive uplift of the Cascades (Kohn et al., 2002; Takeuchi and Larson, 2005) and/or drainage reorganization associated with migration of the Yellowstone Hotspot (Chamberlain et al., 2012). For this reason, we exclude these isotope records in our larger-scale analysis.

3. Interpretation

3.1. Interpretation of isotope records

One of the most striking features of this compilation is the observation that $\delta^{18}O$ values of surface waters increase from the Middle Miocene to Quaternary in many parts of western North America (Fig. 3). Previous studies working with more limited datasets have argued that this increase may be due to: 1) Reduction of Sierra Nevada surface elevation (Poage and Chamberlain, 2002) and/or 2) Increased influence of the North American Monsoon that brought ^{18}O-enriched summer southerly precipitation further north as Basin and Range topography was reduced through extension (Horton and Chamberlain, 2006). Both studies noted that some of the increase results from a change in the $\delta^{18}O$ of the oceans during ice sheet growth. This effect, however, is relatively small and accounts for less than 1.0‰ of the enrichment in ^{18}O over the course of the entire Cenozoic (Zachos et al., 2001). The ice volume effect would be even less during Neogene time as several major glaciations such as the Oi-1 and Mi-1 occurred earlier.

We agree with the above conclusions that neither global cooling nor ice sheet growth can account for the increase in $\delta^{18}O$ since the Middle Miocene. We reject the early conclusions that a lowering of surface elevation and increased influence of the NAM caused the increases in $\delta^{18}O$, however. Our reasoning is as follows. First, there is no compelling geologic or isotope evidence that the surface elevation of the Sierra Nevada has decreased since the Middle Miocene. In contrast, studies argue that the Sierra Nevada has either maintained or increased in elevation since then (Jones et al., 2004; Le Pourhiet et al., 2006; Mulch et al., 2008). Second and more importantly, the $\delta^{18}O$ values from the Middle Miocene to Quaternary in the Rocky Mountain foreland to the east show a similar positive trend to those in the Basin and Range Province. If we assume that the positive increase in $\delta^{18}O_p$ values results from the same processes throughout western North America, this observation is inconsistent with the idea

that reduced surface elevation in the Basin and Range and increased penetration of the NAM were the unique drivers of $\delta^{18}O_p$ change. The foreland basins of the Rocky Mountains have remained at nearly constant elevation since the Middle Miocene. Third, it is unlikely that the NAM has increased in intensity since the warm Middle Miocene. The precipitation regime of western North America is controlled by the competing effects of winter moisture derived from the Pacific and Arctic and summer moisture from the Gulfs of California and Mexico (Bryson and Hare, 1974). These air masses are isotopically distinct, with winter moisture sources depleted in ^{18}O relative to summer moisture sources (Friedman et al., 2002). During warm times in the past the NAM has been more intense, delivering ^{18}O-enriched summer moisture from the south (Sjostrom et al., 2004; Fricke et al., 2010). Therefore, we would expect that global cooling since the Middle Miocene Climatic Optimum (MMCO) should have decreased the intensity of the NAM. Instead, isotope records show the opposite trend, becoming enriched in ^{18}O in the Quaternary relative to the Middle Miocene. Moreover, changes in amount and seasonality of precipitation leading to this isotope pattern are unreasonable, as they require a stronger influence of winter moisture when western North America was warmer than it is today.

Changes in local temperature do not account for the observed $\delta^{18}O$ enrichment trend for several reasons. First, temperature effects are small in comparison with other causes of oxygen isotope change. For example, the combined temperature effects of condensation and calcite–water fractionation are only ±0.35‰ per °C (Rozanski et al., 1993; Kim and O'Neil, 1997). Second, temperature decreases since the MMCO would be associated with decreases in carbonate $\delta^{18}O$ values due to decreased isotope fractionation during condensation and mineral precipitation, which is opposite of the observed trends. Furthermore, decreasing global temperatures are associated with an increase in the isotopic lapse rate of water vapor in the troposphere, leading to lower $\delta^{18}O_p$ values, particularly over the North American Cordillera and other orogens (Poulsen and Jeffery, 2011).

We argue that the positive trend in $\delta^{18}O_p$ is the result of the well-documented increases in: 1) Continental aridity and 2) The expansion of grasslands since the Middle Miocene (Axelrod, 1985; Jacobs et al., 1999). Fossil floras and global climate modeling approaches indicate summer-wet conditions at least for southwestern North America in the Middle Miocene followed by increased aridity into the Late Miocene and Pliocene (Axelrod, 1985; Axelrod and Schorn, 1994; Lyle et al., 2008; Herold et al., 2011). Aridity and increased evaporation leads to the ^{18}O enrichment of

residual soil water, which is recorded in soil carbonate and authi-genic smectite. Increased aridity cannot be solely responsible for the changes in $\delta^{18}O_p$ seen in Neogene North America, however. Fossil ungulate and equid tooth enamel show an increase in $\delta^{18}O$ (Crowley et al., 2008). Mammals differ in their sensitivity to en-vironmental aridity. Differences in behavior and physiology such as panting vs. sweating, grazing vs. browsing, and the amount of surface vs. leaf water ingested can lead to changes in the isotopic composition of bioapatite (Levin et al., 2006). Equids such as those studied by Crowley et al. (2008), however, are obligate drinkers. It is estimated that surface water composition contributes to over 70% of the $\delta^{18}O$ signal in equids (Delgado Huertas et al., 1995). Since it is implausible to assume that the ungulates and equids sampled would exclusively drink from evaporative surface waters, we suggest that the isotopic increases reflect changes in vapor re-cycling upstream from the sampled site. In the Great Plains, equid tooth enamel decreases in $\delta^{18}O$ (Passey et al., 2002). Due to the large amount of scatter in mammalian fossil isotope records as well as the potential physiological, behavioral and evolutionary complications mentioned above, we have chosen to limit this study to oxygen isotope records from paleosols.

3.2. Grasslands as a driver of changes in continental water cycling

The $\delta^{18}O$ and δD values of precipitation, in part, reflect va-por recycling as a result of evaporation and transpiration (Kendall and Coplen, 2001; Dutton et al., 2005; Liu et al., 2010). In gen-eral, $\delta^{18}O_p$ and δD_p values will be higher under conditions of high ET along the moisture track than situations where little or no vapor recycling occurs. Reduced distillation of ^{18}O and D along moisture tracks is readily observed in the modern precipitation within the Basin and Range (Ingraham and Taylor, 1991) and across central and eastern North America (Kendall and Coplen, 2001; Dutton et al., 2005; Liu et al., 2010). Below we elaborate on some of the more important mechanisms of $\delta^{18}O$ change that may have been operating during expansion of grasslands.

3.2.1. Change from open-system Rayleigh distillation to closed-system behavior as water vapor is increasingly recycled by transpiration of grasses

As an air mass moves inland, it will undergo Rayleigh distil-lation, in which ^{18}O and D will be preferentially concentrated in the liquid phase during condensation. Without vapor recycling, this process behaves as an open system, with $\delta^{18}O_p$ decreasing dramat-ically as the air mass becomes progressively depleted in moisture. Evaporation and transpiration from the land surface returns wa-ter vapor back to the atmosphere, affecting overall water balance, and decreasing the magnitude of Rayleigh distillation along the air mass trajectory (Gat and Matsui, 1991). Vapor recycling and clo-sure of the hydrologic system are important features of both the early Cenozoic and the modern hydrologic regime in western North America, particularly in the Basin and Range where the hydrologic balance changes from open west of the Sierra Nevada to closed east of the Sierran crest (Ingraham and Taylor, 1991; Mix et al., 2011). Such a change to more closed hydrologic systems can be induced by vegetation changes. Eddy covariance data from a CO grassland and an NC forest show that grasses transpire more water relative to precipitation than forests (Table 1) (Ferretti et al., 2003; Oishi et al., 2008). Though transpiration itself does not involve an isotopic fractionation step, it will nonetheless enrich atmospheric water in ^{18}O by affecting overall water balance. Thus, a change in plant functional types from forests/shrubs to grasslands would in-duce an increase in the oxygen isotope composition of water vapor.

Table 1
Model variables, evaporation and transpiration fluxes for different vegetation types, and fractionation factors used in our moisture transport model are listed along with the appropriate references.

Moisture transport variables and inputs			
Variable		Source	
Precipitable water (w)		NCEP reanalysis (Kalnay et al., 1996)	
Advection velocity (v)		NCEP reanalysis (Kalnay et al., 1996)	
Precipitation (P)		NCEP reanalysis (Kalnay et al., 1996)	
Surface temperature (T_s)		NCEP reanalysis (Kalnay et al., 1996)	
850 mb temperature (T_{850})		NCEP reanalysis (Kalnay et al., 1996)	
Relative humidity (RH)		NCEP reanalysis (Kalnay et al., 1996)	
$\delta^{18}O$ of atmospheric moisture (δa)		after Hendricks et al. (2000)	
$\delta^{18}O$ of precipitation (δp)		after Hendricks et al. (2000)	
$\delta^{18}O$ of evaporation (δe)		after Hendricks et al. (2000)	
$\delta^{18}O$ of transpiration (δt)		after Hendricks et al. (2000)	
$\delta p - \delta a$ (Δp)		after Hendricks et al. (2000)	
$\delta e - \delta a$ (Δe)		after Hendricks et al. (2000)	
$\delta t - \delta a$ (Δt)		after Hendricks et al. (2000)	

Vegetation inputs			
Vegetation type	E/P	T/P	Source
Modern CO grassland	0.31	0.73	Ferretti et al. (2003)
Modern NC forest	0.1	0.32	Oishi et al. (2008)

Fractionation factors	Ref.
Water–calcite	Kim and O'Neil (1997)
Liquid water–water vapor (eq)	Horita and Wesolowski (1994)
Liquid water–water vapor (kin)	Gonfiantini (1986)

3.2.2. Shorter rooting depth of grasses leads to recycling of evaporitic soil water

Soil waters typically reflect the $\delta^{18}O_p$ of the region (e.g. Tang and Feng, 2001) and exert the dominant control on the isotope composition of transpired vapor (δ_t). However, near-surface evap-oration of soil water leads to $\delta^{18}O$ profiles that decrease in $\delta^{18}O$ with depth. In modern grassland soil profiles in Colorado, soil wa-ter in the upper 10 cm is as much as 10‰ greater in $\delta^{18}O$ than water 1 m below the surface. For native grasslands in the Great Plains, soil waters at the surface are approximately 4‰ greater in $\delta^{18}O$ than those 50 cm below the surface (Ferretti et al., 2003; Nippert and Knapp, 2007). Plants will tap waters of different iso-tope compositions depending on their rooting depth. While trees have roots that can access deep waters by penetrating into frac-tured bedrock, commonly exceeding rooting depths of >2 m in water-limited environments, grasses have fibrous roots concen-trated in the upper half meter of the soil horizon (Lewis and Burgy, 1964; Ehleringer and Dawson, 1992; Sternberg et al., 1996; Schenk and Jackson, 2002). Under wet conditions, plants compete for shallow soil waters. In water-limited environments, rooting depth correlates with mean annual precipitation (less with ET) and absolute rooting depth is expected to be shallower for en-tire ecosystems (Schenk and Jackson, 2002). However, non-grass species such as herbs and shrubs shift to sourcing deeper soil wa-ter, thereby leaving grasses to tap shallow, ^{18}O-enriched soil water (Nippert and Knapp, 2007).

3.2.3. Change in the seasonality of transpiration as vapor recycling of grasslands reflects a shorter growing season

Growing seasons, and therefore the seasonality of transpiration, vary with vegetation type and climate. As $\delta^{18}O_p$ typically changes with season in the mid-latitudes, upstream vegetation and ecosys-tem dynamics should affect the annual mean $\delta^{18}O_p$ of a given region. Grasslands build most of their biomass during the spring and summer months in the Great Plains and Rocky Mountains. During these months, moisture advects inland from the Gulfs of Mexico and California, which is more enriched in ^{18}O than the comparably ^{18}O-depleted Pacific and Arctic-derived moisture deliv-ered during the winter. Even with a single moisture source, $\delta^{18}O_p$

changes over the seasons with lower $\delta^{18}O$ values during the winter as a result of greater rainout fraction and lower condensation temperature. While the long term $\delta^{18}O$ of water reaching a point must equal that of water leaving, vegetation changes will affect the partitioning of that water as either runoff or vapor recycled to the atmosphere. Since grasses have a shorter and more punctuated growing season than woodlands (Running and Coughlan, 1988; Ferretti et al., 2003; Baldocchi et al., 2004) they will preferentially transpire high-$\delta^{18}O$ water vapor to the atmosphere during the summer months and return minimal vapor to the atmosphere during the winter. After acquiring monthly transpiration fluxes for different plant functional types and monthly $\delta^{18}O_p$ data, we calculated annual weighted mean $\delta^{18}O_p$ values indicating that grasses transpire vapor that is approximately 1.6‰ higher than shrubs and trees in western Nebraska (Bowen et al., 2005; Bowen, 2011).

3.3. Vapor transport modeling

3.3.1. Model description and assumptions

In order to quantify the isotopic effects associated with large-scale expansion of grasses, we developed an isotope-tracking model following the work of Hendricks et al. (2000) and Noone and Sturm (2009). We begin with the overall hydrologic cycle, described in dynamical models in terms of the mixing ratio of atmospheric water vapor (q) as,

$$\frac{\partial q}{\partial t} = -V * \nabla q + D\nabla_h^2 q + \frac{\partial}{\partial p}\left(\overline{z'q'}\right) + ET - P + S \qquad (1)$$

The first term on the right describes advection processes with multi-dimensional advection velocity, V. The second and third terms represent the effects of horizontal diffusion and vertical small scale mixing, respectively. Together, these three terms describe overall transport and mixing within the atmosphere, while the last three terms are water sources and sinks. ET refers to surface evaporation and transpiration that serve as the dominant moisture source back to the atmosphere, and P represents condensational processes that remove moisture from the atmosphere in the form of precipitation. Finally, S represents atmospheric chemical processes such as the oxidation of methane that act as sources and sinks of moisture.

In order to evaluate the effects of changing vegetation on the isotope composition of atmospheric water vapor, we eliminated the small scale and atmospheric chemical processes (terms 2, 3, and 6 in Eq. (1)) to simplify the model for quantitative analysis. Our basis for this modification is that changing vegetation should have minimal impacts on these terms, particularly at the atmospheric level of condensation. We modeled specific storm tracks representative of the dominant path of moisture delivery to a given location. This approach allows us to analyze q in one dimension. Disregarding small scale and atmospheric chemical processes and reducing Eq. (1) to one dimension, we solve for the mixing ratio (the molar ratio of a species to the total other constituents) of the isotopic species $H_2^{18}O$ (q_{18}),

$$\frac{\partial q_{18}}{\partial t} = -v \cdot \frac{\partial q_{18}}{\partial x} + ET_{18} - P_{18} \qquad (2)$$

where v represents the one-dimensional advection velocity.

We then separate ET_{18}, the isotopic mixing ratio of ET, into separate terms for evaporation and transpiration as evaporation involves isotope fractionation while transpiration does not. We also expand evaporation, transpiration, and precipitation terms to include the fractionation of isotopes associated with phase changes in order to calculate the fluxes of $H_2^{18}O$ based on overall moisture fluxes. Assuming the isotope composition of water vapor at a given

location is invariant with time, we finalize our storm track isotope model in delta notation as,

$$\frac{d\delta a}{dx} = \frac{E}{vw}\Delta E + \frac{T}{vw}\Delta T - \frac{P}{vw}\Delta P \qquad (3)$$

where symbols are defined in Table 1. Eq. (3) is derived by solving Eq. (2) for steady-state and converting to delta notation.

In this model, precipitation is assumed to be stratiform, the air mass is advected along the specified storm track at the 850 mb level, and we assume no post-condensation isotope fractionation. We ignore the eddy diffusive effects associated with air mass mixing, as the model is meant to specify a specific storm track. The validity of this model is therefore only robust in regions and time periods where the bulk of precipitation originates from a single air mass.

Equilibrium and kinetic fractionation effects associated with precipitation and evaporation are computed using temperature and relative humidity values from NCEP/NCAR Reanalysis Project data (Kalnay et al., 1996) from the 850 mb and surface levels. In addition, precipitation rate, advection velocity, and initial precipitable water come directly from NCEP reanalysis data. Using published evaporation and transpiration rates relative to precipitation, we calculate the isotopic effects of different vegetation cover scenarios along a transect from the Gulf of Mexico to western Nebraska, representing summer precipitation (Fig. 1, Supplemental Fig. 2A) (Alton et al., 2009). Due to kinetic and equilibrium fractionation, $\delta^{18}O$ values of evaporated moisture that is reintroduced to the atmosphere are reduced relative to the original precipitation by approximately 13–14‰. $\delta^{18}O$ values of subsequent transpiration fluxes to the atmosphere are increased relative to the original precipitation as plants tap residual soil water enriched by evaporation. As the ratio of transpiration to evaporation increases, $\delta^{18}O$ of ET approaches that of the precipitation.

We determine the isotope composition of soil water, and therefore transpired water, as a function of depth using the approach given in Barnes and Allison (1983) and Zimmermann et al. (1967) with the appropriate fractionation factors (Supplemental Fig. 2B) and evaporation rates based on vegetative cover as described above. To calculate the isotope composition of soil carbonate, we use the isotope composition of soil water, the temperature at the soil surface, and a carbonate precipitation depth of 35 cm, the bulk accumulation zone for pedogenic carbonates in semi-arid climates (McFadden et al., 1991). For a complete description of the model parameters, assumptions and validation, see the supplement.

3.3.2. Vapor transport model results

We performed several numerical experiments in order to deconstruct the different components of hydrologic change associated with changing land cover type. First, we examined vapor recycling through evaporation and transpiration fluxes only. We simulated ET fluxes using Bowen ratio data from a Colorado shortgrass steppe (Ferretti et al., 2003) and coupled sap flux and eddy covariance data from a mature North Carolina oak–hickory forest (Oishi et al., 2008).

In our first simulation, we held all parameters associated with the isotope composition of evapotranspiration constant and equal to local $\delta^{18}O_p$ in order to isolate the effects of changing water balance on the Rayleigh distillation of the air mass (see Section 3.2.1). $\delta^{18}O_p$ is plotted along the transect for the CO grassland and NC forest. A scenario with no evapotranspiration (open-system Rayleigh distillation) is included as well. Without the contributions of recycled vapor from evapotranspiration, $\delta^{18}O_p$ and $\delta^{18}O$ of soil carbonate ($\delta^{18}O_c$) become more rapidly depleted in ^{18}O with distance (Fig. 4A–B). Under the no ET scenario, $\delta^{18}O_p$ decreases by over 10‰ before 1400 km along the transect, where $\delta^{18}O_p$ values
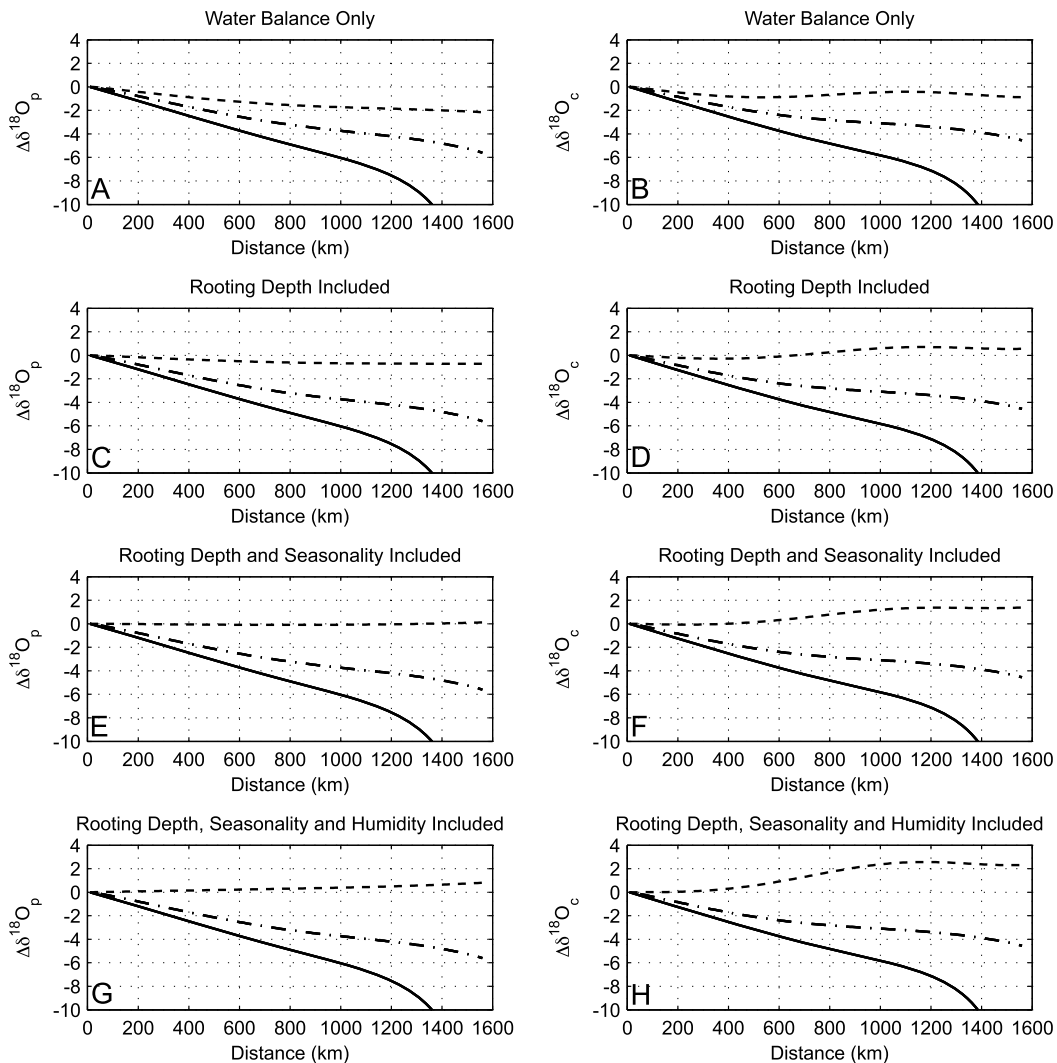
Fig. 4. Results of model experiments. (A–B) Modeled $\delta^{18}O_p$ and $\delta^{18}O_c$ response to differences in evaporation and transpiration fluxes only. (C–D) Modeled $\delta^{18}O_p$ and $\delta^{18}O_c$ response to differences in ET fluxes as well as rooting depth. (E–F) Modeled $\delta^{18}O_p$ and $\delta^{18}O_c$ response to differences in ET fluxes, rooting depth and seasonality of transpiration. (G–H) Modeled $\delta^{18}O_p$ and $\delta^{18}O_c$ response to differences in ET fluxes, rooting depth, seasonality and relative humidity. Colorado grassland: dashed line; North Carolina oak–hickory forest: dash–dot line; No ET: solid line.

then drop precipitously as the air mass runs out of moisture. Under the forest scenario, $\Delta\delta^{18}O_p$ values reach $-6‰$. The grassland, which transpires significantly more water than the modeled forest, produces the most enriched profile, with a $\Delta\delta^{18}O_p$ value of $-2‰$ at the end of the transect. Carbonate $\delta^{18}O$ values follow the same pattern, but decrease by 1–2‰ less than $\delta^{18}O_p$ values along the transect. This is likely due to the important roles of relative humidity, soil water composition and carbonate formation depth in controlling $\delta^{18}O_c$.

In the next simulation, we included the water balance effects discussed above as well as effects associated with vegetation rooting depth. In this simulation, the forest scenario transpires water from 1 m depth in the soil profile, while grasses source water from the top 30 cm of the soil profile (see Section 3.2.2). While the $\delta^{18}O$ of ET is constrained by the $\delta^{18}O$ of precipitation falling at the site, the transpiration of relatively enriched soil waters closer to the soil surface allows the $\delta^{18}O$ of ET in grasslands to more closely approach that of the original precipitation, thereby reducing the isotopic gradient across the storm track. In this scenario then, the grassland produces the most enriched profile, roughly 4–5‰ greater in $\delta^{18}O_p$ than the forest by the end of the transect.

Next, we added a seasonality component to the simulations above. We calculated the annual weighted mean $\delta^{18}O$ of water vapor transpired by different vegetation types based on monthly transpiration and precipitation data, and concluded that grasses transpire vapor that has a $\delta^{18}O$ value 1.6‰ than that of forests (see Section 3.2.3). We added this component to the $\delta^{18}O$ of transpiration for grasses only. Predictably, the grass simulations produce isotope profiles even more enriched in ^{18}O (Fig. 4E–F). The grassland scenario does not decrease in $\delta^{18}O_p$ along the transect while the forest decreases by nearly 6‰.

Finally, we incorporated changes in relative humidity to our land cover change simulations. Transition from a forest ecosystem to a grassland ecosystem would be accompanied by a change in relative humidity. As relative humidity controls the isotope profile of soil water, change in relative humidity will affect the isotope composition of transpired vapor. In this set of simulations, we assigned relative humidities of 0.7 to representative of deciduous forest and 0.5 for grasslands based on the Holdridge life zone classification and mean monthly terrestrial climatology data (Holdridge, 1947; New et al., 1999). Change in relative humidity causes the grassland scenario to increase slightly in $\delta^{18}O_p$ over the transect (Fig. 4G–H). We observe the greatest differences between grassland and forest to occur due to the water balance effects ($\sim$4‰), an additional $\sim$2‰ due to rooting depth effects, with seasonality

and humidity effects responsible for $<1‰$ of difference in $\delta^{18}O_p$ by the end of the 1550 km transect.

3.3.3. Discussion of modeling results

We included a modeling component in this paper to provide a framework for predicting relationships between the development of grassland ecosystems and the hydrologic cycle at a continental scale. Much of the area covered by the Gulf of Mexico–Nebraska transect underwent expansion of C_4 grasslands at the expense of wood and shrublands over the course of the Neogene (Axelrod, 1985; Wing, 1998; Jacobs et al., 1999). Our model results show that this change in vegetation is capable of producing a change in $\delta^{18}O_p$ by as much as $+6‰$ by the time air masses reach western Nebraska. With average $\delta^{18}O_p$ increases of 3.8‰ in the Basin and Range, and 3.4‰ to the south and west of the Basin and Range, the bulk of the isotopic change in western North America could be related to the rise of grasslands. Of course, the effect of moisture recycling by grassland ecosystems will scale in magnitude with distance to the moisture source, and become more pronounced towards the continental interior as air masses interact with progressively recycled water.

We demonstrate that recycling of water vapor must have played an underappreciated role in the current climate and hydrology reconstructions of North America. This observation is highlighted by the degree that our vegetated scenarios differ from a simple open-system Rayleigh curve, modeled by our "no ET" scenario (Fig. 4). Conversion to grassland leads to over 10‰ of enrichment in $\delta^{18}O_p$ values by 1400 km along our transect compared with open-system Rayleigh behavior according to our model results.

Finally, we recognize that our model is designed for first-order observations only. Among the most significant model shortcomings are constant temperature, relative humidity, and the distribution of precipitation while changing vegetation type. Despite the caveats, the argument that change in vegetation types affected continental water balance on geologic and evolutionary timescales remains grounded in the fundamental observations that nearly all $\delta^{18}O$ records increase from the Middle Miocene to Quaternary when grasslands expanded at the expense of woodlands in western North America. Our modeling demonstrates that this change in biomes would have affected the isotope composition of surface waters in a manner consistent with observations.

4. Discussion

We argue that the bulk of the increase in $\delta^{18}O_p$ from the Middle Miocene to the Quaternary in the Basin and Range and Rocky Mountain foreland could be caused by expansion of grasslands. An additional increase of ~0.8 to 1‰ results from the change in oceanic source $\delta^{18}O$ values due to expansion of polar and continental ice sheets during the Neogene. Any remaining regional long-term increase in $\delta^{18}O$ of these records is most likely the result of increased aridity that accompanied grassland expansion (Axelrod, 1985) Certainly evaporation would have contributed to changing soil water isotope composition as regional climate became more arid. While we cannot quantify this effect with our dataset, there are promising methods that should be explored to address the role of aridity in such isotope records (Levin et al., 2006).

Our interpretation that regional changes in plant communities altered the hydrologic regime in western North America is further supported by the observation that the increase in $\delta^{18}O_p$ is diachronous. Although almost all isotope records increase during the Miocene, the timing of the trend to more positive $\delta^{18}O_p$ values differs regionally (Fig. 3). The turnover from forest to grasslands in the Great Plains and Rocky Mountains also occurred in

a diachronous and geographically complex fashion. Despite these complexities, there are some first-order changes in plant communities that should be reflected in terrestrial oxygen isotope records. First, floral and faunal data show that forests covered the modern Great Plains and Rocky Mountains prior to the Middle Miocene (Jacobs et al., 1999). In the Eocene, these forests were composed of broadleaf evergreens, temperate deciduous trees, and even tropical to subtropical species such as palms (Wing, 1998). By the Late Oligocene, Colorado was populated by pinaceous conifers, and scrub, while Utah was covered by arid-adapted herbaceous plants (Crepet and Feldman, 1991; Wing, 1998). As shown by our model, this change in vegetation type should be apparent in oxygen and hydrogen isotope records. These records do not currently extend into the Eocene unfortunately.

Second, the transition from forest- to grass-dominated landscapes was regionally complex as grasses expanded northward in the Middle Miocene (Cerling et al., 1997). Although some grassy vegetation was present in the Early Miocene (Strömberg and McInerney, 2011), the global expansion of C_4 vegetation began around 7 Ma (Cerling et al., 1993; Wang et al., 1994). By the Late Miocene, the Great Plains transitioned from ~20% C_4 biomass to over 70% by the Pleistocene (Fox and Koch, 2003; see also Stebbins, 1981). These grasslands consisted of a mosaic of C_3 vegetation in wetter areas and C_4 grasslands in the drier regions (Wing, 1998). We suggest that the diachronous nature of the positive trends in $\delta^{18}O$ values could be due, in part, to the differences in timing and extent of grassland expansion. While the timing of the isotopic enrichment trends reflects the spatial complexity of Neogene hydrologic change, it broadly matches the timing of several well-known paleoecological transitions (Fig. 5). Positive changes in $\delta^{18}O$ are concurrent with increases in grass abundance in phytolith assemblages (Fig. 5A) (Strömberg, 2005; Strömberg and McInerney, 2011), increases in grazer hypsodonty, cursoriality and size (Fig. 5B) (Bakker, 1983; MacFadden, 1992; Janis et al., 1998, 2000; Strömberg, 2011), all of which predate the rise of C_4 biomass evidenced by the paleosol carbonate $\delta^{13}C$ record (Fig. 5D) (Fox and Koch, 2003).

Links between changes in plant communities and hydrologic balance are well known. For example, precipitation in semi-arid regions such as the Great Plains is particularly sensitive to changes in soil moisture (Koster et al., 2004); and tropical deforestation and replacement by cropland increases precipitation at the cropland boundaries and suppresses rainfall over adjacent forest (Garcia-Carreras and Parker, 2011). Changes in plant communities affect the global hydrologic balance as well. For example, using a general circulation model with vegetated and non-vegetated conditions, Kleidon et al. (2000) showed that a "green planet" could nearly double precipitation in regions particularly sensitive to ET fluxes. Furthermore, the change from non-angiosperm to angiosperm vegetation in the Cretaceous should have profoundly affected the global hydrologic balance. Models show large regional changes in precipitation due to higher transpiration rates of angiosperms (Boyce and Lee, 2010). Such hydrologic changes should be evident in the oxygen isotope record.

As yet there are no similar models that capture the dynamics of grasslands and their affect on water balance. Because current isotopic mass balance models (Hendricks et al., 2000; this study) fix precipitation at each site, we cannot quantitatively assess the degree to which the precipitation regime changes as grasslands replace forests. Could grasslands alter downstream climate, and through feedback mechanisms, engineer their expansion? We speculate that grasslands would change the hydrologic regime downstream by increasing seasonality of precipitation to favor their development. Since grasslands deliver moisture downstream at sharp seasonal intervals, their hydrologic effects would sweep ahead of the grasslands themselves. Grasslands would expand with a hy-
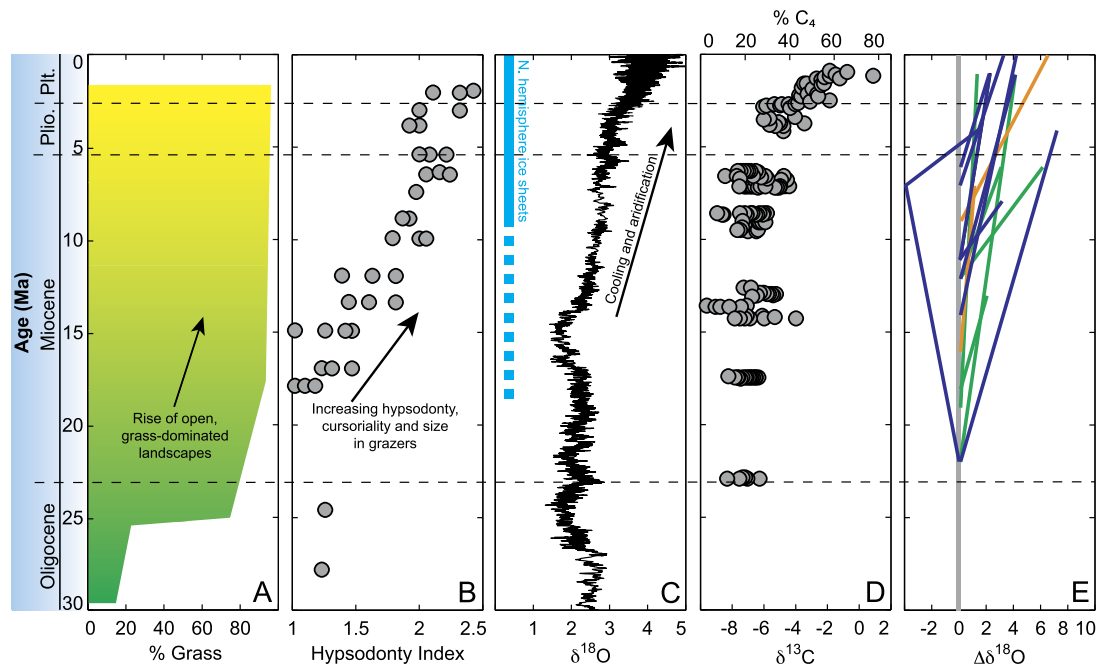
Fig. 5. Summary of paleoenvironmental changes in western North America during the last 30 Ma. (A) Grass abundance in phytolith assemblages. After Strömberg (2005) and Strömberg and McInerney (2011). (B) Mean faunal hypsodonty index after Janis et al. (1998, 2000) and Strömberg (2011). Increases in faunal size and cursoriality from Bakker (1983) and MacFadden (1992). (C) Deep-sea foraminifera record of $\delta^{18}O$ after Zachos et al. (2001). Cooling and aridification in western North America from paleofloral data of Axelrod (1985). (D) $\delta^{13}C$ of paleosol carbonate in the Great Plains. After Fox and Koch (2003). (E) Changes in $\delta^{18}O$ of pedogenic carbonate and smectite in western North America. Records from the Pacific Northwest omitted due to Cascadian uplift. Colors indicate the regions from Fig. 1.

drologic front ahead of them, creating climatic disturbances before invading new territory. In this regard, it is interesting to note that pedogenic $\delta^{13}C$ records indicate that dietary change to C_4 plants in equids began at lower latitudes and swept northward (Cerling et al., 1997). This ecological transition suggests that the comparative advantages of grasslands began in the south, and hydrologic effects could have contributed to the northward advance of grasslands.

How then could this expansion have occurred? Initial establishment of grasslands must have been the result of global climatic changes as they dramatically increased their range worldwide during the Neogene. A widely held explanation for C_4 grassland expansion is that decreasing atmospheric pCO_2 in the Late Miocene led to a threshold where C_4 grasses held a competitive advantage over C_3 vegetation (Cerling et al., 1997; Ehleringer et al., 1997). Some suggest, however, that this pCO_2-threshold mechanism is insufficient and unnecessary. Fox and Koch (2003) argue that the driver was not pCO_2 decrease, but rather global cooling and reduction in the length of the growing season since the MMCO. Nevertheless, once established, grasses may have aided their expansion by increasing the seasonality of precipitation. This effect would have played into fire-induced feedbacks that are central to both the establishment of grasslands in the Miocene as well as the maintenance of grasslands today (Axelrod, 1985; D'Antonio and Vitousek, 1992; Keeley and Rundel, 2005; Beerling and Osborne, 2006). Exactly how this occurred is unknown and likely to be quite complex as vegetation may undergo rapid nonlinear responses to changes in climate and ecological disturbance (Staver et al., 2011; Hirota et al., 2011). Grassland expansion contributes to the development of warm moist growing seasons with high productivity alternating with dry seasons capable of producing fires, critical to the feedback (Keeley and Rundel, 2005). Further study should more thoroughly examine the role of the biosphere both in responding to and driving global change.

Appendix A. Supplementary material

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.epsl.2013.07.032.

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