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Responses of woody species to spatial and temporal ground water changes in coastal sand dune systems

C. Máguas¹, K. G. Rascher^{1,3}, A. Martins-Loução¹, P. Carvalho^{1,2}, P. Pinho¹, M. Ramos¹, O. Correia¹, and C. Werner³

¹Centre for Environmental Biology (CBA), Faculty of Sciences (FCUL), University of Lisbon, FCUL, Campo Grande, Ed. C2, 5 Piso, Campo Grande 1749-016 Lisboa, Portugal

²Division of Plant and Crop Sciences, University of Nottingham, MM, UK

³Experimental and Systems Ecology, University of Bielefeld, Universitätsstrasse 25, 33615 Bielefeld, Germany

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Correspondence to: C. Máguas (cmhanson@fc.ul.pt)

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Abstract

In spite of the relative importance of groundwater in coastal dune systems, the number of studies concerning the responsiveness of vegetation to ground water (GW) variability, in particularly in Mediterranean regions, is scarce. In this study, we established 5 study sites within a meso-mediterranean sand dune *Pinus pinaster* forest on the Atlantic coast of Portugal, taking advantage of natural topographic variability and artificial GW exploitation, which resulted in substantial variability in depth to GW between microsites. Here we identify the degree of usage and dependence on GW of different plant functional groups (two deep-rooted trees, a drought adapted shrub, a phreatophyte and a non-native woody invader) and how GW dependence varied seasonally and between the heterogeneous microsites. Our results indicated that the plant species had differential responses to changes in GW depth according to specific functional traits (i.e. rooting depth, leaf morphology, and water use strategy). The species comparison revealed that variability in pre-dawn water potential (Ψ_{pre}) and bulk leaf $\delta^{13}C$ was related to microsite differences in GW use in deep-rooted (*Pinus pinaster*, *Myrica faya*) and phreatophyte (*Salix repens*) species. However, such variation was more evident during spring rather than during summer drought. The exotic invader, *Acacia longifolia*, which does not possess a very deep root system, presented the largest seasonal variability in Ψ_{pre} and bulk leaf $\delta^{13}C$. In contrast, the response of *Corema album*, an endemic understory drought adapted shrub, across seasons and microsites seemed to be independent of water availability. Thus, the susceptibility to changing GW availability in sand dune plant species is variable, being particularly relevant for deep rooted species and phreatophytes, which have typically been less exposed to GW fluctuations.

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1 Introduction

Vegetation-groundwater interactions are the focus of renewed interest, particularly in semi-arid areas, reflecting the current trend towards a more holistic approach and integrated management of natural resources. Successful conservation of forests and ecosystems requires knowledge on the dependency of vegetation on groundwater (GW) availability and on the feedback between plant functioning and GW. GW extraction and surface water diversions produce dramatic changes in stand structure and species composition (e.g. Valentini et al., 1995; Stromberg et al., 1996; Stromberg and Patten, 1990; Lite and Stromberg, 2005) thereby significantly altering groundwater-dependent ecosystems (e.g. Murray et al., 2003; Lamontagne et al., 2005). To date, very few studies have had the opportunity to use artificial lowering of GW levels at the ecosystem scale, in order to monitor the plant community response to changing groundwater levels (e.g. Stromberg and Patten, 1990). Since 2001, a pine forest, located in the western coastal region of Portugal, has been subjected to artificial lowering of the groundwater table, as a result of industrial water exploitation. This large scale manipulation of the groundwater reservoir provides excellent experimental conditions to study the responses of the plant community to changes in water availability and community functioning in a natural, intact ecosystem of high ecological value.

The patterns of use and redistribution of soil water by plant species have a considerable impact on the hydrological cycles of terrestrial ecosystems (Jackson et al., 2000). For example, within the same community, species may differ substantially in rooting depth and water consumption so that shifts in species composition can significantly alter patterns of ecosystem water use (Canadell and Zedler, 1995; Canadell et al., 1996; Jackson et al., 1995, 2000). However, the water sources and/or depth of soil water uptake by plants have traditionally been difficult to assess (i.e. Ehleringer and Dawson, 1992). Nowadays, considerable progress identifying plant water sources has been achieved by means of stable isotope analyses (hydrogen and/or oxygen) when water sources have distinct isotopic signatures (Phillips and Gregg, 2001; Ehleringer

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and Dawson, 1992; Dawson, 1993; Corbin et al., 2005). Since there is no isotopic fractionation by plant roots during water uptake (White et al., 1985), the isotopic composition of plant xylem water reflects the isotopic composition of water used by the plant (e.g. Dawson and Ehleringer, 1991; Dawson, 1993; Corbin et al., 2005; Dawson and Pate, 2006). Generally, groundwater retains a relatively constant stable isotope signature on an annual basis, which allows the identification of groundwater recharge accurately from isotopically distinct and well-characterised water sources, such as precipitation and soil water (Ehleringer et al., 1991).

In coastal sand dunes, soil moisture availability may vary considerably at small spatial and temporal scales (Pavlik, 1980). The dune water table fluctuates seasonally because of differences in rainfall and evapotranspiration between the summer and winter months. In Mediterranean dune systems, drought is exacerbated by the low water holding capacity of sandy soils and by the likelihood of high salinity and possibility of sea water intrusion (Garcia Novo et al., 2004; Zunzunegui et al., 2005; Costelloe et al., 2008; Antonellini and Molleno, 2010). Moreover, in sand dunes, similar to what has been observed in deserts and semi-arid zones, small-scale variations in vegetation density, soil surface cover, and soil texture determine the amount of water and nutrients available to plants (Rosenthal et al., 2005).

The main objectives were to: (i) determine how co-occurring species differ in groundwater usage and/or dependence on GW, (ii) determine the variability across a range of microsites all located within an 8 km² contiguous sand dune ecosystem; (iii) document species specific responses to the combined stresses of seasonal drought and changes in groundwater level. We hypothesized that species which have consistent access to GW might be less affected by seasonal drought but more susceptible to the lowering of GW levels. This hypothesis was tested by comparing a range of species with different water use strategies: a deep rooted pine (*Pinus pinaster*), an endemic shrub (*Corema album*), native (*Myrica faya*) and invasive (*Acacia longifolia*) woody understory trees, and a phreatophytic willow (*Salix repens ssp. argentea*).

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2 Material and methods

2.1 Site description

The study was conducted at Osso da Baleia in Carriço, Pombal (40°0'3.47" N, 08°54'14.73" W), in inland dunes with some patches of mature pine (*Pinus pinaster*) forest (Fig. 1). Presently, human influence in this coastal dune is very low, with the exception of GW exploitation for the construction of natural gas reservoirs. Systematic GW exploitation has been carried out since 2001. Water is extracted at 20 wells along a 4 km long north-south line (~600 m from the coast) affecting the GW levels in 8.2 km² of dune habitat (Fig. 1). Maximum water extraction at all wells is limited to 600 m³ h⁻¹ and maximum lowering of the ground water table is restricted to 5 m at each well. A network of wells and piezometers (17 in total) allow for a spatially explicit determination of groundwater depth throughout the study area.

For this study, five microsites (letters A to E) were selected nearby to extraction wells and monitoring piezometers, contiguous to the water extraction line in an area of approximately 1 km² (Fig. 1). Microclimatic data were obtained from a Campbell Scientific climate station (Shepshead, UK) which monitored wind velocity and direction, precipitation, air humidity, temperature and solar radiation.

2.2 Plant species

Functionally distinct species were selected in order to assess the overall community effect of GW lowering: (1) *Pinus pinaster* – a native evergreen tree species (archeophyte) with a very broad distribution in the Mediterranean basin, in particularly in the coastal areas of France and the Iberian Peninsula; (2) *Corema album* – an evergreen shrub of the Ericacea family, endemic to the Atlantic coast of the Iberian Peninsula; (3) *Salix repens* ssp. *argentea* – an important species of the dune slack habitat, with the southern limit of its distribution in this region; (4) *Myrica faya*, a naturalized fast growing evergreen shrub or small tree with the capacity to fix atmospheric nitrogen; (5) the

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exotic invasive *Acacia longifolia*, which has characteristic properties of a successful invader, such as a rapid growth rate sustained by efficient resource acquisition (high N-uptake and symbiotic N-fixation), and high seed production. The selected woody native and non-native species present a differential tolerance to drought conditions: *Pinus pinaster* and *Corema album* are typical drought adapted species, in opposition to *Salix repens*, which is a phreatophyte and therefore particularly dependent on GW.

2.3 Water potential

Predawn leaf water potential (Ψ_{pre}) was determined in situ with a Scholander-type pressure chamber (Scholander et al., 1965) (Manofrigido, Lisbon, Portugal) to evaluate the water status of each species at each microsite. Measurements were made on 5 plants per microsite in spring and summer (May and August) 2005.

2.4 Identification of water-sources and their differential utilization by plants

To identify the seasonal water sources used by plant species, the oxygen isotopic composition ($\delta^{18}O$) of precipitation (single rain events and cumulative monthly precipitation) and GW (obtained from piezometers and extraction wells) were analyzed monthly using standard methods with an ISOPrime-IRMS coupled to a multiflow automatic sampler (GV Instruments, UK). At the end of each season, 10 cm branches of 5 plants per species were collected, sealed in glass tubes and immediately placed on dry ice to avoid any water evaporation and consequent isotopic fractionation. Xylem water was then extracted under vacuum in the lab.

2.5 Two-source mixing model for determination of plant water sources

Seasonally, we used the two-compartment linear mixing model of Phillips and Gregg (2001) to estimate the percentage of vegetation water derived from groundwater (P_{GW}):

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$$P_{\text{GW}} = \frac{\delta^{18}\text{O}_{\text{xylem}} - \delta^{18}\text{O}_{\text{rain}}}{\delta^{18}\text{O}_{\text{GW}} - \delta^{18}\text{O}_{\text{rain}}} \quad (1)$$

where, $\delta^{18}\text{O}_{\text{xylem}}$ is the isotope value for water extracted from the vegetation, $\delta^{18}\text{O}_{\text{rain}}$ is the mean seasonal isotope value for rain water and $\delta^{18}\text{O}_{\text{GW}}$ is the mean isotope value for groundwater.

5 Model results indicated that some individual plants had greater than 100% or less than 0% dependence on groundwater. This can result from either neglecting a third water source or measurement error in xylem or source $\delta^{18}\text{O}$ determination (Phillips and Gregg, 2001). Values that were outside the 0 to 100% range by less than 30% (e.g. between -30% and 130%) were assumed to result from $\delta^{18}\text{O}$ measurement error and these plants were subsequently assigned a value of either 0 or 100% dependence on groundwater. When the mixing-model indicated values of groundwater dependence of less than -30% or greater than 130% data were excluded from further analyses.

2.6 Carbon isotope discrimination in plant material

At the end of each season, south-facing sun-exposed leaves ($n = 5$) per species per microsite were collected, dried at 60°C for at least 72 h, ground to a fine powder in a ball mill (Glen Creston Ltd MM 2000, Haan, Germany) and analyzed for $\delta^{13}\text{C}$ in continuous flow mode on an isotopic ratio mass spectrometer SIRA II /VG Isogas (UK) coupled to an automatic sampler EUROEA (EuroVector, Italy). Results are expressed in δ notation and were standardized against Pee-Dee Belemnite.

2.7 Mapping groundwater spatial and temporal variation

In spring and summer GW level (relative to sea level), was calculated using data obtained from the wells and piezometers. Data was interpolated within the study area using ordinary kriging by calculating variograms for each season (Cerena, 2000, geoMs – Geostatistical Modelling Software). A spherical function describing the spatial

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correlation in the data (nugget effect = 0, maximum range = 3200 m and anisotropy in the NE-SW) was fitted to the variograms and then used to interpolate to obtain a continuous map of GW level. Next, a map detailing the distance to GW was calculated as the difference between the GW level map and the ground surface topography, calculated from a digital terrain model detailing the topography of the study area. Mapping and outputs were produced in ArcGis (ESRI, 2008, ArcMap v. 9.2).

2.8 Statistical analysis

Within species, one-way ANOVA was used to determine the effect of microsite, season and the microsite*season interaction on bulk leaf $\delta^{13}\text{C}$, Ψ_{pre} and GW use. GW use data was square root transformed before analysis to satisfy the ANOVA assumptions of normality and homogeneity of variance. Linear regression was used to determine the relationships between $\delta^{13}\text{C}$ and Ψ_{pre} and GW use. All analyses were conducted in R 2.6.2 (R Core Development Team, 2008).

3 Results

3.1 Climate

Osso da Baleia is located in a meso-mediterranean climatic region (Fig. 1). The year 2005 was particularly dry when compared with average years, with precipitation distribution following the characteristic Mediterranean pattern: high rainfall during spring and fall and a relatively early onset of drought in mid-May with only a few minor rainfall events (< 10 mm) until October (Fig. 2a). Minimum and maximum daily temperatures were registered in February ($-0.6\text{ }^{\circ}\text{C}$) and August ($38.5\text{ }^{\circ}\text{C}$) respectively (Fig. 2b).

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3.2 Plant water sources: species differences and seasonal variability

The isotopic signature of GW was distinct from that of precipitation, being in general more enriched than GW (Fig. 3), allowing the evaluation of the relative uptake of surface and deep-water sources by analysis of the isotopic composition of xylem sap water. Groundwater $\delta^{18}\text{O}$ varied slightly throughout the year and was more variable in spring than summer (Fig. 3a and b) but the mean value remained relatively constant (between -4.2‰ and -4.3‰ , Fig. 3). Precipitation $\delta^{18}\text{O}$ signatures varied significantly between spring and summer, which is consistent with precipitation values expected during the cooler spring time (Yurtsever and Gat, 1981). During summer drought, which was characterized by no significant precipitation and very high temperatures, there was likely strong ^{18}O enrichment in soil water, presumably due to high evaporation in the top soil layers.

There was a clear effect of seasonality on the observed source water used by the plant community. Xylem $\delta^{18}\text{O}$ values indicated that most species utilized a mixture between GW and precipitation during spring, with *P. pinaster* being the species with $\delta^{18}\text{O}$ values most similar to GW (on average 4.1‰) and *C. album* having the most variable $\delta^{18}\text{O}$ signatures and differing the most from the GW signature (Fig. 3). During summer drought, due to the combination of decreasing GW levels and no significant precipitation, plants tended to have $\delta^{18}\text{O}$ signatures, which differed from GW signatures, and variability was higher than in spring (Fig. 3). This tendency of more enriched $\delta^{18}\text{O}$ signatures in summer may also be related to the fact that available soil water is more enriched during summer than spring due to higher rates of evaporation from the soil. This observation was particularly relevant for the shallow rooted *A. longifolia*, which had a large number of individuals with relatively enriched xylem water.

In addition to functional variability between the species, we observed a very high variability in GW utilization between the 5 microsites, which clearly revealed heterogeneous access to and utilization of GW within the study area. In general, xylem sap $\delta^{18}\text{O}$ from microsites A, B and C indicated a greater utilization of GW, whereas plants

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at sites D and E appeared to use a mixture of GW and precipitation. During summer, with the lowering of GW, plants in sites A and B showed a larger enrichment in $\delta^{18}\text{O}$ (relative to spring values), indicating a higher susceptibility to drought at these sites. Additionally, plants were differently exposed to significant changes in GW utilization from spring to summer. Thus, microsites A, D (located along the extraction line) and B had the strongest reduction in GW use, from spring to summer as indicated by a large seasonal change in xylem $\delta^{18}\text{O}$ signature (Fig. 4a and b).

This microsite heterogeneity in GW access and the respective distance to GW levels (Fig. 4) results in a very patchy pattern of distance to GW in both seasons (Fig. 4). This spatial heterogeneity between microsites was larger in summer than in spring.

3.3 Linking plant functional traits and groundwater use

An integrated measure of plant water relations and carbon assimilation is given by $\delta^{13}\text{C}$ signatures of bulk leaf material, which varied significantly between the microsites for all species (Table 1a). $\delta^{13}\text{C}$ was similar between seasons for all species except *A. longifolia*, which had a significant enrichment in $\delta^{13}\text{C}$ during the summer drought compared to the wet spring (Table 1a).

Predawn water potentials (Ψ_{pre}) as an instantaneous measure of water status varied significantly by both microsite and season for some species (Table 1b). Ψ_{pre} seasonal effects were significant in all species except the shallow-rooted endemic shrub *C. album*, which did not significantly alter its water potential in response to the changes in climate conditions (Table 1b).

To investigate the effects of microsite variation in groundwater access of different co-occurring species and environmental conditions, we first applied a two-source mixing model (Phillips and Gregg, 2001) to determine the percentage of groundwater vs. rainwater used by each species at each microsite. For all species, with the exception of *C. album*, the percentage of GW use varied significantly across microsites, and between the seasons for *A. longifolia* and *S. repens* (Table 1c).

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The relationship between relative groundwater use and Ψ_{pre} , measured at the five microsites during spring and summer drought, demonstrated clear differences between species and seasons (Fig. 5). *M. faya* and *S. repens* exhibited a significant correlation (Fig. 5a and d; Table 2) between both factors: highest Ψ_{pre} occurred in site A where plants depended almost solely on groundwater (> 75%), while the lowest Ψ_{pre} of -3.0 MPa occurred in summer in site E for *M. faya* where there was practically no access to groundwater (Fig. 5a; Table 2). In fact, *S. repens* exhibited the highest water potential among all species even during summer and a high proportional groundwater use, which remained above 50% GW use during summer at locations D and E (Fig. 5d). This reflects that *S. repens* is a phreatophyte, (a plant species that is dependent upon groundwater, being very sensitive to changes in this water source), tolerating only briefly limitations in ground water. In contrast, the alien invasive, *A. longifolia*, had a broad range in GW utilization coupled with the largest variation in predawn water potential; however the response varied substantially between sites (Fig. 5b), with no consistent relationship between GW use and Ψ_{pre} (Table 2). Furthermore, *A. longifolia* had the greatest reduction in Ψ_{pre} of all the species (down to -3.8 MPa at site B) during summer drought. Similarly, *C. album* did not present any consistent relationship between GW use and Ψ_{pre} either (Fig. 5c). For *M. faya*, *S. repens* and *P. pinaster* there were significant correlations between bulk leaf $\delta^{13}\text{C}$ values and percentage of GW used in spring and also in summer for *P. pinaster* (Fig. 6d and e; Table 2). Decreasing GW use was associated with an enrichment in leaf $\delta^{13}\text{C}$, reflecting increasing stomatal control of water loss as water availability decreased. Consistent with the lack of response in Ψ_{pre} among sites (Fig. 5c), *C. album* did not have a consistent relationship between GW use and $\delta^{13}\text{C}$ (Fig. 6c).

4 Discussion

This work confirms that GW is an important water source for the functioning and survival of plant communities in coastal sand dunes, and that vegetation may be wholly or partially dependent on groundwater sources (e.g. Canadell and Zedler, 1995; Murray et al., 2003; Lite and Stromberg, 2005). Plant species respond to GW changes, and in particularly GW lowering, with species specific responses according to functional traits and microsite GW access. According to earlier studies (Abrunhosa, 2002), the aquifer at our study site was previously very homogeneous. This indicates that the heterogeneity observed here is mainly due to the artificial GW lowering, which is in turn enhanced by the variable topography of the sand dune system. Although only a few studies have considered the interplay between small-scale spatial heterogeneity in site attributes and plant functional response (Stratton et al., 2000), microsite attributes have often been significant predictors of plant responses (Hinckley et al., 1991; Stratton et al., 2000). In this study, we found that spatial heterogeneity in GW use and seasonal drought both determined plant functioning. Accordingly, all species, with the exception of the drought adapted shrub *C. album*, presented a significant difference in GW use across all 5 microsites depending on the site specific distance to GW (Table 1). Moreover, the increase in xylem water $\delta^{18}\text{O}$ variability in all five studied species during summer drought may be the result of evaporative enrichment at the soil surface during that period, as already observed by other authors (Barnes and Turner, 1998; Querejeta et al., 2007). However, it is not possible to state that this was the only reason, since rain events present a similar signature (slightly less enriched $\delta^{18}\text{O}$ values).

In agreement with our original hypothesis, species with deep roots were the most sensitive to GW drawdown while shallow rooted species were not as affected by changing GW availability. Both of the native tree species, *P. pinaster* and *M. faya*, had large variation in GW use across microsites (from almost 100% use to less than 25%). The significant regressions between GW use and Ψ_{pre} and leaf $\delta^{13}\text{C}$ for these species indicated that they responded dynamically to water availability by regulating carbon

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assimilation and water use (Figs. 5a and 6a). At microsites with ready access to GW, *P. pinaster* and *M. faya* could use more water, which resulted in reductions in Ψ_{pre} . A very similar pattern was observed for the phreatophyte, *S. repens*. Differences in plant responses between microsites were more apparent in spring than in summer, reflecting the overall water limitation during the summer drought. In fact, if one considers that variation in $\delta^{13}C$ of plant leaf material not only integrate time that carbon was fixed but also functional traits (Werner and Máguas, 2010), it is expected that only deep-rooted species and phreatophytes would present a significant correlation between GW lowering and $\delta^{13}C$ signature (Lamontagne et al., 2005). Accordingly, the species, which had a significant correlation between GW use and Ψ_{pre} , also had a significant correlation with bulk leaf $\delta^{13}C$. Therefore, the spatial heterogeneity in GW availability led to significant differences in $\delta^{13}C$.

A study on soil water partitioning among *cerrado* species (Jackson et al., 1999) and recently with Mediterranean species (Álvarez-Cansino et al., 2010), showed that, based on their xylem water deuterium values, evergreen shrub species tended to rely more on shallow soil water sources than deciduous shrubs. *C. album*, a drought adapted Mediterranean shrub (Correia and Diaz-Barradas, 2000; Zunzunegui et al., 2011) showed an irregular pattern and no clear relationship between water potential and GW use (Fig. 6c, Table 2). In fact, this species is of very high importance for the structuring of dunes, since it is one of the few species capable of colonizing dune ridges. For this species, factors other than GW access (e.g. light) most likely led to the wide variation in $\delta^{13}C$ signatures.

In contrast to the native species, the exotic invader *Acacia longifolia*, which exhibits a water spender strategy (Peperkorn et al., 2005; Rascher et al., 2010, 2011; Werner et al., 2010; Richardson and Pysek, 2006), responded significantly to both seasonal drought and microsite differences in GW access (Figs. 5 and 6). Indeed, the low values of Ψ_{pre} for *A. longifolia* indicate that, irrespective of microsite GW access, it exhibited little stomatal control of water use. This fits well with recent studies demonstrating that *A. longifolia* contributes significantly to stand water use in an invaded dune pine forest

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(up to 42% seasonally) (Rascher et al., 2011).

New leaf growth of the native species typically occurs in a short flush period in spring and early summer, while in *A. longifolia*, the invasive species, growth can extend into the onset of the drought period. This explains why only *A. longifolia* presented a significant change in leaf $\delta^{13}\text{C}$ signatures between spring and summer, emphasizing the very high metabolic activity and the maintenance of carbon assimilation for longer periods than the native species. This indicates that, for the native species, leaves used for determination of $\delta^{13}\text{C}$ signatures in both seasons may in fact have been from the same cohort of leaves formed during spring thereby resulting in an uncoupling between leaf $\delta^{13}\text{C}$ and xylem water $\delta^{18}\text{O}$ in summer. Therefore, it is not surprising that the correlations between bulk leaf $\delta^{13}\text{C}$ and xylem $\delta^{18}\text{O}$ tended to be stronger in spring than in summer (Fig. 6, Table 2). Overall, $\delta^{13}\text{C}$ was a good indicator of heterogeneity in GW access ($p < 0.001$, Table 2), but a poor indicator of seasonal changes in carbon discrimination which fits with recent studies demonstrating that bulk leaf $\delta^{13}\text{C}$ signatures are not always good tracers of photosynthetic regulation, especially in Mediterranean habitats (Werner and Máguas, 2010).

In conclusion, our study demonstrates that sand dune plant communities contain a broad range of species with significant differences in ecological strategy. Furthermore, the dependence on GW across species and microsites is highly variable and is also dependent on season. Despite the difficulties to assess information on GW use, current mixing models based on $\delta^{18}\text{O}$ or δD signatures of xylem water yield a means for estimating local GW use. This application of standard mixing models to determine dependence on GW revealed a variety of plant water strategies which correlated with species functional traits. In accordance with our initial hypothesis, functional traits that led to direct access to GW, such as deep root systems (*P. pinaster* and *M. faya*) or in case of the phreatophyte (*S. repens*) a particular short distance between roots and GW, are key drivers for a significant response to changing GW levels. The evergreen shrub *C. album* was the only species in which ecophysiological functioning was completely uncoupled from access to GW. Furthermore our study provides further evidence of the

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water-spender strategy of the invasive *A. longifolia*, a trait which distinguishes it from the native vegetation.

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Table 1. P-values from Analysis of Variance with **(a)** bulk leaf $\delta^{13}\text{C}$, **(b)** predawn xylem water potential (Ψ_{pre}) and **(c)** groundwater use as response variables and Site, Season and the Site*Season interaction as predictor variables. ANOVA was conducted for each species and response variable independently. Groundwater use data was square root transformed before analysis to satisfy the ANOVA assumptions of normality and homogeneity of variance. Significant values ($\alpha = 0.05$) are shown in bold.

(a)	$\delta^{13}\text{C}$ (‰)				
	<i>A. longifolia</i>	<i>C. album</i>	<i>M. faya</i>	<i>S. repens</i>	<i>P. pinaster</i>
Site	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Season	0.027	0.981	0.800	0.867	0.380
Site * Season	0.424	0.436	0.823	0.558	0.777
(b)	Ψ_{Predawn} (MPa)				
	<i>A. longifolia</i>	<i>C. album</i>	<i>M. faya</i>	<i>S. repens</i>	<i>P. pinaster</i>
Site	< 0.001	0.133	< 0.001	< 0.001	nd
Season	< 0.001	0.001	< 0.001	0.006	nd
Site * Season	0.002	0.183	< 0.001	< 0.001	nd
(c)	Groundwater Use (%)				
	<i>A. longifolia</i>	<i>C. album</i>	<i>M. faya</i>	<i>S. repens</i>	<i>P. pinaster</i>
Site	0.001	0.866	< 0.001	0.004	< 0.001
Season	0.006	0.652	0.168	0.044	0.522
Site * Season	0.153	0.305	0.084	0.128	0.158

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Table 2. Regression coefficients (R^2) for the dependence between groundwater use and **(a)** bulk leaf $\delta^{13}\text{C}$ and **(b)** predawn xylem water potential (Ψ_{pre}) in spring and summer. Significant regressions ($\alpha = 0.05$) are in bold.

(a)	Groundwater Use vs $\delta^{13}\text{C}$	
	Spring	Summer
<i>A. longifolia</i>	0.036	0.142
<i>C. album</i>	0.069	0.003
<i>M. faya</i>	0.258	0.016
<i>S. repens</i>	0.328	0.114
<i>P. pinaster</i>	0.337	0.553
(b)	Groundwater Use vs Ψ_{pre}	
	Spring	Summer
<i>A. longifolia</i>	0.073	0.142
<i>C. album</i>	0.015	0.001
<i>M. faya</i>	0.362	0.668
<i>S. repens</i>	0.066	0.101
<i>P. pinaster</i>	nd	nd

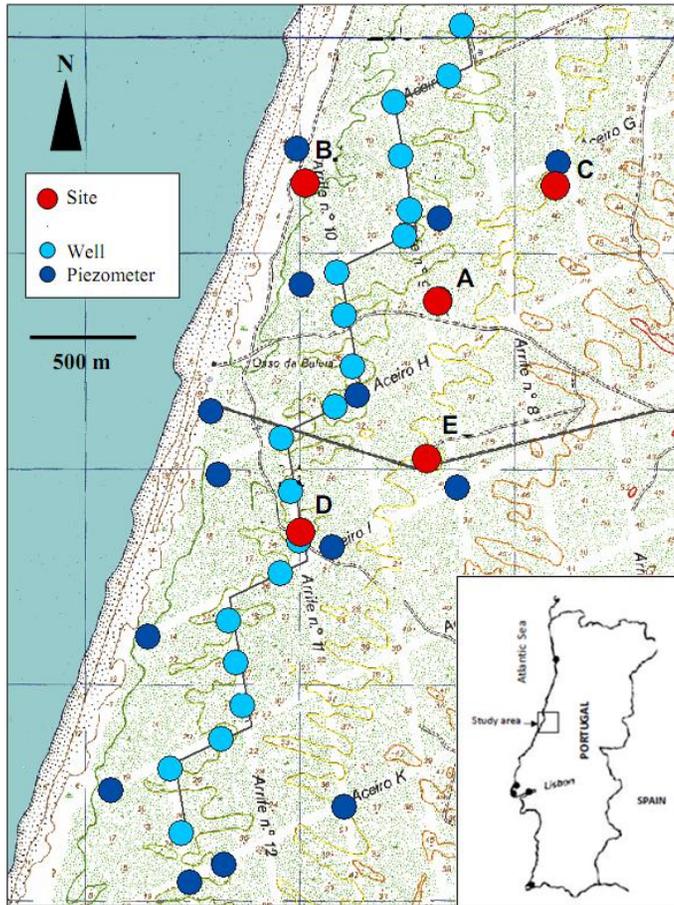


Fig. 1. Map of Osso da Baleia Portugal indicating locations of the water extraction line, wells, piezometers and field site locations.

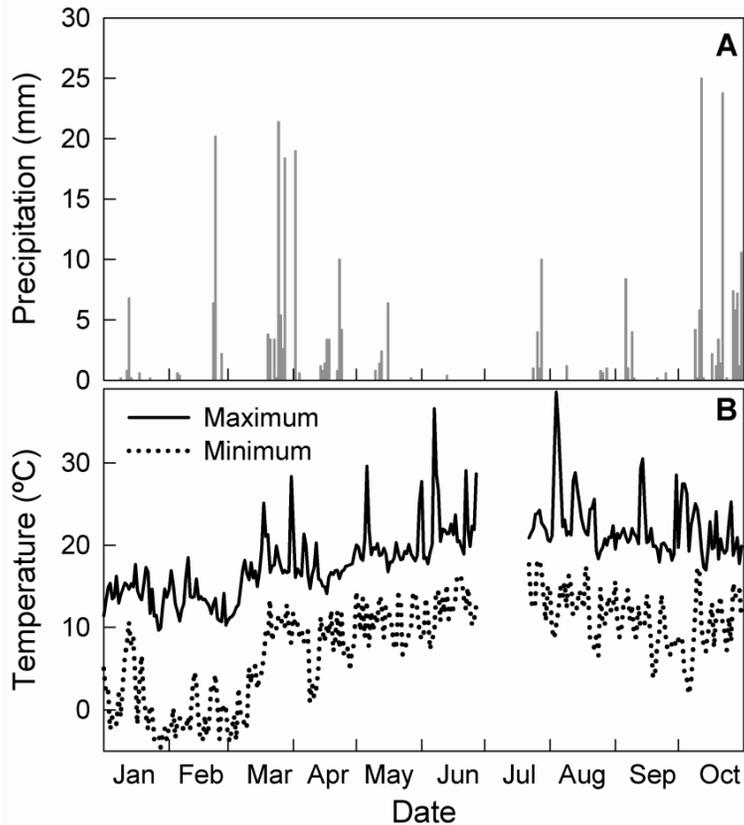


Fig. 2. January through October 2005 (a) precipitation and (b) air temperature for Osso da Baleia, Portugal. Data from 28 June to 21 July 2005 are missing due to data logger failure.

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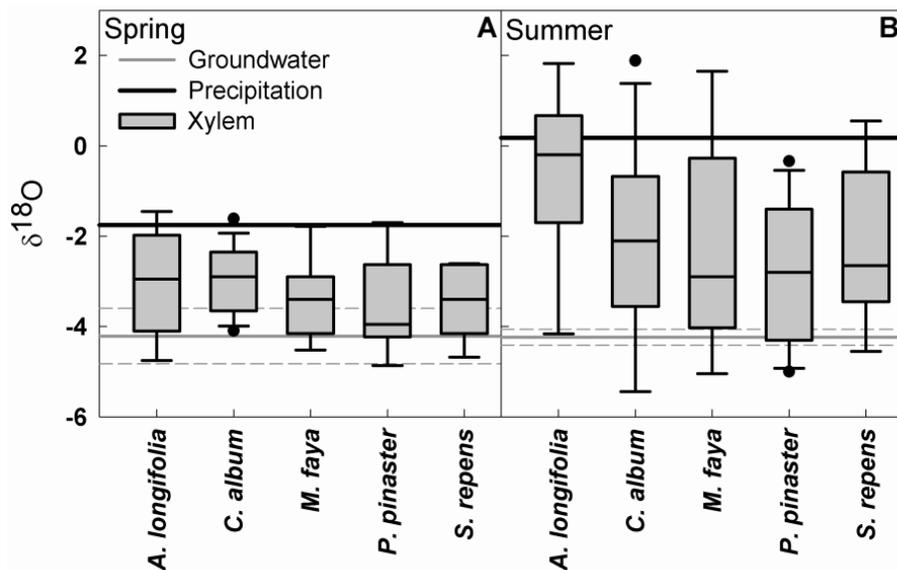


Fig. 3. $\delta^{18}\text{O}$ (‰) of xylem water (boxplot), precipitation (black line) and groundwater (grey line) in (a) spring (May) and (b) summer (August). Boxplots denote the 10th, 25th, median, 75th and 90th percentiles of the xylem $\delta^{18}\text{O}$ for each species. Outlying values are indicated by solid circles denoting the 5th and 95th percentiles. Precipitation $\delta^{18}\text{O}$ for spring is the mean value of the two major rainfall events during May 2005 (12–13 May, $\delta^{18}\text{O} = -1.8\text{‰}$; 25 May, $\delta^{18}\text{O} = -1.7\text{‰}$). There was very little measurable precipitation in August and therefore a long-term mean value of 0.18‰ was used for summer precipitation. Groundwater $\delta^{18}\text{O}$ values are denoted as the monthly mean (solid grey line) \pm SD (dotted grey lines) of groundwater collected approximately monthly from 2002 through 2006.

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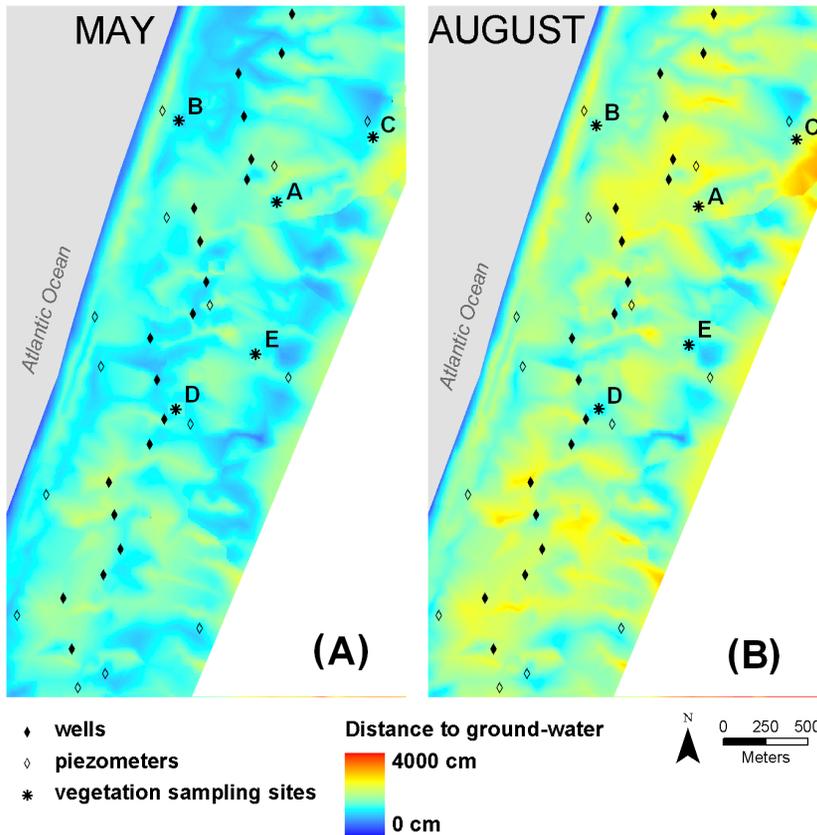


Fig. 4. Maps indicating the depth to groundwater interpolated from measurements at wells and piezometers in (a) spring and (b) summer 2005.

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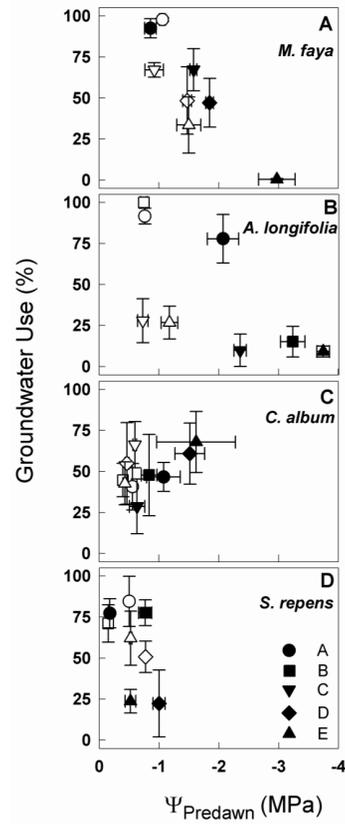


Fig. 5. Relationships between groundwater use (%) and predawn xylem water potential (Ψ) for (a) *M. faya*, (b) *A. longifolia*, (c) *C. album* and (d) *S. repens* in spring (open symbols) and summer (closed symbols) at the five sites: A (○); B (□); C (▽); D (◇) and E (△). Each site is depicted as the mean \pm SE of groundwater use (%) against mean \pm SE of predawn xylem water potential (MPa). $n = 3-5$ plants for each species and site and season.

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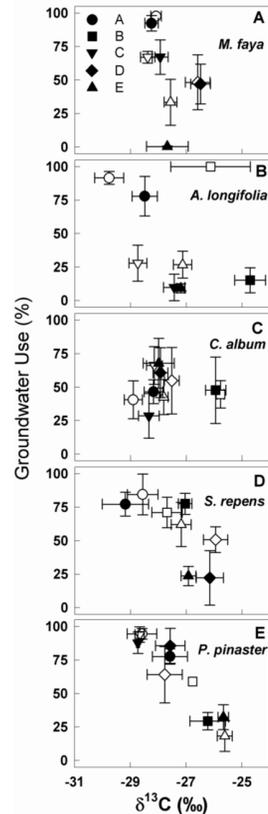


Fig. 6. Relationships between groundwater use (%) and bulk leaf $\delta^{13}\text{C}$ (‰) for **(a)** *M. faya*, **(b)** *A. longifolia*, **(c)** *C. album*, **(d)** *S. repens* and **(e)** *P. pinaster* in spring (open symbols) and summer (closed symbols) at the five sites: A (○); B (□); C (▽); D (◇) and E (△). Each site is depicted as the mean \pm SE of groundwater use (%) against mean \pm SE of bulk leaf $\delta^{13}\text{C}$ (‰). $n = 3 - 5$ plants for each species and season.

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