ECOPHYSIOLOGY

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Summer water use by California coastal prairie grasses: fog, drought, and community composition

Abstract Plants in the Mediterranean climate region of California typically experience summer drought conditions, but correlations between zones of frequent coastal fog inundation and certain species' distributions suggest that water inputs from fog may influence species composition in coastal habitats. We sampled the stable H and O isotope ratios of water in non-photosynthetic plant tissue from a variety of perennial grass species and soil in four sites in northern California in order to determine the proportion of water deriving from winter rains and fog during the summer. The relationship between H and O stable isotopes from our sample sites fell to the right of the local meteoric water line (LMWL) during the summer drought, providing evidence that evaporation of water from the soil had taken place prior to the uptake of water by vegetation. We developed a novel method to infer the isotope values of water before it was subjected to evaporation in which we used experimental data to calculate the slope of the δH versus δO line versus the LMWL. After accounting for evaporation, we then used a two-source mixing model to evaluate plant usage of fog water. The model indicated that 28–66% of the water taken up by plants via roots during the summer drought came from fog rather than residual soil water from winter rain. Fog use decreased as distance from the coast increased, and there were significant differences among species in the use of fog. Rather than consistent differences in fog use by species whose distributions are limited to the coast versus those with broader distributions, species responded individualistically to summer fog. We conclude that fogwater inputs can mitigate the summer drought in coastal California for many species, likely giving an advantage to species that can use it over species that cannot.

Keywords Evaporation · Native perennial grass · Plant–water relations · Stable isotopes

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Introduction

Water is a critical resource that limits the distribution and abundance of vegetation in arid and semiarid regions of the world. A variety of traits allow plants to persist under prolonged drought conditions, such as early flowering, leaf and stem succulence, and deep roots that access permanent water sources. Recent advances in the use of stable isotopes have shown that, while perennial plants in arid and semiarid climates often access water deep in the soil profile to support growth or persistence during dry conditions, many species also support shallow roots to take advantage of brief precipitation events (Ehleringer and Dawson 1992; Lin et al. 1996; Williams and Ehleringer 2000; Dawson et al. 2002). The relative availability of different sources of water, for example in deep versus shallow horizons of the soil, may influence species' distributions through the influence of water availability on survival or the likelihood of population coexistence (Stratton et al. 2000).

Water from fog has been shown to constitute a significant portion of the hydrologic inputs in a variety of ecosystems, including coastal coniferous forests in Chile and northern California (Azevedo and Morgan 1974; Cereceda and Schemenauer 1991; Ingraham and Matthews 1995; Dawson 1998), tropical lowland and montane cloud forests (Feild and Dawson 1998; Martorell and Ezcurra 2002), and New Zealand tussock grasslands (Ingraham and Mark 2000). However, few studies have quantified the degree to which vegetation relies on fog

(but see Ingraham and Matthews 1995; Feild and Dawson 1998; Dawson 1998). One of the best-studied examples is that of coastal redwood forests in California, where, during the summer, 8–42% of the water obtained by redwood trees (*Sequoia sempervirens*) and 6–100% of the water obtained by understory species was derived from fog (Dawson 1998). Water inputs from fog in coastal northern California are of particular ecological significance, because the period of most frequent fog inundations coincide with the severe summer drought that is characteristic of the region's Mediterranean climate (Major 1988).

Though many California grassland ecosystems were converted from perennial bunchgrass domination to Eurasian annual grass and forb domination in the nineteenth century (Mack 1989; Heady et al. 1991), coastal prairie grasslands in California are notable in the persistence of native perennial grasses (Heady et al. 1988; Stromberg et al. 2001; Corbin and D'Antonio 2004). As a result, the conservation of these ecosystems is of particular concern to habitat managers. Unlike the exotic annual species, most of which complete their life cycle before the summer, native perennial bunchgrasses maintain live vegetative tissue throughout the summer drought period. The extent to which coastal prairie vegetation is dependent on fog inputs is not known, but the predictability of summer fog in coastal habitats suggests that it could be an important water source for otherwise drought-stressed species.

Water derived from fog and rain can be distinguished by its hydrogen and oxygen stable isotope ratio (δ^2H and δ^{18}O) (Gonfiantini and Longinelli 1962; Ingraham and Matthews 1990; Dawson 1998). Rainwater that reaches coastal California is relatively depleted in the heavier form of H and O (^{2}H and ^{18}O, respectively) as compared to water from fog (Ingraham and Matthews 1990). The differences in stable H and O isotope values are relatively predictable and can be used to determine the origin of water contained in vegetation or soil (Ingraham and Matthews 1990; Dawson 1998; Dawson and Ehleringer 1998; Dawson et al. 2002). Interpretation of stable water isotope patterns is complicated, however, in cases where water sources available to the plants are likely to experience isotopic fractionation as water evaporates from the soil profile (Craig and Gordon 1965; Clark and Fritz 1997; Kendall and Caldwell 1998). Evaporation leads to the concentration of heavier isotopes of H and O and higher δ^2H and δ^{18}O values in the moisture left behind than was present in the original rain or fog inputs. Previous applications of stable isotope analysis to determine the proportional use of rain versus fog water by vegetation took place in ecosystems in which the effects of evaporation on stable isotope values could be assumed to be negligible (e.g. Ingraham and Matthews 1995; Dawson 1998; Ingraham and Mark 2000), and, thus, water in the soil profile closely reflected the isotope values of source waters. However, water in many ecosystems, particularly exposed or wind-blown ones, may experience significant evaporative enrichment of H and O isotopes prior to plant uptake. If stable isotopes are to be widely used to characterize water use by vegetation, then the evaporative enrichment of water must be factored into the determination of water source use.

We tested the use of fog by coastal prairie vegetation during the summer drought by sampling the stable H and O isotope ratios of water in the soil and non-photosynthetic tissue of seven perennial grass species in four coastal prairie grasslands. Our sites, in Sonoma and Marin Counties, CA, USA fall along a gradient of heavy to light fog inundation. We hypothesized that the grasses would use fog-derived water in the summer. We further hypothesized that populations closer to the coast would use fog to a greater extent than populations further inland. Finally, we hypothesized that species would vary in the extent to which they used fog in the summer, and that this variation would reflect the distributions of these species. Specifically, we expected that species whose distributions are limited to coastal sites with a high incidence of fog, such as *Calamagrostis nutkaensis* or *Deschampsia caespitosa* ssp *holciformis*, would use more water from fog than more widely distributed species such as *Nassella pulchra* or *Elymus glaucus*. In determining the proportional use of fog by coastal prairie grassland species, we applied a novel isotope correction to account for the evaporative fractionation of stable H and O isotopes in the soil profile.

Materials and methods

Study sites

Plant and soil samples were collected at four sites in Marin and Sonoma Counties, CA, USA (Table 1). These sites varied in characteristics that influence the degree of fog inundation such as elevation, distance from the ocean, and topographic features. Bodega Marine Reserve (BMR), adjacent to the Pacific Ocean, received the most frequent and heaviest fog inundation. In contrast, Sky Oaks Meadow (SO), while located only 10 km south and 10 km inland from BMR, experienced the least frequent fog inundation because fog-laden air rarely passes over the Bolinas Ridge to the west (J. Corbin, personal observation). Vegetation composition varied among sites, but all four sites would be classified as coastal prairie grasslands based on the descriptions of Heady et al. (1988) and Stromberg et al. (2001). Dominant species included native perennial bunchgrasses such as *Danthonia californica* Bolander, *D. caespitosa* spp *holciformis* (C. Presl) W. E. Lawr, and *N. pulchra* (A. Hitchc.) Barkworth, exotic annual grasses such as *Bromus diandrus* Roth and *Vulpia myuros* (L.) C. Gmelin, exotic perennial grasses such as *Festuca arundinacea* Schreber and *Holcus lanatus* L., and exotic forbs such as *Erodium botrys* (Cav.) Bertol., *Hypochaeris glabra* L., and *Plantago lanceolata* L. (Nomenclature follows Hickman 1993).

Table 1 Site characteristics and species sampled

Site	BMR	TP	4C	SO	Grove of the old trees[a]
Location	38°19′N	38°13′N	37°54′N	37°58′N	38°24′N
	123°4′W	122°57′W	122°33′W	122°35′W	122°59′W
Elevation (m)	15	25	220	150	300
Distance from ocean (km)	0.4	2.5	4.3	8.4	8
Species sampled					
C. nutkaensis	X				
D. californica		X	X	X	
D. caespitosa	X	X	X		
E. glauca	X	X	X		
F. rubra	X	X	X		
H. lanatus	X	X	X	X	
N. pulchra		X	X	X	

[a]An old-growth redwood forest where rain water was collected for estimate of $\delta^{18}O_{rain}$

Vegetation, soil, and water sampling

Vegetation and soil were sampled periodically from September 2000 to November 2001. Species sampled included abundant native perennial grasses at each site, as well as one exotic perennial grass, *H. lanatus*, whose abundance in coastal prairie grasslands has increased in recent decades. Not all species were present at all sites (Table 1). In order to determine the δ^2H and $\delta^{18}O$ values of water in plant tissue, basal culm and root tissue just below the soil surface level were harvested from each individual, taking care to exclude photosynthetic tissue. This methodology permits the analysis of water (whether from fog or rain) taken up by roots, rather than directly by foliage. It was not possible to collect enough tissue from individual plants for isotopic analysis, so tissue from 3 to 5 randomly selected individuals of each species were pooled to form a single sample at each date. Three soil cores (15 cm depth) from randomly selected points at each site were collected at the same time as vegetation samples in order to determine the δ^2H and $\delta^{18}O$ values of water in the surface soil. All samples were stored in water-tight polyethylene vials with sealed caps and frozen prior to water extraction and isotope analysis.

The interpretation of variation in the stable isotope composition of water in herbaceous plant species, such as the grasses we studied, assumes that evaporative processes have not acted on plant water in non-photosynthetic tissue such as the roots or in the basal culms (Ehleringer and Dawson 1992). Though this assumption has been examined in woody species (see Dawson and Ehleringer 1993), it remains largely untested in herbaceous species. Evaporative enrichment, which leaves behind a greater fraction of the heavier isotopes of hydrogen and oxygen, could constitute a significant source of variation in plant water isotopes between sites or between seasons in some systems. We took care to limit our samples to root and basal culm tissue below the soil surface in order to minimize potential evaporation from plant tissues, though we acknowledge that we cannot entirely rule out the possibility without further and more definitive experiments.

Fog water was collected at each site from March 2001 to September 2001 using 1 m^2 PVC pipe frames equipped with nylon mesh screen oriented perpendicular to the direction of the prevailing wind (modified from Goodman 1995). Collected moisture was used to provide an estimate of the isotopic signature (δ^2H and $\delta^{18}O$) of fog at each site. The quantity of fog collected at SO was not sufficient for isotope analysis; therefore, we substituted the isotope value of fog from the closest site, 4C. Rain was collected at the Grove of Old Trees in Sonoma County (Table 1) following the methods of Dawson (1998). Rain water was collected 37 times, during November–April 2000–2004; the mean "winter" oxygen isotope value of these collections (unweighted by amount) was −9.92 (SE ± 1.14)‰ (see below for notation).

We also sampled soil water for isotope analysis, gravimetric water content (GWC), and root biomass from *N. pulchra* at various depths of the soil profile to provide a gauge as to where plants were getting water, and to understand patterns of water availability and rooting structure. *N. pulchra* was chosen because it is one of the most abundant and widespread of California's native bunchgrasses, and is widely used in grassland restoration. On June 25 and November 8, 2002, during the early and late summer, respectively, basal culm and root tissue were harvested from three *N. pulchra* individuals at the most intensively sampled site, Tom's Point (TP), as above. At the same time, the isotopic gradient in the soil profile was sampled by taking sequential soil cores under each *N. pulchra* individual from 0–5, 5–10, 10–20, 20–40, 40–60, and 60–80 cm depths. A rock layer prevented sampling below 80 cm. The isotopic composition of water in vegetation was assumed to be an integrated measure of the water in the soil horizons from which vegetation actively took up water, and was compared to the gradient of isotopic values through the soil profile (Ehleringer and Dawson 1992). Finally, roots were hand sorted and weighed from November soil samples. Previous research has indicated that the difference between root biomass in June and root biomass in November is negligible (J. Corbin, unpublished data).

Sample water extraction and stable isotope analysis

Water was extracted from vegetation and soil samples using a cryogenic vacuum distillation extraction line (Ehleringer et al. 2000). The stable H and O isotopic composition of the extracted water and of fog/rainfall collections was determined on an isotope ratio mass spectrometer (Finnigan Mat Delta[Plus] *XL*, Germany) at the UC Berkeley Center for Stable Isotope Biogeochemistry. The stable H isotope composition of all water samples was determined using the method outlined by Nelson and Dettman (2001); the stable O isotope composition was determined using a 5-day equilibration of water samples with CO_2 followed by mass spectrometer analysis (Epstein and Mayeda 1953; Brooks and Dawson 2001). Long-term external precision estimates are 0.5 standard deviation of the population for ^2H and 0.14 standard deviation for ^{18}O analysis (P. Brooks, personal communication). Hydrogen and oxygen isotope ratios (as $^2H{:}^1H$ and $^{18}O{:}^{16}O$ respectively) are expressed in delta notation as "per mil" or parts per thousand (‰) relative to V-SMOW (Ehleringer and Dawson 1992).

We used the two-compartment linear mixing model of Phillips and Gregg (2001) in order to estimate the proportion of water in vegetation that derived from summer fog,

$$P_{\text{fog}} = \frac{\delta^{18}O_{\text{vegetation}} - \delta^{18}O_{\text{rain}}}{\delta^{18}O_{\text{fog}} - \delta^{18}O_{\text{rain}}}, \tag{1}$$

where $\delta^{18}O_{\text{fog}}$ is the mean isotope value for fog collected at each site through the year [(Mean ± SE) BMR: -1.73 ± 0.09‰; TP: -1.72 ± 0.22‰; 4C and SO: -2.63 ± 0.15‰], and $\delta^{18}O_{\text{rain}}$ is the mean isotope value of rain collected at the Grove of old trees in Sonoma County during our study period (Mean ± SE: -9.92 ± 1.14‰; Table 1; T. Dawson, unpublished data). The five sites are close enough to each other that the isotope values of rain would not be expected to vary significantly between them (Ingraham and Taylor 1991).

The relationship between δ^2H and $\delta^{18}O$ values in precipitation in California has been shown to deviate significantly from the global meteoric water line, or the relationship between δ^2H and $\delta^{18}O$ in precipitation, as reported by Craig (1961) (Dawson 1998; Kendall and Coplen 2001). As a result, we used the California state meteoric water line reported by Kendall and Coplen (2001) as the local meteoric water line (LMWL) ($\delta^2H = 7.8 \times \delta^{18}O + 5.4$). Rain (data not shown) and fog values (Fig. 1a) closely matched the LMWL.

Correction for evaporative enrichment

The relationship between δ^2H and $\delta^{18}O$ in our vegetation and soil samples suggested that kinetic fractionation via evaporation from the soil surface influenced isotopic values at various times during the year (Fig. 1a; see Results and discussion). The original isotope values of the water prior to evaporation can be inferred, however, by determining the slope of the change in δ^2H and $\delta^{18}O$ as the isotope values deviate from the LMWL (Clark and Fritz 1997; Barnes and Turner 1998; Kendall and Caldwell 1998). In a separate experiment, we calculated the slope of the deviation of δ^2H and $\delta^{18}O$ values in water from the LMWL as water evaporates using measured isotope values from water in soil samples collected as soil moisture evaporated from unvegetated plots (See Appendix). We further assumed that the water in each vegetation or soil sample whose isotopic content deviated from the LMWL had undergone evaporative fractionation after water deposition.

We corrected the isotope values of each vegetation and soil sample following collection and determination of the original values of δ^2H and $\delta^{18}O$ in water. For each sample, we calculated the intersection with the LMWL of a line (evaporation line: slope = 3.5) connecting the isotopic content of the sample ($x = \delta^{18}O$; $y = \delta^2H$) and the LMWL (Appendix; Fig. 1c). The δ^2H and $\delta^{18}O$ of the intersection between the LMWL and the evaporation line were assumed to be the isotopic content of the water source *before* evaporative enrichment. Each corrected $\delta^{18}O$ value was applied to Eq. 1, as above.

Statistical analysis

Estimates of fog use for each species at each site throughout the year were pooled, so that estimates over time were considered independent replicates during statistical analysis. We believe this is a valid assumption given that the same individuals were not sampled each time. We used two separate one-way ANOVAs (SAS Institute 2000) to compare fog use during the summer drought (May–October) between species and the four sites. However, uneven species distributions of species across the sites prevented full analysis of species by site interactions. We therefore identified a subset of species × site combinations in which groups of species were found in at least three sites. Four species (*D. caespitosa, E. glaucus, F. rubra,* and *H. lanatus*) were found at BMR, TP, and 4C; meanwhile, another group of four species, (*D. californica, E. glaucus, H. lanatus,* and *N. pulchra*) were found at TP, 4C, and SO. We tested the importance of species and site within each data subset using two-way ANOVA. Where ANOVA analysis indicated a significant main effect of site for a particular species, we applied the mixing model of Phillips and Gregg (2001) to assign 95% confidence intervals to estimates of fog use. This model considers variation in estimates of source populations as well as fog use, and therefore is more conservative than pair-wise comparisons based on fog use alone. Where ANOVA indicated a significant main effect of species, we performed pair-wise comparisons using Fisher's least-significant-difference test.
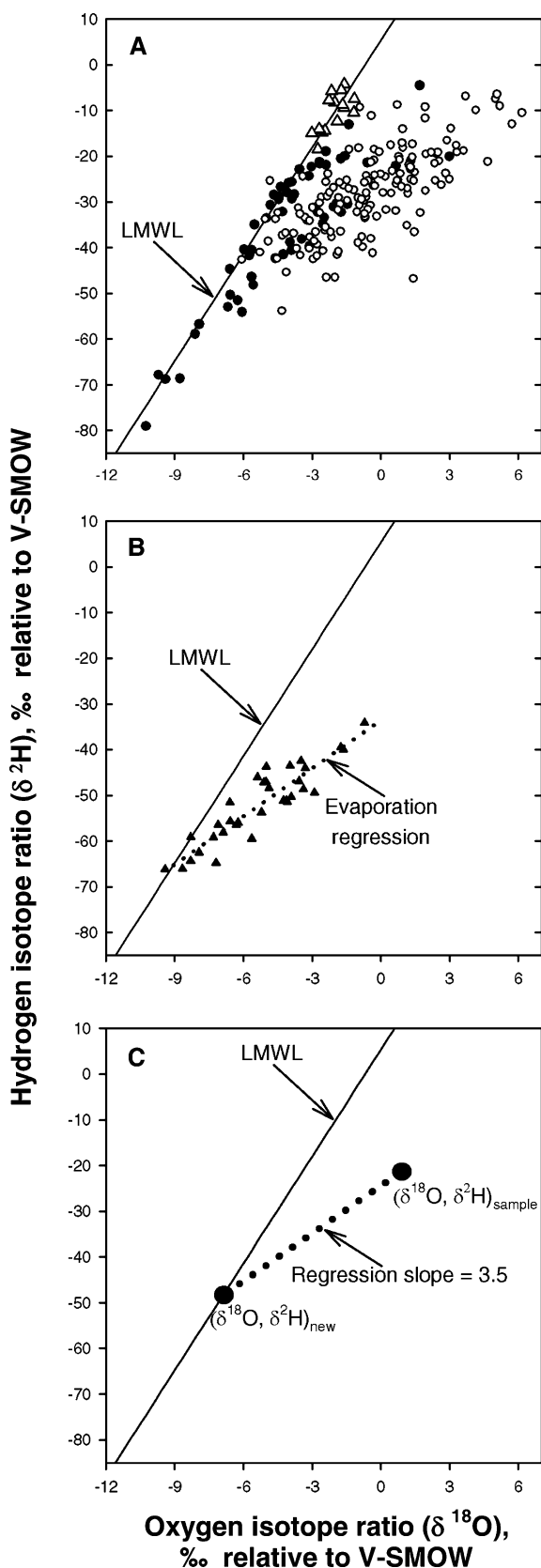
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Fig. 1 Evidence of evaporative fractionation of water, and methodology for inferring original isotope values of water. **a** δ^2H and δ^{18}O water in vegetation, soil, and fog sampled at all four sites in 2000–2001, plotted along with the LMWL reported by Kendall and Coplen (2001). *Filled circle* Soil and vegetation samples collected in winter (December-March); *open circle* soil and vegetation samples collected in spring/summer (April–November); *open triangle* summer fog samples. **b** δ^2H and δ^{18}O of water in the top 2 cm of soil as water evaporated from unvegetated plots on five different days. See Appendix for description of methods. In the case of the 5 days in which the isotope values of the surface soil was sampled, the evaporation line and LMWL intersected at the values δ^2H = −65.5 and δ^{18}O = −9.1; **c** Hypothetical correction for evaporative fractionation, in which the point (δ^{18}O, δ^2H)$_{new}$ is inferred from the evaporation line (slope = 3.5) connecting (δ^{18}O, δ^2H)$_{sample}$ and the LMWL

Results and discussion

Vegetation and soil isotope values

Stable O isotope values (δ^{18}O) in vegetation and the top 15 cm of soil changed substantially over the course of the year (Fig. 2). The uncorrected δ^{18}O values at all four sites were lowest in February–March, then increased substantially through the summer drought period until November, when the fall rains began. The increase in vegetation and soil δ^{18}O as the summer drought progressed is likely due to both increasing use of water from fog by vegetation and evaporative enrichment of water in the soil as temperatures increased.

The relationship between δ^2H and δ^{18}O in vegetation and soil provided evidence that evaporative fractionation of water in the soil had taken place prior to uptake of water by vegetation. The isotopic values of vegetation and soil plotted to the right of the LMWL (Fig. 1a), consistent with an evaporated soil profile (Clark and Fritz 1997; Kendall and Caldwell 1998; Barnes and Turner 1998). The vegetation and soil values that deviated from the LMWL were largely restricted to the summer drought season, when temperatures were highest (Fig. 1a).

Correction for evaporation, using our estimated evaporation line (Appendix, Fig. 1), decreased our estimates of the isotopic values of water in vegetation and soil in nearly all cases (Fig. 2), reflecting the effect of evaporative enrichment on the water taken up by vegetation. The difference between the original and evaporation-corrected isotope values in the summer drought period also varied along the geographical gradient: the decrease in δ^{18}O at BMR (2.7‰), where lower temperatures and frequent cloud cover likely contributed to lower rates of evaporation, was significantly less than the decrease in δ^{18}O at TP (7.5‰), Four Corners (4C) (8.7‰) or SO Meadow (9.1‰) ($F_{3,100}$ = 20.6; $P < 0.0001$).

Use of fog by vegetation

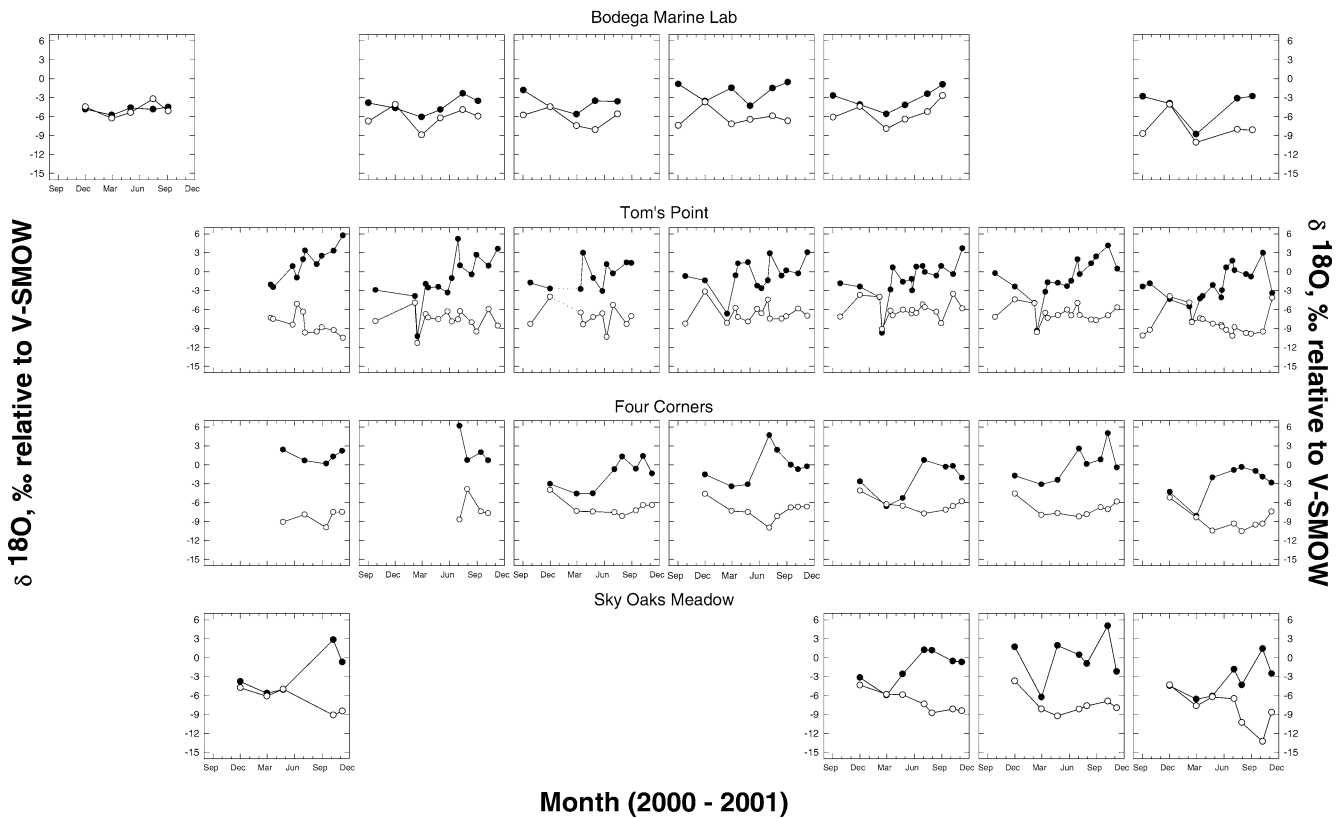After applying the evaporation line to the isotopic content of each plant and soil water sample, output from

Fig. 2 Uncorrected (*filled circle*) and evaporation-corrected (*open circle*) $\delta^{18}O$ values of water in all species and soil at the four sites. See text for description of correction methods

the two-compartment mixing model (Philips and Gregg 2001) confirmed our hypothesis that the perennial grass species at all sites used moisture from fog during the summer drought (May–October 2001) (Figs. 3, 4). The mixing model also indicated that fog contributed a large proportion of water to vegetation in December 2000 (data not shown), although there were no fog events in this time period. Instead, this result was more likely caused by an unusually high $\delta^{18}O$ value in water from a particular storm in the early winter rain season, when isotope values of rain are less distinguishable from fog, as previously shown by Dawson (1998).

We found support for our hypothesis that the importance of fog to the vegetation during the summer drought would vary with distance from the coast ($F_{3,80} = 6.76$, $P < 0.0004$). Fog use at BMR was over 1.5 times higher than at 4C, and two times higher than at SO (Fig. 4). We also found significant differences in the use of fog by various species across all sites ($F_{6,77} = 2.86$, $P < 0.014$; Fig. 4). Mean percent of plant water from fog during the summer drought ranged from 66% by *C. nutkaensis*, a native perennial species whose distribution in California is limited to habitats near the coast and which is not found south of Monterey County, to 28% by *D. californica*. The next highest use of fog after *C. nutkaensis* was by *H. lanatus* and *Festuca rubra*

(Fig. 4). These results are consistent with earlier work in a coastal redwood forest, where species were also found to vary in their fog use (Dawson 1998).

We did not find support for the hypothesis that species whose distributions are limited to coastal habitats would use fog to a greater extent than species that have wider distributions. *C. nutkaensis* used significantly more water from fog than the more widespread species *N. pulchra* or *E. glaucus*, but *D. caespitosa*, another strongly coastal species, did not (Fig. 4). Using a subset of data in order to factor out differences in fog use between species due to the uneven distribution of species across the four sites, two-way ANOVA found that the four species that all occurred at the three most coastal sites (BMR, TP, and 4C)—*D. caespitosa, E. glaucus, F. rubra*, and *H. lanatus*—differed somewhat in their use of fog ($F_{3,47} = 2.21$; $P < 0.098$). Pairwise comparisons indicated that *H. lanatus* relied on fog to a greater extent than *D. californica* and *E. glaucus*; there were no other significant differences between species. This is consistent with information from a variety of sources that suggests *H. lanatus* is sensitive to water availability (e.g. M. Thomsen, unpublished data). Another subset of four species that all occurred at the three most inland sites (TP, and 4C, and SO)—*D. californica, E. glaucus, H. lanatus*, and *N. pulchra*—were not significantly different in their use
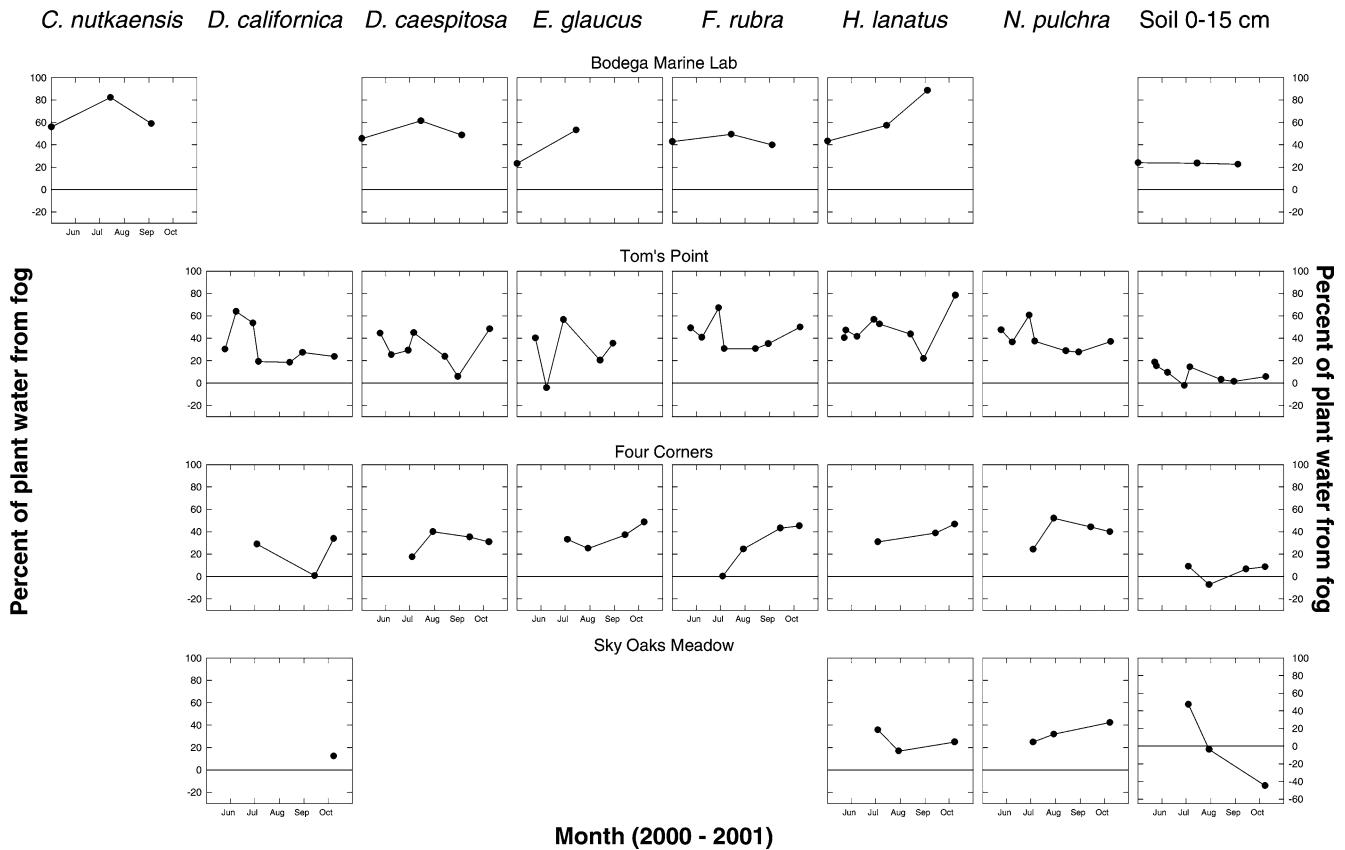
Fig. 3 Percentage of water in vegetation and soil from fog. Note the different scale for percentage of water in soil at SO. See text for description of two-source model used to calculate percentages

of fog ($F_{3,42} = 1.59$; $P < 0.2$) but these sites were generally drier with lower fog inputs in the first place. These results suggest that differences in fog use by species were influenced, in part, by differences in species occurrences across our four sites (Table 1, Fig. 4). It is worth noting, however, that the likelihood of significant differences between species would have been greater had comparisons across all four sites been possible.

We also compared how populations within a species varied in their use of fog during the summer drought. We found marginally significant between-population differences in two species, *D. caespitosa* ($F_{2,11} = 3.06$, $P < 0.09$) and *H. lanatus* ($F_{3,13} = 3.00$, $P < 0.07$): in both cases, there was a non-significant trend of greater use of fog at BMR, decreasing as distance from the coast increased (Fig. 4). There were no other significant differences between populations, though the remaining species exhibited a similar pattern across the coast-inland gradient.

Our estimate of the proportion of water from fog used by vegetation only considers uptake of water through roots, yet fog may influence plant water balance in other ways as well. First, the high humidity, low temperature conditions experienced during fog episodes reduces transpiration and plant water stress (Burgess and Dawson 2004). Second, it is possible that plants are taking up water from fog directly through

their leaves. Plant tissues in our study were not sampled in a way to distinguish the relative importance of foliar versus root uptake of fog water. Evidence from redwood forests suggests that the quantity of water taken up via leaves is likely a much smaller fraction than that taken up through roots (Burgess and Dawson 2004). It is possible, however, that the ecological importance of foliar uptake is greater than its relative quantity if it takes place during periods when plants are especially water stressed. Therefore, our estimates of the importance of fog to coastal prairie vegetation may be conservative, in that they only examine direct fog use via root uptake and not other effects, such as foliar uptake of fog or reduced transpiration, on plant–water relations.

Use of shallow versus deep soil water

We compared $\delta^{18}O$ values of water in *N. pulchra* individuals and in the soil horizon at TP in order to determine the relative importance of shallow versus deep soil horizons for water uptake. The most likely zone of active water use in early (June) and late (November) summer 2002 was at approximately 10 cm depth, in spite of the fact that GWC was greatest at the deepest soil horizons (Fig. 5). This is likely because

Fig. 4 Mean percentage of water in vegetation from fog at each site and in each species during the summer drought (May–October 2001), when fog frequency is highest. Sites: *BMR* Bodega Marine Reserve; *TP* Tom's Point; *4C* Four Corners; *SO* Sky Oaks Meadow. Species: CN *C. nutkaensis*; DAN *D. californica*; DES *D. caespitosa*; EG *E. glaucus*; FR *F. rubra*; HL *H. lanatus*; NP *N. pulchra. Bars with different letters* (A, B, C) in each figure are significantly different from each other
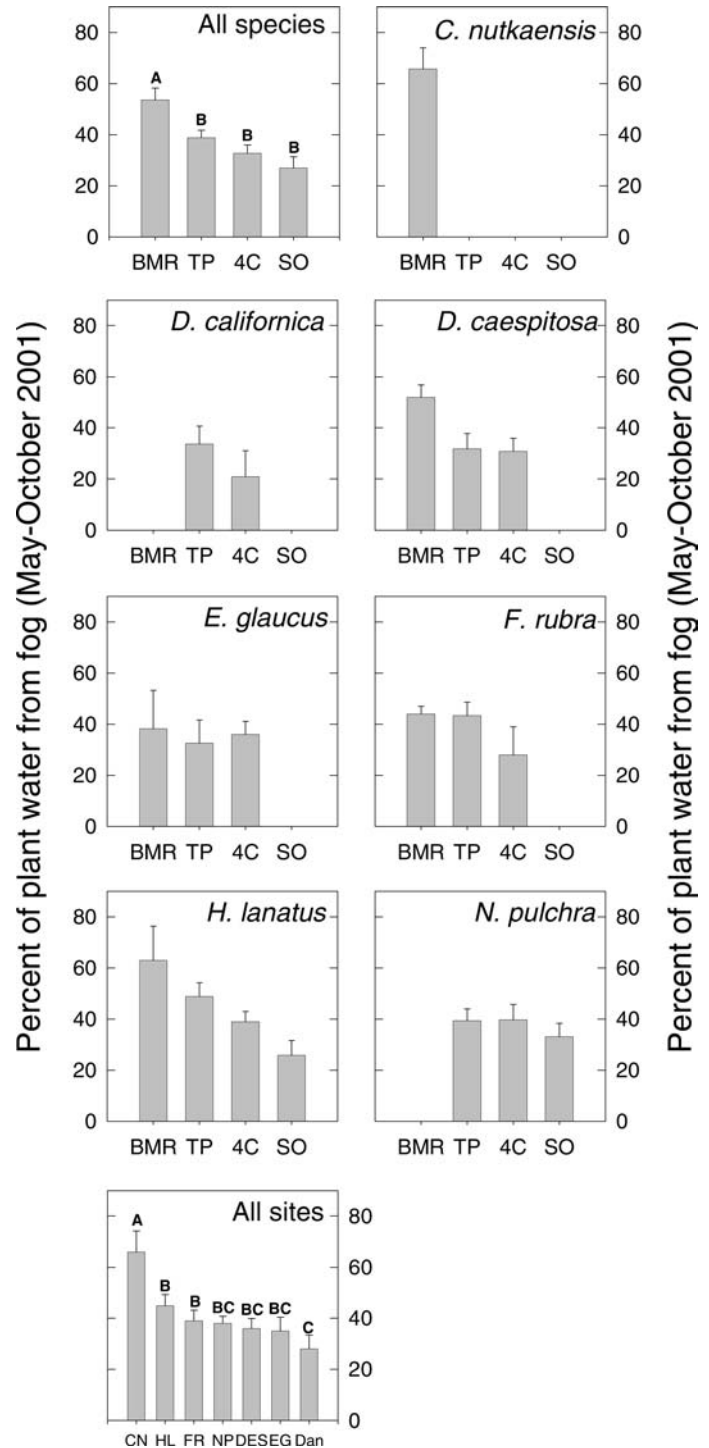
root biomass was greatest in shallow horizons where uptake of fog moisture inputs would be most efficient (Fig. 5). We also found that proportion of water from fog in the top 15 cm of soil was consistently lower than in vegetation at all sites during the summer 2001 (Fig. 3), suggesting that water from fog was available in the shallowest soil horizons. We conclude that *N. pulchra* did not take up water from deeper soil layers, but instead maintained active roots in shallow soil horizons that took advantage of the frequent moisture

inputs from fog. Our findings are consistent with those of Dawson and Pate (1996), working in *Banksia* woodlands, and Williams and Ehleringer (2000), in pinyon-juniper forests, that plants in arid and semiarid ecosystems rely on shallow root water uptake where precipitation is relatively predictable. Coastal prairie grassland species, therefore, may contrast with those in interior California grasslands, where perennial grasses are generally assumed to access water > 0.5 m below the soil surface during the summer (Holmes and Rice
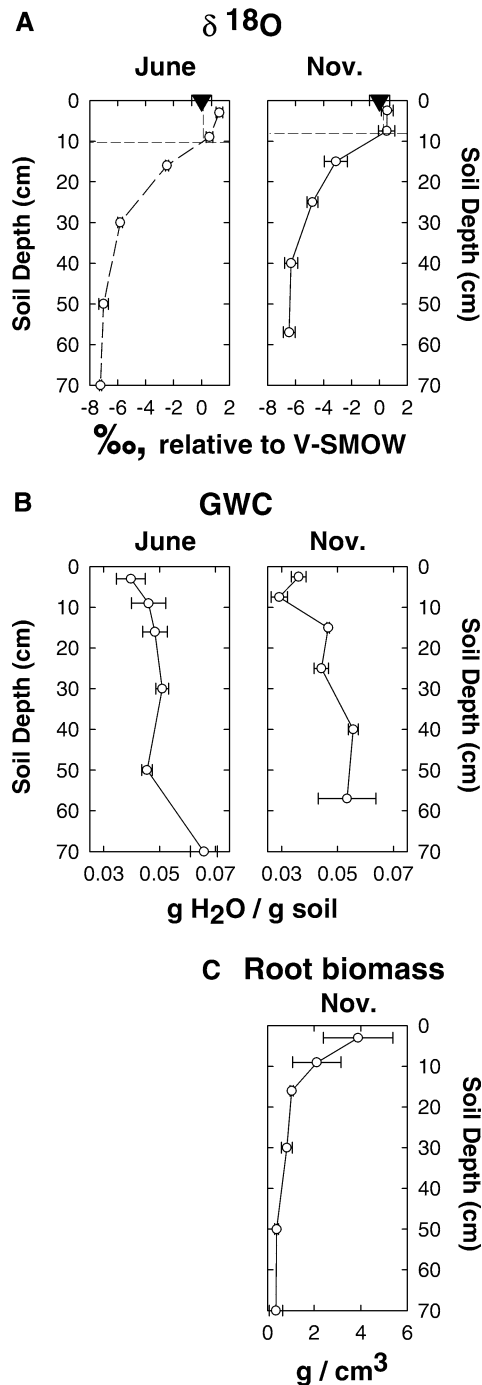
Fig. 5 a Soil water $\delta^{18}O$, **b** GWC, and **c** root biomass through the soil profile (*open circle*) and $\delta^{18}O$ of *N. pulchra* (*filled inverted triangle*) at TP in June and November 2001. *Dashed lines* in (**a**) indicate the match between vegetation isotope values and soil depth, and the most likely zone of water use by *N. pulchra*. Root biomass was only sampled in November 2001. Values are means (*n* = 3) ± 1SE

1996; Dyer and Rice 1999). Reliance on shallow roots to access summer precipitation is likely to vary along gradients of water availability (Ehleringer and Dawson 1992), and vegetation further inland, away from the zone of frequent fog inundation—such as California's Central Valley—is less likely to rely on shallow roots for their primary water acquisition during the summer drought season.

Implications for species distributions and the invasion of exotic species in coastal prairie grasslands

Availability of moisture has frequently been shown to influence species' distributions in other ecosystems (e.g. Barton 1993; Royce and Barbour 2001), and it has been suggested that the distribution of certain vegetation types, including coastal redwood forests (Kerfoot 1968; Azevedo and Morgan 1974; Dawson 1998), Loma vegetation in Peru (Aravena et al. 1989), tropical mountain rainforests (Grubb and Whitmore 1966), and vascular epiphytes in the northeastern United States (Weathers and Likens 1997), may be dependent on the presence of fog. Our results suggest that the grass species that make up coastal prairie grasslands respond individualistically to summer fog through their ranges and exhibit various degrees of dependence on fog. At one extreme, *C. nutkaensis*, which obtained 60–80% of its summertime water from fog at BMR, seems, in California, to be restricted to habitats in which fog inputs are relatively dependable. It is the largest species with the highest leaf area, potentially making it highly susceptible to dessication. At the other extreme, *D. californica* obtained less than 30% of its summertime water from fog across three sites, yet it is an important constituent of many coastal prairie grasslands (Heady et al. 1988). It has relatively narrow leaves, low leaf area and is prostrate, characteristics that might aid in drought avoidance. Species such as *E. glaucus* and *N. pulchra* that are found in both inland habitats such as the Sierra foothills, where there is no summer fog, and coastal prairie grasslands likely differ in their reliance on fog across their range: plants are able to survive where there is no fog, but use fog where it is available.

The ability of coastal prairie grass species to access water during the summer drought likely plays a role in the persistence of remnant patches of native-dominated grasslands in coastal California. The invasion of Eurasian annual grass and forb species has converted grasslands in much of the state from ones dominated by perennial grasses to ones dominated by exotic annual species (Mack 1989). The exotic annual grasses have been shown to suppress native perennial grasses in inland habitats (e.g. Dyer and Rice 1999; Hamilton et al. 1999). In contrast, native perennial bunchgrasses in coastal prairies have been shown to be strong competitors against exotic annual grasses (Corbin and D'Antonio 2004). Fog provides summer moisture inputs that the native perennial species can use and may extend their growing period—a potentially significant advantage over exotic annual species that complete their life cycles in the spring and have died by the summer fog season. It is notable, however, that *H. lanatus*, an exotic perennial grass, used fog. In the last

20 years, exotic perennial grasses including *H. lanatus* have begun to invade a variety of annual-dominated or co-dominated grasslands in coastal ecosystems, raising the possibility that coastal prairies are undergoing another significant compositional shift. Thomsen (unpublished data) has found that *H. lanatus* has high stomatal conductance and is sensitive to water availability in the field. Hence, fog may aid invasion of coastal prairie sites by alleviating water stress. The ability of these perennial grass invaders to use summer moisture inputs from fog, thereby lengthening their growing season and increasing the probability of persistence, may threaten the remnant native-dominated coastal prairie grasslands that have, thus far, been able to resist invasion by exotic annual species.

Appendix

Details of the experiment to estimate the evaporation line: the slope of the change in δ^2H and $\delta^{18}O$ values in water from LMWL as water evaporates

We calculated the slope of the deviation of δ^2H and $\delta^{18}O$ values in water from the LMWL as water evaporates by measuring isotope values in water in soil samples collected as soil moisture evaporated over the course of four separate days at TP (13 June 2002, 25 June 2002, 14 September 2003, and 9 October 2003) and one day at BMR (29 August 2003). On each day, surface soil (0–2 cm depth) was sampled once every 1–2 h in a single 1 m^2 area without vegetation cover. The stable H and O isotopic composition of the water in each soil sample ($n = 32$) was analyzed using methods described above.

The slope of the relationship between δ^2H and $\delta^{18}O$ values of the water in the soil samples as evaporation took place was analyzed using linear regression between δ^2H and $\delta^{18}O$. The resulting "evaporation line" was $\delta^2H = 3.5 \times \delta^{18}O - 33.6$ ($F_{1,31} = 143.7$, $P < 0.0001$; $r^2 = 0.82$; Fig. 1b; Slope SE = 0.3; Intercept SE = 1.6), and represents the pooled effect of evaporation on the isotopic content of water in soil over repeated episodes of evaporation at two different coastal California habitats. The slope of the resulting equation, 3.5, is comparable with estimates of the relationship between δ^2H and $\delta^{18}O$ in other systems, including slopes of 2–5 in an experimental soil column using dune soils, (Allison 1982), and 4.0 in a Mexican aquitard (Ortega-Guerrero et al. 1997). Our

slope and those reported by Allison (1982) and Ortega Guerrero et al. (1997), all using non-saturated soils, are lower than slopes derived from saturated soils or free water bodies (Gonfiantini 1986; Barnes and Turner 1998).

Climatic conditions ranged significantly, from heavy fog cover and high humidity to clear conditions and low humidity, during sampling to determine the evaporation line. Temperature and relative humidity were measured on 14 September and 9 October 2003 at TP using a Hobo data logger (Onset Computer Corp., Bourne, MA, USA). Temperature ranged from 11.4°C to 25.2°C, while relative humidity ranged from 38.1% to 99.1%. Relative humidity, in particular, is known to influence the kinetic fractionation in non-saturated soils (Allison et al. 1983; Barnes and Turner 1998) and, therefore, the slope of the evaporation line. Variation in the slope of the evaporation line as we sampled sites further inland (where humidity is lower) could call into question our conclusion that coastal and inland sites varied in their use of fog if decreasing humidity resulted in a decrease in the slope of the evaporation line. This would cause a spurious pattern of lesser "apparent fog use" in inland sites. However, Allison (1982), examining the effect of humidity on the slope of the δ^2H–$\delta^{18}O$ relationship in sandy, non-saturated columns much like our soils, reported that decreasing humidity resulted in an increase in the slope of the evaporation line, though the effect was small. If we apply Allison's scenario of increasing slopes as we move inland, then we would have found marginally greater differences in fog use between our coastal and inland sites than we found using a single slope.

To test what effect different evaporation conditions might have for our estimates of fog use by coastal prairie vegetation, we simulated shifts of the evaporation line slope to the 95% confidence intervals (slope = 2.9–4.1). Increasing the evaporation line slope from 3.5 to 4.1 decreased mean summer fog use by vegetation ($n = 84$ samples) from 38% to 24%; decreasing the evaporation line slope to 2.9 increased mean fog use to 49%. As a result, while use of a different evaporation line may change the quantitative estimate of plants' fog use, it would likely not influence the conclusion that coastal prairie vegetation relies on summer fog to a considerable extent.

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