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Fluctuating deposition of ocean water drives plant function on coastal sand dunes

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Abstract

Sea-level rise will alter the hydrology of terrestrial coastal ecosystems. As such, it becomes increasingly important to decipher the present role of ocean water in coastal ecosystems in order to assess the coming effects of sea-level rise scenarios. Sand dunes occur at the interface of land and sea. Traditionally, they are conceived as freshwater environments with rain and ground water as the only water sources available to vegetation. This study investigates the possibility of ocean water influx to dune soils and its effect on the physiology of sand dune vegetation. Stable isotopes are used to trace the path of ocean water from the soil to the vegetation. Soil salinity, water content and $\delta^{18}O$ values are measured concurrently with stem water and leaf tissue of eight species during the wet and dry season and from areas proximal and distal to the ocean. Our results indicate the dune ecosystem is a mixed freshwater and marine water system characterized by oceanic influence on dune hydrology that is spatially heterogeneous and fluctuates temporally. Ocean water influx to soil occurs via salt spray in areas 5–12 m from the ocean during dry season. Accordingly, vegetation nearest to the sea demonstrate a plastic response to ocean water deposition including elevated integrated water use efficiency ($\delta^{13}C_{leaf}$) and uptake of ocean water that comprised up to 52% of xylem water. We suggest physiological plasticity in response to periodic ocean water influx may be a functional characteristic common to species on the leading edge of diverse coastal habitats and an important feature that should be included in modeling coastal ecosystems. Rising sea level would likely cause a repercussive landward shift of dune species in response to encroaching maritime influences. However, human development would restrict this process, potentially causing the demise of dune systems and the protection from land erosion they provide.

Keywords: coastal ecology, eco-physiology, island ecology, ocean water, oxygen isotopes, plant distribution, sea-level rise, water sources

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Introduction

As global warming proceeds, sea levels are predicted to continue rising driven by both thermal expansion of ocean water and melt water from the polar ice caps (Hegerl & Bindoff, 2005). Coastal dunes will be among the first ecosystems threatened by sea-level rise (Feagin *et al.*, 2005), a process that will erode coastlines. Sand dune ecosystems protect many coastlines from erosion by mitigating energetic and potentially catastrophic surges of ocean water from daily wave action and storm events (Liu *et al.*, 2005). Vegetation plays a valuable role in dune stabilization. Roots bind sandy soils, a process that promotes dune building by way of sand accretion and decreases sediment flow into near-shore ocean environments. Rising sea levels will also increase oceanic influence on terrestrial hydrology. Soil hydrology is known to be an important environmental variable that affects the distribution, water relations and survivorship of vegetation in coastal ecosystems including salt marshes, mangroves and hardwood forests (White, 1983; Haines & Dunn, 1985; Sternberg & Swart, 1987; Williams *et al.*, 1999). However, clear links between hydrologic conditions, the distribution of vegetation and the physiology of vegetation on coastal dunes have yet to be established.

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Tropical and temperate dunes alike exhibit zonal distributions of plant species from the ocean toward the inland (Cowels, 1899; Doing, 1985; Barbour, 1992; Reinert *et al*., 1996; Musila *et al*., 2001; Greaver, 2005). Zonal distribution is characteristic of ecotonal communities and is driven by gradients of environmental factors across the dune. One such driving factor is ocean water, which may deposit more salt to proximal soils causing salinity gradients to occur across the dune. However, since the turn of the 20th century, debate has ensued over the importance of soil salinity in driving the distribution of coastal dune vegetation (Oosting & Billings, 1942; Van der Valk, 1974; Maun & Perumal, 1999; Wilson & Sykes, 1999). This debate has been fueled by inconsistent observations among investigators who alternatively supported and reproved the notion that gradients of soil salinity even existed (Kearny, 1904; Boyce, 1954; Wilson & Sykes, 1999). The conflicting reports suggest that salinity gradients may not be a permanent feature of dune ecosystems.

The function of ocean water on dune ecosystems beyond its role in salt deposition is not well investigated. Traditionally, dunes are conceived as environments with only freshwater sources, where plants uptake rain or ground water to fuel the transpiration stream and metabolic processes. However, ocean water may be present in dune soil where it would be taken up by vegetation and influence plant physiology. Evidence for ocean water in dune soils would offer new directions to more accurately incorporate dunes into models that investigate the effects sea-level rise on terrestrial ecosystems.

Here, we propose that ocean water influx to soil forms an ephemeral gradient creating spatial and/or temporal fluctuations of salinity and ocean water content that drive plant function. We use stable isotopes as a water tracer to link soil hydrology and plant physiology by identifying sources of water in the environment taken up by dune vegetation. We proceed to determine if the water sources accessed by a plant species affects its water use efficiency (WUE). Specific hypothesis are: (1) soil pore water salinity and proportion of ocean water will fluctuate spatially (horizontally and vertically) and temporally, (2) plant water source will differ between season, species and with proximity to the ocean, (3) plant WUE, as measured by δ^{13}C values of leaf tissue, will depend on water source.

Methods

Site description

The coastal dune systems studied was Bill Baggs (25°68′N, 80°15′W) in Key Biscayne, Florida. Key Biscayne (KB) is a coastal barrier island located in the outer margin of the south Florida inner continental platform (Enos, 1977). This site is characterized by low elevation and gently sloping geomorphology; the highest elevation is 1.86 m above sea-level and the water table is horizontal across the dune at a depth equal to sea-level (Greaver, 2005). The dune makes a transition into upland hammocks, is characterized by quartz and carbonate soil and a humid subtropical climate with approximately 1325 mm of annual precipitation, of which 80% occurs from June to November.

Stem, soil and water collection and δ^{18}O analysis

All stem, soil and water samples were collected in October 2001 (wet season) and February 2002 (dry season), except for rain water which was collected over the period of July–October for the wet season and October–February for the dry season.

The first 5–12 m inland above the high-tide mark was designated the fore dune (FD). The distance between the onset of vegetation and inland boundary of the dune is 60 m, therefore the segment between 45 and 55 m from the high-tide mark was designated the back dune (BD). The spatial component of distance from the ocean is represented by the FD and BD positions that are the extremes of a potential gradient across the dune.

For each dune position and season, three soil cores were made 30 m apart in a transect running parallel to the ocean ($N = 6$ cores season^{-1}). Soil samples were collected by a sand auger through the vadose layer, from 0.1 m depth to the level of water saturation. Samples were divided at the time of collection into separate vessels to measure conductivity, gravimetric content and stable isotope ratios of soil water. Soil samples were weighed and then dried at 60 °C for 5 days to calculate the gravimetric water content (θ_m), according to the definition of Or & Wraith (2001). After samples were dried, 10 mL of deionized water was added and agitated for 1 min before measurement of the electrical conductivity (μS) of the soil water (Oakton portable conductivity meter (Oakton Instruments, Vemon Hills, IL, USA)). Salinity (ppt) was calculated from conductivity and soil water content Alpha *et al*., 1996). Three-way ANOVAS (JMP Version 4.0.4, SAS Institute, Cary, NC, USA) tested the effects of depth, dune position, season and their interactions on the moisture content and salinity of soils at each site.

Stem and leaf samples were collected from four species in the FD and four different species in the BD. Species were selected to represent the vegetation association in each dune position and they were chosen based on their distribution (Greaver, 2005). For example, a species collected in the FD either only occurred within the FD or occurred in the FD in the greatest abundance compared with other dune positions. FD species were: *Ipomoea pes-caprae* (L.) R. Br., *Iva imbricata* Walter., *Scaevola plumieri* (L.) Vahl and *Sesuvium portulacastrum* (L.) L. BD species were: *Caesalpinia bondoc* (L.) Roxb., *Coccoloba uvifera* (L.) L., *Lantana involucrata* L. and *Suriana maritima* L. During each season, four stem samples were collected from each species, placed in pyrex tubes and sealed by threaded caps that were secured with parafilm for transport to the lab where the samples were frozen until analysis. To prevent water loss from the stems by evaporation/transpiration, care was taken to collect well-suberized stems.

Water was distilled from the soil and stem samples by vacuum distillation (Sternberg *et al*., 1986) for isotopic analysis. Oxygen isotope ratios of water were determined by a technique originally developed by Epstein & Mayeda (1953), modified so that a 1 mL aliquot of the sample water was equilibrated with 5 mL of CO_2 gas for 2 days at 25 °C. The CO_2 was then extracted by cryogenic distillation and its isotopic value measured using an isotope-ratio gas mass spectrometer (VG Prism, Micromass, Middlebury, UK) with a precision of ± 0.1‰. Isotopic values were expressed in δ units, described by the following equation:

$$\delta(‰) = \left[\frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}} - 1\right] \times 1000, \qquad (1)$$

where R_{sample} represents the molar ratio of heavy to light isotope and R_{standard} is the molar ratio of the Vienna-Standard Mean Ocean Water (V-SMOW). Meaningful statistical comparisons of δ^{18}O values of soil water cannot be made among seasons because the δ^{18}O values of environmental source waters shift. The within season affect of dune position and depth on the δ^{18}O value of soil water is tested using a two-way ANOVA.

Mixing model

Traditionally, it was difficult to determine stem water composition of vegetation in a system with more than two water sources because of the 2*n*-member limitation of mass-balance mixing models. However, a recently published three-source mixing-model (Zencich *et al*., 2002) allows us to calculate the relative contribution of ground water (saturated region of the soil), rain water and ocean water to stem water from the δ^{18}O value of the stem water. This model does not give a discrete solution, but calculates a range of possible solutions. If the mixing model yielded a range of possible solutions in which the lower limit is zero, we conclude the species was not an obligate user of ocean water.

Leaf collection and δ^{13}C analysis

Integrated WUE by δ^{13}C analyses was measured for leaves collected from five different individuals of each species for which stems were collected. Leaves were collected from terminal internode positions because those were most likely borne during the season in which they were collected. If a species had very small leaves, then several leaves from the same individual were collected and ground together to be counted as one sample. Leaves were dried for 3 days at 50 °C then ground to mesh 20. CO_2 was extracted and purified from approximately 5 mg of biomass tissue based on the methods of Buchanan & Corcoran (1959).

Carbon isotope ratios of the purified CO_2 were measured by mass spectrometry (VG Prism, Micromass) in delta units (Eqn (1)), where R_{sample} represents the molar ratio of heavy to light isotope and R_{standard} is the molar ratio of *Belemnita americana* fossil carbonate from the Pee Dee geological formation in South Carolina (PDB). The precision of analysis is ± 0.1‰ (1σ). Two-way nested ANOVA tested the effects of season, dune position and species nested within dune position on δ^{13}C values.

Results

Depth of soil sample has a significant effect on soil water content at all sites (three-way ANOVA, $P < 0.0001$). Water content is least in the shallow soil samples (~3%) and greatest in the deepest soil layers (~25%) (Fig. 1). There is no significant effect of dune position or season on water content of the soil (three-way ANOVA, $\alpha = 0.05$). Salinity of soil water shows significant effects of the interaction between season and dune position ($P < 0.001$, Table 1). The FD is significantly more saline during the dry season across all depths (19.38 ± 1.08 ppt) than the BD during both seasons and the FD during the wet season (BD wet = 1.89 ± 0.13 ppt, BD dry = 1.90 ± 0.10 ppt and FD wet = 2.69 ± 0.15 ppt; Tukey–Kramer HSD, $\alpha = 0.05$). Both dune position and depth have a significant effect on δ^{18}O value of soil water during dry season (Fig. 1, two-way ANOVA, $P < 0.01$). During the dry season, the average δ^{18}O of soil water across all depths is significantly more enriched in the fore than BD (FD = 0.7‰, BD = −1.6‰, Tukey–Kramer HSD, $\alpha = 0.05$, $P \leq 0.05$) and δ^{18}O values are more enriched in shallow soils. There is no significant effect of dune position or depth during the wet season.

The mixing model yields zero as a possible solution for the ocean water component of stem water for all FD and BD species during the wet season (Fig. 2). We interpret the results of the model conservatively, so that if zero is in the range of solutions we conclude that the

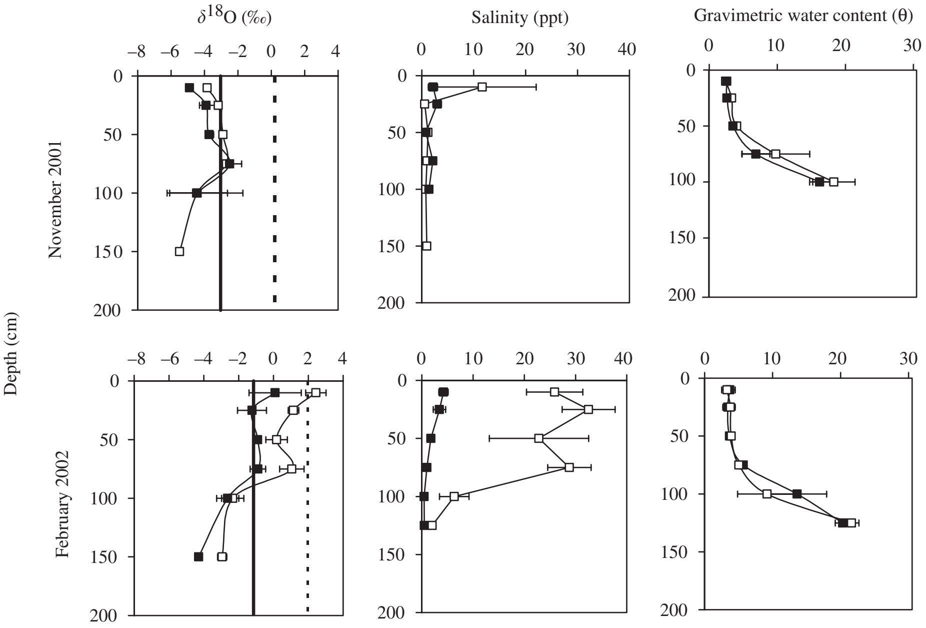

Fig. 1 Soil profiles of δ^{18}O values and salinity in the wet season (November 2001) and the dry season (February 2002). Markers indicate the mean value ($N = 3$) and ±1 SE. Fore dune is indicated by open squares (□) and back dune is indicated by closed squares (■). The stippled line (- - - -) indicates δ^{18}O value of ocean water and the solid line (——) indicates δ^{18}O value of rain water. The signature of source water changes between seasons.

water source in question is not used. In contrast, the δ^{18}O values of three out of four species in the FD suggest ocean water is a component of the stem water during the dry season. The minimum percentage of ocean water in the stem water is 4% for *S. portulacastrum*, 14% for *S. plumieri* and 52% for *I. pes-caprae* (Fig. 2).

There is a significant effect of dune position, species nested within dune position and the interaction between dune position and season on the δ^{13}C values of leaf tissue (two-way nested ANOVA, $P<0.01$, Table 1). The leaves from species in the FD during both seasons had significantly more enriched δ^{13}C values (FD wet = −27.1 ± 0.19‰ and FD dry = −26.2 ± 0.19‰) than the BD during both seasons (BD wet = −28.8 ± 0.19‰, BD dry = −29.1 ± 0.10‰, Tukey–Kramer HSD, $\alpha = 0.05$). There was no significant difference between wet and dry season in the BD, but δ^{13}C values were significantly more enriched in the FD during the dry season than the wet season (Tukey–Kramer HSD, $\alpha = 0.05$).

Discussion

The results provide strong evidence that spatial gradients and temporal fluctuations of ocean water deposition into soils drive the water uptake patterns and WUE of dune vegetation. During the wet season there is no difference in the salinity of soil pore water with respect to distance from the ocean, however during the dry season the FD is significantly more saline than the BD (Fig. 1). These episodes of high salinity found closest to the ocean cause the formation of an ephemeral gradient of soil salinity. The periods of drought during the dry season may facilitate the accumulation of salt from ocean water spray within the soil, which would otherwise be leached out by rainfall (Kearny, 1904; Boyce, 1954).

The enriched δ^{18}O values of soil water in the FD give further evidence that ocean water mixes into the soil profile during the dry season. There are two possible causes of enriched δ^{18}O values of soil water: ocean water deposition or evaporative enrichment. Ocean water is more enriched than either rain or ground water, thus ocean water input into surface soils by sea spray would cause enrichment of soil water. Likewise, the process of evaporation causes enrichment of δ^{18}O values because the heavier ^{18}O accumulates in the soil as the lighter ^{16}O preferentially moves out of the soil profile and into the gaseous stage (Allison *et al*., 1983). The BD experiences higher air deficit saturation and air temperature, two factors that cause elevated levels of evaporation from the soil surface and would cause isotope enrichment equal to or greater than that of the FD (Greaver, 2004). However, we conclude that evaporation is not the cause of the enriched δ^{18}O values of soil water in the FD during the dry season because significant enrichment of δ^{18}O values is not observed in the BD. Instead, the evidence supports the elevated

Table 1 ANOVA results for soil and leaf characteristics. (A) Two-way nested ANOVA for the effects of season, dune position, depth and their interactions on the salinity of soil water, (B) two-way ANOVA for δ^{18}O value of vadose soil water during the wet and dry season, (C) two-way nested ANOVA table for δ^{13}C value of leaf tissue from fore and back dune species during the wet and dry season

	R^2 adjusted	df	Sum of squares	P-value
***(A)** Soil salinity*				
Whole model	0.68	9	6146.81	<0.001*
Error			1651.74	
Effects test				
Season		1	82.21	0.17
Dune position		1	99.47	0.1335
Depth		4	219.28	0.28
Season × dune position		1	646.81	0.0004*
Season × depth		4	90.01	0.71
Depth × dune position		4	337.05	0.11
Depth × dune position × season		4	299.19	0.15
***(B)** δ^{18}O soil water*				
Wet Season				
Whole model	0.29		22.74	0.072
Error			23.61	
Effects test				
Dune position		1	1.88	0.22
Depth		5	13.94	0.02*
Depth × dune position		5	1.60	0.71
Dry Season				
Whole model	0.65		125.58	<0.0001*
Error			38.14	
Effects test				
Dune position		4	20.34	0.0024*
Depth		1	93.50	<0.0001*
Depth × dune position		4	4.72	0.73
***(C)** δ^{13}C leaf tissue*				
Whole model	0.64	13	5798.72	<0.0001*
Error			2300	
Effects test				
Season		1	5.56	0.71
Dune position		1	93.42	0.1445
Species nested within dune position		6	2015.91	<0.0001*
Season × dune position		1	1952.73	<0.0001*

*Significance ($\alpha = 0.05$) designated by asterisk.

δ^{18}O values of soil water in the FD are due to ocean water deposition in the soil that likely accumulates between rainfall events during the dry season.

The presence of ocean water in the soil profile is directly linked to the presence of ocean water in the xylem of FD vegetation, as a result water uptake by the FD and BD species differ between seasons. During the wet season both FD and BD vegetation use mixtures of ground and rain water (Fig. 2). BD species continue to take up freshwater sources in the dry season and all species exhibit the same water harvesting strategy (Fig. 2). This result is consistent with that reported for four species of phanerophytes in Mediterranean consolidated dunes that also used freshwater during the wet and dry periods, however, those species used water exclusively from the water table (Alessio *et al.*, 2004). In comparison, when ocean water is present in the upper 100 cm of the FD soil during the dry season there is a concomitant enrichment of the δ^{18}O values of stem water in three out of four FD species tested, indicating up to 52% ocean water in the xylem for one of the species. The uptake of ocean water by dune vegetation has not been previously reported.

WUE of leaves further illustrates the physiological response of dune species to ocean water in the soil. Stable isotopes of C (δ^{13}C) provide information about the WUE of a plant based on stomatal control that is integrated over the lifespan of a leaf. In general, less

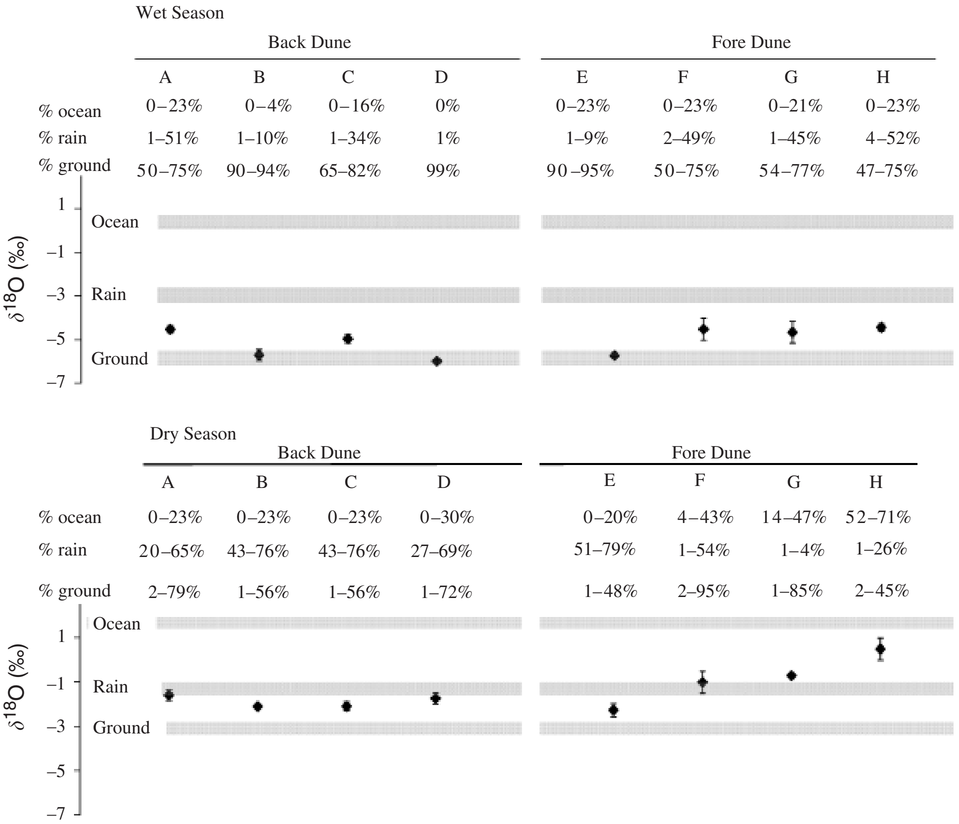

Fig. 2 The δ^{18}O value of stem water and percentage uptake of source waters by fore and back dune vegetation at Bill Baggs State Park, Florida. Markers (◆) indicate mean δ^{18}O values and error bars denote ±1 SE. Gray bars indicate the δ^{18}O value of source waters, note these values change between seasons. Percentage ocean, ground and rain water indicate the values of source water that compose the stem water as calculated by the three-component mixing model. The zeros indicate the water source was may not be present in the stem water, while ranges indicate the water source was taken up by the species. Species are designated by the following letters: A, *Caesalpinia bondoc*; B, *Coccoloba uvifera*; C, *Lantana involucrata*; D, *Suriana maritima*; E, *Iva imbricata*; F, *Sesuvium portulacastrum*; G, *Scaevola plumieri*; H, *Ipomoea pes-caprae*.

negative δ^{13}C values indicate higher WUE (Farquhar *et al*., 1982). FD species have leaf tissue with δ^{13}C values that indicate greater WUE than BD species for both seasons (Fig. 3). During the wet season soil hydrology and xylem water are not significantly different between the FD and BD, therefore, the FD species may have inherently higher WUE than those species in the BD under the same environmental conditions. Alternatively, the elevated WUE of the FD species may be in response to ephemeral periods of high salinity that occurred during the wet season, but before the sampling date. In comparison, during the dry season leaves of the FD species have less negative δ^{13}C values, and therefore higher integrated WUE, than the same species during the wet season. Because there is no difference in soil moisture content (Fig. 1), these results indicate that elevated soil salinity is the most probable cause of increased WUE by FD vegetation. This observation is consistent with a greenhouse study of *Scaevolea sericea*, a dune shrub common in Hawai'i, in which elevated soil salinity caused higher integrated WUE (Alpha *et al*., 1996).

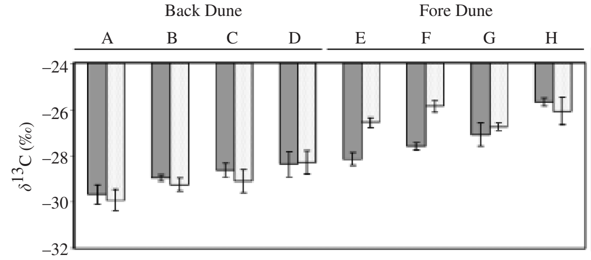

Fig. 3 The mean ±1 SE of δ^{13}C values of leaf tissue that were collected from fore and back dune species. Samples collected from the wet season are dark gray and those collected in the dry season are light gray. Species are designated by the following letters: A, *Caesalpinia bondoc*; B, *Coccoloba uvifera*; C, *Lantana involucrata*; D, *Suriana maritima*; E, *Iva imbricate*; F, *Sesuvium portulacastrum*; G, *Scaevola plumieri*; H, *Ipomoea pes-caprae*. $N = 5$ for each bar.

The synthesis of soil hydrology, xylem water and WUE of leaves is an effective approach to understand the soil–plant continuum on coastal dunes. The results indicate that WUE is lowest for BD species even when soil conditions are constant across the dune, suggesting that species on the BD uptake water from the water table that is consistently abundant and nonsaline. In contrast, ocean water input causes elevated soil salinity near the ocean, thereby creating a spatial gradient across the dune during the dry season. FD vegetation respond to the elevated salinity with physiological plasticity that is demonstrated by their ability to both uptake ocean water and improve WUE during the dry season. Many environmental factors influence distribution and succession on coastal dunes (Van der Putten *et al*., 1993; Henriques & Hay, 1998; Garcia-Mora *et al*., 1999). Wilson & Sykes (1999) suggest soil salinity is the most dominant influence on species distribution in coastal dunes of New Zealand. In support of their observation, we show that plant species make physiological adjustments to tolerate periods of high soil salinity that occur in the FD. It is likely that BD species are unable to thrive in FD areas that become very saline during the dry season, and soil salinity may inhibit the establishment of young seedling that have poorly developed root systems, as is suggested to occur in salt marshes (Young *et al*., 1994).

Mangrove ecosystems are similar to dunes because they also occur at the interface of land and sea. However, mangroves typically grow along shores with low energy waves where soil is often flooded for long periods of time by up to several meters of water. In mangroves, ocean water flooding occurs in fringe habitats nearest to the ocean causing elevated soil salinity and subsequent physiological adjustment by vegetation. Like dunes, mangrove species living close to the ocean can use both ocean water and freshwater; however, they are restricted to the shoreline, likely out competed in the inland environments by hardwood hammock species that uptake only freshwater (Sternberg & Swart, 1987). Thus, an overarching pattern emerges for the distribution of species in coastal ecosystems that is consistent between dunes and mangroves. Species that live closest to the ocean have the ability to take up mixtures of ocean water and freshwater and demonstrate physiological plasticity in response to periodic salinity. Additional investigation would test whether this pattern is common to all coastal ecosystems.

As discussed, our results indicate ocean water plays an important role in the structure and function of dune ecosystems, especially during the dry season. El-Niño Southern Oscillation (ENSO) events have been tightly coupled with precipitation anomalies within the global tropics, some geographic areas receive above-average precipitation while others experience drought (Lyon, 2004). It is predicted that global climate warming will cause ENSO events to become more frequent (Tsonis *et al*., 2005). In south Florida, ENSO events cause above-average precipitation during the dry winter months (Cronin *et al*., 2002). In contrast, many coastal areas in southern Mexico, along the NE coast of South America and the SE coast of Africa experience more severe droughts associated with ENSO events (Lyon, 2004). The dune ecosystem accumulates salty ocean water in the absence of rain during dry periods; therefore any pronounced decrease in rainfall would likely elevate levels of salinity and create additional stress for dune species.

Climate warming scenarios also predict sea-level rise, a process that will shift the interface between land and sea, resulting in the inland extension of maritime related flooding and elevated soil salinities. After examining sea-level rise over the last 100 years, Williams *et al*. (1999) conclude the increased soil salinity, not flooding, that occurs during sea-level rise inhibits hammock tree species from regenerating and drives their retreat further inland. Sand dunes will likely follow a similar process of retreat. Depending on the pace of rise, the salt tolerant species of the leading edge could respond to the encroaching sea by establishing further inland as conditions give them the competitive edge in these previously freshwater-species dominated areas. Rising sea level would likely cause a repercussive landward shift of all dune species; however future work focused on salinity tolerance thresholds of individual species would improve predictions of how this shift may proceed. Unfortunately, many coastlines are developed by human settlement immediately landward of the dunes. Therefore, the space required for the dune species to proceed through succession via reproduction, dispersal and growth is likely unavailable (Feagin *et al*., 2005). In such a case the dune plants and the protection from land erosion they provide will likely disappear between the sea and human settlement.

References

Alessio GA, De Lillis M, Brugnoli E *et al*. (2004) Water sources and water-use efficiency in Mediterranean coastal dune vegetation. *Plant Biology*, **6**, 350–357.

Allison GB, Barnes CJ, Hughes MW (1983) The distribution of deuterium and ^{18}O in dry soils. 2. Experimental. *Journal of Hydrology*, **64**, 377–397.

Alpha CG, Drake DR, Goldstein G (1996) Morphological and physiological responses of *Scaevola sericea* (Goodeniaceae) seedlings to salt spray and substrate salinity. *American Journal of Botany*, **83**, 86–92.

Barbour MG (1992) Life at the leading edge: the beach plant syndrome. In: *Coastal Plant Communities of Latin America* (ed. Seeliger U), pp. 291–307. Academic Press Inc., London, UK.

Boyce SG (1954) The salt spray community. *Ecological monographs*, **24**, 29–67.

Buchanan DL, Corcoran EJ (1959) Sealed tube combustion for the determination of ^{14}C and carbon isotopes. *Annals of Chemistry*, **31**, 1635–1638.

Cowels HC (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. The Botanical Gazette 27. In: *Foundations of Ecology: Classic Papers with Commentaries* (eds Real LA, Brown JH), pp. 95–117. The University of Chicago Press, Chicago, USA.

Cronin TM, Dwyer GS, Schwede SB *et al*. (2002) Climate variability from the Florida Bay sedimentary record: possible teleconnections to ENSO, PNA and CNP. *Climate Research*, **19**, 233–245.

Doing H (1985) Coastal fore-dune zonation and succession in various parts of the world. *Vegetatio*, **61**, 65–75.

Enos P (1977) Holocene sediment accumulations of the south Florida shelf margin. In: *Quaternary Sedimentation in South Florida, Part I* (eds Enos P, Perkins RE), pp. 1–130. Geological Society of America Memoir, Boulder, CO, USA.

Epstein S, Mayeda T (1953) Variation of ^{18}O content of water from natural sources. *Geochimica Cosmochimica Acta*, **42**, 213–224.

Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, **9**, 121–137.

Feagin RA, Sherman DJ, Grant WE (2005) Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. *Frontiers in Ecology and the Environment*, **3**, 359–364.

Garcia-Mora MR, Gallego-Fernandez JB, Gracia-Novo F (1999) Plant functional types in coastal foredunes in relation to environmental stress and disturbance. *Journal of Vegetation Science*, **10**, 27–34.

Greaver TL (2004) Heterogeneous reflected light influences asymmetry in leaf anatomy and gas exchange. *American Journal of Botany*, **91**, 1998–2001.

Greaver TL (2005) Booktitle: Eco-hydrology and physiological water relations of vegetation along coastal dune ecotones on subtropical islands. Dissertation, University of Miami, Coral Gables, FL.

Haines BL, Dunn EL (1985) Coastal marshes. In: *Physiological Ecology of North American Plant Communities* (eds Chabot BF, Monney HA), pp. 323–341. Chapman & Hall, New York.

Hegerl GC, Bindoff NL (2005) Warming the World's Oceans. *Science*, **309**, 254–255.

Henriques RPB, Hay JD (1998) The plant communities of a foredune in southeastern Brazil. *Canadian Journal of Botany*, **76**, 1323–1330.

Kearny TH (1904) Are plants of sea beaches and dunes true halophytes. *Botanical Gazette*, **37**, 424–436.

Liu PL-F, Lynett P, Fernando H *et al*. (2005) Observations of the international tsunami survey team in Sri Lanka. *Science*, **308**, 1595.

Lyon B (2004) The strength of El Niño and the spatial extent of tropical drought. *Geophysical Research Letters*, **31**, L21204.

Maun MA, Perumal J (1999) Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. *Ecology Letters*, **2**, 14–18.

Musila WM, Kinyamario JI, Jungerius PD (2001) Vegetation dynamics of coastal sand dunes near Malindi, Kenya. *African Journal of Ecology*, **39**, 170–177.

Oosting JH, Billings WD (1942) Factors effecting vegetational zonation on coastal dunes. *Ecology*, **23**, 131–142.

Or D, Wraith JM (2001) Soil water content and water potential relationships. Chapter 3. In: *Soil Physics Companion* (ed. Warrick EW), pp. 49–82. CRC Press LLC, Boca Raton, FL, USA.

Reinert F, Roberts A, Wilson JM *et al*. (1996) Gradation in nutrient composition and photosynthetic pathways across the restinga vegetation of Brazil. *Botanica Acta*, **110**, 135–142.

Sternberg L da SL, DeNiro MJ, Johnson HB (1986) Oxygen and hydrogen isotope ratios of water from photosynthetic tissues of CAM and C_3 plants. *Plant Physiology*, **82**, 428–431.

Sternberg LdSL, Swart PK (1987) Utilization of freshwater and ocean water by coastal plants of Southern Florida. *Ecology*, **68**, 1898–1905.

Tsonis AA, Elsner JB, Hunt AG *et al*. (2005) Unfolding the relation between global temperature and ENSO. *Geophysical Research and Letters*, **32**, L09701.

Van der Putten WH, Van Dijk C, Peters BAM (1993) Plant-specific soil-borne diseases contribute to succession in fore-dune vegetation. *Nature*, **362**, 53–56.

Van der Valk AG (1974) Environmental factors influencing the distribution of forbes on coastal fore dunes on Cape Hatteras National Seashore. *Canadian Journal of Botany*, **52**, 1057–1073.

White DA (1983) Plant communities of the lower Pearl River basin, Louisiana. *American Midland Naturalist*, **110**, 381–396.

Williams K, Ewel KC, Stumpf RP *et al*. (1999) Sea-level rise and coastal forest retreat on the west coast of Florida, USA. *Ecology*, **80**, 2045–2063.

Wilson JB, Sykes MT (1999) Is zonation on coastal sand dunes determined primarily by sand burial or by salt spray? A test in New Zealand dunes. *Ecology Letters*, **2**, 233–236.

Young DR, Erickson DL, Semones SW (1994) Salinity and small-scale distribution of the barrier island shrubs. *Canadian Journal of Botany*, **72**, 1365–1372.

Zencich SJ, Froend RH, Turner JV *et al*. (2002) Influence of groundwater depth on the seasonal sources of water accessed by *Banksia* tree species on a shallow sandy coastal aquifer. *Oecologia*, **131**, 8–19.