

Ecosystem and understory water and energy exchange for a mature, naturally regenerated pine flatwoods forest in north Florida¹

Thomas L. Powell, Gregory Starr, Kenneth L. Clark, Timothy A. Martin, and Henry L. Gholz

Abstract: Eddy covariance was used to measure energy fluxes from July 2000 – June 2002 above the tree canopy and above the understory in a mature, naturally regenerated slash pine (*Pinus elliottii* Engelm. var. *elliottii*) – longleaf pine (*Pinus palustris* Mill.) flatwoods forest. Understory latent energy (λE) and sensible heat (H) fluxes accounted for 45% and 55% of whole-ecosystem fluxes, respectively, with strong seasonal variation in the proportion of λE attributable to the understory. The partitioning of net radiation (R_{net}) to λE and H also changed seasonally, with half-hourly mean ecosystem H in the winter peaking at $175 \text{ W}\cdot\text{m}^{-2}$, almost twice as large as λE . In contrast, half-hourly ecosystem λE and H remained almost equal throughout the day in July and August, with mean midday peaks of approximately $200 \text{ W}\cdot\text{m}^{-2}$. Maximum hourly evapotranspiration (ET) in the months of July and August was 0.32 and $0.29 \text{ mm}\cdot\text{h}^{-1}$ for 2000 and 2001, respectively. For a variety of environmental conditions, mean daily ET was approximately 2.7 mm in the summer and 1.3 mm in the winter. Annual ET for the first year was 832 mm , or 87% of annual precipitation (956 mm). Although leaf area index was higher in the second year, annual ET was only 676 mm , which is considerably lower than that of the previous year, but it still accounted for approximately the same proportion (84%) of the much lower annual precipitation (811 mm). Canopy conductance declined as soils dried, changing patterns of partitioning of R_{net} to λE .

Résumé : La méthode de covariance des turbulences a été utilisée pour mesurer les flux d'énergie de juillet 2000 à juin 2002 au-dessus du couvert forestier et au-dessus de la végétation du sous-bois d'une forêt mature d'origine naturelle, établie sur terrain plat et composée de pin d'Elliott typique (*Pinus elliottii* Engelm. var. *elliottii*) et de pin des marais (*Pinus palustris* Mill.). Les flux de chaleur latente (λE) et sensible (H) de la végétation du sous-bois représentaient respectivement 45 et 55 % des flux de tout l'écosystème et de fortes variations saisonnières dans la proportion de λE ont été causées par la végétation du sous-bois. La répartition du rayonnement net (R_{net}) entre λE et H a aussi varié selon les saisons avec des valeurs mi-horaires moyennes de H de l'écosystème atteignant un maximum de $175 \text{ W}\cdot\text{m}^{-2}$ pendant l'hiver, soit presque le double de λE . Au contraire, les valeurs mi-horaires de λE et H de l'écosystème sont demeurées presque égales tout au long des journées en juillet et août avec des valeurs maximales de mi-journée d'environ $200 \text{ W}\cdot\text{m}^{-2}$. L'évapotranspiration (ET) horaire maximale au cours des mois de juillet et août a atteint respectivement $0,32$ et $0,29 \text{ mm}\cdot\text{h}^{-1}$ pour les années 2000 et 2001. Pour toute une gamme de conditions environnementales, la moyenne journalière de ET était d'environ $2,7 \text{ mm}$ pendant l'été et $1,3 \text{ mm}$ pendant l'hiver. La valeur annuelle de ET pour la première année était de 832 mm , soit 87 % des précipitations annuelles (956 mm). Même si la valeur de l'indice de surface foliaire était supérieure pendant la deuxième année, la valeur annuelle de ET a atteint seulement 676 mm , ce qui est considérablement plus faible que la valeur de l'année précédente. Cette valeur correspond environ à la même proportion (84 %) des précipitations annuelles (811 mm) de 2001 qui ont été beaucoup plus faibles qu'en 2000. La conductance du couvert forestier a diminué avec l'assèchement du sol, ce qui a changé le patron de répartition de R_{net} sous forme de λE .

[Traduit par la Rédaction]

Received 20 June 2004. Accepted 18 March 2005. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 10 August 2005.

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¹Journal Series R-10682 of the Florida Agricultural Experiment Station, Gainesville, Florida.

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Introduction

Pine flatwoods are a widespread ecosystem type on the southeastern US Coastal Plain, occupying approximately 5.35×10^6 ha (Smith et al. 2001). Flatwoods are particularly important in Florida, where they account for about half of the terrestrial landscape, in a mixture of about two-thirds pine uplands and one-third forested wetlands (Myers and Ewel 1990). Prior to European settlement, these ecosystems were characterized by open-canopy forests of mixed longleaf pine (*Pinus palustris* Mill.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*), with low, but dense shrub understories (Abrahamson and Hartnett 1990). Over the last century, the structure of the pine uplands has changed considerably, and much of the naturally occurring pine forests have been replaced by artificially regenerated plantations of slash pine, and to a lesser extent loblolly pine (*Pinus taeda* L.). These plantations are managed with varying degrees of silvicultural intensity (Brown 1996). Plantations differ in structure and function from their naturally regenerated predecessors in a number of ways. Compared with most naturally regenerated forests, pine plantations have higher stem density, higher tree canopy leaf area index (LAI), lower understory LAI, smaller mean tree size, and a smaller range of tree sizes and tree ages. In addition, the low-intensity, high-frequency fires that characterized presettlement forests are essentially excluded from pine plantations. The effects of these contrasting structural and functional attributes on the energy balance and water fluxes of the landscape are not known, although many public and some nonindustrial private forest landowners in the region are increasingly turning to natural regeneration and uneven-aged silviculture on their lands (Owen 2002).

Variations in water flux and energy balance across space and time are a function of interactions among environmental conditions, ecosystem characteristics, and land management regimes. A complex mosaic of land uses within landscapes induces energy gradients that influence local and regional water dynamics (Baldocchi et al. 1996). Evaluating the effects of even-aged forest management on ecosystem and regional water budgets on the southeastern Coastal Plain has been the focal point of considerable research (Riekerk 1982, 1989; Golkin and Ewel 1984; Liu 1996; Liu et al. 1998; Martin 2000; Gholz and Clark 2002). This research has shown that evapotranspiration (ET) is the largest component of the flatwoods water balance and accounts for 60%–90% of annual precipitation. Furthermore, ET plays a large role in surface and ground water dynamics because shifts in the ratio between ET and precipitation can change the amount of precipitation that ends up in groundwater storage or streamflow (Allen 1982).

The goal of this study was to quantify ecosystem water and energy budgets for a mature, naturally regenerated pine flatwoods ecosystem in north-central Florida, and to understand the key environmental variables that determine these budgets. The research had three primary objectives: (1) to quantify the water budget for this forest over a 2-year period; (2) to determine the dominant environmental factors controlling the seasonal partitioning of net radiation (R_{net}) into the main energy budget components of latent energy flux (λE) and sensible heat flux (H); and (3) to determine the role of understory vegetation in ecosystem exchanges of water and energy.

Table 1. Characteristics of the naturally regenerated *Pinus palustris* – *Pinus elliottii* stand in the Austin Cary Memorial Forest.

Stand area	41 ha (95% pine uplands, 5% cypress wetlands)
Stem density	$325 \pm 36 \text{ ha}^{-1}$
Canopy height	$22.1 \pm 0.55 \text{ m}$
Tree DBH (2001)	$25.7 \pm 1.17 \text{ cm}$
Tree basal area (2001)	$18.0 \pm 0.95 \text{ m}^2 \cdot \text{ha}^{-1}$
Tree canopy LAI ^a	2000–2001: summer, 3.4; winter, 2.6 2001–2002: summer, 3.8; winter, 2.6
Understory LAI ^a	Jan. 2001: <i>Serenoa</i> , 0.7; <i>Ilex</i> , 0.2 Feb. 2002: <i>Serenoa</i> , 1.0; <i>Ilex</i> , 0.2

Note: Values are mean \pm 1 standard error.

^aAll-sided leaf area index.

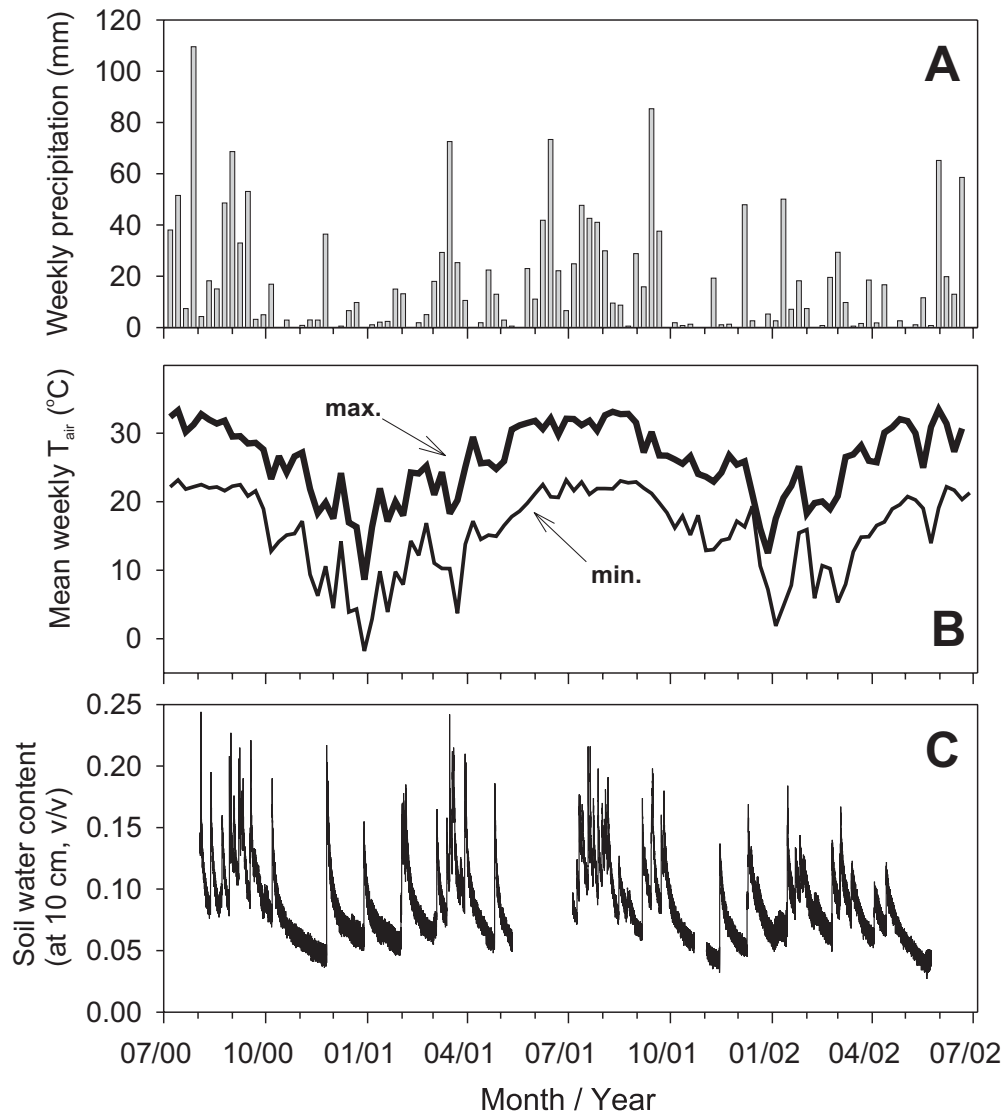
Study site and methods

This study was conducted on the University of Florida's Austin Cary Memorial Forest (ACMF), 15 km northeast of Gainesville, Alachua County, Florida, USA (29°44'N, 82°09'30'W). The elevation of the site is 50 m and the topography is flat. The study stand (Table 1) was a naturally regenerated, 41-ha, mixed slash pine and longleaf pine stand (64% and 36% of the stand basal area, respectively). Prior to state purchase in 1936, the forest had been selectively harvested for timber and otherwise utilized as grazing land. A current management objective is ultimately to restore elements of forest structure and function typical prior to European settlement, including large, widely spaced trees; a vigorous understory plant community; and frequent, low-intensity fires. The stand was thinned in 1991, removing 27% of the basal area, and the most recent prescribed fire occurred 4 years prior to this study. The stand is well stratified, with a 22.1 m tall, relatively open tree canopy 15 m above a 1.5 m tall understory. Tree ages ranged from 20 to 80 years in 2001, with a mean age of 60 years. The understory was well developed, consisting of naturally occurring native species dominated by saw palmetto (*Serenoa repens* (Bartr.) Small), gallberry (*Ilex glabra* (L.) Gray), wax myrtle (*Myrica cerifera* L.), and wiregrass (*Aristida stricta* Michx).

The soils of this site are poorly drained Ultic Alaquods that have a discontinuous spodic horizon (30–60 cm depth) and a deeper argillic horizon (100–140 cm depth, Gaston et al. 1990). During the study period, the watertable ranged from 1.3 m depth in September 2000 to nearly 3 m in depth in July 2000 and June 2001 (Fig. 2E), with the average considerably deeper than the long-term average of 1–2 m (Abrahamson and Hartnett 1990).

Long-term (1961–2004) mean annual precipitation recorded 5 km from the site was 1259 mm, with 52% falling from June to September (National Climatic Data Center 2004). Annual precipitation during the study period was 956 and 811 mm during the first and second years, respectively (Fig. 1A). Long-term mean maximum and minimum temperatures for the months of January and July were 19.0 °C and 6.1 °C, and 32.6 °C and 21.8 °C, respectively (National Climatic Data Center 2004). During the study, mean maximum and minimum temperatures for January and July were 17.6 °C and 5.6 °C, and 31.8 °C and 22.9 °C, respectively (Fig. 1B).

Fig. 1. (A) Weekly precipitation, (B) maximum and minimum air temperature, and (C) volumetric soil water content at 10 cm depth for the two measurement years.



Energy flux measurements

Net fluxes of latent heat (λE) and sensible heat (H) were measured using standard eddy-covariance methods (e.g., Clark et al. 1999, 2004). λE was estimated as

$$[1] \quad \lambda E = \rho_a \overline{w'c'}$$

where ρ_a is the density of air, w' is the instantaneous deviation of vertical wind speed from the mean vertical wind speed ($w' = \bar{w} - w$), c' is the instantaneous deviation of water vapor concentration from the mean water vapor concentration ($c' = \bar{c} - c$), and the overbar denotes a time averaged, 200-s running mean.

A 30-m walk-up scaffolding tower was erected in the center of the stand, extending 8 m above mean canopy height. A mobile 3-m antenna tower was also erected to measure above-understory fluxes (λE_u and H_u). We assumed that λE_u and H_u fluxes transferred across a horizontal plane existing between the bottom of the canopy and the understory (Baldocchi and Vogel 1996, 1997). The understory tower was moved be-

tween three fixed locations (30–40 m from the tower) to dampen local effects of understory heterogeneity, and data were pooled for analysis. Wind speed was measured with 3-dimensional sonic anemometers mounted 2 m above the top of the canopy tower and 1 m above the understory tower (Windmaster Pro, Gill Instruments Ltd., Lymington, UK). Closed-path infrared gas analyzers (IRGA) (LI-6262, LI-COR, Inc., Lincoln, Nebraska) were used to measure H_2O concentrations at 10 Hz. The gas samples were pumped at $6.0 \text{ L}\cdot\text{min}^{-1}$ from the anemometers to the IRGAs through 4 mm i.d. Teflon[®] coated tubes. Mean gas sample lag times between the anemometers and the IRGAs were approximately 10 and 12 s for the canopy and understory towers, respectively. Nitrogen was run at a rate of $0.10 \text{ L}\cdot\text{min}^{-1}$ through a desiccant and into the IRGA reference cells to establish a water-free baseline. The IRGAs were calibrated every 2 to 3 days using a dew point generator (LI-610, LI-COR, Inc.).

Flux calculation software was used to rotate the horizontal wind velocities to obtain turbulence statistics perpendicular

to the local streamline using Reynolds detrending (200-s constant, Katul et al. 1999). Net scalar fluxes were averaged at half-hour intervals. Fluxes were collectively corrected for attenuation of the gas concentrations in the sampling tube, the nonideal frequency response of the LI-6262, and sensor separation loss using transfer functions (Moncrieff et al. 1997).

The data were screened to eliminate spurious or incomplete half-hourly data resulting from system malfunction or environmental disturbance. Half-hour values were eliminated if they met any of the following criteria: (1) 10-Hz data were incomplete because of interruptions for calibration or maintenance, (2) data were collected during rain events, (3) data were collected when atmospheric conditions were stable, leading to poor coupling between canopy air and atmospheric air (we defined stable conditions as half hours with friction velocity (u^*) $< 0.2 \text{ m}\cdot\text{s}^{-1}$ (Goulden et al. 1996; Clark et al. 1999, 2004)), or (4) 10-Hz data exhibited unusually high or unusually low variation. In total, ecosystem fluxes were measured $\sim 70\%$ of the time and about one-third of those data were eliminated by the screening criteria. There was no apparent temporal bias in the distribution of screened data.

Water and energy budget calculations

Interception (I) was calculated by subtracting throughfall (TF) and stemflow (SF) from precipitation and was measured on an event basis periodically in the summer and winter to include seasonal variation in LAI. TF was collected in twenty 1 m long (808 cm^2) troughs that were slightly angled and drained by funnels into 4-L containers. TF depth was determined by dividing the volume of water collected in each trough by the collection area. SF was estimated as 1% of precipitation (P) when the event was $> 2.5 \text{ mm}$ (Allen and Gholz 1996), otherwise SF was assumed to be negligible. Interception for rainfall events in which TF was not measured was estimated from a regression of (TF + SF) on P .

Annual ET was estimated by summing half-hourly above-canopy eddy covariance ecosystem latent heat flux (λE_e) values. For half hours with missing data, λE_e was estimated by substituting R_{net} , vapor pressure deficit (VPD), aerodynamic conductance (g_a), and canopy conductance (g_c) into the Penman–Monteith equation (Monteith 1965). R_{net} and VPD were obtained from the weather station, and g_a was calculated as $g_a = u^2/u_z$ (Kelliher 1993; Baldocchi and Vogel 1997), where u_z is horizontal wind speed at the sonic anemometer height (30 m). If sonic anemometer data were not available for a time period, the median observed g_a value was used. A model was used to simulate g_c from measured R_{net} and VPD data (Jarvis 1976; Martin et al. 1997):

$$[2] \quad \hat{g}_c = f(R_{\text{net}}) \times f(\text{VPD})$$

where \hat{g}_c is the predicted bulk canopy conductance, and $f(R_{\text{net}})$ is a function relating g_{max} to R_{net} , where g_{max} is defined as the hypothetical g_c under a given R_{net} when there is no reduction in g_c due to VPD. A vapor pressure deficit function, $f(\text{VPD})$, derived from boundary line analysis (Martin et al. 1997) was then used to reduce g_{max} and produce the final estimate of g_c . We parameterized the model with a data set of measured bulk g_c calculated by substituting meteorological data, g_a , and λE_e into the inverted Penman–Monteith equation (Baldocchi and Vogel 1997; Martin et al. 1997). To

keep the g_c model simple and parsimonious, we designed the model to only capture typical variation in g_c , and therefore eliminated unusually high or low g_c values from the model parameterization data set using the following criteria: (1) parameterization data were restricted to those half hours when λE_e was within 50% of λE_e predicted from the regression between λE_e and R_{net} (40% of parameterization data); (2) g_c values $> 0.012 \text{ m}\cdot\text{s}^{-1}$ were eliminated ($< 4\%$ of parameterization data); (3) data were screened when $R_{\text{net}} < 200 \text{ W}\cdot\text{m}^{-2}$ and $g_{\text{max}} > 0.002 \text{ m}\cdot\text{s}^{-1}$ ($< 1\%$ of parameterization data). When the gap-filling model was compared with a validation eddy-covariance data set ($n = 829$ randomly selected half hours) that was not used for model parameterization, residuals showed slight underprediction at very high VPD ($> 2.5 \text{ kPa}$) and very low VPD ($< 0.5 \text{ kPa}$), but the measured and modeled λE sums were within 10% of each other.

When the canopy was wet, the Penman–Monteith equation was reduced to the Penman equation (Penman 1948) by removing g_c from the equation, assuming water only evaporated from exterior surfaces until the canopy dried. For gap-filling λE_e during rain events, the Penman model was used for half hours that had precipitation and subsequent half hours until the Penman model evaporated the depth of I . Once I was evaporated, the model incorporating the Penman–Monteith equation and eq. 2 resumed.

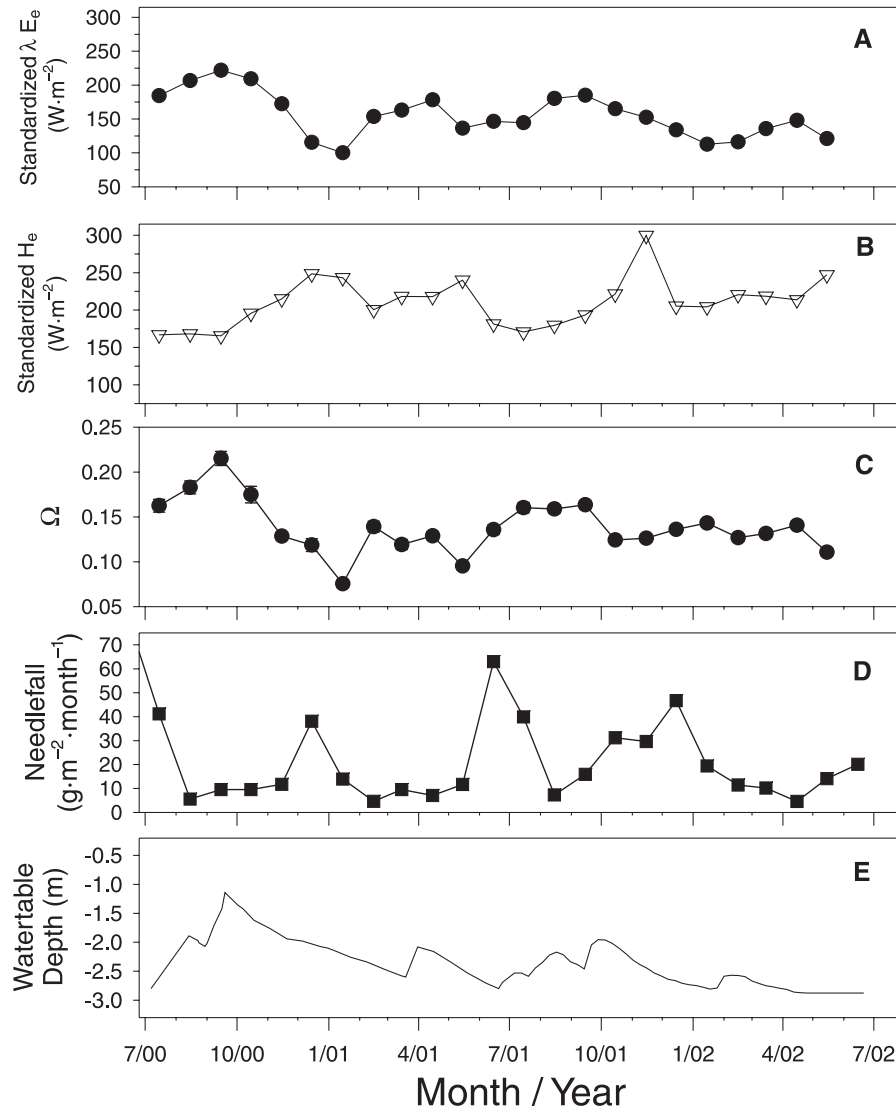
To facilitate analysis of seasonal variation in λE_e and ecosystem sensible heat flux (H_e), we created standardized monthly values of these variables. We performed monthly regressions of λE_e and H_e versus R_{net} , and we used the predictions at $R_{\text{net}} = 500 \text{ W}\cdot\text{m}^{-2}$ as the standardized values. To estimate the relative importance of g_c and g_a for controlling evapotranspiration, the decoupling coefficient Ω was calculated as described by Jarvis and McNaughton (1986).

Biomass and leaf area estimates

A 50 m \times 50 m inventory plot was randomly located in each of four quadrants around the tower. The inventory plots were used for measurements of tree diameter and height, canopy and understory LAI, and throughfall. LAI was calculated from annual litterfall collected monthly from ten 1- m^2 litter traps randomly located within the inventory plots following the method described in Martin and Jokela (2004). Litterfall was dried for 3 days at 70 $^\circ\text{C}$ in an oven, and needles were separated and weighed to the nearest 0.1 g. The needlefall year was defined as March 1 through February 28, since new needle flushing begins in March. A needlefall curve was integrated with a needle-accretion curve calculated from a logistic equation (Gholz et al. 1991; Dougherty et al. 1995) to estimate seasonal changes in canopy foliage biomass. Multiplication by the appropriate specific leaf areas of each cohort produced area equivalents (Dalla-Tea and Jokela 1991; Gholz et al. 1991).

Allometric equations were used to determine all-sided LAI of understory saw palmetto from measurements of frond blade length and rachis length made in a 25 m \times 25 m subplot at the center of each inventory plot (Gholz et al. 1999). Gallberry LAI was estimated using measurements of total stem height (centimetres) of individual plants made in twenty 1- m^2 subplots distributed randomly in census plots, using a previously derived equation based on destructive sampling:

Fig. 2. Monthly values of ecosystem latent energy (λE_e) (A) and sensible heat (H_e) (B) fluxes standardized at a net radiation (R_{net}) of $500 \text{ W}\cdot\text{m}^{-2}$, derived from monthly regressions of λE_e and H_e against R_{net} ; mean monthly midday (1000–1400 hours) values of the Ω decoupling coefficient (C), monthly needlefall (D), and watertable depth (E).



leaf area (cm^2/plant) = (total height \times 6.652) - 110.2 ($n = 30$, H.L. Gholz, unpublished data).

Meteorological and soil measurements

Meteorological data were continuously collected during the study period by scanning standard meteorological sensors every 5 min and then averaging every half hour with a datalogger (Easylogger EL824-GP, Omnidata International, Ogden, Utah). Sensors were mounted on top of the tower for measuring incident solar radiation, photosynthetically active photon flux density (LI-200 and LI-190, respectively, LICOR, Inc.), net radiation (Q7, Radiation and Energy Balance Systems, Inc., Seattle, Washington), wind speed and direction (3001-5, R. M. Young Company, Traverse City, Michigan), temperature and relative humidity (HMP 45C, Vaisala, Inc., Helsinki, Finland), and precipitation (tipping bucket, Sierra Misco, Inc., Berkeley, California). Watertable depth was measured 15 m from the instrument tower with a Steven's water depth gage (F-68, Leupold and Stevens, Inc., Beaverton,

Oregon). Volumetric soil moisture content, θ , and soil temperature, T_s , were monitored with combination thermistor - dielectric capacitance probes (Hydra, Stevens Vitel, Inc., Chantilly, Virginia). Ecosystem soil heat flux (G) was estimated by averaging soil heat flux measurements calculated from three soil heat flux plates (HFT-3.1, Radiation and Energy Balance Systems, Inc.) buried 10 cm below the soil surface in three separate locations, 8 m from the tower. The soil heat flux for each sensor was calculated as the sum of soil heat flux measured at sensor depth (10 cm) and the energy stored in the soil above the sensor, S ($G = G_{10\text{cm}} + S$). Soil bulk density of $0.72 \text{ g}\cdot\text{cm}^{-3}$ (Schmalzer et al. 2001) and a soil heat capacity of $840 \text{ J}\cdot\text{kg}^{-1}\cdot\text{K}^{-1}$ were used with local half-hourly measurements of T_s and θ to calculate S (HFT-3.1 technical reference).

Statistical analysis

Regression analysis using SigmaPlot 5.0 Regression Wizard (SPSS Science, Chicago, Illinois) and the GLM procedure of

Table 2. Energy budget equations and above and below canopy flux equations for net radiation (R_{net}), latent energy (λE), sensible heat (H), and soil heat flux (G).

	Equation	R^2	p value	n
Above-canopy energy balance, October 2000 – May 2002	$(\lambda E_e + H_e + G) = 0.80R_{\text{net}} - 17.0$	0.83	<0.0001	6962
Above-canopy latent energy flux				
2000–2001	$\lambda E_e = 0.29R_{\text{net}} + 17.5$	0.51	<0.0001	4021
September 2000	$\lambda E_e = 0.42R_{\text{net}} + 13.7$	0.65	<0.0001	278
January 2001	$\lambda E_e = 0.18R_{\text{net}} + 12.2$	0.42	<0.0001	340
2001–2002	$\lambda E_e = 0.29R_{\text{net}} + 6.1$	0.59	<0.0001	4666
September 2001	$\lambda E_e = 0.34R_{\text{net}} + 14.1$	0.64	<0.0001	374
January 2002	$\lambda E_e = 0.26R_{\text{net}} + 5.7$	0.58	<0.0001	311
Above-canopy sensible heat flux, 2000–2002	$H_e = 0.45R_{\text{net}} - 19.0$	0.81	<0.0001	8757
Understory fluxes				
2000–2001 ^a	$\lambda E_u = 0.51\lambda E_e + 14.2$	0.62	<0.0001	2102
	$H_u = 0.55H_e - 7.2$	0.81	<0.0001	2102
2001–2002 ^a	$\lambda E_u = 0.43\lambda E_e + 19.4$	0.52	<0.0001	1553
	$H_u = 0.45H_e - 3.9$	0.77	<0.0001	1582

Note: All units are watts per square metre. September and January are shown to represent the highest and lowest months associated with the energy components of the system.

^aPooled across three understory tower locations.

SAS 8.1 (SAS Inc., Cary, North Carolina) was conducted to explore relationships between λE and H and environmental variables. Analysis of covariance with indicator variables was used to detect differences between seasonal regressions. Census plot plant measurement data were analyzed using Statistica (StatsSoft, Inc., Tulsa, Oklahoma) with the non-parametric Kruskal–Wallis test to determine whether there were significant interactions ($p = 0.05$) between plots and individual samples within the plots (Stevens 1996). No significant plot effects were found, so all plot data were pooled.

Results

Meteorological data

During the study, Florida was experiencing a “100-year drought”, with total precipitation of 956 and 811 mm during the first and second years, respectively, with approximately 60% falling during July to October each year (Fig. 1A). There were 86 days when $P > 1$ mm in the first year and 78 days when $P > 1$ mm during the second year. Volumetric soil water content (θ) at 10 cm depth varied widely, from field capacity (25% for the sandy soils at this site) to as low as 3.5% after long periods with low precipitation (Fig. 1C). The low θ values of 3.5% are equivalent to soil matric potential of approximately -0.78 MPa, based on soil moisture release curves generated for local Spodosols (H.L. Gholz unpublished data).

Needlefall and leaf area dynamics

In addition to the normal fall pulse of needlefall (Gholz et al. 1991), there were premature needlefall pulses in May and June of 2000 and 2001, where 50% of the annual needlefall occurred (Fig. 2D). Canopy LAI (all-sided) had a seasonal trend with peak values between 3.4 and 4.0 in August and minimum values between 2.2 and 2.6 in March. Understory LAI was 0.9 in January 2001 and 1.2 in January 2002 (Table 1).

Exchanges of momentum and energy

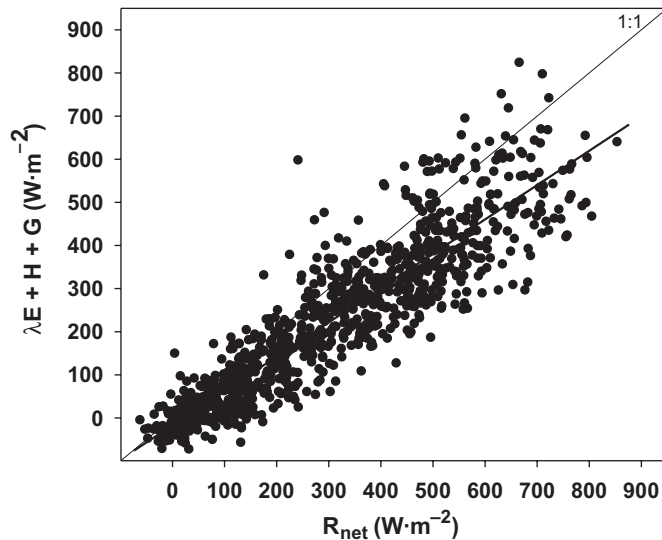
The relationship between friction velocity (u^* , metres per second) and horizontal wind speed (u_z , metres per second) was linear ($u^* = 0.241u_z - 0.086$; $R^2 = 0.72$, $n = 11997$). This relationship included data from all wind directions and indicates that eddies penetrated the open canopy in a relatively uniform manner. Net radiation was linearly related to incident solar radiation, R_g ($R_{\text{net}} = 0.77R_g - 14.2$; $R^2 = 0.98$, $n = 4373$). A mean albedo of 0.23 was calculated from the complement of the slope of this relationship. A comparison between the sum of λE_e , H_e , and G and R_{net} revealed that the annual energy balance at this site closed to within 20% (Table 2, Fig. 3).

Ecosystem λE was linearly related to R_{net} and accounted for approximately 30% of R_{net} (Table 2, Fig. 4A). The relationship between λE_e and R_{net} was significantly different between the 2 years (slope $p = 0.04$, intercept $p < 0.0001$). Ecosystem sensible heat flux (H_e) was also linearly related to R_{net} , and, on average, accounted for about 40% of R_{net} . This relationship did not vary between the two measurement years (Table 2, Fig. 4B).

Bimodal patterns were observed each year in time series of λE_e and H_e standardized to $R_{\text{net}} = 500 \text{ W}\cdot\text{m}^{-2}$ (Figs. 2A and 2B). A minor peak in standardized λE_e occurred in April, and a major peak occurred in September of each year. A minor trough occurred in June and July 2001, and a major trough occurred each January. The September peaks coincided with maximum LAI in each year, while each trough was associated with a major pulse of litterfall (Fig. 2D). Trends in standardized H_e were generally complementary to variation in standardized λE_e (Fig. 2B).

The partitioning of R_{net} to λE_e varied with both VPD and soil moisture (Fig. 5). As VPD increased from 0.00 to 0.75 kPa, the proportion of R_{net} dissipated as λE_e increased linearly from about 17% to 30%. Under dry soil conditions (θ at 10 cm depth $< 6\%$, soil water potential < -0.45 MPa), $\lambda E_e/R_{\text{net}}$ remained steady at 0.30 until VPD reached

Fig. 3. Annual energy balance for the University of Florida's Austin Cary Memorial Forest during October 2000 – May 2002. For clarity, a 15% random sample of the data points is plotted. See Table 2 for corresponding equations and statistics.



2.0 kPa, at which point the ratio began declining. Under wet soil conditions, $\lambda E_e/R_{net}$ increased linearly to 0.40 at a VPD of 1.25 kPa and then remained relatively constant. Weekly non-light-limited g_c (photosynthetically active photon flux density $>1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was positively but weakly correlated with θ ($g_c = 0.003 + 0.0316\theta$; $R^2 = 0.21$).

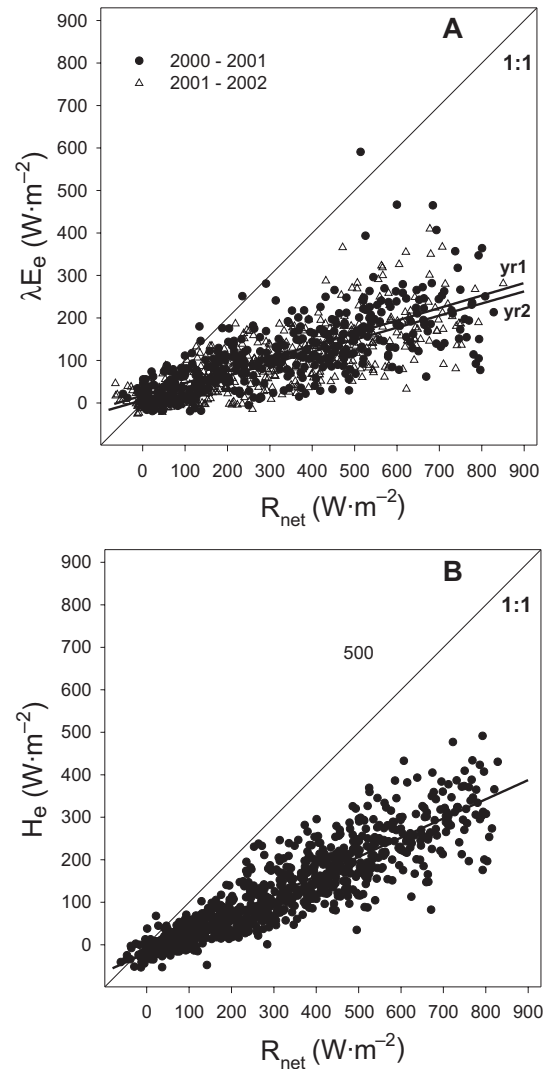
Diurnal patterns of ecosystem and understory λE and H in winter months (December and January) and summer months (July and August) highlighted seasonal shifts in energy partitioning (Fig. 6). In December and January, H_e dominated ecosystem energy balance, with mean midday values of $175 \text{ W}\cdot\text{m}^{-2}$, almost twice as large as λE_e (Fig. 6A). In contrast, mean λE_e and H_e remained almost equal throughout the day in July and August (Fig. 6B). Understory energy partitioning was much less variable over seasons, with λE_u and H_u remaining approximately equal throughout the day in both summer and winter months (Fig. 6).

Understory (understory vegetation plus litter layer and soil) latent energy (λE_u) and sensible heat (H_u) fluxes were a significant proportion of λE_e and H_e (Figs. 6 and 7). On an annual basis, λE_u and H_u accounted for 45%–55% of whole-ecosystem fluxes (Table 2). Maximum half-hourly λE_u and H_u were approximately 200 and 300 $\text{W}\cdot\text{m}^{-2}$, respectively. There was a major contrast in the proportion of λE_e accounted for by λE_u in midsummer (July and August) versus midwinter (December and January). In midwinter λE_u dominated λE_e , with understory latent heat loss accounting for 75% to almost 100% of ecosystem water loss at some points during the diurnal cycle (Fig. 6A). During midsummer, λE_u accounted for about 50% of λE_e throughout most of the day (Fig. 6B). The proportion of H_e accounted for by H_u remained steady throughout the year (Fig. 6).

Conductances and ET modeling

We used a screened subset of the eddy-covariance data to investigate “typical” variation in canopy conductance (g_c) with environmental drivers, and to create a model for filling

Fig. 4. (A) The relationship between net radiation (R_{net}) and ecosystem latent energy flux (λE_e) for 2000–2001 (yr1) and 2001–2002 (yr2). The slopes and intercepts were significantly different between years. (B) The relationship between R_{net} and ecosystem sensible heat (H_e) for all data pooled over both years. There was no significant difference in this relationship between years. For clarity, a 10% random sample of the data points is plotted. See Table 2 for corresponding equations.



in missing values from the eddy-covariance time series (Table 3). Aerodynamic conductance (g_a) in this data set ranged from 0.02 to $0.33 \text{ m}\cdot\text{s}^{-1}$ and had a weak linear relationship with u_z (Table 3).

Canopy conductance (g_c) was highly variable, but declined nonlinearly from 0.048 to $0.001 \text{ m}\cdot\text{s}^{-1}$ with increasing VPD (Table 3). Maximum canopy conductance, the value of g_c that would be expected without VPD limitations, increased linearly with R_{net} (Table 3). Evapotranspiration estimated by substituting the modeled g_c values into the Penman–Monteith equation agreed well with eddy-covariance results for a validation data subset ($R^2 = 0.61$, $p < 0.0001$, $n = 1657$). A sensitivity analysis revealed that annual ET estimates varied by less than 2% when the gap-filling model parameters (eq. 2) were individually changed by $\pm 10\%$.

Fig. 5. Relationship between ecosystem latent energy flux (λE_c) normalized by net radiation (R_{net}) and vapor pressure deficit for dry soil conditions (volumetric soil water content (SWC) <6%) and moist soil condition (SWC >6%).

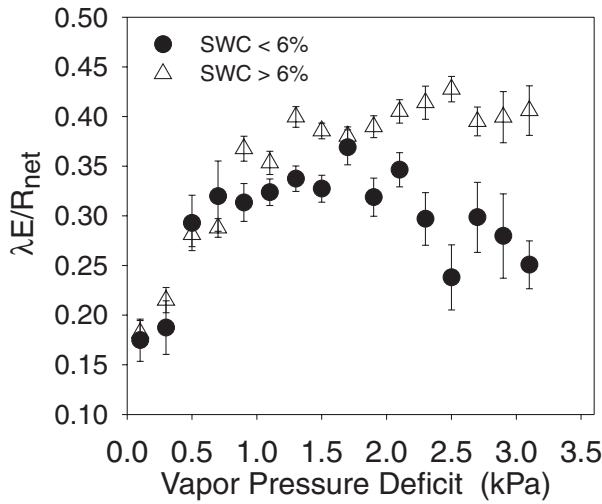


Fig. 6. Diurnal course of ecosystem and understory energy flux components for (A) midwinter months (December and January) and (B) midsummer months (July and August).

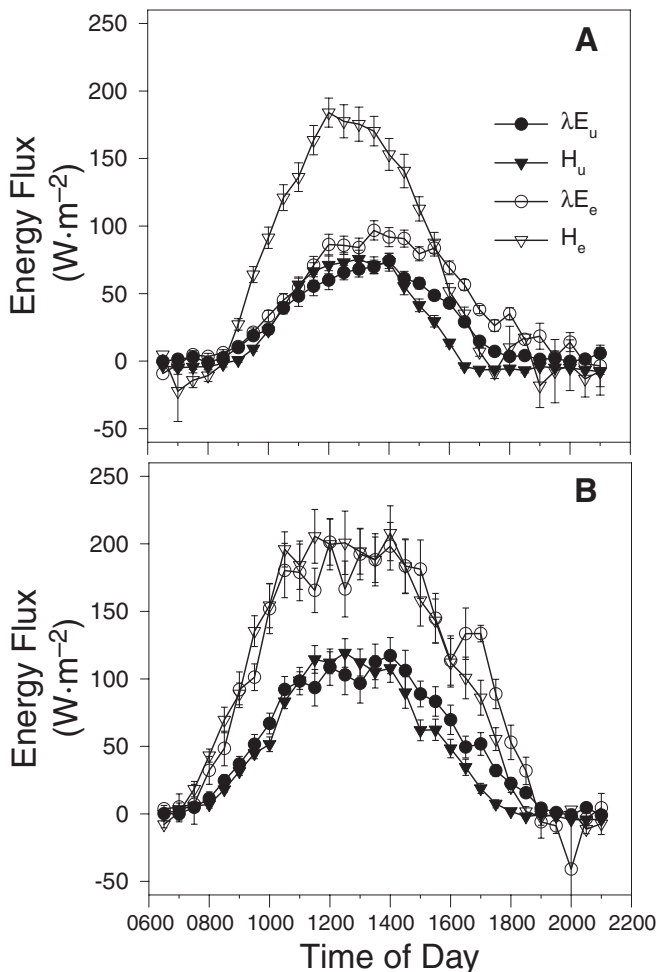
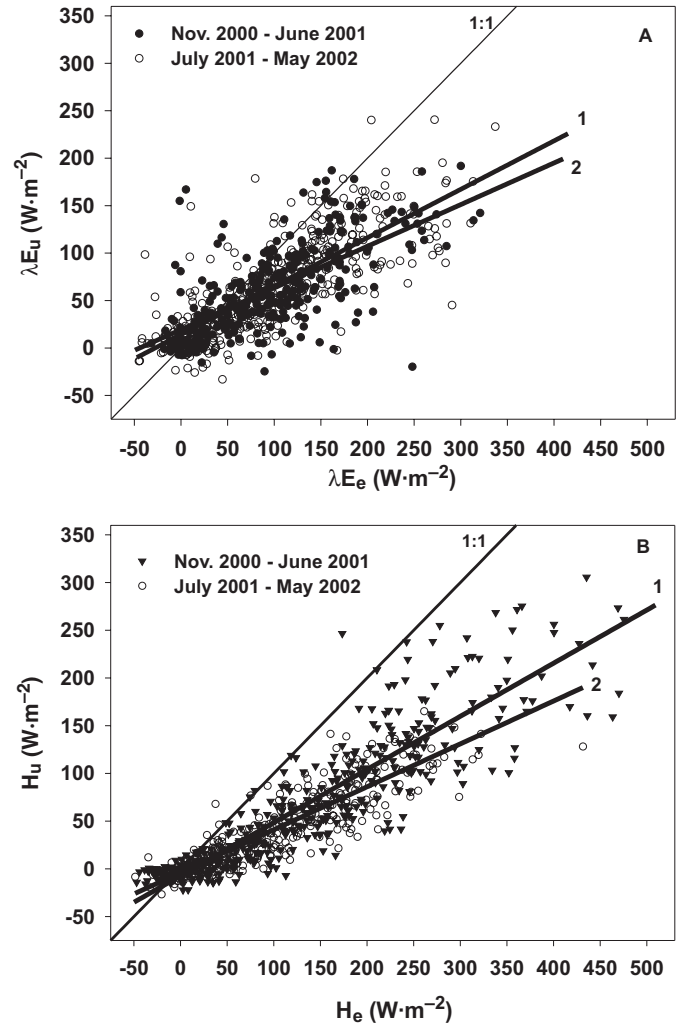


Fig. 7. Proportion of ecosystem latent energy (λE_c) and sensible heat (H_c) accounted for by the understory latent energy (λE_u) (A) and sensible heat (H_u) (B) for November 2000 – June 2001 (1, closed symbols) and July 2001 – May 2002 (2, open symbols). For clarity, a 20% random sample of the data points is plotted. See Table 2 for corresponding equations and statistics.



The mean value of the decoupling coefficient Ω varied monthly throughout the study period, ranging between 0.07 and 0.22 (Fig. 2C), indicating strong coupling or stomatal control of transpiration. Variation in Ω followed fluctuations in the watertable depth (Fig. 2E). Monthly mean Ω was positively but weakly correlated with θ at 10 cm depth ($\Omega = 0.05 + 0.966\theta$; $R^2 = 0.23$, data not shown).

Precipitation, evapotranspiration, and canopy interception

Total precipitation (P) was 956 and 811 mm during the first and second years of the study, respectively, with approximately 60% falling from July to October each year. Annual evapotranspiration (ET) was estimated to be 832 and 676 mm for the 2 years. Throughfall (TF) was measured during the first year and the sum of TF plus stemflow (SF) was strongly related to P ($TF + SF = 0.82P - 0.1897$; $R^2 = 0.99$, $p < 0.0001$). This relationship can also be expressed in terms of canopy interception loss ($I = 0.1761P + 0.1897$; $R^2 =$

Table 3. Equations defining the relationship between aerodynamic conductance (g_a) and horizontal wind speed (u_z), and functions for modeling bulk canopy conductance (g_c), where predicted $\hat{g}_c = f(\text{VPD}) \times f(R_{\text{net}})$.

	Equation	R^2	p value	n
Aerodynamic conductance	$g_a = 0.033u_z - 0.061$	0.22	<0.0001	4599
VPD function ^a	$f(\text{VPD}) = e^{(-0.7727\text{VPD})}$	—	—	301
R_{net} function	$f(R_{\text{net}}) = 3 \times 10^{-5}R_{\text{net}} + 0.0021$	0.5	<0.0001	2933

^aVPD, vapor pressure deficit; R_{net} , net radiation. This function was fitted through the top 10% of the data set to define the upper boundary rather than to describe the mean response, and therefore regression statistics are not reported.

0.86, $p < 0.0001$), where the intercept represents the canopy storage capacity in millimetres. Annual I for this stand was estimated to be 205 mm for year 1 and, by applying the same relationship, 177 mm for year 2.

Over the course of the study, mean daily ET was approximately 2.7 and 1.3 mm·day⁻¹ during summer (July–September) and winter (December–February), respectively. Mean hourly ET peaked at 0.32 mm·h⁻¹ during the summer of 2000 and 0.29 mm·h⁻¹ during the summer of 2001. The mean diurnal course of ET during the summer of the second year was asymmetrical, with a distinct midafternoon depression. The diurnal course of ET during the winter of both years was symmetrical, occurring over a 12-h period and peaking at 0.23 mm·h⁻¹ at 1300 hours. Weekly ET tracked seasonal fluctuation in R_{net} more closely than did LAI or environmental conditions. There did not appear to be a watertable threshold below which ET rates were markedly reduced, yet when λE was normalized by R_{net} , it did tend to decrease over time as the watertable continued to decline over the study period (Fig. 2).

Discussion

During the study, Florida was experiencing a “100-year drought”, with annual precipitation falling about 30% below long-term averages. Typically, pines in these ecosystems shed most of their needles in the mid to late fall, with a much smaller needlefall peak in May to June (e.g., Dalla-Tea and Jokela 1991; Gholz et al. 1991). However, up to half of the needlefall occurred in May–June during this study, with only about a quarter during the normal fall period. The premature needlefall caused summer LAI to be lower than usual and the seasonal range to be consequently dampened (about 30% compared with 40% in studies from wetter years, Gholz et al. 1991). Within-year variation in ET and energy exchange for other local ecosystems are closely linked to LAI (Liu 1998; Liu et al. 1998; Gholz and Clark 2002), which suggests that seasonal fluctuations over time in forests in the region may be high as they experience and then recover from periodic droughts.

Over the study period, mean albedo was 0.23, which is at the low end of the range reported for other conifer forests (Jarvis et al. 1976; Baldocchi and Vogel 1996). This value is higher than the 0.18 reported for nearby closed-canopy plantations (Gholz and Clark 2002). In fact, it is closer to that of a nearby 2-year-old stand (Gholz and Clark 2002), probably because of the relatively low canopy LAI and greater radiation interception by understory vegetation (which is similar to that regrowing in the understory of the 2-year-old stand).

The degree of energy budget closure is one way to assess the accuracy of component measurements in energy-balance studies. If measurements are taken without error, the sum of the energy dissipation terms (λE_e , H_e , and G) should equal net energy input (R_{net}), if it is assumed that energy storage in canopy air or biomass is negligible. On average, summed measurements of λE_e , H_e , and G in our study were about 20% lower than R_{net} (Table 2, Fig. 3). Similar departures from full energy budget closure were found in a naturally regenerated, semi-arid ponderosa pine (*Pinus ponderosa*) forest in Oregon (Anthoni et al. 1999), which also has an open canopy. While the 20% departure from closure is of similar magnitude to the potential error of measurement for Q7 R_{net} sensors ($\pm 20\%$, Twine et al. 2000), it is also possible that the position of the R_{net} sensor, 8 m above the mean canopy height, may not have been high enough to obtain a representative spatial characterization of R_{net} for the entire flux footprint area. Additional error in our hourly flux estimates may have occurred because we did not measure heat storage in the canopy air or biomass, which can approach 100 W·m⁻² under some midday conditions (Baldocchi and Vogel 1997).

Comparisons of λE and H between this ecosystem and other pine forests suggest similarities in the partitioning of net radiation across greatly contrasting environments. For example, a ponderosa pine forest in Oregon (Anthoni et al. 1999), a maritime pine (*Pinus pinaster*) forest in Portugal (Berbigier et al. 1996), a Scots pine (*Pinus sylvestris*) forest in Siberia (Kelliher et al. 1998), and a boreal jack pine (*Pinus banksiana*) forest in Saskatchewan (Baldocchi and Vogel 1996) all utilized 27%–36% of R_{net} for λE_e , which is similar to both the naturally regenerated stand in this study as well as the adjacent pine plantations (Table 4). The relatively low partitioning of available energy to λE_e is typical of pine forests, which generally have low LAI and low leaf-level stomatal conductance, in contrast to many temperate broad-leaved forests, which tend to have higher LAI and leaf-level stomatal conductance. As a result, many temperate broadleaf forests partition 70% or more of R_{net} to λE_e (Baldocchi and Vogel 1996; Schmid et al. 2000; Wilson et al. 2002).

Comparing the local Florida pine stands with contrasting management histories indicates that the ACMF stand and the plantations both utilized similar amounts of R_{net} for λE_e . At an R_{net} of 500 W·m⁻², λE_e in the current study was 158 W·m⁻² (averaged over the 2 years) compared with 164 W·m⁻² in surrounding plantation stands (Gholz and Clark 2002). However, smaller seasonal differences in λE_e were observed for the ACMF in comparison with the closed-canopy plantations. For example, summertime λE (normalized to $R_{\text{net}} = 500 \text{ W}\cdot\text{m}^{-2}$)

Table 4. Water vapor exchange for present study and other selected sites.

Forest type	LAI (all-sided)	Stems-ha ⁻¹	λE_e (% of R_{net})	λE_u (% of λE_e)	Mean ET (mm-day ⁻¹)	Reference
Florida pine flatwoods						
Naturally regenerated, summer	3.4	325	33	50–60	2.7	This study
Naturally regenerated, winter	2.6	325	28	70–85	1.3	This study
<i>Pinus elliotii</i> plantation						
Rotation-aged, summer	6.6	1300	38	—	3.6	Gholz and Clark 2002
Rotation-aged, winter	4.0	1300	27	—	2.0	Gholz and Clark 2002
<i>Pinus taeda</i> plantation, winter ^a	6.9	1150	—	—	1.8	Martin 2000
<i>Pinus banksiana</i>	4.0	1875	36	10–40	0.5–2.5	Baldocchi and Vogel 1996, 1997
<i>Pinus ponderosa</i>	3.2	620	—	44 (early spring), 22–33 (summer)	~1.6–1.7	Anthoni et al. 1999; Law et al. 2000
<i>Pinus pinaster</i>	—	300	31	15	2.1	Berbigier et al. 1996
Siberian <i>Pinus sylvestris</i>	4.4	290	30	54	—	Kelliher et al. 1998
Temperate deciduous	9.8	—	77	5	—	Baldocchi and Vogel 1996

Note: “—” indicates that data are not available. LAI, leaf area index; λE_e , ecosystem latent energy flux; λE_u , understory latent energy flux; R_{net} , net radiation, ET, evapotranspiration.

^aSapflow measurements on overstory only.

in the plantation was 40% greater than wintertime λE , while the summertime λE for the ACMF was only about 25% greater than wintertime λE . The smaller range for the ACMF was likely due to drought effects on g_c , which would have been affected by reductions in both LAI and leaf-level stomatal conductance. Seasonal differences in standardized H_e for the plantations (11%) were similar to the seasonal range for the ACMF (12%–23%).

The relatively few studies that have quantified understory energy balance have shown substantial variation in the proportion of ecosystem energy flux contributed by the understory (Table 4; see also review by Black and Kelliher 1989). As might be expected, forests with sparse or no understory tend to have a smaller contribution of λE_u to λE_e than forests with well-developed understory vegetation. For example, of the Douglas-fir (*Pseudotsuga menziesii*) stands reviewed by Black and Kelliher (1989), those with “sparse” or no understory vegetation had $\lambda E_u/\lambda E_e$ ratios ranging from 0.03 to 0.21, versus 0.30 to 0.65 for stands with understory projected LAI of 1.0 to 3.0. The stand in the present study would probably fall into the latter category, with understory all-sided LAI of 0.9 to 1.2, and $\lambda E_u/\lambda E_e$ of about 0.50. To some extent, the relationships among overstory LAI, understory LAI, and $\lambda E_u/\lambda E_e$ may be homeostatic. For instance, Roberts (1983) suggested that similarities in annual evapotranspiration among forest stands in Europe with widely varying overstory LAI may be partially attributable to compensatory water loss from understory vegetation in stands with lower overstory LAI.

The $\lambda E_u/\lambda E_e$ ratio in the current study changed seasonally, with λE_u contributing as much as 85% of ecosystem λE in the winter and 50%–60% in the summer (Fig. 6). Studies in other open-canopy pine forests have also shown seasonal variation in $\lambda E_u/\lambda E_e$. The $\lambda E_u/\lambda E_e$ ratio in the ponderosa pine forest studied by Law et al. (2000) declined from 0.44 in spring to 0.22–0.33 in summer. They attributed this change to decreased soil evaporation from the sparsely vegetated understory as drought developed. In contrast, Black and Kelliher (1989) cited several studies in *Pinus* and *Pseudotsuga* for-

ests that demonstrated increases in $\lambda E_u/\lambda E_e$ with decreasing soil water availability (e.g., Tan et al. 1978; Roberts et al. 1980; Kelliher et al. 1986). Black and Kelliher (1989) attributed this phenomenon to differences between overstory and understory coupling. They hypothesized that the well-coupled forest overstories, with Ω approaching 0.0, have strong stomatal control of λE and thus show reduced λE under soil or atmospheric drought conditions that induce stomatal closure. In contrast, they postulate that understory vegetation in these stands tended to have higher Ω because of its short stature and exposure to low wind speeds, which resulted in λE_u being more responsive to R_{net} than to VPD (Jarvis and McNaughton 1986; Martin et al. 2001).

We did not estimate Ω for our understory because of the additional complexities and assumptions associated with those calculations, but it does not appear that $\lambda E_u/\lambda E_e$ in our stand responds to drought in the same way as it does in the stands described in Black and Kelliher (1989). We hypothesize that the decline in $\lambda E_u/\lambda E_e$ from winter to summer in the current study resulted primarily from increased overstory λE associated with elevated LAI during the summer, rather than from any differences between overstory and understory response to θ caused by differences between overstory and understory Ω . The fact that overstory tree LAI was correlated with mean monthly midday λE_e ($r = 0.44$, $p = 0.0481$) but not with λE_u ($r = 0.12$, $p = 0.6059$) supports this hypothesis.

The canopy water-holding capacity of 0.19 mm for the ACMF stand was much lower than the 0.42–0.50 mm for closed-canopy plantations (Liu 1998; Gholz and Clark 2002), reflecting the lower LAI of this stand. However, canopy interception was 20% of annual precipitation at the ACMF in both years, whereas interception was only 8% of precipitation for the plantation stands (Gholz and Clark 2002). The high interception but lower water-holding capacity for the natural stand is probably related to the much higher annual precipitation during the Gholz and Clark study. However, it is also likely that water intercepted during individual rain events evaporated more rapidly from the more exposed surfaces of the more open structured ACMF canopy.

Evapotranspiration has been estimated for numerous Florida flatwoods ecosystems using a range of techniques, including weighing lysimeters, mass balance models, sap flux gauges, soil moisture changes, and micrometeorology (Allen et al. 1982; Riekerk 1982, 1985, 1989; Golkin and Ewel 1984; Liu 1996; Liu et al. 1998; Gholz and Clark 2002). Allen et al. (1982) used the mass balance equation in computer simulations of ET for watersheds in south Florida that were at least 50% pine and estimated ET to be 70% of annual precipitation. Using weighing lysimeters, Riekerk (1982) found that annual ET accounted for 60%–90% of precipitation for young slash pine stands. Using a process based model, Liu (1996) estimated annual ET to be 783–876 mm-year⁻¹ for 1991–1993 for nearby slash pine stands that had similar maximum canopy LAI values (2.6) and somewhat higher stocking (544 stems-ha⁻¹) as compared with the ACMF forest. On a daily basis in the winter of 1997–1998, sap flux density measurements of a young managed flatwoods plantation revealed that for identical climate conditions, loblolly pine transpired 1.8 mm-day⁻¹, while slash pine transpired 1.5 mm-day⁻¹ (Martin 2000). Therefore, the ACMF annual ET estimates of 676–832 mm-year⁻¹ and daily ET estimates of 1.3–2.7 mm-day⁻¹ from this study compare well with previous pine flatwoods ET estimates made at various spatial and temporal scales and with very contrasting methodologies.

Although previous research in pine flatwoods forests in this region has suggested that soil or atmospheric drought seldom impacts tree physiological function (Nearby et al. 1990; McMurtrie et al. 1994; Teskey et al. 1994), the present study took place in two remarkably dry years, and the impacts on ecosystem function were evident. The effects of drought on energy partitioning were manifested in several ways. First, reduced canopy conductance in response to elevated VPD (presumably caused primarily by stomatal closure) resulted in moderation of the partitioning of radiation to λE as VPD increased, even when soils were relatively moist (Fig. 5). This response was modified as soils dried below 6% volumetric water content, with $\lambda E/R_{\text{net}}$ actually declining as VPD increased above 1.75 kPa (Fig. 5). This was a consequence of both an overall decline in g_c with drying soil and a probable increase in the sensitivity of g_c to VPD (Ewers et al. 2001). Finally, monthly patterns of radiation-normalized λE appeared to be sensitive to short-term reductions in LAI associated with drought-induced needlefall pulses (Fig. 2). While these responses are not unusual in terms of general forest drought effects (e.g., Irvine et al. 1998; Ewers et al. 2001), they are out of the ordinary for these flatwoods ecosystems, where soil water availability is seldom an issue because of the presence of a watertable within 1 m of the surface (Abrahamson and Hartnett 1990; Teskey et al. 1994). It is likely that the receding watertable during the course of this study (Fig. 2) induced or enhanced physiological responses to VPD and drying surface soil in this forest.

The Ω decoupling coefficient varied monthly and appeared to be closely tied to the depth of the watertable (Fig. 2). The decline in g_c as soils dried was a primary driver of monthly variation in Ω (data not shown). Ω is essentially an index of the ratio g_c/g_a (Jarvis and McNaughton 1986). Since g_a had no discernible seasonal trends, variation in g_c was the main determinant of changes in Ω in our study. Despite noticeable monthly variation in Ω , even the highest values were well

within the ranges reported for conifer forests, where low g_c and high g_a tends to be the norm, leading to strong control of ET by g_c and VPD (Jarvis and McNaughton 1986; Martin et al. 2001).

While variation in annual precipitation precludes strict comparison of the magnitude of annual ET between the ACMF stand and surrounding plantations, the proportions of precipitation consumed by the pine stands in the region are similar: 80%–86% for the ACMF and the 2-year-old stand, and 92%–113% for the closed-canopy plantations (Gholz and Clark 2002). In other words, annual ET for the various Florida pine systems seems to fluctuate with precipitation, while maintaining a relatively constant ET/P. This contrasts with a ponderosa pine forest in Oregon with annual precipitation of 595 and 188 mm during 2 years, which maintained similar annual ET of 430 and 400 mm, but where the ET/P ratios were 0.72 and 2.12 (Anthoni et al. 1999). One interpretation is that the Florida pines avoid drought by closing their stomata to regulate water loss, whereas the ponderosa pine tolerate droughts and maintain ET by accessing alternative water sources with deep taproots (Anthoni et al. 1999).

In conclusion, this naturally regenerated pine flatwoods ecosystem partitions net radiation into λE and H in proportions similar to those of other conifer forests. Local silvicultural practices affect canopy structure and hence the transfer of momentum from the atmosphere and albedo, and the partitioning of energy between λE and H . However, silviculture and stand age do not seem to affect annual ET as much as do fluctuations in annual precipitation. Clearly, the understory in the open-canopy stand in the present study plays a more significant role in ecosystem hydrology because of the greater understory LAI and enhanced penetration of radiation through the overstory canopy. For this reason, a priority for future research should be a better understanding of the hydrologic consequences of the frequent, low-intensity fires that characterize flatwoods managed under nonintensive silvicultural regimes, and which result in the removal and regrowth of the understory during each burning cycle.

Acknowledgements

This research was supported by the Biological and Environmental Research Program, US Department of Energy, through the Southeast Regional Center of the National Institute for Global Environmental Change; the NASA Land Cover and Land Use Change Program; and the University of Florida School of Forest Resources and Conservation. We also thank Ryan Atwood, Jose Luis Hierro, Jennifer Staiger, Jennifer Jacobs, and Julie Graves for their contributions to this work.

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