# Variation in soil moisture in relation to rainfall, vegetation, gaps, and time-since-fire in Florida scrub[1]

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*Abstract*: Florida scrub is a pyrogenic shrubland ecosystem occurring on well-drained sands derived from contemporary and relictual beach dunes. Despite average annual precipitation > 1300 mm, Florida scrub is dominated by xeromorphic plants. We monitored spatio-temporal variation in soil moisture to determine if the distribution of Florida scrub communities reflects patterns in soil moisture variation. Using frequency domain reflectometry, we measured soil moisture at 24 sampling stations (3 depths per station) in 3 Florida scrub communities (rosemary scrub, scrubby flatwoods, and oak–hickory scrub) at Archbold Biological Station for 3 y (October 1998–September 2001). Stations were arrayed to sample 2 microhabitats (gaps, shrubs) and 2 burn histories. Soil moisture closely tracked cumulative rainfall across widely varying precipitation in the 3 y studied. Soil moisture changed through time and differed significantly among habitats; it was generally highest in scrubby flatwoods, particularly during the wettest periods, and lowest in oak–hickory scrub. Soil moisture was generally greater at deeper depths, in more recently burned sites, and in gaps. Burn effects were particularly pronounced in rosemary scrub, where lack of resprouting dominants after fire maintains more distinct, larger gaps. Burn and gap effects were small in absolute terms, but burned sites and gaps consistently had greater soil moisture than unburned and matrix sites. These small differences may be critical to the germination, establishment, and growth of narrowly endemic plants, particularly in Florida rosemary scrub. However, factors such as competition for nutrients, cryptobiotic soil crusts, litter accumulation, gap size, and allelopathy may be more important in influencing distributions of endemic scrub plants.
*Keywords*: fire, Florida scrub, frequency domain reflectometry, seasonal variability, shrublands, soil moisture.

*Résumé* : Les broussailles de Floride sont un écosystème arbustif pyrogène qui se retrouve sur des sables bien drainés dérivés de dunes de plage contemporaines ou reliques. Malgré une moyenne annuelle de précipitation > 1300 mm, les broussailles de Floride sont dominées par des plantes xéromorphes. Nous avons suivi la variation spatio-temporelle de l'humidité du sol afin de déterminer si la distribution des communautés de broussailles de Floride reflétait les patrons de variation de l'humidité du sol. En utilisant la réflectométrie dans le domaine fréquentiel, nous avons mesuré l'humidité du sol dans 24 stations d'échantillonnage (3 profondeurs par station) dans 3 communautés de broussailles de Floride (broussailles de romarin, plateaux broussailleux, broussailles de chêne et de caryer) à la Station biologique Archbold durant 3 ans (octobre 1998 – septembre 2001). Les stations étaient organisées de façon à échantillonner 2 microhabitats (ouvertures et arbustaies) et 2 historiques de feu. L'humidité du sol suivait de près les précipitations cumulatives et ce pour de grandes variations de précipitation et pour les 3 années étudiées. L'humidité du sol variait dans le temps et différait de façon significative entre les habitats, elle était généralement plus élevée dans les plateaux broussailleux, particulièrement lors des périodes les plus humides, et plus basse dans les broussailles de chêne et de caryer. L'humidité du sol était généralement plus élevée en profondeur, dans les sites récemment brûlés et dans les ouvertures. Les effets du feu étaient particulièrement prononcés dans les broussailles de romarin où l'absence de rejets dominants après feu maintien des ouvertures plus grandes et plus distinctes. Les effets du feu et des ouvertures étaient faibles en termes absolus mais l'humidité du sol était toujours plus élevée dans les sites brûlés et dans les ouvertures que dans les broussailles et dans les sites non brûlés. Ces petites différences peuvent être critiques pour la germination, l'établissement et la croissance de plantes endémiques rares, particulièrement dans le cas des broussailles de romarin. Cependant, des facteurs tels que la compétition pour les nutriments, les croûtes cryptobiotiques, l'accumulation de litière, la taille des ouvertures et l'allélopathie peuvent être plus importants en terme d'influence sur la distribution des broussailles endémiques.
*Mots-clés* : arbustaies, broussailles de Floride, feu, humidité du sol, réflectométrie dans le domaine fréquentiel, varaibilité saisonnière.

*Nomenclature*: Wunderlin & Hansen, 2003, except where another authority is noted.

## Introduction

Soil moisture plays an important role in the distribution of plant communities at a global scale (Boyer, 1982; Francis & Currie, 2003). Soil moisture availability is governed by rainfall, hydraulic properties of the soil, evaporation, and transpiration. Areas with similar rainfall patterns may harbour diverse plant communities due to differences in water holding capacity (Kursar, Engelbrecht & Tyree, 2005), depth to the water table (Watson & Burnett, 1993), or disturbance history (D'Odorico, Francesco & Ridolfi, 2005). In particular, fire may increase or decrease soil moisture availability by altering vegetation structure and thereby affecting rates of transpiration (Sakalauskas *et al.,* 2001; Nardoto & Bustamante, 2003).

Florida scrub is a globally threatened (Dobson *et al.,* 1997; Estill & Cruzan, 2001) pyrogenic shrubland ecosystem (Myers, 1990; Menges, 1999) consisting of plant communities arrayed along a gradient of depth to the water table (Abrahamson *et al.,* 1984). Several variants of Florida scrub occur (*e.g.,* Florida rosemary scrub, scrubby flatwoods, oak–hickory scrub), differing in geographic location, geological age, elevation, soil type, natural fire frequency, community structure, and species composition (Myers, 1990; Menges, 1999; Boughton *et al.,* 2006). All variants occupy well-drained to excessively well-drained sandy entisols or droughty spodisols derived from quartz sands (Brown, Stone & Carlisle, 1990). Florida scrub experiences moderate to heavy rainfall (mean of about 1300 mm annually) of which ~60% falls during the 4-month summer (June–September) rainy season (Chen & Gerber, 1990). As in shrublands in South Africa and Australia, Florida scrub is dominated by sclerophyllous shrubs despite high annual rainfall. Some aspects of Florida scrub are comparable to Mediterranean ecosystems that have far lower precipitation and a winter, rather than a summer, rainy season. (Carrington & Keeley, 1999).

Florida scrub plant morphology, phenology, and physiology suggest that partitioning of soil water could be an important mechanism explaining the distribution and abundance of scrub plants. However, it is not clear how soil moisture varies seasonally in response to seasonality of rainfall, among scrub variants differing in community structure and species composition, with time-since-fire, or among gap and shrub matrix microsites. For example, if transpiration is the major source of water loss from scrub soils, one would expect more open areas (recently burned or persistent gaps among dominant shrubs) to have higher soil moisture. As gaps close, water availability may decrease as the shrub matrix encroaches both above- and belowground (Petru & Menges, 2003). Gap closure and drying are likely to have deleterious effects on the many endemic perennial forbs and low woody plants that have evolved to specialize in these microsites (Christman & Judd, 1990; Quintana-Ascencio & Morales-Hernandez, 1997; Menges & Quintana-Ascencio, 2004; Menges *et al.,* in press).

Only one study has previously documented soil moisture in a Florida scrub habitat. Using time domain reflectometry, Hungate *et al.* (2002) found that soil moisture at depths varying from 3–10 to 60–65 cm tracked rainfall over an 8-month period that included a 4-month-long summer drought in an oak-dominated coastal scrub.

In this study, we used frequency domain reflectometry (Veldkamp & O'Brien, 2000) to investigate seasonal variability in soil moisture in 3 Florida scrub communities. Within these communities, we compared percent soil moisture at 3 depths, in recently burned *versus* long-unburned sites, and in gap *versus* shrub matrix microhabitats. We specifically addressed the following questions: What is the relationship between rainfall and seasonal patterns of soil moisture? How does soil moisture vary seasonally among Florida scrub communities? How does it vary with depth and between shrub matrix and open gap microsites? How is soil moisture affected by the fire history of a site? We also considered whether soil moisture differences are likely to be one of the explanations for the specialization of many Florida scrub species for gaps and recently burned sites.

## Methods

### Climate and study sites

This study was conducted at Archbold Biological Station, a 2000-ha research area and preserve located in Highlands County, Florida, near the southern terminus of the 160-km-long Lake Wales Ridge in south-central peninsular Florida (27° 11' N, 81° 21' W). The site comprises a mosaic of shrub-dominated xeric uplands, mesic flatwoods, and seasonal wetlands (Abrahamson *et al.,* 1984).

The climate of south-central Florida is characterized by warm, wet summers and cool, dry winters. Mean annual rainfall at Archbold (1932–2005, recorded to the nearest 0.01 inches) is 1366 mm, with ~60% falling during the summer (June–September) rainy season (Figure 1). However, El Niño years result in higher than normal winter rainfall; for example, during the extreme El Niño event of 1997–1998, total dry season (October 1997–May 1998) rainfall at Archbold was almost twice the long term average (1015 *versus* 547 mm). Mean annual temperature at Archbold (1952–2005) is 22.3 °C. January is the coldest month of the year with a mean of 15.9 °C; the mean maximum January
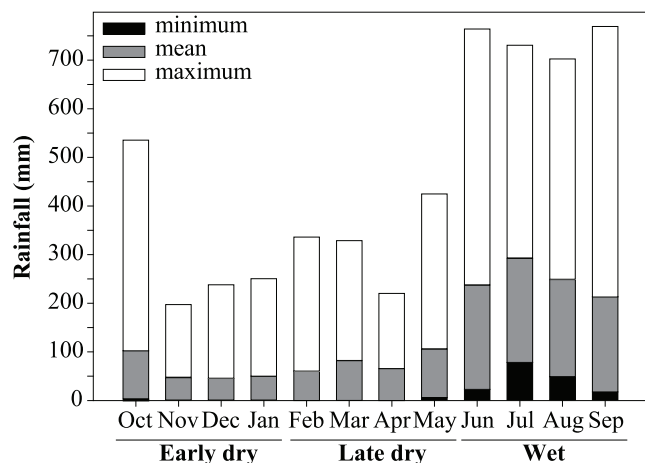


FIGURE 1. Minimum, mean, and maximum monthly rainfall at Archbold Biological Station (1932–2005) by soil moisture season. Note that in some dry season months, minimum rainfall is zero.

temperature is 23.3 °C and the mean minimum is 8.3 °C. August is the hottest month with a mean of 27.4 °C; the mean maximum August temperature is 34.0 °C and the mean minimum is 20.8 °C.

The 36-month sampling period encompassed by this study included the driest calendar year on record at Archbold (2000) and one of the wettest (1999). Total rainfall based on the annual dry-to-wet soil moisture cycle (October–September) in 1998–1999 was 1569.5 mm, 14.5% above the 73-y average (1932–2005); May, June, July, and September were ~50 mm above normal, and August was 177.8 mm above normal. In contrast, total rainfall in 1999–2000 was 828.8 mm, 39.5% below average. The most extreme deviations from normal seasonal rainfall patterns occurred during the 2000 summer drought, when rainfall was 42.3% below normal, and summer 2001, when rainfall was 40.5% above normal (Figure 2).

We measured soil moisture in 3 Florida scrub communities characteristic of the Lake Wales Ridge scrub ecosystem:

(1) The rosemary scrub community is characterized by a discontinuous shrub matrix dominated by Florida rosemary (*Ceratiola ericoides*; Ericaceae) and many open sandy gaps, with variable abundances of herbs, including several species of endemic gap specialists (Menges & Hawkes, 1998; Menges *et al.,* in press);

(2) The scrubby flatwoods community is characterized by a relatively continuous shrub matrix dominated by clonal oaks (especially *Quercus inopina*) and relatively few gaps, with variable abundances of herbs, including a few endemics (Abrahamson *et al.*, 1984; Abrahamson & Hartnett, 1990; Menges, 1999); and

(3) The oak–hickory scrub community is characterized by a relatively dense shrub matrix dominated by *Quercus myrtifolia* and *Carya floridana*, with relatively few gaps and few endemics ("southern Ridge sandhill/hickory phase" of Abrahamson *et al.*, 1984; Menges, 1999).
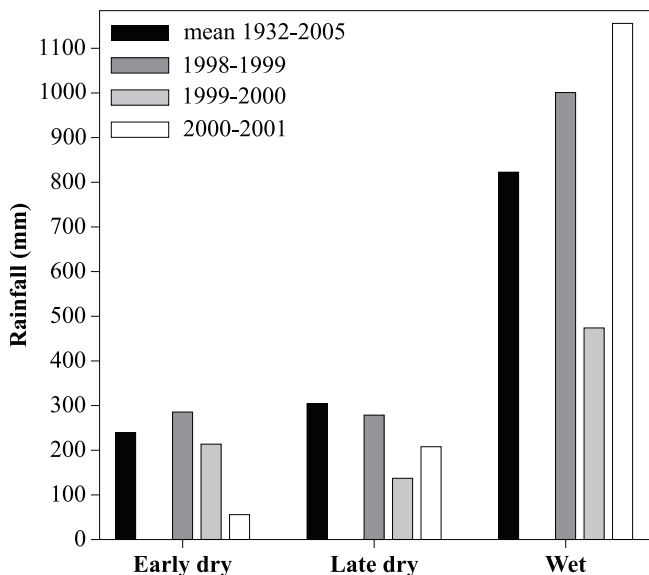


FIGURE 2. Comparison of total seasonal rainfall at Archbold Biological Station for the 3 study years to the 73-y mean.

Natural fire return intervals in these scrub habitats vary from < 10 y in oak–hickory scrub (Menges *et al.,* 2006) to several decades in Florida rosemary scrub (Myers, 1990; Menges, 1999; Menges, 2007). In scrubby flatwoods and oak–hickory scrub, the shrub dominants (*e.g.,* clonal oaks and repent palmettos [*Serenoa repens, Sabal etonia*] resprout following fire; in contrast, Florida rosemary [*Ceratiola ericoides*] is killed by fire and recruits from a soil seedbank).

EXPERIMENTAL DESIGN AND SAMPLING PROTOCOL

We installed 72 PVC tubes (schedule 40, 100 cm long and 10.2 cm in diameter) into 3 community types × 3 sites × 2 times-since-fire categories (burned *versus* unburned) × 2 microsites (gap *versus* matrix) × 2 replicates. Tubes were installed vertically so that about 5 cm protruded above the soil surface. Between sampling sessions, tubes were closed off with PVC caps to prevent intrusion by rain, sand, litter, or animals. In each community we sampled 4 sites. We chose 2 sites that were recently burned (3–5 y previously at the start of the study; 6–8 y by the close of the 3-y data set reported here) and 2 that were long unburned (> 20 y). Some recently burned and long unburned sites were contiguous. At each sampling site, tubes were paired: 1 tube within the shrub matrix and another within an adjacent shrub-free gap. At each tube, we measured soil moisture at 3 depths (10, 50, and 90 cm) using a Sentry 200-AP frequency domain reflectometry system (Troxler Electronics Lab, Research Triangle Park, North Carolina, USA). Depths were chosen to span the range of rooting depths observed in most Florida scrub species.

We sampled the 72 tubes weekly from 1 October 1998 through 9 June 1999 and every second week from 23 June 1999 though 3 October 2001. For the current analysis we used only bi-weekly data. Three sampling sessions were separated by 3 weeks due to technical difficulties. On each of the resulting 78 sampling dates we collected 216 data points (72 tubes × 3 depths). During the wettest periods, ground water intrusion into the tubes was recorded as evidence of soil saturation at the depth at which water was encountered by the probe. Saturation was recorded as 40% soil moisture by volume.

The Sentry 200-AP uses the dielectric constant of water to measure the moisture content of soil. It consists of a probe containing two electrodes separated by a spacer. The electric field of the electrodes has a resonance frequency that shifts based on the soil water content. The greater the soil moisture content, the greater is the resonance frequency shift. To calibrate the Sentry 200-AP, we compared instrument readings to gravimetric estimates of soil moisture. Instrument readings were obtained by lowering the probe 50 cm into a PVC tube inserted into a 30-gal plastic barrel filled with sand saturated with water. Gravimetric estimates were obtained by simultaneously collecting sand at the same depth. We repeated both measurements at frequent intervals as evaporation dried the soil. The data were used in a regression to develop the following relationship:

percent soil moisture = $D \times 49.887 + 3039.543$

where D is the resonance frequency shift measured by the Sentry 200-AP. This equation was programmed into the

Sentry 200-AP, which calculated percent soil moisture by volume, the variable used in the analyses below.

DATA ANALYSIS

We evaluated the relationship between our soil moisture measurements and rainfall by plotting mean percent soil moisture against cumulative bi-weekly rainfall totals. We used a multivariate Repeated Measures ANOVA procedure (SPSS, 2003) to assess differences over time in soil moisture among the 3 scrub communities, the 3 depths, between open-gap and shrub matrix microhabitats, and between sites with and without recent fire; we also examined all 2- and 3-way interactions among these main effects. To reduce heterogeneity of variances, we used natural log transformed soil moisture values. We report Pillai's Trace statistic because it is robust to departures from the assumptions of the multivariate procedure (Potvin, Lechowicz & Tardif, 1990).

We analyzed the soil moisture data at 2 temporal scales: (1) based on the 78 bi-weekly sampling sessions as described above; and (2) based on the annual soil moisture cycle. We divided the annual soil moisture cycle into 3 seasons (Figure 1): early dry season (October through January), late dry season (February through May), and wet season (June through September). With few exceptions, the results of the ANOVAs were qualitatively the same at the 2 scales; unless otherwise indicated, statistics reported below are based on the seasonal analysis.

## Results

RAINFALL AND VARIATION IN SOIL MOISTURE

Bi-weekly rainfall totals between 17 September 1998 and 2 October 2001 (the 2-week totals preceding the first and last soil moisture samples, respectively) ranged from 0 to 358.6 mm; during this period mean percent soil moisture ranged from 0.44 to 20.4%. Soil moisture generally tracked cumulative rainfall for the 2-week period preceding sampling (soil moisture [natural log transformed] = 1.8534· rainfall [natural log transformed] − 0.0258; $r^2$ = 0.4548, $P$ < 0.001), with particularly high peaks occurring after extended periods of heavy rainfall (Figure 3). We recorded the highest mean soil moisture (20.4%) in late September 1999, following an exceptionally wet summer with monthly rainfall totals 50.0–177.8 mm above normal from May–September. In contrast, the lowest reading (0.44%) occurred in February 2001 following the 2000 drought, the driest year on record at Archbold. Although the highest bi-weekly rainfall total (358.6 mm, 25 July 2001) did not result in a sharp increase in soil moisture, the second highest bi-weekly rainfall (240.0 mm, 19 September 2001) produced the highest peak in soil moisture since late 1999.

High soil moisture values occasionally reflected sampling conducted in the proximate aftermath of unseasonably high rainfall. For example, on 5 November 1998 tropical storm Mitch dropped 102.6 mm of rain on Archbold and the relatively high percent soil moisture (9.03%) recorded on 11 November 1998 (Figure 4) reflected this event.

Soil moisture varied significantly among seasons in all 3 y (ANOVA, $P$ < 0.001 for all pairwise comparisons), but the pattern of variation differed among years (Figure 4), reflecting both the Archbold record-breaking wet year of 1999 and the extremely dry year of 2000. Thus, the 1999–2000 dry season began with soil moisture values more than double the average annual values, and in contrast the 2000–2001 dry season began with values only half the annual
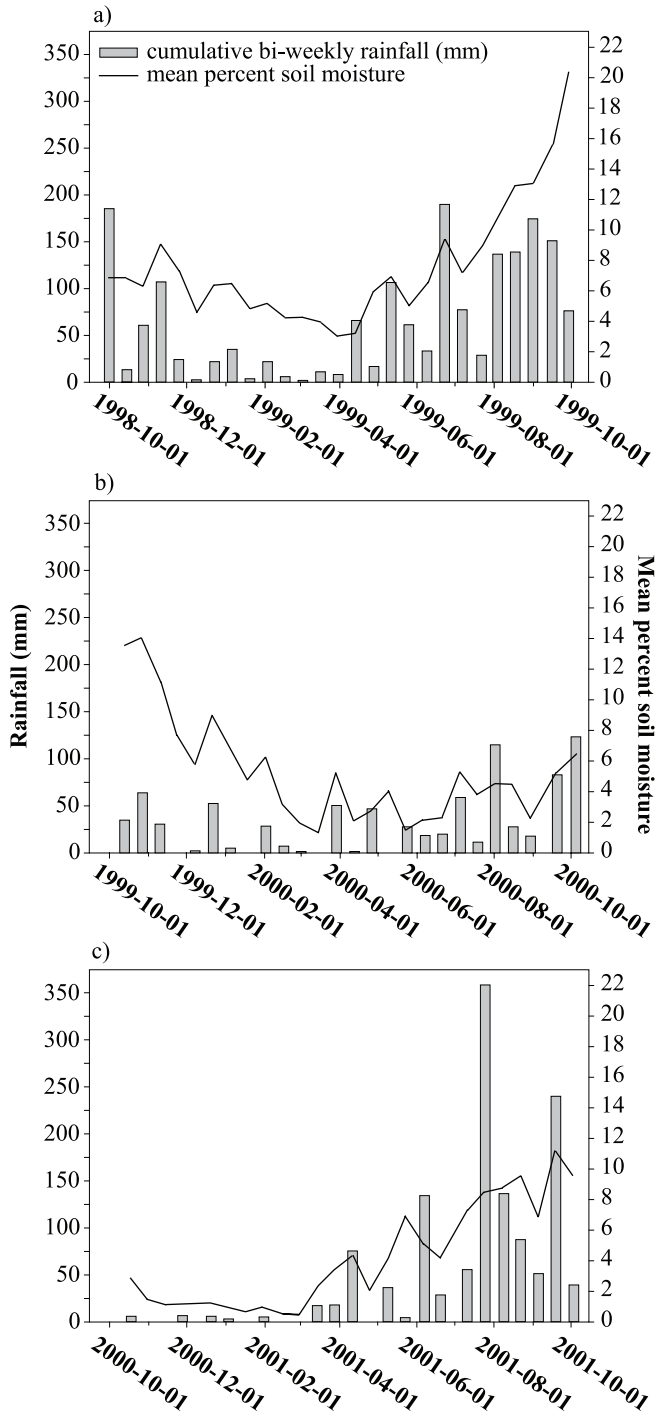


FIGURE 3. Cumulative bi-weekly rainfall in mm (left Y-axis) and mean percent soil moisture based on bi-weekly sampling sessions (right Y-axis) for (a) October 1998–September 1999; (b) October 1999–September 2000; (c) October 2000–September 2001.

average. Soil moisture values rose sharply in late May 2001 in response to increases in bi-weekly rainfall totals at the end of the dry season. Soil moisture values recorded between late May 2001 and late October 2001 (generally between 4 and 10%), corresponded more closely to an average rainfall year than either 1999 or 2000.

In repeated-measures ANOVA, percent soil moisture showed strong seasonal changes (Table I). Soil moisture was highest during the wet season; in 2 of 3 y it was lowest in the late dry season and intermediate during the early dry season (Figure 3).

SOIL MOISTURE BY SCRUB TYPE, DEPTH, TIME-SINCE FIRE, AND GAP/MATRIX MICROHABITAT

Percent soil moisture differed significantly among scrub communities, along the depth gradient, between recently burned and long-unburned sites, and between shrub matrix and gap microhabitats (Table I). Interactions between community and depth, time-since-fire class, and microhabitat (gap *versus* matrix) also differed significantly over time (Table I).

Over time, soil moisture was generally highest in scrubby flatwoods and lowest in oak–hickory scrub (Figure 5; Table I: season × vegetation), with differences most pronounced during wetter periods (*e.g.,* fall 1999). The 3 scrub communities generally followed the same trajectories. Averaged over all readings (between-subject effects), soil moisture also differed significantly among the 3 communities (Table II), with scrubby flatwoods > rosemary scrub > oak–hickory scrub ($P \leq 0.013$ for all pairwise comparisons).

Averaged over all measurements, we detected a significant vertical soil moisture gradient with 90 > 50 > 10 cm ($F = 107.273$, df = 2, $P < 0.001$; $P < 0.001$ for all pairwise comparisons). The most notable exception to this trend occurred in summer 2000 during the driest period on record at Archbold when there was little difference in percent soil moisture among the 3 depths for any of the 3 communities. When measurements were taken shortly after heavy rainfall,

values were occasionally higher at 10 cm than at the lower depths. The community by depth interaction (Figure 6) was also significant (Table II). Differences among depths were most pronounced for rosemary scrub and scrubby flatwoods during the wettest periods (*e.g.,* late 1999, mid-July, late September 2001), reflecting extended soil saturation in some scrubby flatwoods tubes at 90 cm. In contrast, oak–hickory scrub showed less difference in soil moisture among depths.

Overall, soil moisture was significantly higher ($F = 45.044$, df = 1, $P < 0.0001$) in recently burned than in long-unburned sites (6.04 *versus* 5.28%). This effect (Figure 7) was most pronounced in recently burned rosemary scrub sites, where mean soil moisture was about 30% higher than in long-unburned rosemary scrub (6.12 *versus* 4.73%); it was less evident in scrubby flatwoods (7.41 *versus* 7.05%) and in oak–hickory scrub (4.79 *versus* 4.28%).

TABLE I. Pillai's Trace statistic for repeated measures ANOVA on 5 factors affecting changes in percent soil moisture in 3 Florida scrub communities (rosemary scrub, scrubby flatwoods, oak–hickory scrub). Burn refers to time-since-fire class. Data represent seasonal means of 78 bi-weekly samples collected between 1 October 1998 and 3 October 2001, constituting 3 annual soil moisture cycles. We divided the annual soil moisture cycle into 3 seasons: early dry (October–January), late dry (February–May), and wet (June–September). We show all 2- and 3-way interactions.

| Factor | $F$-statistic | Hypothesis df, error df | $P$-value |
|---|---|---|---|
| Season | 804.530 | 8, 173 | < 0.001 |
| Season × vegetation | 15.780 | 16, 348 | < 0.001 |
| Season × depth | 23.127 | 16, 348 | < 0.001 |
| Season × burn | 4.970 | 8, 173 | < 0.001 |
| Season × gap | 2.356 | 8, 173 | 0.020 |
| Season × vegetation × depth | 6.217 | 32, 704 | < 0.001 |
| Season × vegetation × burn | 3.709 | 16, 348 | < 0.001 |
| Season × vegetation × gap | 1.780 | 16, 348 | 0.032 |
| Season × gap × depth | 0.902 | 16, 348 | 0.567 |
| Season × gap × burn | 1.464 | 8, 173 | 0.173 |
| Season × burn × depth | 0.881 | 16, 348 | 0.983 |
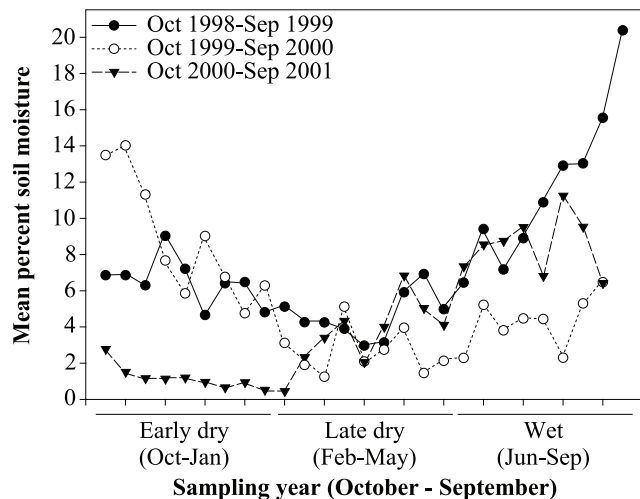


FIGURE 4. Comparison of mean percent soil moisture for 3 annual soil moisture cycles comprising early dry (October–January), late dry (February–May), and wet (June–September) seasons.
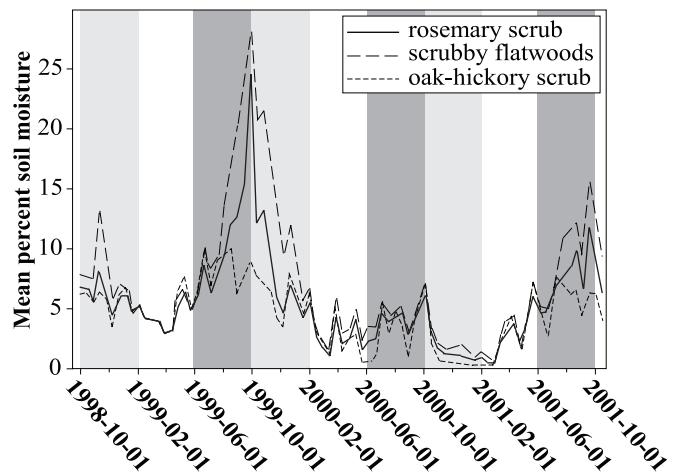


FIGURE 5. Comparison of mean percent moisture for 3 scrub habitats (rosemary scrub, scrubby flatwoods, and oak–hickory scrub) from October 1998 through September 2001. Light grey areas denote early dry season, clear areas denote late dry season, and dark grey areas denote wet season.

Averaged across all years, soil moisture was slightly but significantly higher (Table II) in gaps than in matrix microsites (5.80 *versus* 5.53%). This effect (Figure 8) was slightly more pronounced in gaps in rosemary scrub (5.76 *versus* 5.10%) than in scrubby flatwoods (7.31 *versus* 7.15%) or in oak-hickory scrub (4.56 *versus* 4.50%). Absolute gap *versus* matrix differences were not more pronounced during wetter *versus* drier times (Figure 8). However, relative soil moisture differences between gap and matrix were strongest in dry periods, especially in rosemary scrub (*e.g.,* 66% more soil moisture in gaps than matrix during a dry period *versus* a 45% difference during a wet period).

## Discussion

Soil moisture in Florida scrub varied among years and soil moisture seasons in response to cumulative rainfall patterns. Within a soil moisture season, Florida scrub communities differed in soil moisture. More soil moisture was generally available at greater depths, in gaps, and shortly after fire. Our 3-y sampling period fortuitously encompassed both an extremely wet and an extremely dry soil moisture year (October 1998–September 1999 and October 1999–September 2000, respectively), thereby revealing soil moisture dynamics that were not evident in a less extreme soil moisture year (October 2000–September 2001). However, these extremes may be irrelevant to the population dynamics of the herbs endemic to these Florida scrub communities because in extraordinarily wet years seedling and herb mortality due to drought stress is non-existent and in extraordinarily dry years mortality due to drought stress is ubiquitous. Of greater interest is the impact of relatively small seasonal differences in soil moisture during "average" years. Differential seasonal soil moisture patterns, mediated by scrub type, gap *versus* matrix, and time-since-fire, may contribute substantially to an understanding of the structure of scrub communities and to the distribution of rare and endemic herbs within the Florida scrub ecosystem.

TABLE II. Between-subject effects from repeated measures ANOVA on 4 factors affecting changes in percent soil moisture in 3 Florida scrub communities (rosemary scrub, scrubby flatwoods, oak–hickory scrub). Burn refers to time-since-fire class. Data represent overall means of 78 bi-weekly samples collected between 1 October 1998 and 3 October 2001. We show all main effects and 2-, 3-, and 4-way interactions.

| Factor | *F*-statistic | df | *P*-value |
|---|---|---|---|
| Vegetation | 59.263 | 2 | < 0.001 |
| Depth | 107.273 | 2 | < 0.001 |
| Burn | 45.044 | 1 | < 0.001 |
| Gap | 1.751 | 1 | 0.005 |
| Vegetation × depth | 10.435 | 4 | < 0.001 |
| Vegetation × burn | 13.059 | 2 | < 0.001 |
| Vegetation × gap | 4.387 | 2 | 0.014 |
| Burn × depth | 0.560 | 2 | 0.572 |
| Burn × gap | 11.065 | 1 | 0.001 |
| Gap × depth | 1.899 | 2 | 0.153 |
| Vegetation × gap × depth | 0.623 | 4 | 0.647 |
| Vegetation × burn × depth | 1.310 | 4 | 0.268 |
| Vegetation × burn × gap | 2.375 | 2 | 0.096 |
| Burn × gap × depth | 0.311 | 2 | 0.733 |
| Vegetation × burn × gap × depth | 0.069 | 4 | 0.991 |

Soil moisture patterns revealed in this study suggest a large disparity in spatial and temporal distribution of soil moisture between Florida scrub and other subtropical and Mediterranean-type ecosystems. In chaparral ecosystems, because soil moisture availability is limited to the top 30 cm of soil during the dry season, most species are shallow rooted (Canadell *et al.,* 1996). In contrast, this paper has shown that soil moisture often increases with depth in Florida scrub, leading to plants with a diversity of rooting morphologies (S. Saha, unpubl. data). With a greater per-
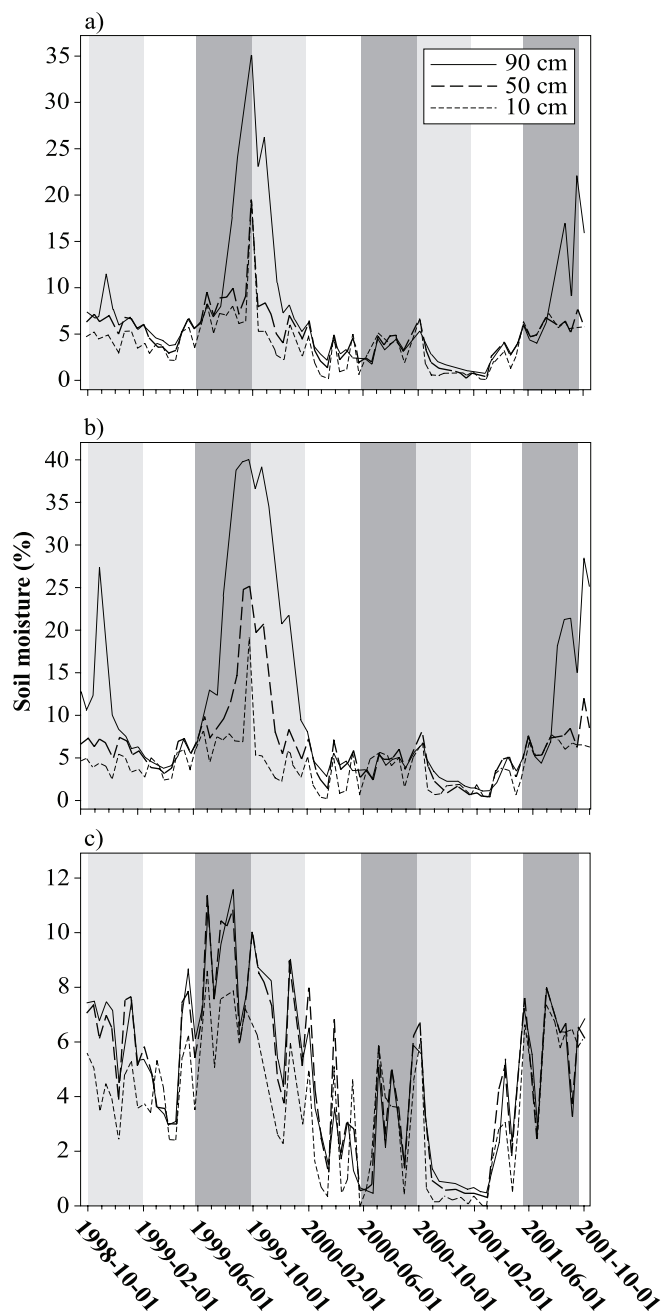


FIGURE 6. Percent soil moisture at 3 depths (90, 50, and 10 cm) for (a) rosemary scrub, (b) scrubby flatwoods, and (c) oak–hickory scrub. Light grey areas denote early dry season, clear areas denote late dry season, and dark grey areas denote wet season. Note different scales for Y-axes.

centage of clay and loam compared to Florida scrub soils, other Mediterranean-type ecosystems and subtropical savannas retain greater moisture in soils, thus yielding higher soil moisture values after the rainfall events (Jipp *et al.,* 1998; Oliviera *et al.,* 2005).

Soil moisture varied significantly among the 3 Florida scrub communities. The ordering (scrubby flatwoods > rosemary scrub > oak–hickory scrub) reflects relative elevation and distance from the water table (Abrahamson *et al.*,

1984). Within the study area, oak–hickory scrub sites were on elevated ridges, rosemary scrub sites on less elevated knolls, and scrubby flatwoods on broad plateaus. Scrubby flatwoods sites are clearly closer to the surficial water table (some tubes flooded for 4–5 months in wet years), followed by rosemary scrub (1–2 months) and by oak–hickory scrub (never flooded). Thus, soil moisture differences among scrub communities may contribute to differences in species composition.
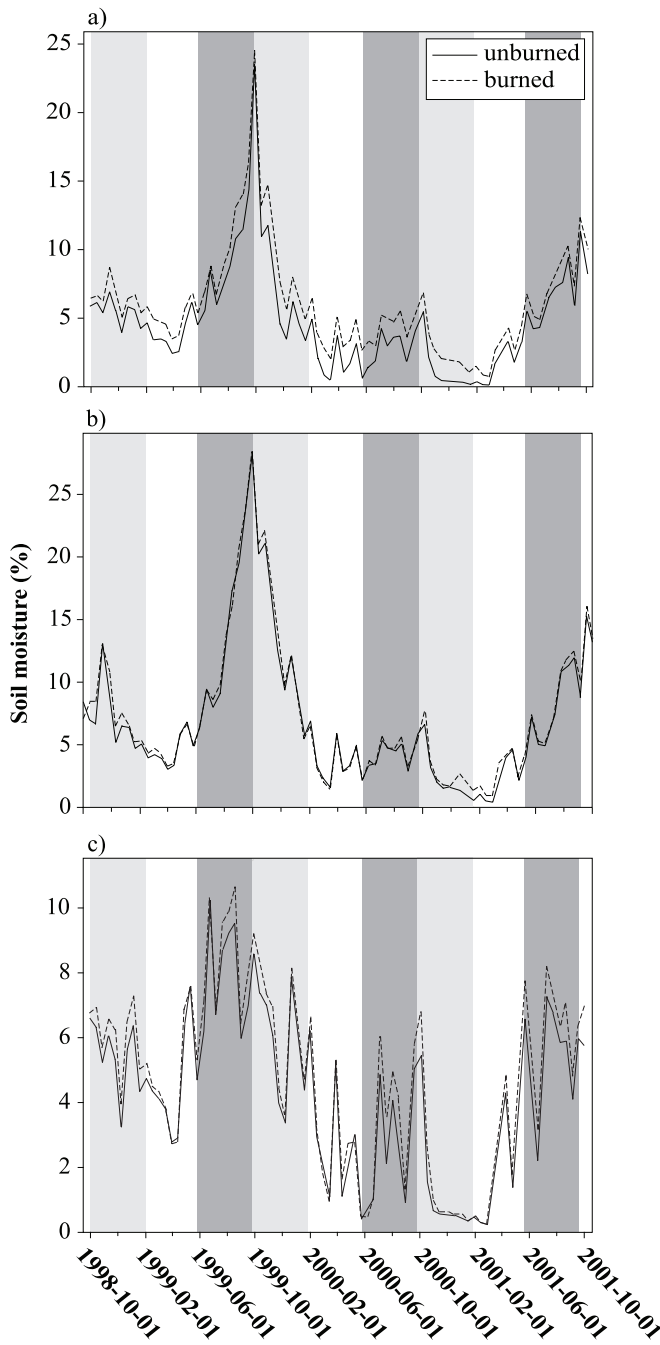


FIGURE 7. Percent soil moisture in burned and unburned sites for (a) rosemary scrub, (b) scrubby flatwoods, and (c) oak–hickory scrub. Light grey areas denote early dry season, clear areas denote late dry season, and dark grey areas denote wet season. Note different scales for Y-axes.
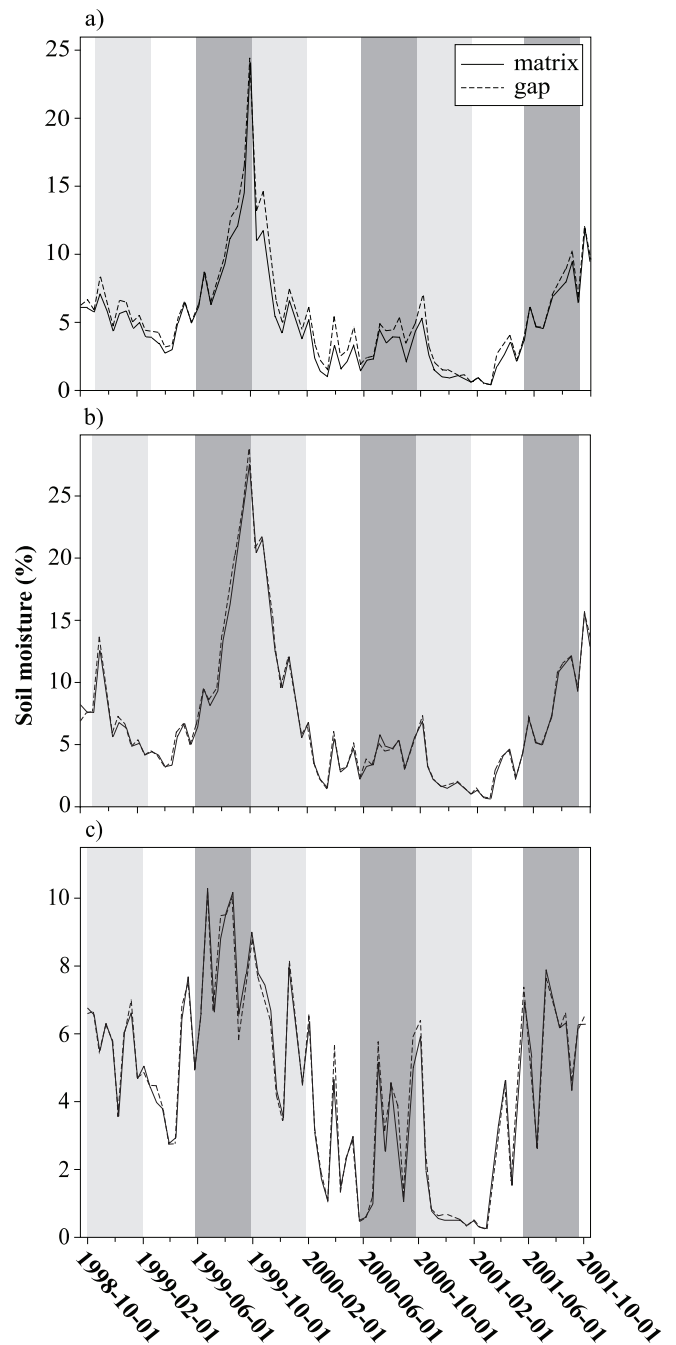
FIGURE 8. Percent soil moisture in gap and matrix sites for (a) rosemary scrub, (b) scrubby flatwoods, and (c) oak–hickory scrub. Light grey areas denote early dry season, clear areas denote late dry season, and dark grey areas denote wet season. Note different scales for Y-axes.

In all 3 scrub communities, the seasonal mean soil moisture was generally higher at the greater depths (typically, 90 > 50 > 10 cm). The most notable exception to this pattern occurred during the 2000 summer drought, when there was no significant difference within any of the scrub communities in percent soil moisture at the 3 depths (although the greater depths still had somewhat higher soil moisture). The depletion of soil moisture resulted in noticeable wilting of scrub oaks and other xeromorphic species, as well as marked declines in seedling recruitment (C. W. Weekley & E. S. Menges, pers. observ. and unpubl. data). On the other hand, we suspect that water-logged soils at the 90-cm depth for periods up to 5 months during wet years may limit the penetration of roots into the soil, imposing a maximum limit on aboveground shrub biomass in some plant communities. High water tables cause increased mortality of *Pinus elliottii* var. *densa* Little & K.W. Dorman in seasonal ponds in the Archbold scrub landscape (Menges & Marks, in press).

Across scrub communities and soil moisture seasons, soil moisture was generally higher in open sand gaps than in the surrounding shrub matrix, especially in rosemary scrub. Maliakal-Witt, Menges, and Denslow (2005) also found that soil moisture was significantly lower near Florida rosemary plants than in open sand gaps. These findings are consistent with the expectation that water loss via transpiration exceeds that of evaporation from open soil, and that overall water loss would therefore be lower in areas with lower vegetation cover. Such differences are also consistent with higher soil moisture values in unvegetated sand roads at Archbold (C. W. Weekley & E. S. Menges, unpubl. data). The small absolute difference between gaps and matrix soil moisture may be partly due to the fact that aboveground gaps are colonized by roots of shrubs whose aboveground parts are adjacent to the gap (Hunter & Menges, 2002; Petru & Menges, 2003).

Across habitats and seasons, most recently burned sites tended to have higher mean soil moisture than long-unburned sites. This contrasts with patterns in forests, where charcoal additions postfire increase hydrophobicity, thereby reducing soil moisture (Certini, 2005). Our results are consistent with the expectation that postburn reductions in aboveground plant biomass would result in higher soil moisture by reducing transpiration-driven water loss. In addition, the effect of time-since-fire should be strongest in rosemary scrub, where postburn biomass recovery is slow due to the obligate seeding life history of the dominant Florida rosemary (Johnson, 1982; Johnson & Abrahamson, 1990). Our finding that soil moisture was ~30% higher in recently burned (3–8 y) *versus* long-unburned (> 20 y) rosemary scrub sites supports this hypothesis. Even greater differences might be expected 0–3 y postfire, when little aboveground biomass exists in rosemary scrub, but we currently have no data on soil moisture in sites < 3 y postfire.

Recently burned areas and gaps, particularly in rosemary scrub and to a lesser extent in oak–hickory scrub, provide habitat for many narrowly endemic herbs (Christman & Judd, 1990; Johnson & Abrahamson, 1990; Menges & Hawkes, 1998; Menges *et al.*, in press). Rosemary scrub gap specialists include *Eryngium cuneifolium* (Menges & Quintana-Ascencio, 2004), *Hypericum cumulicola* (Quintana-Ascencio, Menges & Weekley, 2003), *Polygonella basiramia* (Hawkes & Menges, 1995), and *Lechea cernua* (S. Maliakal-Witt, unpubl. data). In oak–hickory scrub, several *Dicerandra* species are gap specialists (Menges, 1992; Menges *et al.*, 1999; Menges *et al.*, 2006). These species also tend to be postfire specialists to a greater or lesser extent. Long-unburned areas have smaller gaps than areas burned in the last few decades (Menges *et al.*, in press), and the area of bare sand decreases with postfire age in several types of scrub (Menges & Hawkes, 1998; Greenberg, 2003; Schmalzer, 2003). Gaps and postfire areas are favourable sites for these species because they provide safe sites for seedling recruitment and good conditions for plant growth and reproduction (Quintana-Ascencio, Menges & Weekley, 2003; Menges & Quintana-Ascencio, 2004). Recently burned sites have markedly higher seedling recruitment (Johnson & Abrahamson, 1990; Quintana-Ascencio, Menges & Weekley, 2003; Weekley & Menges, 2003; Menges & Quintana-Ascencio, 2004), perhaps due to postfire germination cues, postfire nutrient pulses (Alexis *et al.*, 2007), and/or higher soil moisture.

Differences in the structure and species composition of Florida scrub communities are unlikely to be driven solely by differences in soil moisture, and several other factors acting alone or in combination with soil moisture undoubtedly contribute to the shaping and dynamics of scrub communities. Many of these potential factors, including soil moisture, are affected by fire. For example, cryptobiotic soil crusts, which develop only in gaps, may facilitate herb seedling recruitment (Hawkes, 2004). However, litter (Menges *et al.*, 1999) and ground lichen cover (Hawkes & Menges, 2003) may suppress seedling recruitment. Thus, by removing litter and ground lichens, fires increase available habitat for herbs and subshrubs recruiting from soil seed banks.

Many of the endemic herbs and subshrubs are shallowly rooted and may be poor competitors with deeply rooted shrubs. Experimental removal of roots within gaps increases spontaneous seedling recruitment (Petru & Menges, 2003). Species that have their best demographic performance in the centres of gaps (Menges & Kimmich, 1996) perform poorly when planted next to gap-bordering shrubs (Quintana-Ascencio & Morales-Hernandez, 1997; Quintana-Ascencio & Menges, 2000). Indeed, gap area is a strong predictor of gap occupancy for most species occurring in rosemary scrub gaps (Menges *et al.*, in press). Florida rosemary plants have particularly negative effects on gap herbs and subshrubs (Quintana-Ascencio & Menges, 2000). Rosemary roots grow outward into gaps, competing for soil moisture and soil nutrients, or directly inhibit germination through allelopathy (Hunter & Menges, 2002).

What role does soil moisture availability play in generating these patterns, particularly in Florida rosemary scrub? The effects of gaps and recent burning on soil moisture are generally quite small (on average < 1.5% absolute difference in soil moisture), even in the case of the largest differences (rosemary scrub, recently burned *versus* long-unburned sites). In addition, differences due to burn history are most pronounced during the wet season. It seems

unlikely that recently burned areas and gaps offer a high enough contrast in soil moisture to be the sole driver of gap specialization in Florida scrub plants. Nonetheless, relative differences between gaps and matrix in rosemary scrub sites during droughts may be one of several key filters controlling species distributions in the Florida scrub landscape.

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