

# Linking the patterns in soil moisture to leaf water potential, stomatal conductance, growth, and mortality of dominant shrubs in the Florida scrub ecosystem

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**Abstract** Patterns in soil moisture availability affect plant survival, growth and fecundity. Here we link patterns in soil moisture to physiological and demographic consequences in Florida scrub plants. We use data on different temporal scales to (1) determine critical soil moisture content that leads to loss of turgor in leaves during predawn measurements of leaf water status ( $\Psi_{\text{crit}}$ ), (2) describe the temporal patterns in the distribution of  $\Psi_{\text{crit}}$ , (3) analyze the strength of relationship between rainfall and soil moisture content based on 8 years of data, (4) predict soil moisture content for 75 years of rainfall data, and (5) evaluate morphological, physiological and demographic consequences of spring 2006 drought on dominant shrubs in Florida scrub ecosystem in the light of water-uptake depth as determined by stable isotope analysis ( $\delta^{18}\text{O}$ ). Based on 1998–2006 data, the soil moisture content at 50 cm depth explained significant variation in predawn leaf water potential of two dominant

shrubs, *Quercus chapmanii* and *Ceratiola ericoides* ( $r^2=0.69$ ). During 8 years of data collection, leaves attained  $\Psi_{\text{crit}}$  only during the peak drought of 2000 when the soil moisture fell below 1% by volume at 50 and 90 cm depth. Precipitation explained a significant variation in soil moisture content ( $r^2=0.62$ ). The patterns in predicted soil moisture for 75 year period, suggested that the frequency of drought occurrence has not increased in time. In spring 2006, the soil reached critical soil moisture levels, with consequences for plant growth and physiological responses. Overall, 24% of plants showed no drought-induced damage, 51% showed damage up to 50%, 21% had intense leaf shedding and 2% of all plants died. Over the drought and recovery period (May–October 2006), relative height growth was significantly lower in plants with greater die-back. All species showed a significant depression in stomatal conductance, while all but deep-rooted palms *Sabal etonia* and *Serenoa repens* showed significantly lower predawn ( $\Psi_{\text{pd}}$ ) and mid-day ( $\Psi_{\text{md}}$ ) leaf water potential in dry compared to wet season. Plants experiencing less severe die-back exhibited greater stomatal conductance, suggesting a strong relationship between physiology and morphology. Based on results we suggest that the restoration efforts in Florida scrub should consider the soil moisture requirements of key species.

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## Abbreviations

$g_s$	stomatal conductance
$\Psi_{pd}$	predawn leaf water potential
$\Psi_{crit}$	predawn leaf water potential at turgor loss
$\Psi_{md}$	mid-day leaf water potential
PWP	permanent wilting point
RWC	relative water content, $\delta^{18}\text{O} = (R_{\text{sample}} / R_{\text{SMOW}} - 1) \times 1,000$ , in which $R_{\text{sample}}$ and $R_{\text{SMOW}}$ represent the heavy to light isotopes ratio of the sample and standard (Vienna standard mean ocean water) respectively

## Introduction

Annual rainfall and length of dry periods between rainfall events are important ecosystem determinants of plant distribution, physiognomy, and functional diversity (e.g. Barton and Teeri 1993; Fay et al. 2002; Gitlin et al. 2006), and are regulated by natural phenomena such as Atlantic Multidecadal Oscillations or by anthropogenic forcing (Enfield et al. 2001; Jones and Mann 2004; Mann 2007). The effects of rainfall deficiencies are mediated through changes in soil moisture availability that affect leaf area index, leaf water status, photosynthetic rates, productivity and plant growth rates (Orwig and Abrams 1997; Allen and Breshears 1998; Leuzinger et al. 2005; Krishnan et al. 2006; Li et al. 2007). However, the majority of studies examining the effects of drought on plants use rainfall data (Warwick 1975) and few studies use soil moisture in conjunction with precipitation to examine the effects of drought (Jones 2007).

Prolonged droughts at the ecosystem level can compromise plant growth and productivity by decreasing carbon fixation, documented after the 2003 drought in Europe (Ciais et al. 2005; Gobron et al. 2005) and in boreal forests of North America (drought occurring from 2000–2003, Klujn et al. 2006; Krishnan et al. 2006). Drought may affect species composition in an ecosystem if populations are eliminated or reduced. For example, *Pinus edulis* suffered 40–100% drought-induced mortality in the southwestern US (Gitlin et al. 2006). At a community level, persistent drought may favor the spread of drought-adapted species at the cost of drought-sensitive species (Swemmer et al. 2006), such as drought tolerant *Tamarix* spp. replacing *Populus* and *Salix* spp. in Arizona (Lite and Stromberg 2005).

Soil moisture reductions lead to declines in gas-exchange and leaf water potential, possibly leading to plant die-back or mortality, depending on the drought severity (Borchert 1994; Breshears et al. 2005; Saha et al. 2005; Gitlin et al. 2006; Otieno et al. 2006). For example, a 30% decrease in soil moisture, compared to the control, led to a mean decline of 53% in stomatal conductance ( $g_s$ ) for isohydric (leaf water potential stable across seasons) *Quercus ilex* (Asensio et al. 2007). Throughfall exclusion in eastern Amazonian forests negatively affected the photosynthetic capacities, but not the leaf water status of common tree species over a period of 2 years (Nepstad et al. 2002). Severe drought (soil moisture below 35% of field capacity) led to a significant decline in both leaf water potential and  $g_s$  in *Leymus chinensis* (Xu et al. 2007) 3 months after the drought treatment was imposed. Strong seasonal drought in Australian savannas led to soil moisture dropping below the permanent wilting point, causing mortality in *Eucalyptus* spp. (Fensham and Fairfax 2007). Thus the plant responses depend on the extent of soil moisture reduction, which in turn depends on precipitation, soil texture, and depth to water table.

Here we examine a mechanistic link between soil moisture and plant physiological and morphological responses in the Florida scrub ecosystem. We use 8 years of soil moisture, precipitation, and pre-dawn leaf water potential ( $\Psi_{pd}$ ) data to calculate the soil moisture levels that cause leaves to attain leaf water potentials low enough causing turgor loss during pre-dawn measurements ( $\Psi_{crit}$ ). Turgor loss among leaves is a crucial hydraulic threshold point (Brodribb and Holbrook 2003). Upon losing turgor, the cells cannot expand or grow and fail to hydrate (Nobel 1999). We use  $\Psi_{pd}$  as an indicator of drought stress because  $\Psi_{pd}$  is known to equilibrate with soil moisture (Petrie and Hall 1992; Ameglio et al. 1998; but see Donovan et al. 2001). The patterns in  $\Psi_{pd}$  are utilized by agronomists to infer drought stress in crops and to manage irrigation patterns (Pellegrino et al. 2004; da Silva et al. 2005), but the relationship between soil moisture,  $\Psi_{pd}$  and demography is rarely studied in natural landscapes, which is a novel aspect of this study. We use physiological variables such as  $\Psi_{pd}$ , mid-day leaf water potential ( $\Psi_{md}$ ) and  $g_s$ , in conjunction with morphological variables such as drought-induced damage, plant growth and mortality to assess the impacts of an abnormal spring drought.

In addition, we evaluate physiological and demographic effects of the 2006 drought in the light of water-uptake depth as determined by stable isotope analysis ( $\delta^{18}\text{O}$ ).

The specific questions we address are: (1) what is the critical soil moisture content that leads to loss of turgor in leaves during predawn measurements of leaf water status ( $\Psi_{\text{crit}}$ ), (2) are there temporal patterns in the distribution of  $\Psi_{\text{crit}}$ , (3) how strong is the relationship between rainfall and soil moisture content, (4) can we predict the soil moisture content for 75 years of rainfall data, based on 8-years of relationship between soil moisture and rainfall and, (5) what are the morphological, physiological and demographic consequences of spring 2006 drought on dominant shrubs?

## Materials and methods

### Study site

The study was conducted at the 2,000 ha Archbold Biological Station (ABS, 22° 11' N, 81° 21' W), located at the southern boundary of the Lake Wales Ridge in central Florida. The Ridge, which is 160 km long and 10 km wide, is oriented north-south along the center of the Florida peninsula (Weekley et al. 2007). The climate includes hot and wet summers from June to September and mild, dry winters. Typically, temperatures are highest in August and lowest in January (Abrahamson et al. 1984). Average annual rainfall is 1,365 mm, with 60% falling between June–September (wet season), and intermittent rainfall occurs during the 8-month long dry season and may account for 40% of total annual rainfall (Chen and Gerber 1990). ABS has weather data from 1932 onwards with daily records of precipitation, and bimonthly records of ground water wells. Depth to the water table, measured at the main grounds of Archbold Biological Station, varies from 0.5 to 1.8 m annually (ABS weather station data). During 2006, the period between April and early June was unusually dry with 75% less rainfall than the spring average at ABS and in central Florida (<http://www.drought.unl.edu/dm/monitor.html>, National Drought Monitor Center, University of Nebraska-Lincoln. Accessed on Oct 6, 2006). Since the 40% of total annual rainfall occurs

during the dry season when many species exchange leaves and exhibit leaf expansion, we define a 75% reduction in the dry season rainfall as abnormal.

Rainfall patterns in south Florida are shaped by the Atlantic multidecadal oceanic phenomenon (AMO; Kerr 2000). The multidecadal oscillation of sea surface temperature encompasses cool and warm phases that show dampened to high variability respectively in Florida's rainfall (Enfield et al. 2001). Given our aim of explaining the trends in precipitation and soil moisture on plant responses, we examine our data in the light of rainfall patterns attributed to AMO.

The ABS area is characterized by a mosaic of scrub, flatwoods, and seasonal ponds (Abrahamson et al. 1984; Menges 1999). Upland Florida scrub vegetation is divided into three major assemblages described in detail by Abrahamson et al. (1984): (1) Sand pine scrub with *Ceratiola ericoides* Michx. (rosemary scrub) or oaks, (2) scrubby flatwoods, and (3) flatwoods. Rosemary scrub and scrubby flatwoods are generally open and characterized by white sands belonging to satellite soil series, which are hypothermic uncoated Aquic Quartzipsamments (Carter et al. 1989). Fire plays an important role in governing species composition and plant stature, with fire-return-intervals estimated from 8–16 years for scrubby flatwoods to 15–30 years for rosemary scrub (Menges 2007). Rosemary scrub and scrubby flatwoods are the most common upland assemblages at ABS and thus were selected for the analysis of drought effects in this study.

We documented the effects of soil moisture variation on six species of woody shrubs that comprised 80% of all the biomass in the study area. Focal species consisted of three clonal oaks that resprout post-fire, two evergreen species of palms that exchange leaves all through the year and resprout post-fire, *Serenoa repens* (W. Bartram) Small, and *Sabal etonia* Swingle ex Nash, and the evergreen *C. ericoides*, an obligate seeder that shows post-fire mortality but requires fire for seedling recruitment. *Quercus chapmanii* Sarg., *Quercus geminata* Small, and *Quercus inopina* Ashe, *Q. chapmanii* and *Q. inopina* are brevideciduous species that complete leaf expansion by early spring, and *Q. geminata* is an evergreen species that exchanges leaves throughout the spring and early summer. We follow Wunderlin and Hansen (2004) for taxonomic authorities.

Measurements of soil moisture and  $\Psi_{pd}$ 

We examined soil moisture, rainfall, and  $\Psi_{pd}$  data to study the effects of soil moisture and rainfall on  $\Psi_{pd}$ , and to analyze the strength of relationship between soil moisture and precipitation. In 1998, a total of 55 soil moisture tubes were installed at five independent sites encompassing the gradient from scrubby flatwoods to Rosemary scrub at ABS (Weekley et al. 2007). At these sites, we measured soil moisture with a Sentry AP 200 probe (Troxler Inc., NC, USA), which utilizes frequency domain reflectometry to estimate volumetric soil moisture (% moisture by volume, Rundel and Jarrell 1989; Weekley et al. 2007). At each sampling occasion we recorded soil moisture at three soil depths (10, 50, and 90 cm). Due to a lag in soil moisture response to precipitation, we explored cumulative rainfall over varying lengths of time that might be the best predictor of soil moisture. We determined that the cumulative rainfall over a period of 4 weeks prior to the soil moisture measurement was the best predictor of soil moisture, as opposed to 2-, 6-, and 8-week prior rainfall values.

We collected data on  $\Psi_{pd}$  for *Ceratiola* and *Q. chapmanii* from 1998–2006, on two plants (one leafy branch/plant) at each site, every 2 weeks to 4 months depending on accessibility to the sites due to the flooding of access roads. Rosemary scrub-scrubby flatwoods get cut-off from the access roads especially when the seasonal ponds get flooded and the water overflows on to the access roads. At each sampling event the plants were chosen randomly, and were located at least 5 m from the edge of the site with the minimum distance of 5 m between two plants.

We used leaf water potential ( $\Psi_1$ ) at turgor loss, derived from pressure volume curves, to obtain  $\Psi_{crit}$ . Eight expanded and mature leaves per species were collected from the study sites to get pressure-volume data.  $\Psi_{crit}$  was defined as the predawn leaf water potential ( $\Psi_{pd}$ ) causing turgor loss in leaves. Description of the theory behind the derivation of turgor loss is beyond the scope of this manuscript, interested readers can refer to Koide et al (1989) and Tyree and Jarvis (1982). We used a pressure chamber (Soil moisture Equipment Corp., Santa Barbara, CA, USA) that withstood pressurization up to 4 MPa. Due to this instrument limitation, we were uncertain that we obtained complete pressure–volume data for palm leaves. However we compared our data on palms with

published data on pressure–volume curves of a closely related palm, *Sabal palmetto* (Holbrook and Sinclair 1992) to scrutinize if the leaf tissue properties were comparable. Equipment did not impose restrictions on oaks because an earlier study indicated that Florida scrub oaks lose turgor in the range of  $-1.8$  to  $-2.5$  MPa (Abrams and Menges 1992).

## Monitoring morphological and physiological variables during the spring drought of 2006

To study the effects of the spring 2006 drought, we chose five sites harboring rosemary scrub-scrubby flatwoods gradients at ABS and sampled one line transect per site. Transects had been chosen randomly and established for an earlier study (Boughton et al. 2006), and had a mean length of 45 m. We marked ten points on each transect, every 5 m, and sampled one permanently marked individual per species within 3 m of each point, without sampling an individual more than once. For each individual, we recorded the number of stems, plant height, maximum crown length and perpendicular crown width. For multi-stemmed species, we counted all stems within 12 cm of the closest stem. Along our sample transects, the most common species were *Q. inopina* and *S. repens* (relative abundance of 23% each), followed by *Q. chapmanii* (21%), *C. ericoides* (13%) and both *S. etonia* and *Q. geminata* (10%). Throughout the manuscript we refer to the focal species as *Ceratiola*, *Q. chapmanii*, *Q. geminata*, *Q. inopina*, *Sabal* and *Serenoa* (Table 1).

Between 20th May and 1st June 2006 we characterized drought damage for each plant as the percentage of total plant canopy with dead branches and/or dead ramets that are leafless or harbor wilted and dead leaves. We did not sample plants with visible and significant insect damage. We categorized each plant into one of the five damage classes (0% or no damage, 1–25%, 26–50%, 51–75%, 76–100%) based on damage as percentage of total canopy area. Plants were re-sampled at the end of wet season and early dry season, between 29th September and 30th October 2006. Scrub plants exhibit stem elongation and leaf production through late summer (Myers 1990) and therefore the drought recovery can be assessed only after the expansion of the new flush is complete. We recorded the same data immediately after the end of wet season but also noted death of

**Table 1** Summary of plant morphological and physiological traits monitored in this study, and depth of water uptake data

Species	Height (m)	Rooting depth/depth of water uptake	Data
<i>Ceratiola ericoides</i> <sup>a</sup>	2.5	50 cm	$\Psi_{pd}$ (1998–2006), physiology, morphology (2006)
<i>Quercus chapmanii</i> <sup>b</sup>	4	40–140 cm <sup>b</sup>	$\Psi_{pd}$ (1998–2006) physiology, morphology (2006)
<i>Quercus geminata</i> <sup>b</sup>	2	40–80 cm <sup>b</sup>	Physiology, morphology (2006)
<i>Quercus inopina</i> <sup>b</sup>	3	20–40 cm <sup>b</sup>	Physiology, morphology (2006)
<i>Sabal etonia</i> <sup>c</sup>	1.5	0–2.5 m or water table	Physiology, morphology (2006)
<i>Serenoa repens</i> <sup>c</sup>	1.8	0–2.5 m or water table	Physiology, morphology (2006)

<sup>a</sup>Depths of water uptake and rooting depths for six focal shrub species were estimated by excavating adult plants. ( $\Psi_{pd}$  signifies predawn leaf water potential)

<sup>b</sup>Depths of water uptake and rooting depths for six focal shrub species were estimated with stable isotope technique. ( $\Psi_{pd}$  signifies predawn leaf water potential)

<sup>c</sup>Depths of water uptake and rooting depths for six focal shrub species were estimated from literature (Brown et al. 1990). ( $\Psi_{pd}$  signifies predawn leaf water potential)

individuals. Using plant height and crown area (crown dimensions along two perpendicular axes in N–S, and E–W directions) we measured height and crown growth rates over a 4 month period using the equations that yielded relative growth rates in the units of centimeter per centimeter per month.

$$RGR_{ht} = [\ln(\text{height}_2) - \ln(\text{height}_1)]/4$$

$$RGR_{\text{crown}} = [\ln(\text{crown area}_2) - \ln(\text{crown area}_1)]/4$$

We measured  $g_s$  on all marked plants per transect. Two canopy leaves per plant were sampled to obtain a mean value per plant for  $g_s$  using a LI-COR 1600 steady state promoter (LI-COR Inc., Lincoln, NE, USA) during drought (May 2006) and wet seasons (September 2006). Concurrently, we measured  $\Psi_{md}$  and  $\Psi_{pd}$  on all the marked plants and a subset of three plants respectively per species per site. We sampled one leafy branch per plant in case of all species but palms. For measuring  $\Psi_1$  of palm leaves we used 2 cm long tip of the leaflets from a frond.

#### Determination of water uptake depth

Stable isotope analyses ( $\delta^{18}\text{O}$ ) were used to measure depth of water uptake of each of the three oak species (*Q. inopina*, *Q. geminata*, *Q. chapmanii*). Five mature (plants that reproduce) *Ceratiola* plants were excavated for estimation of rooting depths. We compared our data on *Ceratiola* rooting depths to studies done by Hawkes and Casper (2002) that used tracer dye

analyses. Published data on rooting depths of *Serenoa* and *Sabal* (Brown et al. 1990) were used. While the analysis of stable isotopes and root excavations are fundamentally different methods, the information they provide can be used to infer the depth of water uptake by plants. Samples of five individuals of each of the *Quercus* sp. were collected at during May 2006 and February 2007 during the dry season as we wanted to determine the depth of water uptake during the most critical time of the year. Suberized twigs approximately 10 mm in diameter and 50–80 mm long were cut from the canopy and decorticated to avoid contamination of xylem water by isotopically enriched phloem water (Ehleringer and Dawson 1992). Clipped twigs were immediately placed in a capped vial, wrapped in parafilm, and stored in the freezer until water extraction. Surface (0–10 cm) soil samples were collected with a hand-driven probe to measure water content and isotopic composition of oxygen ( $\delta^{18}\text{O}$ ) in of soil water. Soil cores were excavated in order to characterize all possible sources of water for plants during the dry season. Two soil cores per site were excavated to the depth of 250 cm or until the water table was reached. Seven soil samples per core were taken at the following intervals: 0–10, 10–20, 20–40, 40–80, 80–140, 140–200, 200–250 cm. Freshly collected soil samples were placed in capped vials, wrapped in parafilm and stored in the freezer until water extraction for stable isotope analyses and water content.

Oxygen stable isotope analysis was conducted at the Stable Isotope Laboratory of the University of Miami to obtain  $\delta^{18}\text{O}$  values with the  $\text{CO}_2\text{:H}_2\text{O}$

equilibration method where 500  $\mu\text{l}$  of the extracted water was injected into airtight vials flushed with 2,000 or 3,000 ppm  $\text{CO}_2$  in He. After 48 h,  $\text{CO}_2$  in the head space was analyzed for its oxygen isotope ratio with an Isoprime IRMS (Manchester, UK). Analytical precision was  $\pm 0.1\text{‰}$  for  $\delta^{18}\text{O}$ .

#### Data analysis

We used regression analysis to examine which of the variables, soil moisture at 10, 50 and 90 cm depths, and rainfall were the best predictor(s) of  $\Psi_{\text{pd}}$ . Soil moisture and 4-week precipitation data were transformed to obtain normalized residuals.

Linear regression was used to examine the relationship between 4-week rainfall and percentage soil moisture for the 8 year dataset. Using the regression parameters we predict soil moisture content from rainfall data of 75 years. To assess the validity of prediction, we calculated the statistical parameters describing the distribution of precipitation for both 8 and 75 years of data. The mean 4 week rainfall was 11.3 and 11.9 cm, and the variance was 3.01 and 3.39 for 75 and 8 years of rainfall data respectively. The frequency distributions of rainfall data for both time intervals were identical ( $\chi^2=4.46$ ,  $P=0.1$ ). We removed the records from 75 years data, that were outside the range (0–47.4 cm) exhibited by 8 years data. It led to removal of two data points, 52 and 55 cm from the 75 year data.

Chi-square analysis of the total number of plants per species in each damage-class category was conducted to examine if species were differentially damaged by drought. We eliminated the damage class 75–100% from the analyses as none of the plants exhibited greater than 75% damage to the canopy. To test for differences in  $\text{RGR}_{\text{ht}}$  and  $\text{RGR}_{\text{crown}}$  among species, one-way analysis of variance was performed. Stomatal conductance and leaf water potentials were compared between dry and wet season among species using a two-way ANOVA, as the assumptions of normality and homoscedasticity were met.

We performed a non-parametric Kruskal–Wallis test to assess if plants experiencing greater degree of die-back (a non-normal variable) also showed greater reduction in  $g_s$  and  $\Psi_{\text{md}}$ . We performed a set of correlation tests between  $\text{RGR}_{\text{ht}}$ ,  $\text{RGR}_{\text{crown}}$ , and each of the physiological variables based upon the measurements made on the same plant. SPSS 11.5

(SPSS, Inc., Chicago IL, USA) was utilized for data analyses.

## Results

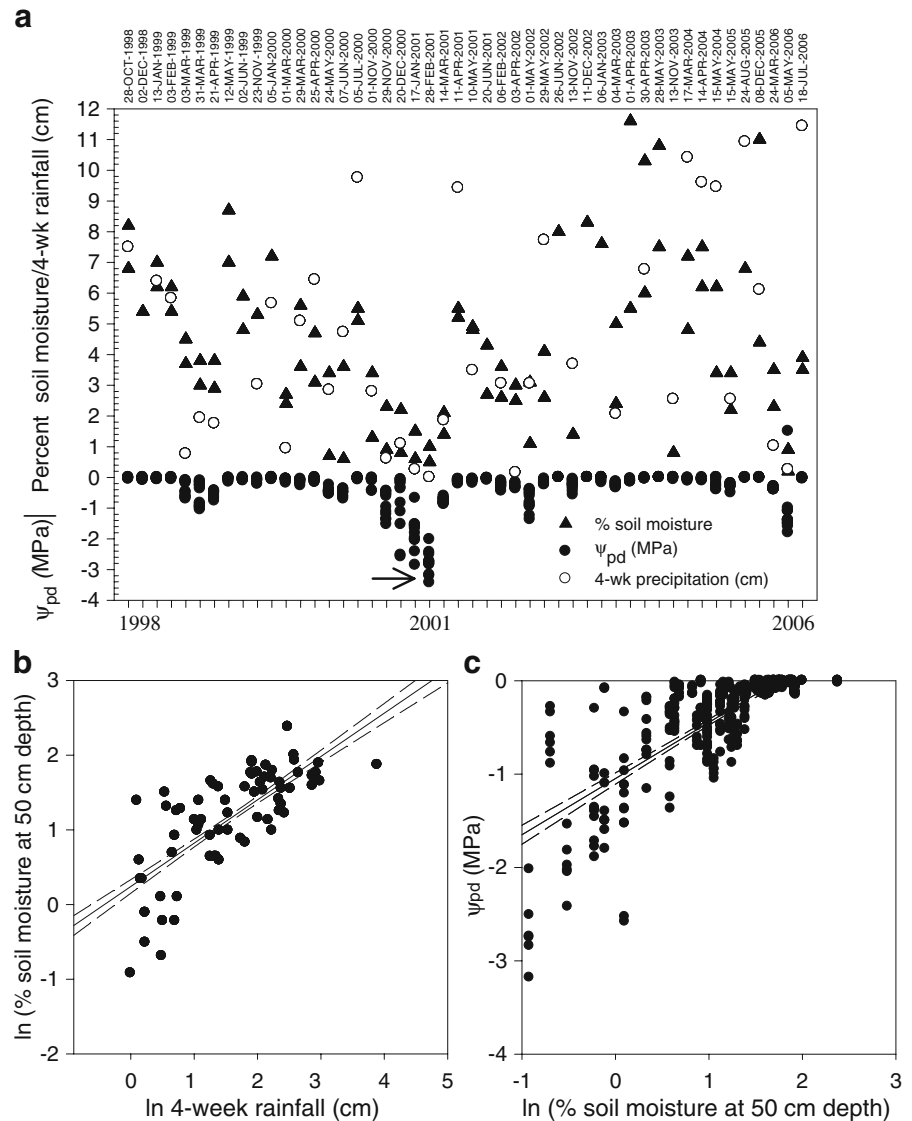
#### Relationship between soil moisture, predawn leaf water potential and precipitation

From 1998 to 2006,  $\Psi_{\text{pd}}$  was never below  $-0.20$  MPa during the wet season (Fig. 1a). Plants experienced severe drought during the early dry seasons of 2000 and 2001. During the period of severe drought, on four sampling occasions between Dec 2000 and Feb 2001 (highlighted with an arrow on Fig. 1a), both *Q. chapmanii* and *Ceratiola* exhibited  $\Psi_{\text{crit}}$  ( $\Psi_{\text{pd}} < -2.50$  MPa for *Q. chapmanii*, and less than  $-1.5$  MPa for *Ceratiola*). Occurrence of  $\Psi_{\text{crit}}$  in leaves was paralleled by low soil moisture values of  $<1\%$  at 50 and 90 cm depths. The soil moisture was replenished in late February and March 2001 causing leaves to hydrate as indicated by greater  $\Psi_{\text{pd}}$  in subsequent measurements.

Soil moisture at 50 cm depth and 4-week prior precipitation were strongly correlated ( $r^2=0.62$ ,  $P < 0.001$ , Fig. 1b). Soil moisture at 50 cm depth alone explained significant variation in  $\Psi_{\text{pd}}$  for *Q. chapmanii* ( $r^2=0.69$ ,  $P < 0.001$ , Fig. 1c); however, the model improved marginally with inclusion of soil moisture at 90 cm depth and 4 week rainfall ( $r^2=0.70$ ,  $P < 0.001$ ). For *Ceratiola*, soil moisture at 50 cm depth was the strongest predictor of  $\Psi_{\text{pd}}$  as revealed by stepwise linear regression ( $r^2=0.50$ ,  $P < 0.001$ ). The soil moisture at 10 cm depth did not significantly contribute to the model for either species.

From the best fit model describing the relationship between soil moisture and  $\Psi_{\text{pd}}$ , we derived the values of percent soil moisture content that led to turgor loss among leaves of both species. Soil moisture contents of 0.57% at 50 cm depth and 0.85% at 90 cm depth generated  $\Psi_{\text{crit}}$  among leaves of *Q. chapmanii*, while soil moisture content of 0.45% at 50 cm depth generated  $\Psi_{\text{crit}}$  among leaves of *Ceratiola*. On only one sampling occasion was the percent soil moisture at the depths of 50 and 90 cm lower than 1% (28<sup>th</sup> Feb 2001). At this time both species developed  $\Psi_{\text{crit}}$  and exhibited severe leaf loss, but plants showed subsequent recovery after a strong rainfall event.

**Fig. 1** Eight years of data on soil moisture and 4-week rainfall (positive values on the  $y$ -axis) and predawn leaf water potential of *C. ericoides* and *Q. chapmanii*.  $\Psi_{pd}$  is denoted by negative values on the  $y$  axis. Arrow highlights the extreme drought of 2000–2001 for which  $\Psi_{crit}$  was recorded for four consecutive occasions in *Q. chapmanii* and *C. ericoides* leaves. The top  $x$  axis lists the dates on which measurements were made, while the bottom  $x$  axis points out landmark years marking occurrence of critical soil moisture (a). The relationship between soil moisture and 4-week rainfall ( $r^2=0.62$ ,  $P<0.001$ ) was used to extrapolate soil moisture for the years 1932–2006 (b). The positive relationship ( $r^2=0.69$ ,  $P<0.001$ ) between soil moisture and  $\Psi_{pd}$  was used to determine soil moisture causing  $\Psi_{crit}$  among leaves (c). The dashed lines on both b and c depict 95% CI bands



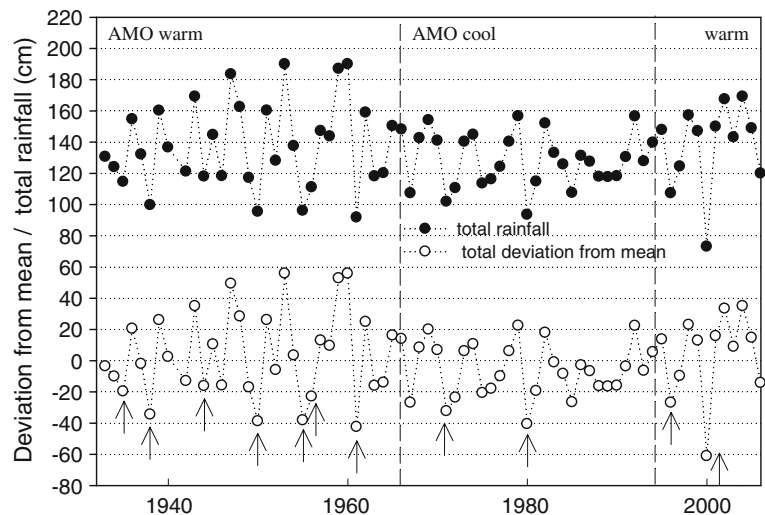
Analysis of 75 year data on rainfall suggested that only in 2000 strong negative deviation from the mean rainfall (>50% reduction) was observed with deficient rainfall in all seasons (Fig. 2). We used the best fit regression model to predict soil moisture at 50 cm depth from rainfall as the predictor variable for 1932–2006 monthly rainfall data.

$$\ln(\text{soil moisture}) = 0.2683 + [0.5626 \times \ln(4 \text{ week rain})]$$

Years with strong negative deviations from the mean rainfall coincided with the years that were

predicted to have critical soil moisture levels leading to  $\Psi_{crit}$  (arrows depicting the years predicted to bear critical soil moisture, Fig. 2). Analysis of predicted soil moisture suggested that values low enough to cause  $\Psi_{crit}$  (turgor loss at predawn), occurred on 16 occasions during 75 years, distributed over a period of 11 years in total (14% of years). The mean return interval for critical turgor loss was 7 years, and did not show an increase in recent years. During warm AMO phases Archbold soils are predicted to have greater variation in soil moisture and overall greater mean soil moisture values. Our predicted values of soil moisture indicate that the warm AMO phase initiated in 1994 has experienced critical soil moisture

**Fig. 2** Annual rainfall data and deviations from average rainfall recorded at Archbold Biological Station from 1932–2006. Arrows depict years when the soil moisture was predicted to fall below critical levels. Superimposed are the AMO periods trends



levels in 1998 and 2000 (the latter can be easily seen in Fig. 2). In contrast, during the AMO's cool phase the variation in soil moisture across years was minimal and critical moisture occurred twice during the first cool phase spanning a total of 20 years.

Leaf water potential at turgor loss, inferred from pressure–volume relationships occurred at  $-2.5$  MPa for *Q. chapmanii* and *Q. inopina* (RWC at turgor loss was 92% for both species). Turgor loss occurred at  $-1.7$  MPa for *Q. geminata* (RWC at turgor loss was 90%) and  $-1.5$  MPa for *C. ericoides* (RWC at turgor loss was 81%). RWC of *Serenoa* and *Sabal* leaves was 89% at  $\Psi_1$  of  $-4$  MPa (highly comparable with *S. palmetto*). As we could not pressurize further, we could not determine  $\Psi_1$  at turgor loss. To reiterate we categorized plants as experiencing  $\Psi_{crit}$  when  $\Psi_{pd}$  was  $-2.5$  MPa for *Q. chapmanii* and *Q. inopina*,  $-1.7$  for *Q. geminata*,  $-1.5$  for *Ceratiola*, and less than  $-4$  MPa for *Serenoa* and *Sabal*.

#### Morphological and physiological responses during the spring drought of 2006

Drought caused observable damage, but only 2% mortality of dominant shrubs in Florida scrub. Only four of 231 individuals (three *Ceratiola* and one *Q. inopina*) did not recover from the drought and were dead at the second sampling in September. Species showed some variation in their distributions among damage classes (Table 2;  $\chi^2=38$ ,  $df=20$ ,  $P<0.01$ ). During the drought, damage ranged from none to  $\leq 75\%$  of the total plant canopy (Table 2). Overall,

24% of plants showed no damage, 53% showed  $\leq 50\%$  damage, 21% plants showed intense leaf shedding and 2% of the plants died. Species such as *Q. inopina* and *Q. chapmanii* that usually complete leaf flushing and expansion by early spring experienced the maximum leaf and branch die-back. In addition, the terminal and lateral leaf buds that were to flush new leaves, had turned brown and had started to shed, thus postponing the leaf production into the wet season. *Ceratiola* and *Q. geminata* experienced moderate drought damage, while the palms were least damaged by drought.

During the 2006 drought, growth varied among species. We found a significant difference in relative crown growth rate among species using one-way ANOVA ( $F_{5, 228}=9.33$ ,  $P<0.01$ ; Fig. 3). *Ceratiola* exhibited the greatest and *Q. geminata* and *Q. inopina* the lowest  $RGR_{crown}$  among all dominant species. No significant variation in  $RGR_{ht}$  occurred across species ( $F_{5, 228}=2.27$ ,  $P>0.05$ ). We found a significantly greater  $RGR_{ht}$  for plants suffering lower degree of drought damage, compared to the plants that suffered greater die-back ( $P<0.05$ ,  $\chi^2=9.23$ ; Fig. 3). However we did not find a significant difference in  $RGR_{crown}$  among drought-induced damage classes ( $\chi^2=0.873$ ,  $P>0.05$ ).

Stomatal conductance varied significantly between wet and dry seasons for all species. (Fig. 4a;  $F_{1, 231}=47.60$ ,  $P<0.05$ ). Species showed a significant difference ( $F_{5, 231}=16.08$ ,  $P<0.05$ ), and the interaction of species and season was significant as well ( $F_{5, 231}=17.70$ ,  $P<0.05$ ). All species had lower conductance

**Table 2** Percentage of each species distributed across the categories of drought-induced damage suggests that plants did not experience severe die-back

Species ( <i>n</i> )	Damage class				
	0% (none)	1–25%	25–50%	50–75%	75–100%
<i>Ceratiola ericoides</i> (28)	21	36	18	25	0
<i>Quercus chapmanii</i> (42)	16	44	22	11	0
<i>Quercus geminata</i> (23)	9	43	17	30	0
<i>Quercus inopina</i> (52)	13	44	29	13	0
<i>Sabal etonia</i> (24)	50	33	17	0	0
<i>Serenoa repens</i> (52)	35	44	13	8	0

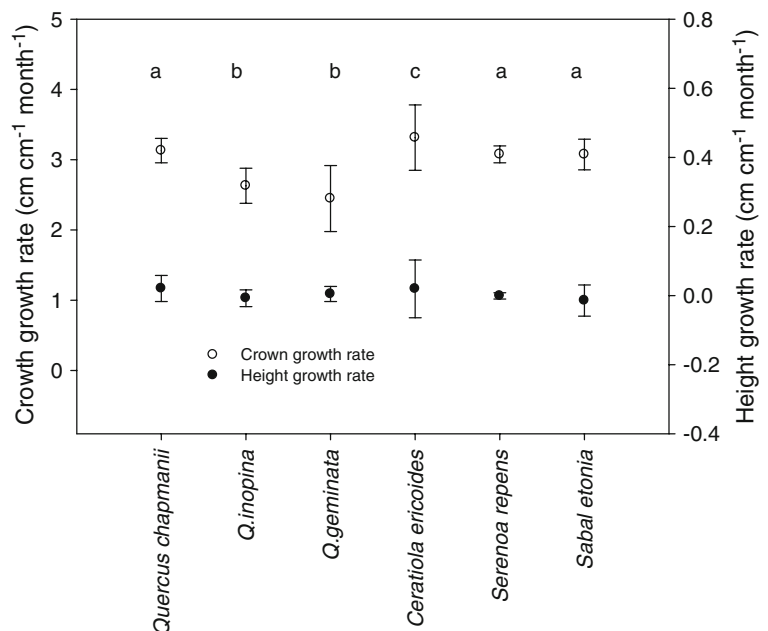
Damage classes are based on percentage of total canopy showing die-back among leaves or stems as sampled during spring drought of 2006.

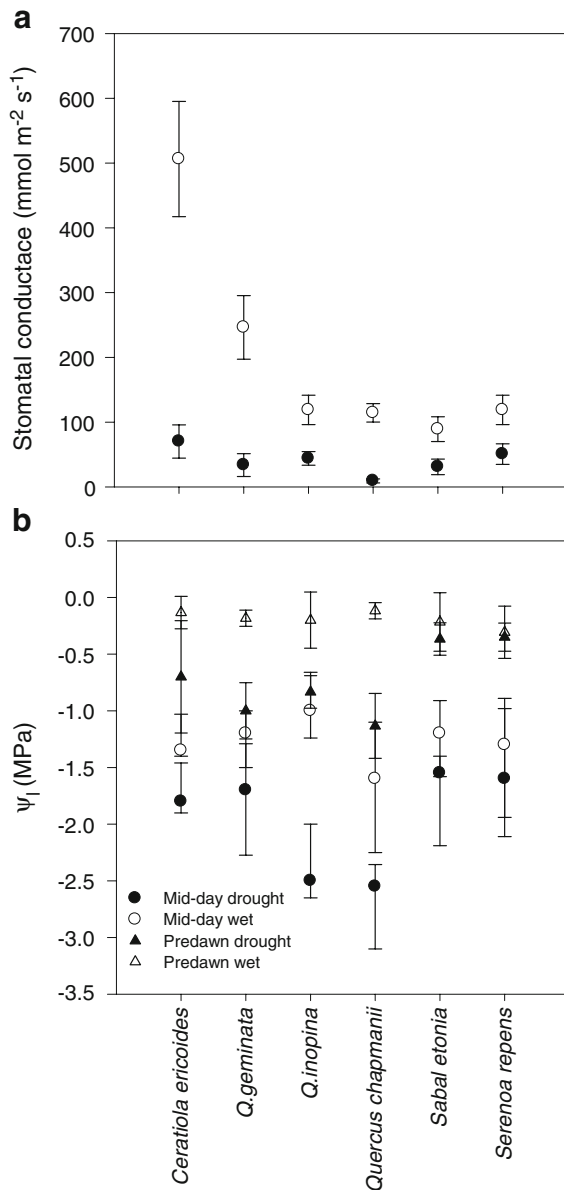
during drought, but the degree of difference was not homogeneous. A post hoc test (Tukey HSD) showed that the  $g_s$  of *Ceratiola* leaves was the greatest and significantly different from all other species ( $g_s$  in dry and wet season was  $70.19 \pm 10.87$  and  $506.21 \pm 40.38$   $\text{mmol m}^{-2} \text{s}^{-1}$  respectively), followed by *Q. geminata* which was significantly different from all other species as well ( $g_s$  in dry and wet season was  $33.81 \pm 8.22$  and  $246.28 \pm 22.30$   $\text{mmol m}^{-2} \text{s}^{-1}$  respectively). No other pairs of species showed significant differences, including *Q. inopina* ( $g_s$  in dry and wet season was  $44.01 \pm 5.51$  and  $118.87 \pm 10.58$   $\text{mmol m}^{-2} \text{s}^{-1}$  respectively), *Serenoa* ( $g_s$  in dry and wet season was  $67 \pm 7.54$  and  $118.91 \pm 10.33$   $\text{mmol m}^{-2} \text{s}^{-1}$

respectively), *Q. chapmanii* ( $g_s$  in dry and wet season was  $9.35 \pm 1.52$  and  $114.38 \pm 6.62$   $\text{mmol m}^{-2} \text{s}^{-1}$  respectively), and *Sabal* ( $g_s$  in dry and wet season was  $31.00 \pm 5.33$  and  $89.20 \pm 7.44$   $\text{mmol m}^{-2} \text{s}^{-1}$  respectively). *Q. chapmanii* was the only species that showed almost complete stomatal closure during the dry season.

Seasonal differences between mid-day leaf water potential were also significant; plants showed lower  $\Psi_{\text{md}}$  during drought compared to the wet season (Fig. 4b;  $F_{1, 141} = 389.90$ ,  $P < 0.01$ ) with a significant species effect ( $F_{5, 141} = 67.20$ ,  $P < 0.01$ ) and a significant interaction of species and season ( $F_{5, 141} = 47.60$ ,  $P < 0.01$ ). *Q. chapmanii* had the most negative  $\Psi_{\text{md}}$

**Fig. 3** Relative crown and height growth rates (mean  $\pm$  95% confidence intervals) of six dominant scrub species during and after the 2006 drought (May–September 2006). Points topped by the same letter are not significantly different in crown growth rate between pairs of species ( $P < 0.05$ ) as revealed by Turkey's post-hoc test





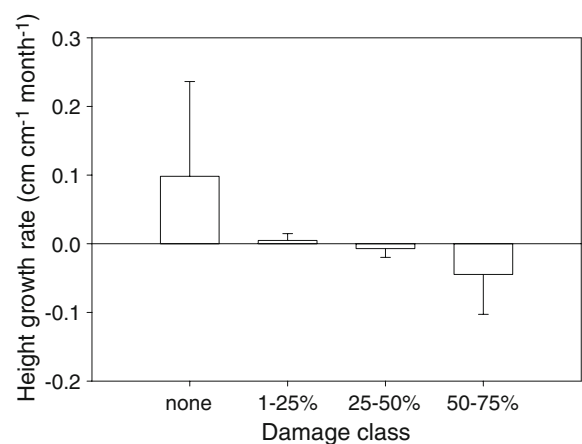
**Fig. 4** Stomatal conductance (mean±95% confidence intervals) of dominant shrub species during drought and wet seasons (a). Leaf water potential ( $\Psi_l$ ) measured at predawn ( $\Psi_{pd}$ ) and mid-day ( $\Psi_{md}$ ) during drought and wet seasons (b)

( $-2.62 \pm 0.06$  MPa), followed by *Q. inopina* and *Sabal* with  $\Psi_{md}$  of  $-2.40 \pm 0.05$  and  $-1.96 \pm 0.25$  MPa respectively. Similar patterns were obtained for predawn leaf water potential with a significant difference due to species ( $F_{5, 82} = 15.29$ ,  $P < 0.001$ ), season ( $F_{1, 82} = 63.45$ ,  $P < 0.001$ ) and a significant interaction of species and season ( $F_{5, 82} = 13.94$ ,  $P < 0.001$ ; Fig. 4b). While the wet season  $\Psi_{pd}$  was high or close to

saturation, *Q. chapmanii* ( $-1.13 \pm 0.01$  MPa) had the lowest  $\Psi_{pd}$  during the dry season, followed by *Q. geminata* ( $-1.00 \pm 0.06$  MPa) and *Q. inopina* ( $-0.9 \pm 0.03$  MPa) respectively. In the dry season species such as *Q. chapmanii* and *Q. inopina* showed poor recovery from drought stress as inferred from low predawn water status.

Differences within species between wet and dry season were compared with Student's *t*-tests. *Ceratiola* showed the greatest difference in conductance between seasons followed by *Q. geminata*. We adjusted the probability values using Bonferroni corrections. All species showed a significantly greater conductance during the wet season compared to dry season ( $P < 0.01$ ). Mid-day leaf water potential ( $\Psi_{md}$ ) was significantly lower for all species during drought except *Serenoa* and *Sabal*, which showed comparable leaf water potential between seasons ( $t = -1.10$ ,  $P > 0.1$ ). Palms did not show a significant difference in  $\Psi_{pd}$  ( $P > 0.05$ ) between seasons as well, while the oaks and rosemary had significantly more negative  $\Psi_{pd}$  in drought compared to wet season ( $P < 0.01$ ).

Stomatal conductance was significantly lower among plants that incurred greater drought-induced damage, such as loss of branches and leaves (Kruskal Wallis  $\chi^2 = 10.31$ ,  $df = 3$ ,  $P < 0.05$ , Fig. 5), while  $\Psi_{md}$  was marginally non-significant ( $\chi^2 = 6.07$ ,  $df = 3$ ,  $P = 0.08$ ) among plants in different damage classes. Neither  $RGR_{ht}$  nor  $RGR_{crown}$  was significantly correlated with  $g_s$  or  $\Psi_{md}$  during drought.



**Fig. 5** Height growth rate (mean±95% confidence intervals) of plants among drought induced die-back classes. Height growth was lower among plants experiencing greater damage ( $P < 0.05$ )

## Depth of water uptake

*Q. inopina* had the shallowest depth of water uptake (20 cm) as indicated by stable isotope analysis (Fig. 6). The depth of water uptake of *Q. geminata* and *Q. chapmanii* ranged from 40–200 cm, though *Q. chapmanii* showed a non-significantly higher depth of water uptake than *Q. geminata*. Depth of water uptake was significantly different among the oak species, though the difference was marginal ( $P=0.05$ ,  $F_{1, 28}=3.17$ ). Depth of water uptake was shallower in *Q. inopina* compared to *Q. geminata* and *Q. chapmanii* as revealed by Tukey post hoc test ( $P=0.052$ ). *Ceratiola* had rooting depths of only up to 50 cm as measured by root excavation. The rooting depths of *Ceratiola* determined with excavation were comparable to the results of Hawkes and Casper (2002), which showed lateral expansion of *Ceratiola* roots up to 1 m away from the root crown, while the rooting depths were reported to be less than 1 m. Our observations that the *Serenoa* and *Sabal* roots reach up to the depths of 2.5 m were parallel to published data on rooting depths of these palms (Brown et al. 1990).

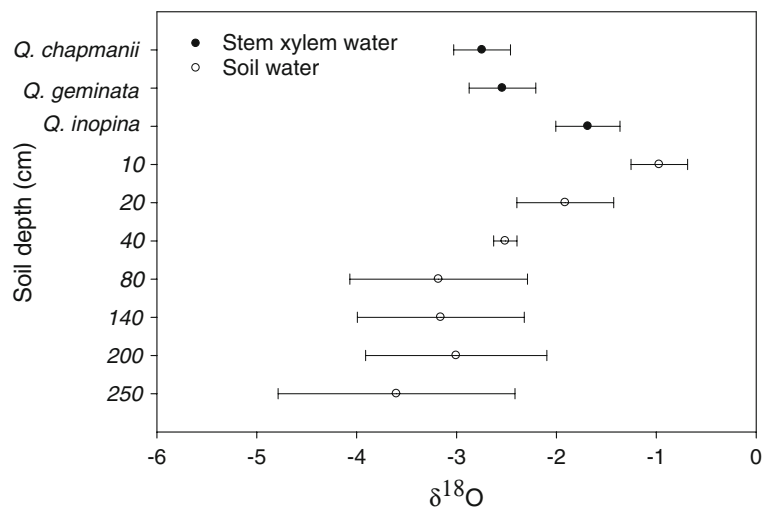
## Discussion

Differential effects of soil moisture on plant responses are poorly delineated because simultaneous records of soil and plant water status are lacking. With simultaneous data on soil moisture and predawn leaf water status for two species, we show that soil moisture

explained a substantial percentage (69%) of variation in  $\Psi_{pd}$ . The dominant species in Florida scrub ecosystem spanned an array of morphological and physiological responses to differential soil moisture decline. For example, *Q. chapmanii* leaves showed predawn saturation over a range of soil moisture content (5–30% soil moisture at 50 cm depth) and developed  $\Psi_{crit}$  at 0.57% and 0.85% soil moisture at the depth of 50 at 90 cm respectively. In addition, *Q. chapmanii* exhibited low  $\Psi_{pd}$ , some leaf shedding and branch die-back at 0–1% soil moisture during the spring drought of 2006. On the other hand, *Serenoa* and *Sabal*, the two palms maintained comparable leaf water status during the spring drought and wet season of 2006, and exhibited 0% mortality during the severe drought of 2000 (Abrahamson and Abrahamson 2002).

Patterns in Floridian rainfall are driven by Atlantic Multidecadal Oscillation phenomenon (Sutton and Hudson 2005). The predicted soil moisture for 75-year period echoed the patterns in rainfall. We suggest that the predicted soil moisture is a good proxy of real soil moisture pattern. The unexplained variation of 38% in the best fit model of soil moisture against 4-week rainfall can be attributed to recurring values of saturation soil moisture during wet season. Surficial water table ranges from 0.5 to >2.5 m in the scrub ecosystem and responds quickly to rainfall events causing soil saturation at 50 and 90 cm depth. Conditions of soil saturation can persist for several weeks or months in a row, during the wet season and also in early dry season reflecting the lag effect of strong rainfall events. However our results do not

**Fig. 6** Values of  $\delta^{18}\text{O}$  (mean $\pm$ SE) in water extracted from stem xylem of three oak species ( $n=5$  individuals per site) five individuals per species per site and water from soil samples at different depths



undermine the predicted values of soil moisture during dry season. Our predictions based on 8 year of simultaneous rainfall and soil moisture data yielded conservative but accurate estimate of critical soil moisture (0.57% at 50 cm depth), which was slightly lower than the actual values that occurred during year 2000–2001 (0.6% at 50 cm depth). Based on our predictions of soil moisture over a period of 75 years, we hypothesize that the frequency of drought occurrence affecting dominant shrubs of Florida scrub has not increased with time in any discernible fashion.

Our results echoed the well documented correlations between physiology and morphology. The morphological effects such as leaf shedding in response to spring drought indicates that even though the leaves did not attain  $\Psi_{\text{crit}}$ , the incomplete cycles of leaf water recovery (from midday to predawn) inflicted irreversible leaf tissue damage. Incomplete recovery of leaves from drought induced tensions causes irreparable damage to functional leaves, while soil moisture depletion may further arrest the growth of newly flushing and expanding leaves. However, when leaf shedding was accompanied by stem and branch die-back the likely cause was drought-induced xylem failure (Tyree and Zimmermann 2002). The first and foremost physiological response of soil dry-down is a decline in  $g_s$  (Zhang and Davies 1989; Tardieu and Davies 1993; Jones 1998; Buckley 2005). Leaf water status declines with complete stomatal closure as well (Kanemasu and Tanner 1969; Comstock and Mencuccini 1998; Lambers et al. 1998). Thus if the drought is persistent, stomatal closure does not prevent irreversible turgor loss in leaves, because of cavitation-induced disruption of water supply to leaves, as demonstrated in Mediterranean oaks (Griffin 1973; Damesin and Rambal 1995), and non-oak species (Sakcali and Ozturk 2004) experiencing abnormal drought conditions, and by *Q. chapmanii* and *Ceratiola* in this study.

Our finding that only 2% plants showed mortality in spring 2006 suggest that longevity of critical soil moisture during the drought in 2006 was not substantial enough to cause dramatic plant mortality such as experienced by dominant species in the southwestern US and Europe during the drought of 2000–2003 (Breshears et al. 2005; Gobron et al. 2005; Gitlin et al. 2006). Plants of dominant eucalypts in central Australia experienced widespread mortality

when soil moisture reached permanent wilting point and caused turgor loss among leaves (Fensham and Fairfax 2007). Similarly, leaf water potential near turgor loss point led to 50% mortality in a *Nothofagus* species under simulated drought (Piper et al. 2007). The patterns in total rainfall, rainfall distribution and soil texture might play a role in determining the longevity of critical soil moisture across ecosystems (Rodriguez-Iturbe et al. 2001). The plants in Florida scrub experience large fluctuations in soil moisture availability during the dry season because the highly porous sands expedite the drainage and recharge of water (Carter et al. 1989), but do not experience extended dry period because 40% of the annual rainfall occurs during the dry season (Chen and Gerber 1990). In addition to wide fluctuations in soil moisture, the shallow water table might buffer the plants against persistently low soil moisture values in the dry season. We hypothesize that Florida scrub plants are equipped to survive large fluctuations in soil moisture availability but do not possess the mechanisms to cope with persistently dry soils because the persistently low soil moisture conditions occur rarely in Florida scrub soils.

Our results suggest that the drought effects on plants during spring 2006 were stronger than a normal dry season experienced by plants in scrub ecosystem. Plants experiencing greater degree of die-back showed lower  $g_s$ , compared to plants that showed no die-back or lower degree of die-back. Though we do not have data on plant growth rates for an average dry season, our data on physiological parameters collected during spring 2005 suggests that mean  $g_s$  and  $\Psi_{\text{pd}}$  was greater during spring 2005 than spring 2006 for all species except the palms. During the normal spring of 2005 the mean  $g_s$  and  $\Psi_{\text{pd}}$  of *Q. chapmanii* was  $110 \pm 23.11 \text{ mmol m}^{-2} \text{ s}^{-1}$ , and  $-0.3 \pm 0.02 \text{ MPa}$  respectively. Besides, all plants experiencing a higher degree of drought-damage showed dampened height growth rate in relation to plants that showed minimal to no drought induced damage, suggesting that differential soil moisture decline translates to decline in  $\Psi_{\text{pd}}$  and stomatal conductance rates, which in effect has a negative effect on plant growth rate.

Access to deeper soil water resources and the abilities of plants to extract water may explain differences in responses to drought among species (Otieno et al. 2005). Greater rooting depth confers drought tolerance

compared to shallow-rooted species within a plant community and may have a direct effect on fitness by enhancing plant productivity (Ho et al. 2005; Pinheiro et al. 2005; Padilla and Pugnaire 2007). Responses of scrub species to drought may be related to their rooting morphologies. Deeper rooted species (i.e. palms) were less significantly affected by drought than the shallower rooted *Ceratiola* and *Q. inopina*, and moderately rooted *Q. geminata* and *Q. chapmanii*. Based on the physiological responses, deep rooted palms are isohydric plants, which maintain constant leaf water potentials and stomatal conductance across seasons by having access to water throughout the year (Franks et al. 2007). The wider distribution of rooting depths permits a plant to shift the depth of soil water uptake, as shown by *Quercus suber* and *Erica* spp. in Mediterranean forests and shrubland ecosystems (Silva and Rego 2003; Otieno et al. 2006), and by *Serenoa* and *Sabal* in this study. *Sabal* and *Serenoa* did not undergo any mortality even during severe drought of 2000 (Abrahamson and Abrahamson 2002) and barely showed any leaf die-back during the spring drought of 2006.

Co-occurring plant species within a plant community use diversity of responses such as documented in Brodribb et al. (2002), Gebrekirstos et al. (2006), and our study. Our findings have implications for restoration of Florida scrub ecosystem and highlight that soil moisture content and its distribution in space and time is critical to understanding of species responses as observed in this study. The patterns of plant and soil water status, and their effects on plant growth and mortality might be utilized for planning restoration of plant communities. Water table in scrub ecosystem is close to surface, and buffers many plant species against short-term drought (Weekley et al. 2007). However, severe droughts are likely to have the differential effects on Florida scrub species, and will be particularly damaging to young transplants used in restorations. Thus it is important that the restoration efforts address the measures to achieve the native patterns of soil hydrology required for successful establishment of plant communities that harbor species with well defined requirements of soil moisture.

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