



Environmental and biological controls on water and energy exchange in Florida scrub oak and pine flatwoods ecosystems

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[1] Scrub oak and pine flatwoods are two contrasting ecosystems common to the humid subtropical climate of Florida. Scrub oak forests are short in stature (<2 m) and occur on well-drained sandy soils, and pine flatwoods are much taller and occur in areas with poorly drained soils. Eddy covariance measurements were made from January 2001 to February 2003 over a scrub oak forest and from January 2002 to February 2003 over an adjacent pine flatwoods located on in central Florida, USA, and exposed to similar atmospheric conditions to evaluate how the dynamics of latent heat (λE) and sensible heat (H) exchanges are affected by environmental and biological variables. Annual evapotranspiration (Et) for the scrub oak was 737 and 713 mm in 2001 and 2002, respectively. Et was comparatively higher, 812 mm, in 2002 at the pine flatwoods due to higher soil moisture and leaf area. In both ecosystems, springtime increases in λE coincided with increasing leaf area and evaporative demand. However, H was the main energy-dissipating component in the spring due to the seasonal decrease in soil water content in the upper soil profile. In the spring, mean weekly Bowen ratio (β , i.e. $H/\lambda E$) values reached 1.6 and 1.2 in the scrub oak and pine flatwoods, respectively. With the onset of the summertime rainy season, λE became the dominant energy flux and β falls to < 0.4. In both ecosystems, β was strongly controlled by the interaction between leaf area and soil moisture. The lowest values of the decoupling coefficient (Ω , 0.2 and 0.25 scrub oak and pine flatwoods, respectively) also occurred during the dry springtime period indicating that surface conductance (g_s) was the mechanism controlling energy partitioning causing high β in both ecosystems. Et increases in the spring, when water in the upper soil profile was scarce and strongly retained by soil particles, indicated that plants in both ecosystems obtained water from deeper sources. The results from this research elucidate how energy partitioning differs and is regulated in contrasting ecosystems within the Florida landscape, which is important for refining regional hydrological and climate models.

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1. Introduction

[2] Landscape level exchanges of water and energy are highly dynamic in time and space owing to differences in both ecosystem structure and biological responses to envi-

ronmental variation [e.g., *Wilson and Baldocchi*, 2000; *Gholz and Clark*, 2002; *Law et al.*, 2002; *Wever et al.*, 2002; *Humphreys et al.*, 2003; *Baldocchi et al.*, 2004]. Many studies have found that water supply is a key variable in regulating vegetation type and evapotranspiration rates across a landscape [*Wetzel and Chang*, 1987, 1988; *Jipp et al.*, 1998; *Hutley et al.*, 2001; *Baldocchi et al.*, 2004]. Peninsular Florida in the southeastern United States is a complex mosaic of terrestrial, aquatic and coastal ecosystems that are classified based on differences in physiognomy, species composition, topography and soil drainage [*Ewel*, 1990; *Menges and Hawkes*, 1998]. Most Florida ecosystems have a relatively shallow water table (i.e. within 1–3 m) and generally experience similar precipitation patterns in the humid subtropical climate—i.e. warm dry springs, hot humid summers, and relatively mild dry winters

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[Chen and Gerber, 1990]. Yet, natural differences in species composition occur, in part, due to large differences in surface soil (i.e. top 1–2 m) hydrology resulting from small changes in topography [Ewel, 1990]. For example, two hydrologically and structurally distinct ecosystems, scrub oak and pine flatwoods, are often adjacent and such a contrast implies that evapotranspiration (E_t) and energy partitioning is highly variable across the region.

[3] Scrub oak is a xeromorphic, low-stature (1–2 m) shrub ecosystem dominated by evergreen oak species (*Quercus geminata*, *Q. myrtifolia*, *Q. chapmanii*), saw palmetto (*Serenoa repens*), and other ericaceous shrubs (e.g., *Lyonia fruticosa* and *L. lucida* [Schmalzer and Hinkle, 1992b]). Scrub oak is very important to the region because of its biological diversity; high endemism and the high number of endangered and threatened species it supports [Christman and Judd, 1990; Myers, 1990]. However, it is disappearing rapidly because of land development [Myers, 1990; Menges, 1999; Duncan et al., 2004]. Its structural features are maintained in large part by a fire return cycle of 7 to 10 years [Schmalzer and Hinkle, 1992a]. Scrub oak is discontinuously distributed in coastal and inland areas and occupies well-drained sandy ridges that are low in nutrients [Myers, 1990]. Oak species dominance increases with the distance to the water table [Schmalzer and Hinkle, 1992b] and most of the xylem water content comes from the water table during the driest time of the year [Hungate et al., 2002]. Leaf area is seasonal with a minimum in February–March, rapid increase during the spring, and maximum between July and October [Hymus et al., 2002; Powell et al., 2006].

[4] Pine flatwoods occur throughout the southeastern coastal plain of the United States and cover approximately 50% of terrestrial Florida ecosystems [Abrahamson and Hartnett, 1990]. Pine flatwoods are characterized by flat topography and poorly drained soils [Abrahamson and Hartnett, 1990; Myers, 1990]. Historically, pine flatwoods ranged from relatively dense to sparsely populated stands of slash (*Pinus elliottii*) and longleaf (*P. palustris*) pine with a dense understory comprised of many species common to the scrub oak community [Abrahamson and Hartnett, 1990]. Currently, 18% of Florida's forests are naturally managed pine forests [Conner and Hartsell, 2002]. Evaluating the effects of forest management on E_t has been the focus of several studies in Florida pine flatwoods [e.g., Liu et al., 1998; Sumner, 1996; Knowles, 1996; Sumner, 2001; Gholz and Clark, 2002; Powell et al., 2005]. These studies have shown that E_t represents a large proportion (60% to 90%) of annual precipitation. Evapotranspiration from these ecosystems is driven by environmental fluctuations and leaf area development [Gholz and Clark, 2002; Powell et al., 2005].

[5] A comparison of direct measurements of latent heat (λE) and sensible heat (H) fluxes of adjacent scrub oak and pine flatwoods ecosystems enables us to contrast the biophysical controls over λE and H while they are subjected to similar dominant climatic conditions. Stomatal closure has been shown to be an important control over water use in ecosystems that are water-limited seasonally [Magnani et al., 1998; Hutley et al., 2000, 2001; Malhi et al., 2002; Vourlitis et al., 2002; Priante-Filho et al., 2004]. *Quercus* species have been found to be relatively resistant to

droughty conditions [Ni and Pallardy, 1991; Oren and Pataki, 2001; Pataki and Oren, 2003] and can maintain stomata conductance at low soil and leaf water potentials by relying on deeper water sources [Hasting et al., 1989; Rambal et al., 2003; Xu and Baldocchi, 2003; Baldocchi et al., 2004]. However, stomatal conductance in pine forests has been shown to be quite responsive to droughty conditions [Liu et al., 1998; Powell et al., 2005].

[6] Estimates of seasonal and annual evapotranspiration from constituent ecosystems are necessary for water management plans in Florida. Ground water is the main source for human and industrial use and water demand is increasing because of urban expansion [Knowles et al., 2002]. Therefore, these types of measurements are also useful to validate land surface models [Sridhar et al., 2002] that can evaluate how change in land cover influences energy distribution.

[7] The objectives of this study were to (1) quantify and compare λE and H fluxes of these two adjacent, hydrologically contrasting Florida ecosystems, and (2) determine and compare the biological and environmental factors affecting the partition of the available energy into evapotranspiration and sensible heat flux between the two ecosystems. The proximity of the study sites—i.e. within 17 km—coupled with the use of eddy covariance allowed for an ideal scenario of making simultaneous measurements in both ecosystems while exposed to the same dominate weather patterns. Additionally, the scrub oak measurements were made during two consecutive years with contrasting precipitation—a dry year and an average year. We hypothesized (1) that seasonally, the partitioning between H and λE in both ecosystems would be regulated by both soil moisture and leaf area, (2) the scrub oak ecosystem would be more conservative, relative to the pine flatwoods, in its water-use due to its well-drained and often dry surface soils, and (3) the scrub oak would be similar to temperate oak forests [Pataki and Oren, 2003] by being conservative in water use between years despite differences in precipitation.

2. Materials and Methods

2.1. Study Sites

[8] The study was conducted in scrub oak (28° 36'N, 80° 42'W) and pine flatwoods (28° 27'N, 80° 40'W) ecosystems located in the John F. Kennedy Space Center on the east coast of central Florida. The climate is warm and humid with mean maximum temperatures of 22°C in January and 33°C in July, mean minimum temperatures of 10°C in January and 22°C in August, respectively [Mailander, 1990]. Long term (1983–2002) mean annual precipitation recorded by the National Atmospheric Deposition Program (NADP, Monitoring Location FL99 Kennedy Space Center) was 1273 ± 285 mm (mean ± SD), with 63% falling between June and October. Soil moisture deficits in this region typically occur between mid-March and May and between November and December [Mailander, 1990].

[9] The scrub oak study site was situated in a 10 ha forest that was dominated by three oak species *Q. myrtifolia*, *Q. geminata* and *Q. chapmanii*, and saw palmetto (*Serenoa repens*). The site has been maintained by periodic fires (5–7 years) with a complete burn in August 1995. In the spring of

1996, it was completely covered with natural shoot regeneration from roots and rhizomes and LAI was $1.4 \text{ m}^2 \text{ m}^{-2}$ when this study commenced in January 2001. Mean canopy height during the study was 1.5 m. The fetch was >200 m in all directions. The ecosystem occurs on Pomello (Arenic Haplohumod) sands that are well drained and low in organic matter and nutrients [Huckle *et al.*, 1974; Schmalzer and Hinkle, 1992b, 1996; Schmalzer *et al.*, 2001]. The sandy soil profile extends down to more than 2 meters. The A horizon extends down to 1.5 m and below which, the B horizon extends to 1.8 m depth and contains coarse and fine roots. The top of the B horizon is dark with a soil organic matter content that can reach 6%. Hydraulic conductivity is 113 cm h^{-1} , 71.5 cm h^{-1} and 77.4 cm h^{-1} for A, B, and C horizon, respectively [Huckle *et al.*, 1974].

[10] The pine flatwoods study site was located in a 310 ha forest approximately 17 km south of the scrub oak site. The fetch was 400m to the west and >600 m in all other directions. The forest was traversed with pine uplands and swale marshes that were <1 m difference in elevation. This site has been managed as an uneven-aged forest and prescribed fires have been used to control understory fuel load since 1969 [Duncan *et al.*, 1999]. The site was last burned in February 1995; 7 years before the commencement of this study in January 2002. A sparse canopy of slash pine represented $<15\%$ of the total canopy coverage [Breininger *et al.*, 2002]. Slash pine stem density was 18 ± 8 stems ha^{-1} and canopy height was approximately 13 m. A dense, 2 m understory was predominantly comprised of three oak species, *Q. geminata*, *Q. myrtifolia*, *Q. chapmanii* (around 40%), and saw palmetto. *Lyonia* species, *Ilex galbra* and grasses also occurred in the understory. Because of structural and compositional characteristics, this ecosystem resembled a “scrubby” flatwoods, considered by some authors as an ecotone between scrub oak and pine flatwoods [Abrahamson and Hartnett, 1990; Duncan *et al.*, 1999]. The soil type is Myakka (Aeric Haplaquod), a poorly drained, acidic sandy soil [Schmalzer and Hinkle, 1992b; Schmalzer *et al.*, 2001]. The A horizon of the soil profile extends to between 0.2 to 0.65 m depth. The B horizon extends to 1.2 m and is formed by weakly cemented sands, which decreases its dryness. Organic matter content of the B horizon can reach 7%, which increases its soil moisture retention relative to the scrub oak ecosystem and therefore, fine roots are more common. Saturated hydraulic conductivity is 65 cm h^{-1} and 1.7 cm h^{-1} for A and B horizons, respectively [Huckle *et al.*, 1974].

[11] The normalized difference vegetation index ($NDVI$) was used to determine the seasonal behavior of leaf area in both ecosystems [Huete *et al.*, 2002; Ferreira and Huete, 2004; Ratana *et al.*, 2005]. $NDVI$ values were generated from MODIS at 250-m resolution in 16-day composite periods (<http://LPDACC.usgs.gov>). $NDVI$ values were compared to measured LAI values in the scrub oak to serve as a validation (results reported below). Leaf area index at the scrub oak was estimated applying Beer’s Law to PAR transmission through the canopy. The extinction coefficient was a linear function of PAR measurements. Values were compared against destructive measurements of LAI [Hymus *et al.*, 2002].

2.2. Eddy Covariance and Meteorological Measurements

[12] The eddy covariance technique was used to measure latent (λE) and sensible (H) heat fluxes continuously [Aubinet *et al.*, 2000; Baldocchi *et al.*, 2001]. Both eddy covariance systems consisted of a closed-path infrared gas analyzer, IRGA (LI 6262, LI-COR, Inc., Lincoln, NE, USA) and a three-dimensional sonic anemometer (Solent R3, Gill Instruments Ltd., Lymington, UK) mounted 3.5 m above the soil at the scrub oak and 18 m above the soil at the pine flatwoods. Eighty percent of the cumulative daytime fluxes were within 140 and 550 m upwind of the towers for the scrub oak and pine flatwoods, respectively [Schmid, 1997]. Flux data were logged at 20 Hz and averaged over 30 min periods. Data reported here are from January 2001 to February 2003 and from January 2002 to February 2003 for the scrub oak and pine flatwoods, respectively. The fluxes were corrected for the damping of high frequency fluctuations, sensor separation, sampling frequency, and misalignment of wind sensors with respect to the mean streamline [Moncrieff *et al.*, 1997; Aubinet *et al.*, 2000].

[13] Eddy covariance data were rejected during periods of rain, equipment maintenance, and low turbulent mixing that caused the canopy to become decoupled from the atmosphere. The threshold for decoupled conditions was established using a critical friction velocity (u_*) value that was seasonally determined (scrub oak range: 0.07 to 0.15 m s^{-1} , pine flatwoods range: 0.10 to 0.15 m s^{-1}) by regressing scalar variances against u_* . Over 68% of the data remained after the screening process. Linear interpolation was used to gap-fill when only single half-hourly flux data were missing. The linear relationship between λE or H and net radiation (R_n) was used to gap-fill each flux for periods >30 min using a ± 7 day moving average relationship. During periods when R_n was not available, the 24-hr flux was estimated from linear interpolation of surrounding days [Falge *et al.*, 2001].

[14] Net radiation ($Q^*7.1$, REBS, Inc., Bellevue, WA, USA), air temperature (T_a , copper/constantan thermocouple, Omega, CT, USA), relative humidity (RH , 1400-104, LI-COR, Inc.) and precipitation (P , TE525 tipping bucket, Campbell Scientific, Logan, UT, USA) were measured continuously above the canopy at each site. Soil temperature (copper/constantan thermocouple, Omega) was measured continuously at each site at depths of 0.02 and 0.1 m. Soil moisture (θ) was measured continuously at the surface (integrated 0–0.20 m) at each site and horizontally at 0.50 m at the pine flatwoods using a water content reflectometer (CS615, Campbell Scientific). Soil water content at 0.45 m and 0.65 m was also measured at 8 permanent sites adjacent to the scrub oak tower every two weeks for discontinuous periods using time-domain reflectometers (Soil Moisture Equipment Inc., San Diego, CA). Soil water content sensors were calibrated at the site against known gravimetric soil water content [Hungate *et al.*, 2002]. Water table depth was measured at the scrub oak site using pressure transducers [Keeland *et al.*, 1977] or by hand inspection. Surface soil heat flux (G) was calculated by adding the measured soil heat flux at 0.08 m using two soil heat flux plates (HFT3, REBS, Inc.), to the calculated energy stored in the layer above the heat flux plates.

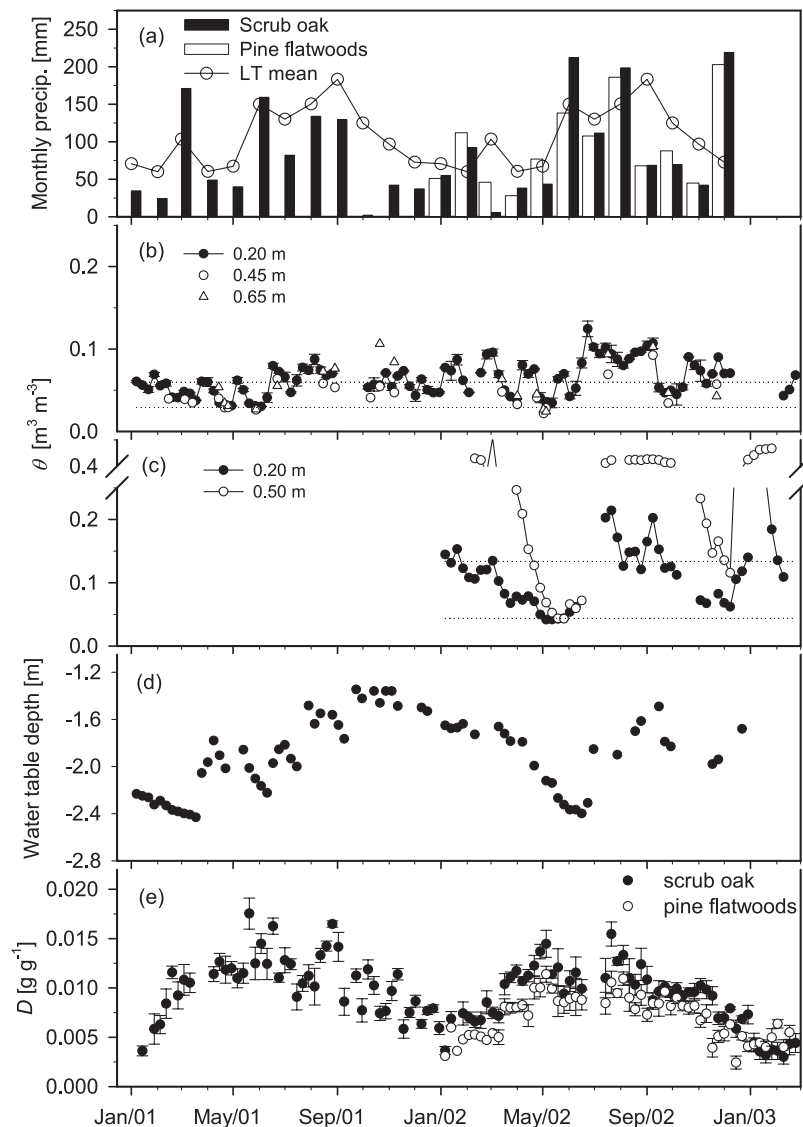


Figure 1. (a) Monthly precipitation (mm) in the scrub oak and pine flatwoods. (b) Weekly average of soil water content (θ , $\text{m}^3 \text{m}^{-3}$) for scrub oak and (c) pine flatwoods at different depths. Dotted lines represent the field capacity (upper line) and permanent wilting point (lower line) for each site [Huckle *et al.*, 1974]. (d) Depth to the water table at the scrub oak. (e) Specific humidity deficit (D g g^{-1}) for both ecosystems.

[15] Bulk surface parameters, such as the Bowen ratio, ($\beta = H/\lambda E$), surface conductance (g_s) and the decoupling coefficient (Ω) were calculated to characterize and compare canopy exchange processes within and between the two ecosystems. Surface conductance for water vapor (g_s), was calculated to evaluate the biological controls over Et by using an inverted form of the Penman-Monteith equation [Kelliher *et al.*, 1995]:

$$\frac{1}{g_s} = \left(\frac{\epsilon + 1}{g_a} \right) \left(\frac{\epsilon(R_n - G)}{(\epsilon + 1)\lambda E} \right) + \frac{\rho_a D}{E} \quad (1)$$

where ϵ , was the rate of change of the latent heat content of saturated air with change in sensible heat content (i.e. $(\lambda/C_p)dq^*/dT_a$, λ was the latent heat of vaporization of

water (J g^{-1}), C_p was the specific heat of air ($\text{J g}^{-1} \text{K}^{-1}$), q^* was the saturation specific humidity at a reference height above the surface (g g^{-1}), g_a was the aerodynamic conductance (m s^{-1}), $R_n - G$ was the available energy (Wm^{-2}), ρ_a was the air density (g m^{-3}), D was the specific humidity deficit above the canopy (g g^{-1}), and E was the evaporation rate ($\text{g m}^{-2} \text{s}^{-1}$). Conductance in m s^{-1} was converted to $\text{mmol m}^{-2} \text{s}^{-1}$ using the ideal gas law. Aerodynamic conductance for water vapor (g_a) was calculated using wind speed and friction velocity and corrected for the excess resistance to the transfer of momentum and sensible heat [Thom, 1972, 1975], as:

$$g_a = \frac{u_z k^2}{\left[\ln\left(\frac{z-d}{z_0}\right) \right]^2 + \left(1.35 u_*^{1/3} \right) k \ln\left(\frac{z-d}{z_0}\right)} \quad (2)$$

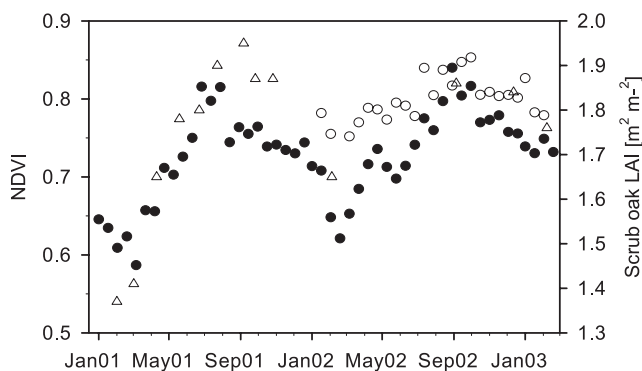


Figure 2. Calculated NDVI for the scrub oak (closed circles) and pine flatwoods (open circles) and measured leaf area index (LAI) at the scrub oak (open triangles), January 2001 to January 2003.

where u_z is wind velocity at height z , k is von Karman constant (0.42), d is zero plane displacement, z_0 is roughness length.

[16] Surface conductance is an integration of whole canopy stomatal conductance, soil and wet canopy evaporation [Raupach and Finnigan, 1988; Granier and Loustau,

1994; Kelliher *et al.*, 1995]. In order to minimize the effect of soil and wet canopy evaporation on g_s , days with recorded precipitation or periods within two days of a rain event >10 mm were excluded from calculations of g_s .

[17] The decoupling coefficient, Ω [Jarvis and McNaughton, 1986], was calculated as:

$$\Omega = \left[1 + \left(\frac{\gamma}{s + \gamma} \right) \frac{g_a}{g_s} \right]^{-1} \quad (3)$$

where s was the slope of the saturation vapor pressure as a function of T_a , and γ was the psychrometric constant. Omega ranges between 0 and 1. When $\Omega \rightarrow 0$, $g_a \rightarrow \infty$ resulting in an efficient transfer of mass and energy, and D at the canopy surface becomes equal to that in the external boundary layer resulting in a strong coupling to external conditions. In this situation, Et is controlled by surface conductance and any change in g_s produces a proportional change in Et . Conversely, when $\Omega \rightarrow 1$, $g_s \rightarrow \infty$, and Et is proportionally controlled by energy input and is independent of D . When changes in g_s produce a small change in Et , the canopy surface is described as decoupled from

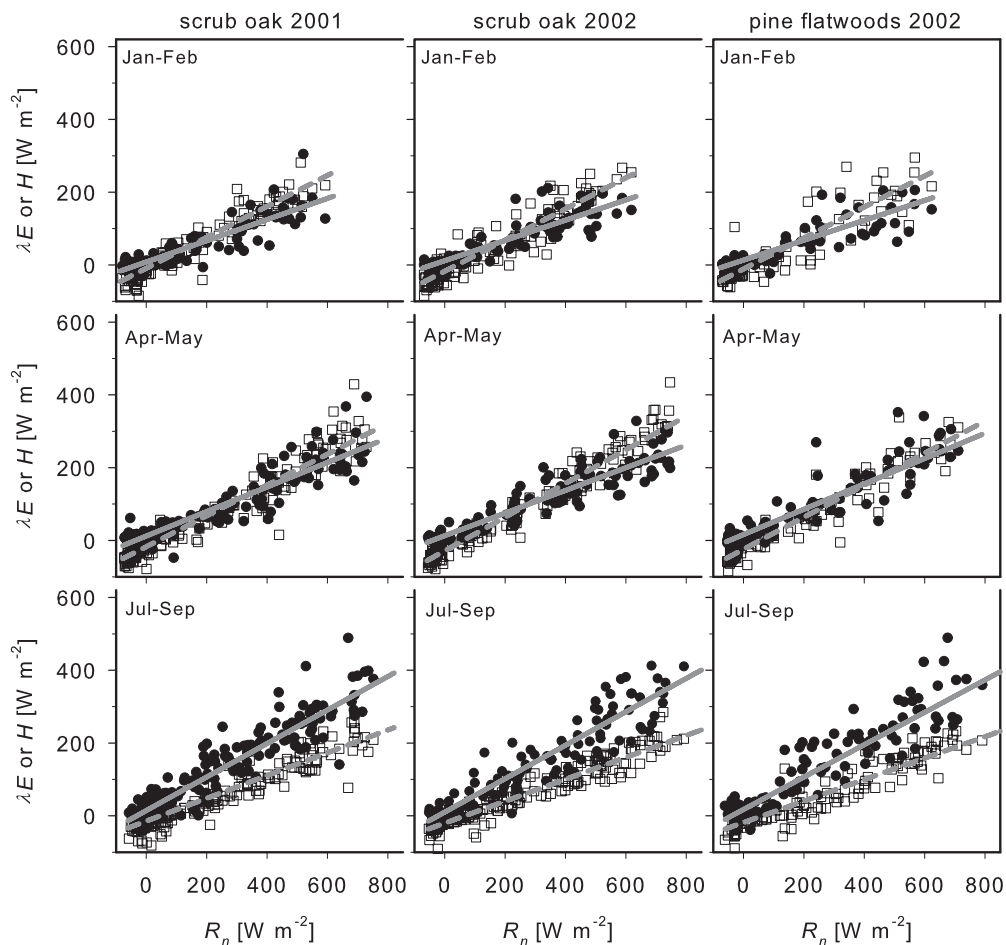


Figure 3. Relationship between latent heat flux (λE , W m^{-2} , closed circles, solid line) or sensible heat flux (H , W m^{-2} , open squares, dashed line) and net radiation (R_n , W m^{-2}) in the scrub oak and pine flatwoods ecosystems for representative months of each season. January–February: dry winter, April–May: dry spring, July–September: wet summer. Regression parameters and statistics are given in Table 1.

Table 1. Regression Parameters and Statistics for the Annual Energy Budgets and the Relationship Between Net Radiation (R_n , $W m^{-2}$) and Either Latent Heat (λE , $W m^{-2}$) or Sensible Heat (H , $W m^{-2}$) Fluxes for the Scrub Oak and Pine Flatwoods Ecosystems (Soil Heat Flux: G , $W m^{-2}$)^a

Site and Year	Equation	r^2	N	Season
Scrub oak 2001	$H + \lambda E = 0.85(R_n - G) - 12.1$	0.94	11150	all year
	$\lambda E = 0.29R_n + 8.22$	0.92	2185	dry winter
	$\lambda E = 0.34R_n + 12.01$	0.89	2697	dry spring
	$\lambda E = 0.46R_n + 14.28$	0.89	3123	wet summer
	$H = 0.42R_n - 9.19$	0.92	2785	dry winter
	$H = 0.42R_n - 17.31$	0.94	2929	dry spring
	$H = 0.31R_n - 14.69$	0.91	4417	wet summer
	Scrub oak 2002	$H + \lambda E = 0.87(R_n - G) - 11.7$	0.95	10720
$\lambda E = 0.28R_n + 11.62$		0.77	1551	dry winter
$\lambda E = 0.31R_n + 12.79$		0.86	1831	dry spring
$\lambda E = 0.46R_n + 9.92$		0.90	2240	wet summer
$H = 0.43R_n - 17.28$		0.88	2342	dry winter
$H = 0.46R_n - 28.61$		0.95	2392	dry spring
$H = 0.30R_n - 20.31$		0.92	2923	wet summer
Pine flatwoods 2002		$H + \lambda E = 0.86(R_n - G) - 11.5$	0.93	10320
	$\lambda E = 0.27R_n + 13.25$	0.77	1259	dry winter
	$\lambda E = 0.35R_n + 16.11$	0.86	1874	dry spring
	$\lambda E = 0.45R_n + 17.24$	0.86	2415	wet summer
	$H = 0.43R_n - 11.26$	0.80	1262	dry winter
	$H = 0.44R_n - 24.30$	0.92	1796	dry spring
	$H = 0.30R_n - 18.57$	0.87	2611	wet summer

^aRepresentative months were selected for each season. January–February: dry winter, April–May: dry spring, July–September: wet summer.

external conditions. [Jarvis and McNaughton, 1986; Monteith and Unsworth, 1990].

3. Results

3.1. Environmental Conditions

[18] Annual precipitation over the scrub oak was 905 mm in 2001 and 1156 mm in 2002. Precipitation over the pine flatwoods was 1149 mm in 2002. Compared to long-term mean annual precipitation, 2001 was relatively dry and 2002 was average. Each year precipitation followed the seasonality characteristic of central Florida (Figure 1a.). Soil water content (θ) of both ecosystems tracked precipitation both in terms of individual events and seasonality, where it increased rapidly after rain events and decreased gradually as the sandy soils drained and dried out (Figures 1b and 1c). The annual minimum occurred between March and May and the annual maximum occurred between July and September (Figures 1b and 1c). At the scrub oak site, weekly mean minimum θ in the first 0.20 m was $0.031 m^3 m^{-3}$ and the maximum reached $0.12 m^3 m^{-3}$. Periodic measurements of θ at 0.45 m and 0.65 m (Figure 1b) tracked continuous measurements of surface θ (0–0.20 m) and matched minimum values recorded during the dry season (April and May of each year). In the pine flatwoods, weekly mean surface θ (0–0.20 m) ranged from $0.04 m^3 m^{-3}$ and $0.30 m^3 m^{-3}$, with the minimum values occurring in May 2002 and maximum values occurring in July 2002 and January 2003 (Figure 2c). Soil water content at 0.50 m decreased rapidly from values around $0.4 m^3 m^{-3}$ at the end of January to $0.04 m^3 m^{-3}$ in May and rapidly increased to $0.4 m^3 m^{-3}$ with the onset of the rainy season. (Data gaps in Figures 1b and 1c were the result of sensor failures.) The dotted lines in Figures 1b and 1c indicate the field capacity (upper line, $0.06 m^3 m^{-3}$ and $0.13 m^3 m^{-3}$ for the scrub oak and pine flatwoods, respectively) and the permanent wilting point (lower line, $0.03 m^3 m^{-3}$ and $0.04 m^3 m^{-3}$

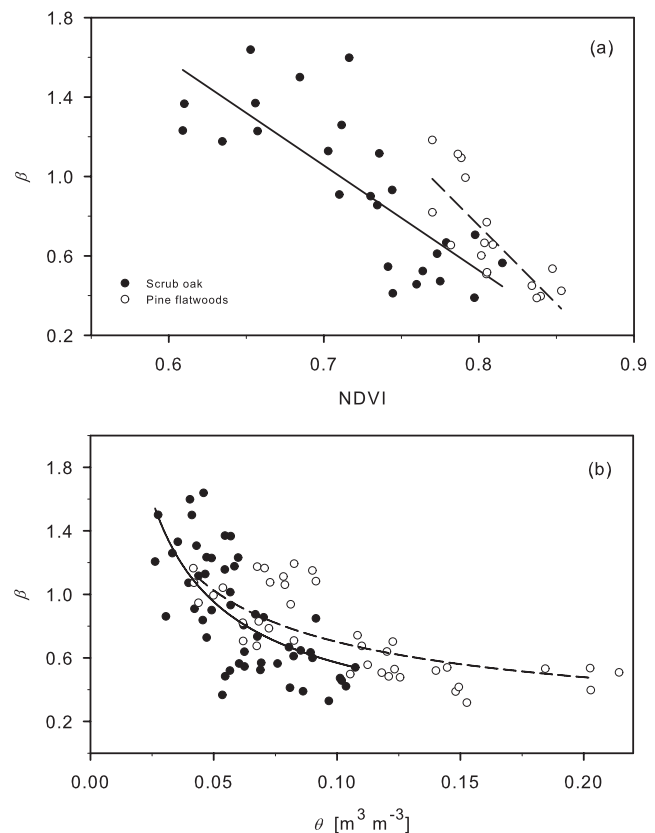


Figure 4. Relationship between Bowen ratio (β) and (a) leaf area (NDVI) and (b) soil water content (θ , $m^3 m^{-3}$) for the scrub oak and pine flatwoods. Continuous lines represent the regressions for the scrub oak, and dashed lines represent the regressions for pine flatwoods.

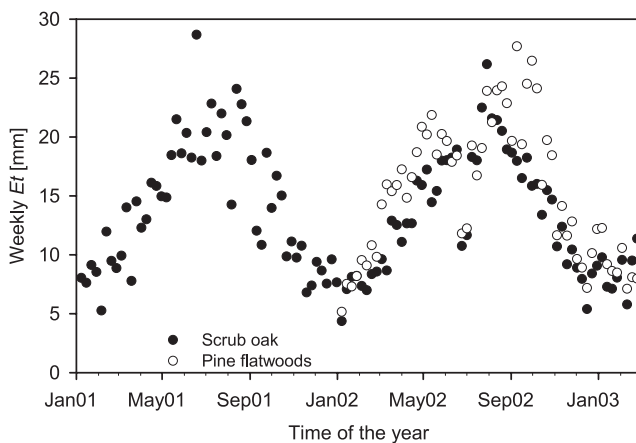


Figure 5. Weekly evapotranspiration (E_t , mm) for scrub oak and pine flatwoods during the time of measurements.

scrub oak and pine flatwoods, respectively) for the 0–0.2 m of the soil profile at each site [Huckle *et al.*, 1974]. Water contained in the soil between these two points was available for the plants. Soil moisture at all three measurement levels in the scrub oak dropped to the wilting point during the spring of both years. Similarly, soil moisture at both measurement levels in the pine flatwoods fell to the permanent wilting point in the spring of 2002. At the scrub oak, each year the maximum water table depth was the same, –2.4 m, but occurred at different times—March 2001 vs. June 2002 (Figure 1d). Minimum water table depth, –1.4 m, occurred at the end of the rainy season (September) each year. No relationship was found between surface θ and the depth to the water table. Water table depth was not measured at the pine site. However, measurements of soil water content at 0.5 m indicated that water table was above this point between January and February, August and October and late December 2002.

[19] Throughout this study, above canopy air temperature (T_a) was similar at both sites and followed the typical seasonal trend for central Florida [Mailander, 1990], where mean weekly T_a was 15.4°C and 19.3°C in January 2001 and 2002, respectively and around 30°C in July in both years. Mean weekly D measured above the canopy of the scrub oak site increased from approximately 0.004 g g⁻¹ each January to > 0.012 g g⁻¹ between May and September (Figure 1e). Mean weekly D at the pine flatwoods followed a similar seasonal trend, but was usually 20% lower compared with the scrub oak D values (Figure 1e).

3.2. NDVI and Leaf Area Index

[20] There was strong agreement between the seasonality of $NDVI$ and LAI for the scrub oak site, thus validating $NDVI$ as an approximation for the seasonal behavior of leaf area in these ecosystems (Figure 2). The seasonal evolution of $NDVI$ at the scrub oak was similar each year with the exception of May and June (Figure 2). For both years, minimum values occurred in February–March and were followed by a rapid increase that coincided with the flush of new leaves in the spring. In 2001, $NDVI$ reached its annual maximum in June. In contrast, $NDVI$ declined during May and June 2002, and then reached its annual maximum in

August. $NDVI$ for the pine flatwoods showed similar seasonality as the scrub oak, but was lower in amplitude and the absolute values were on average greater than $NDVI$ values at the scrub oak ($t = 4.14$, $P < 0.001$) (Figure 2).

3.3. Energy Partitioning and Evapotranspiration

[21] Annual energy balance closure was within 85% for both sites (Table 1). Daily integrated G summertime magnitude was relatively small compared to λE and H and represented less than 2% of R_n . Latent and sensible heat fluxes were linear functions of R_n and these relationships were seasonal (Table 1 and Figure 3). During midday in the winter and spring, λE accounted for approximately one third of R_n (i.e. when $R_n = 500 \text{ W m}^{-2}$) in both sites and H accounted for approximately 40% (Table 1 and Figure 3). In contrast, midday summertime λE accounted for a little less than half of R_n in both sites and H accounted for >30%. The seasonality of the partitioning of R_n between λE and H , as expressed by β , was controlled by fluctuations in soil moisture and leaf area. The Bowen ratio was inversely related to fluctuations in leaf area and explained 61% ($P < 0.001$) of its variation (Figure 4a) at both sites. The slope of the relationship between β and $NDVI$ at the pine site was higher than at the scrub oak. Soil moisture and β were curve linearly related where β rapidly increased above 1.0 as θ decreased below the field capacity at both sites (Figure 4b). The variation in surface soil moisture (0–0.2 m) explained 51% ($P < 0.001$) and 59% ($P < 0.001$) of the seasonal variability in β at the scrub oak and pine flatwoods, respectively. A nonlinear model (Systat Software Inc., Richmond, CA) indicated that simultaneous variations in soil moisture and leaf area explained 80% ($F = 46$, $P < 0.0001$) and 82% ($F = 29.8$, $P < 0.0001$) of the variability in β for the scrub oak and pine flatwoods, respectively.

[22] Simultaneous measurements of net radiation were not different between the two ecosystems during the study ($t = 0.98$, $P = 0.32$). λE at the pine flatwoods was generally 23% greater than λE at the scrub oak during all parts of the year ($t = 3.208$, $P = 0.001$).

[23] Mean maximum daily E_t was 3 mm for both the scrub oak and pine flatwoods and occurred during the summer time. On a seasonal basis, weekly E_t in both ecosystems was 7 mm during the winter and 25 mm during the summer (Figure 5). At the pine flatwoods, annual E_t was 812 mm for 2002. Scrub oak annual E_t was 737 mm in 2001 and 713 mm in 2002 and 2002, which was relatively stable between the two years compared to the 250 mm increase in precipitation from 2001 to 2002. Similarly, E_t during the dry period from January to May was 234 mm in 2001

Table 2. Nonlinear Model Parameters and Statistics for Factors Controlling Variations in E_t in a Scrub Oak and Pine Flatwoods^a

	Scrub Oak		Pine Flatwoods	
	$r^2 = 0.82$		$r^2 = 0.82$	
ANOVA	F = 94.52	P = 0	F = 44.61	P = 0
Variable	Coeff.	P-value	Coeff.	P-value
b	-46.862	0.0	-55.59	0.05
NDVI	61.75	<0.001	67.79	0.06
D	3008	0.0	4430	0.0

^aNDVI (unitless), air specific humidity deficit (D , g g⁻¹).

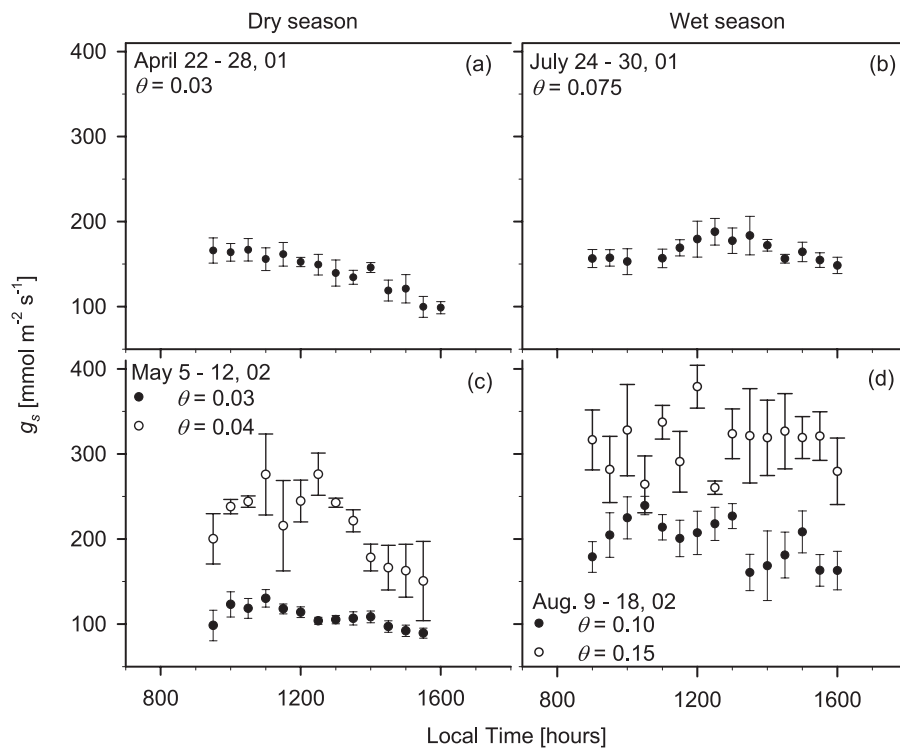


Figure 6. Weekly average of half hour surface conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$) for representative weeks during the peak dry and wet seasons in 2001 (a and b) and 2002 (c and d) for the scrub oak (closed symbol) and pine flatwoods (open symbol). Mean midday soil water content (θ , $\text{m}^3 \text{m}^{-3}$) is given for each period.

vs. 220 mm in 2002; yet precipitation was 34% lower during this period in 2002 compared to 2001. During prolonged dry periods, water losses from the upper soil profile (i.e. 0–0.65 m at the scrub oak and 0–0.5 m at the pine flatwoods) did not match Et losses. For example from January to May of both years, water losses in this horizon at the scrub oak represented 22% to 28% (6 to 8 mm) of measured Et . In contrast, water losses from the upper soil horizon at the pine flatwoods represented only 11% (5 mm) of Et for the same dry period in 2002.

3.4. Factors Controlling Evapotranspiration

[24] The effects of leaf area ($NDVI$), and D on Et at both sites were assessed using a nonlinear regression analysis (Table 2). Simultaneous variations in leaf area and D explained 82% of the variability in Et at both systems. Effects of changes in leaf area at the pine site were significant at 90% probability. The individual effect of D was higher at the pine site than at the scrub oak.

[25] Maximum weekly values of midday surface conductance (g_s), were approximately $200 \text{ mmol m}^{-2} \text{s}^{-1}$ and $350 \text{ mmol m}^{-2} \text{s}^{-1}$ at the scrub oak and pine flatwoods, respectively, and were reached during summer time when leaf area and soil moisture peaked (Figure 6). A regression analysis indicated that weekly averages of g_s at the pine flatwoods was 25% higher than those in the scrub oak ($r^2 = 0.56$, $P < 0.001$). The average diurnal trend in surface conductance (g_s) for periods of differing θ and leaf area were somewhat contrasting between the two ecosystems.

Surface conductance at the scrub oak during dry periods and intermediate leaf area (Figures 6a and 6c) reached a maximum of 130 to $166 \text{ mmol m}^{-2} \text{s}^{-1}$ by midmorning and then progressively decreased by approximately 40 to $60 \text{ mmol m}^{-2} \text{s}^{-1}$ through the afternoon; thus indicating a stomatal response to increases in D (Figures 6a and 6c). Lower g_s in the dry season of 2002 compared to 2001 corresponded with greater water stress in 2002. Maximum weekly g_s values at the scrub oak were similar in the morning during the dry and wet season in 2001 (Figures 6a and 6b) and in contrast only about half during the dry season as compared to the wet season in 2002 (Figures 6c and 6d). During dry periods, a function in the form $g_s = a + b \cdot \ln(D)$, where a and b are regression coefficients, explained 52% ($P < 0.0001$) and 46% ($P < 0.0001$) of the variation in hourly g_s at the scrub oak and pine flatwoods, respectively. In contrast with the scrub oak during the dry period, mean maximum g_s in the pine flatwoods was $275 \text{ mmol m}^{-2} \text{s}^{-1}$ and the magnitude of its midday suppression was 2 times greater at approximately $120 \text{ mmol m}^{-2} \text{s}^{-1}$ (Figure 6c). During the wet season, mean maximum g_s was 240 vs. $380 \text{ mmol m}^{-2} \text{s}^{-1}$ in the scrub oak and pine flatwoods, respectively. In both ecosystems, mean g_s linearly increased with R_n and explained 68% ($P < 0.001$) and 50% ($P < 0.001$) of its variation at the scrub oak and pine flatwoods, respectively.

[26] Aerodynamic conductance (g_a) was ten times higher than surface conductance in both ecosystems. The value of g_a was 35% higher ($r^2 = 0.70$, $p < 0.0001$) over the pine

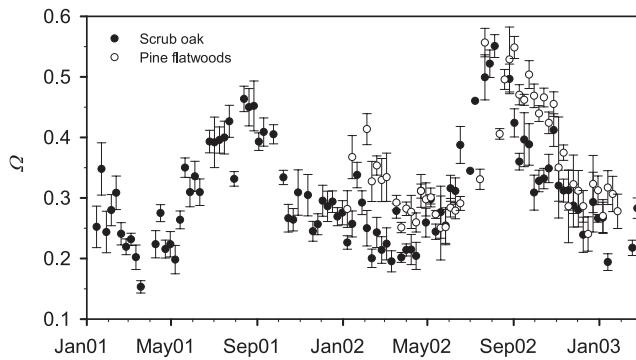


Figure 7. Weekly midday average of the decoupling coefficient Ω at the scrub oak from January 2001 to March 2003 and from January 2002 at the pine flatwoods.

flatwoods than over the scrub oak, thus reflecting the difference in canopy structure on gas exchange in these two ecosystems.

[27] Weekly average values for the decoupling coefficient (Ω) was also seasonal in both ecosystems (Figure 7). Minimum weekly average of midday Ω (0.19 and 0.25 for the scrub oak and pine site, respectively) were reached during the peak dry period. Omega increased with the onset of the raining season, reaching weekly average values above 0.55 in both ecosystems. A paired *t*-test indicated that mean weekly average Ω of the pine flatwoods was significantly higher both during the dry period ($t = 3.35$; $P = 0.0026$) and during the year of comparison ($t = 2.46$;

$P = 0.015$) than mean weekly average Ω values of the scrub oak.

4. Discussion

[28] This study compared energy fluxes and Et in two adjacent Florida ecosystems (scrub oak and pine flatwoods), where both were exposed to the same dominant climatological conditions, but each with differences in soil drainage, water holding capacity, and ecosystem structure. Our study also included responses of Et in the scrub oak system over a two year period with differences in precipitation; showing that scrub oak maintained similar rates of annual Et despite a difference of 22% in annual precipitation.

[29] The lack of energy closure at both sites was within 15% and compares favorably with a global closure within 20% reported for 22 sites across the FLUXNET network [Wilson *et al.*, 2002a]. This imbalance is explained by an underestimation of λE and H or an overestimation of the available energy. Similar to other Florida pine and deciduous ecosystems [Sumner, 2001; Gholz and Clark, 2002; Powell *et al.*, 2005], latent and sensible heat fluxes in both the scrub oak and pine flatwoods were linearly related to net radiation (Figure 3). Also similar to other managed and unmanaged Florida pine forests, in both ecosystems H was the dominant energy flux in the wintertime and dry periods and λE dominated in the summer coincident with peak leaf area and the raining season [Gholz and Clark, 2002; Powell *et al.*, 2005]. The proportion of net radiation dissipated as λE in both ecosystems was similar to the range of values (winter: 18% to 40%, summer 36% to 52%) reported for

Table 3. Annual Evapotranspiration (Et) and $Et:P$ Ratios for Different Ecosystems in Florida, United States

Ecosystem Type	Annual Et (mm)	$Et:P$	Reference
Scrub oak	737	0.81	This work
	713	0.62	
Pine flatwoods	812	0.71	This work
Southern Florida flatwoods	927–1040		Allen <i>et al.</i> [1982]
Managed pine flatwoods	760–1170	0.71; 0.91	Riekerk [1989]
Slash pine	1280		Ewel and Gholz [1991]
Pine flatwoods type	1060		Bidlake <i>et al.</i> [1996]
Slash pine	795		Liu <i>et al.</i> [1998]
Watershed (Pine Flatwoods-Cypress)	916	0.74	Sumner [2001]
	1070	0.76	
Slash pine (clear cut)	959	0.85	
Slash pine (midrotation)	951	1.01	Gholz and Clark [2002]
Slash pine (rotation – aged)	1110	0.93	
Natural regenerated	676–832	0.82	Powell <i>et al.</i> [2005]
Pine flatwoods	832	0.84	
Discontinued swamp	860		Ewel and Smith [1992]
Dry prairie	1010		
Marsh vegetation type	990		Bidlake <i>et al.</i> [1996]
3 m deep lake	1510		
9 m deep lake	1280		Sacks <i>et al.</i> [1994]
Cattails and mixed marsh	1200		Abtew [1996]
Cypress wetland	974		Liu <i>et al.</i> [1998]
Cypress swamp	970		
Subtropical estuary	1580	1.31	Sumner and Belaine [2005]
Herbaceous successional vegetation	680	0.51	Sumner [1996]
Orange trees	920	0.53	Fares and Alva [2000]
Pasture	787	0.68	Sumner and Jacobs [2005]
Watershed in South Florida	890		Allen <i>et al.</i> [1982]
Sylver Spring basin Florida	963		
Rainbow Spring basin	978		Knowles [1996]

intensively managed (excluding recently clearcut land) and natural pine forests in Florida [Sumner, 2001; Gholz and Clark, 2002; Powell et al., 2005]. The energy partitioning (β) in both ecosystems was explained by fluctuations of leaf area and soil moisture at 0–0.2 m depth. The effect of leaf area on β was more pronounced at the pine flatwoods as indicated by a steeper slope (Figure 4a). The interaction of both factors explained over 80% of the energy partitioning at both sites. Despite springtime increases in leaf area, the strong coupling of the canopy to the boundary-layer (low Ω) indicated that stomata controlled the energy distribution resulting in H frequently being greater than λE (i.e. $\beta > 1$) in both ecosystems. Stomata conductance was also important controlling the energy partitioning at different ecosystems within the Fluxnet sites [Wilson et al., 2002b]. Stronger coupling at the scrub oak led to higher β compared to the pine flatwoods, which can produce energy gradients between the two ecosystems. Leaf area was also determined to be an important variable regulating energy partitioning in other intensively and naturally managed pine forest across Florida [Sumner, 2001; Gholz and Clark, 2002; Powell et al., 2005].

[30] In contrast to the scrub oak (and pine flatwoods), temperate and tropical broadleaf forests dissipate 65% to >90% of R_n as λE [Wilson et al., 2002b; Loescher et al., 2005; Stoy et al., 2006]. We attribute this energy-partitioning difference to the difference in leaf area, where scrub oak leaf area is as much as one third of that compared to the much larger temperate and tropical broadleaf forests. Scrub oak energy partitioning also contrasts that of an evergreen Mediterranean *Q. Ilex* forest, which had much higher mean summertime β values (range: 1.73 to 2.25) largely because it experiences its dry season during the summer [Wilson et al., 2002b]. This difference emphasizes the important role soil moisture can have in regulating energy partitioning across different oak forests.

[31] Higher annual Et at the pine flatwoods (812 mm) compared with the scrub oak (713 mm) was explained by differences in plant water availability and leaf area. Annual Et values in Florida (Table 3), range from less than 700 mm in ecosystems with shallow root systems and a relatively deep water table [Sumner, 1996] to close to 1600 mm in open water ecosystems [Sumner and Belaine, 2005]. Annual Et from the scrub oak (737 mm and 713 mm in 2001 and 2002, respectively) is on the low end of the range presented in Table 3 indicating that scrub oak is more conservative in its water-use, regardless of precipitation, compared to other Florida ecosystems. Annual Et from the pine flatwoods reported here was on the low range of values reported for different pine ecosystems in Florida (Table 3), which is reflective of its comparatively low stem density and therefore leaf area. Differences in annual Et in pine ecosystems are driven by fluctuations in environmental conditions [Gholz and Clark, 2002; Powell et al., 2005] and management practices [Riekerk, 1989; Sumner, 2001]. Annual Et from the two subtropical ecosystems reported here was lower than values reported for tropical rain forests (1300–2300 mm) with high leaf area index and a larger annual energy input [Bruijnzeel, 1989; Kumagai et al., 2005; Loescher et al., 2005]. On the other hand, annual Et was higher than the range (340–550 mm) reported for

broadleaf and coniferous temperate forests, which experience lower evaporative demand, stronger seasonality in leaf area, and lower annual integrated energy input [Wilson and Baldocchi, 2000; Valentini et al., 2000; Law et al., 2002; Wilson et al., 2002b]. $Et:P$ indicates that between 51% (for shallowed-root ecosystems) to more than 100% of precipitation (for wetlands and open water ecosystems) returns to the atmosphere as Et (Table 3). These ratios depend on environmental fluctuations, soil, vegetation type, and management. $Et:P$ for the scrub oak varied between years and is typical of ecosystems with access to deep soil water sources [Anthoni et al., 1999].

[32] In the spring time, when soil moisture in the upper soil profile decreases, transpiration at the leaf-level decreases per unit of leaf area in *Q. myrtifolia* [Li et al., 2003], which is one of the dominant species in the scrub oak and pine flatwoods' understory. Interestingly, Et at the ecosystem level increased during the springtime in both ecosystems because the reduction in leaf-level transpiration was more than compensated by the flush of new leaves (Figure 2) and relatively high evaporative demand (Figure 1e). Similarly, the seasonality of leaf area produced seasonal variations in Et in different Florida ecosystems [Liu et al., 1998; Sumner, 2001; Gholz and Clark, 2002] and Et from drier uplands were more sensitive to changes in environmental conditions compared to poorly drained depressions [Liu et al., 1998].

[33] Continuous canopy activity of both ecosystems during the spring, demonstrated by continuous stomatal conductance (Figure 6) when water content in the upper soil profile (0–0.2 m) reach the permanent wilting point, suggests that these two ecosystems avoid drought by accessing deep water. Maintenance of the physiological activity by reaching deep water allowed increases in leaf area. However, strong coupling of the canopy to atmospheric conditions indicated that there was strong stomata control over water losses and that Et was mainly driven by D , especially during the dry periods. Measured stomata conductance was reduced during dry periods in *Q. myrtifolia* [Li et al., 2003]; however, a 50% increase in leaf area from its minimum value at the scrub oak allowed for an increase in Et .

[34] Roots below 0.5 m represent an important fraction in the 1 m root profile at the scrub oak site [Dilustro et al., 2002; Day et al., 2006]. Deep roots explain the discrepancy between Et and water losses from the upper soil profile during the driest periods of the year in both ecosystems. Considering that water losses from the upper soil profile was only 22% to 28% for the scrub oak and 11% for the pine flatwoods during the driest periods in 2001 and 2002, then the residual amount of water used (over 72% at the scrub oak and 89% of the pine flatwoods) must have been supplied from the water table. These results support plant level measurements in this ecosystem where 79% and 95% of the water in the xylem of *Q. myrtifolia* and *Q. geminata* (the two dominant species), respectively, was from the water table during the peak dry season when the water table was almost 3 m deep [Hungate et al., 2002]. Higher Et at the pine flatwoods during the same dry period was related to higher soil moisture conditioned by a lower hydraulic conductivity of the upper soil horizons [Huckle et al., 1974], and greater total leaf area compared to the scrub

oak. This pattern of deep soil water extraction for scrub oak species during the dry season is similar to that reported for the eastern Amazon forest where deep root systems (2 to 8 m) maintain green canopies during the dry season [Nepstad *et al.*, 1994]. It is also similar to cerrado savannas of central Brazil where between 67% and 82% of the water used during the dry season was extracted from below 1 m [Oliveira *et al.*, 2005]. Other ecosystems that also experience a seasonal dry period have shown similar results—e.g. oak-grass savanna, evergreen oak, riparian woodlands and a natural jarrah [Baldocchi *et al.*, 2004; David *et al.*, 2004; Scott *et al.*, 2004; Silberstein *et al.*, 2001].

[35] Our results suggest that scrub oak, with its deeper rooting system, is able to maintain similar annual evapotranspiration in years with significantly lower precipitation when compared with years having average precipitation. This characteristic is important because scrub oak species are then able to maintain significant carbon fixation rates during the dry season or drought years [Powell *et al.*, 2006]. The ecological importance of these adaptations for scrub oak species (deep roots and strong control on water losses) extends beyond their capacity to buffer the effect of long dry season or dry years. The combination of deep roots accessing the water table and physiological controls over water loss (strong coupling to the atmosphere) during the driest periods provides a competitive advantage to scrub oak species thus enabling them to establish and maintain dominance on landscapes characterized by sandy well-drained soils and this advantage would be especially important in the driest years. This hypothesis is supported by the fact that oak species have been found to maintain stomata conductance at low soil and leaf water potential when established in places where they rely primarily on deep water sources [Hasting *et al.*, 1989; Ni and Pallardy, 1991; Oren and Pataki, 2001; Pataki and Oren, 2003; Rambal *et al.*, 2003; Xu and Baldocchi, 2003; Baldocchi *et al.*, 2004]. Furthermore, an oak-hickory deciduous forest at the bottomlands of the Duke Forest was able to maintain similar transpiration rates under drought or normal water supply conditions [Pataki and Oren, 2003].

[36] In Florida, one future implication of this research is that the relative importance of scrub oak may increase in areas where it coexists with pine flatwoods as the water table recedes, which is a possibility owing to projected increases in ground water demands of over 100% by 2020 [Knowles *et al.*, 2002]. This hypothesis is supported by both a nearby study that concluded the occurrence of scrub oak species in the landscape increases with distance to the water table [Schmalzer and Hinkle, 1992b], and historical pollen records that indicate vegetation like scrub oak and oak species occupied a greater extent of the landscape in the southeastern United States during drier periods [Watts, 1971, 1980]. Also, total leaf area and or coverage of both ecosystems can be highly dynamic in time and space due to natural seasonal processes, active management or replacement by suburban development and other land uses [Menges, 1999; Gholz and Clark, 2002; Duncan *et al.*, 2004; Powell *et al.*, 2005, 2006]. Consequently, our results also support the hypothesis that such a dynamic landscape can produce strong energy gradients between contrasting, adjacent land uses that can potentially alter local weather

patterns and water budgets [Dirmeyer, 1994; Pielke *et al.*, 1999, 2002].

5. Summary and Conclusions

[37] This study explored energy partitioning and physiological responses of two characteristic ecosystems of central Florida, scrub oak and pine flatwoods, exposed to similar atmospheric variation in a year (2002) with average precipitation. This study also examined how the scrub oak ecosystem responded to two hydrologically contrasting years—drought (2001) versus average precipitation (2002).

[38] Latent and sensible heat fluxes were driven by R_n , with λE being higher at the pine flatwoods. However the distribution of the R_n into λE and H was modulated by leaf area and the response of stomata conductance to dry surface soil conditions. Higher Et at the pine flatwoods compared to the scrub oak was related to higher availability of soil water and greater leaf area. Increases in leaf area and strong surface coupling to external atmospheric conditions resulted in an increase in Et despite a decrease in θ in the upper soil profile decreased. Moreover, both ecosystems maintained significant Et through the use of tap roots when soil water was scarce or not available in the upper soil horizon above the relatively shallow water table. Coupling to the external conditions was more pronounced in the scrub oak than in the pine flatwoods. Stomatal conductance played a major role in the energy distribution at the landscape level.

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