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Monsoonal influences on evapotranspiration of savanna vegetation of northern Australia

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Abstract Data from savannas of northern Australia are presented for net radiation, latent and sensible heat, ecosystem surface conductance (G_s) and stand water use for sites covering a latitudinal range of 5° or 700 km. Measurements were made at three locations of increasing distance from the northern coastline and represent high- (1,750 mm), medium- (890 mm) and low- (520 mm) rainfall sites. This rainfall gradient arises from the weakened monsoonal influence with distance inland. Data were coupled to seasonal estimates of leaf area index (LAI) for the tree and understorey strata. All parameters were measured at the seasonal extremes of late wet and dry seasons. During the wet season, daily rates of evapotranspiration were 3.1–3.6 mm day⁻¹ and were similar for all sites along the rainfall gradient and did not reflect site differences in annual rainfall. During the dry season, site differences were very apparent with evapotranspiration 2–18 times lower than wet season rates, the seasonal differences increasing with distance from coast and reduced annual rainfall. Due to low overstorey LAI, more than 80% of water vapour flux was attributed to the understorey. Seasonal differences in evapotranspiration were mostly due to reductions in understorey leaf area during the dry season. Water use of individual trees did not differ between the wet and dry seasons at any of the sites and stand water use was a simple function of tree density. G_s declined markedly during the dry season at all sites, and we conclude that the savanna water (and carbon) balance is largely determined by G_s and its re-

sponse to atmospheric and soil water content and by seasonal adjustments to canopy leaf area.

Keywords Eddy covariance · Tree water use · Surface conductance · Understorey evaporation · Leaf area index

Introduction

Evaporation is a fundamental process of terrestrial ecosystems and is particularly relevant to any study of seasonally water-limited ecosystems such as savanna. The relationship between water availability and savanna structure and dynamics has been a focus of savanna research over the last three decades (Eamus and Prior, in press). Savanna distribution is largely determined by plant available moisture (PAM) and plant available nutrient (PAN) (Hutley and Walker 1982; Ben-Shahar 1991; Scholes and Archer 1997). For savannas of northern Australia, the overriding determinant is PAM. While PANs and fire are also of significance, they are of secondary importance (Williams et al. 1996; Walker and Langridge 1997). In recent years, a number of studies have examined the interactions of savanna vegetation with the environment of northern Australia. These studies have been conducted at leaf (Duff et al. 1997; Fordyce et al. 1997; Myers et al. 1997; Prior et al. 1997a, 1997b), tree (O'Grady et al. 1999) and stand (Cook et al. 1998; Hutley et al. 2000) scales. Such studies have contributed significantly to our understanding of the interactions of plant communities with the tropical monsoonal environment. However, they have been conducted at the wettest end of the rainfall gradient and we have little knowledge of savanna function at drier, inland sites.

Environmental gradients have been used increasingly in ecophysiological and vegetation-atmosphere exchange studies (Shuttleworth 1994). Examples include the BOREAS study (Sellers et al. 1997), where an 800-km transect spanning the northern and southern edges of the Canadian boreal forest was used to quantify exchanges of radiation, water and CO₂ between the forest and lower

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atmosphere. In savanna ecosystems, previous broad-scale transect studies include the HAPEX-Sahel experiment (Goutorbe et al. 1994), the SALT transect (Leroux et al. 1994) and the Kalahari transect (Scholes and Parsons 1997; Ringrose et al. 1998). Similarly, for savanna ecosystems of northern Australia, the North Australian Tropical Transect (NATT) has been established (Egan and Williams 1996). This transect spans approximately 1,000 km and 7° latitude between Darwin and Tennant Creek, Northern Territory, Australia. Although changes in vegetation structure and composition along the NATT are well documented (Egan and Williams 1996; Williams et al. 1996; Ludwig et al. 1999b), attempts to determine the cause of such changes have poor success, because the scale of measurement (point measures of soil water content or clay content; e.g. Williams et al. 1996) and the scale of prediction (regional savanna structure) are so disparate. In this paper, we present a set of measurements made at a larger scale that will contribute to our understanding of savanna functioning over a large rainfall gradient.

At a regional scale, vegetation has significant influences on fluxes of moisture, heat, momentum and CO₂ from land surfaces. Most soil-vegetation atmosphere transfer models and atmospheric circulation models use prescribed boundary conditions (Hatton et al. 1997). However, sensitivity analyses have consistently shown the significance of spatial variation of surface features of vegetation such as leaf area index (LAI) and canopy conductance to simulated energy fluxes (Li and Avissar 1994). Values for these parameters are therefore vital for improved descriptions of land surface condition, and data of this type for northern Australia at this spatial scale do not currently exist. The aim of this study was to characterise surface energy balance, conductance, tree stand water use and vegetation structure at three savanna sites along a large rainfall gradient, during wet and dry conditions. We present such data and pose the following questions. What are the consequences of large reductions in annual rainfall to daily and seasonal patterns of energy balance and water use by savanna vegetation of northern Australia? To what extent does the dry season reduce canopy water use? What are the relative contributions of the soil, understorey and tree canopy to actual evapotranspiration in the wet and dry seasons? To answer these questions, high-, moderate- and low-rainfall NATT sites were chosen, each with vegetation representative of the region.

Materials and methods

NATT sites

We used three NATT sites which spanned a 700-km and 1,350-mm rainfall gradient. These sites were Howard Springs (high-annual-rainfall site, 1,750 mm per annum), Katherine (moderate-rainfall site, 870 mm per annum) and the most inland site, Newcastle Waters (low-rainfall site, 520 mm per annum). Soil type was similar at each site, removing the confounding influence of soil hydraulics on interpretations of vegetation water use. Soils were well drained with a surface texture commonly of sandy loam grading to sandy clays and clay sub-soils at depths greater than 1–1.5 m with a massive and earthy structure. At these depths, ferricrete boulders can occur in a matrix of mottled, heavy clays forming a duricrust of low permeability and variable depth. Rounded ferricrete gravels also occurred on the soil surface and throughout the profile, and are between 20 and 50% by volume.

Vegetation

The vegetation of the high-rainfall site, Howard Springs, approximately 35 km south-east of Darwin (12.5° S), consisted of a mosaic of eucalypt-dominated woodlands, open forests, closed forests (*sensu* Specht 1981), seasonally flooded swamps and wetlands. In the Howard River catchment, eucalypt open-forest dominates and all measurements were made in this community type. The overstorey was dominated by two evergreen species, *Eucalyptus tetrodonta* (F. Muell.) and *E. miniata* (Cunn. Ex Schauer) which form a canopy of about 50% cover and are 14–15 m in height. These two species account for approximately 80% of the tree basal area of 8–10 m² ha⁻¹ (O'Grady et al. 2000). Overstorey LAI varies seasonally due to the presence of a mid-stratum consisting of brevifoliate, semi- and fully deciduous tree species and typically ranges from 0.6 during the dry to 0.95 during the wet season (Table 1). The understorey consists of semi-deciduous and deciduous small trees and shrubs but was dominated by the C4 grass *Sorghum* spp. This grass senesces early in the dry season, and understorey LAI remained low throughout the dry season (approximately 0.02; Table 1).

The moderate-rainfall site, Katherine, approximately 360 km south of Darwin (14.7° S), was broadly similar, structurally and floristically, to the Howard Springs site. The main difference was a reduced abundance of mid-stratum tree species, which were replaced by smaller scattered shrubs. The overstorey was dominated by *E. umbonata* (DJ Carr and SGM Carr) and *E. tetrodonta* open forest with a mean canopy height of approximately 10–12 m and basal area of 7.5 m² ha⁻¹. This site represents the southern limit of *E. miniata* and while present at the site, its abundance was low. Overstorey LAI typically increased from 0.4 at the end of the dry season to 0.75 at the end of the wet season (Table 1). Understorey vegetation was also dominated by *Sorghum* spp. and shrubs were sparse.

Vegetation at the low-rainfall site, Newcastle Waters, approximately 720 km south of Howard Springs (17.07° S), differed significantly from Howard Springs and Katherine sites by being a low open woodland. The open overstorey consisted of *E. terminalis* (F. Muell.) and *E. capricornia* (D Carr and S Carr) and a thick understorey dominated by *Acacia* shrubs. Mean tree height was approximately 8 m with a basal area of 4.8 m² ha⁻¹ and an LAI of

Table 1 Overstorey, understorey and total leaf area index for the wet and dry season for each NATT site. Data for the wet season at Newcastle Waters from Hoogerwerf and van Wieringen (1999)

Site	Wet season			Dry season		
	Overstorey	Understorey	Total	Overstorey	Understorey	Total
Howard Springs	0.9	1.2	2.1	0.6	0.05	0.65
Katherine	0.75	0.5	1.25	0.42	0.05	0.47
Newcastle Waters	0.05	0.20	0.25	0.07	0.05	0.12

0.07, which changed little between the wet and dry season (Table 1). The dense understorey consisted of shrub species *Acacia lysiphloia* (F. Muell.), which grew to a maximum height of 2 m with *A. shirleyi* (Maiden) and *Sorghum* spp also present. Understorey LAI was much more seasonally dynamic than that of the trees and increased fourfold between seasons (Table 1).

Climate

Climate at the high- and moderate-rainfall sites (Howard Springs and Katherine) is wet-dry tropical, with a strong monsoonal influence and a predictable wet season occurring from December to March (Taylor and Tulloch 1985). This period accounts for approximately 95% mean annual rainfall (Fig. 1a). This is followed by an essentially rainless dry season, lasting from May to September/October. The months of October and November are transitional and characterised by increases in humidity and temperature, occasional thunderstorms and the onset of canopy flushing by many of the tree and shrub species (Williams et al. 1997). Annual totals of pan evaporation (E_{pan}) are high and for Darwin, Katherine and Newcastle Waters are 2,656, 2,279 and 2,789 mm respectively (Fig. 1b). In general, E_{pan} is relatively aseasonal compared to non-monsoonal climates of Australia (Linacre and Hobbs 1977) with maximal rates of approximately 8 mm day⁻¹ during September and October when solar inclination and solar radiation loads are largest (Vardavas 1987). Wet season rates of E_{pan} range from 5.5 to 6.5 mm day⁻¹ and are lower than dry season values due to increased cloud cover and vapour pressure. A more pronounced seasonality of E_{pan} is evident at the semi-arid Newcastle Waters site (Fig. 1).

Temperatures at the high- and moderate-rainfall sites vary little annually. Mean daily maximum temperatures at Darwin Airport (20 km from the Howard Springs field site) range from 30.4°C (July) to 33.1°C (October and November) and for Katherine from 30.4°C (June) to 37.8°C (October and November). Mean daily minimum temperatures at Howard Springs and Katherine are 19.3 and 12.8°C, respectively. Newcastle Waters experiences a slightly larger range of temperature, with a mean maximum of 38.7°C (November) dropping to a mean daily minimum of 11°C (June). Minimum temperatures can drop to less than 1°C during this month.

Measurements of water use

Actual evapotranspiration E_a (mm day⁻¹) comprises transpiration from vegetation plus soil evaporation and evaporation from canopies of intercepted water following rainfall. In this study, we used eddy covariance techniques to provide seasonal maximum and minimum rates of water vapour flux from savanna communities at the three sites. We also employed heat pulse techniques to determine the contribution of tree transpiration to total vapour flux. No measurements occurred immediately after rainfall, so canopy interception losses were zero. Understorey evaporation was assumed to be the difference between actual evapotranspiration and tree stand water use, as previously shown for the Howard Springs site (Hutley et al. 2000). At the Howard Springs site, wet season measurements were made during March 1998, with dry season measurements conducted during September and October 1998. For the Katherine and Newcastle Waters sites, late wet season measurement were made during March 1999 and late dry season measurements during September 1999. For wet season estimates, all sites received average or higher than average rainfalls the month prior to measurement and significant rainfall (40–60 mm) fell in the week prior to measurement.

Eddy covariance

Each site had adequate (~1 km) fetch in all directions with slopes of less than 1°. Measurements were conducted for 5 consecutive

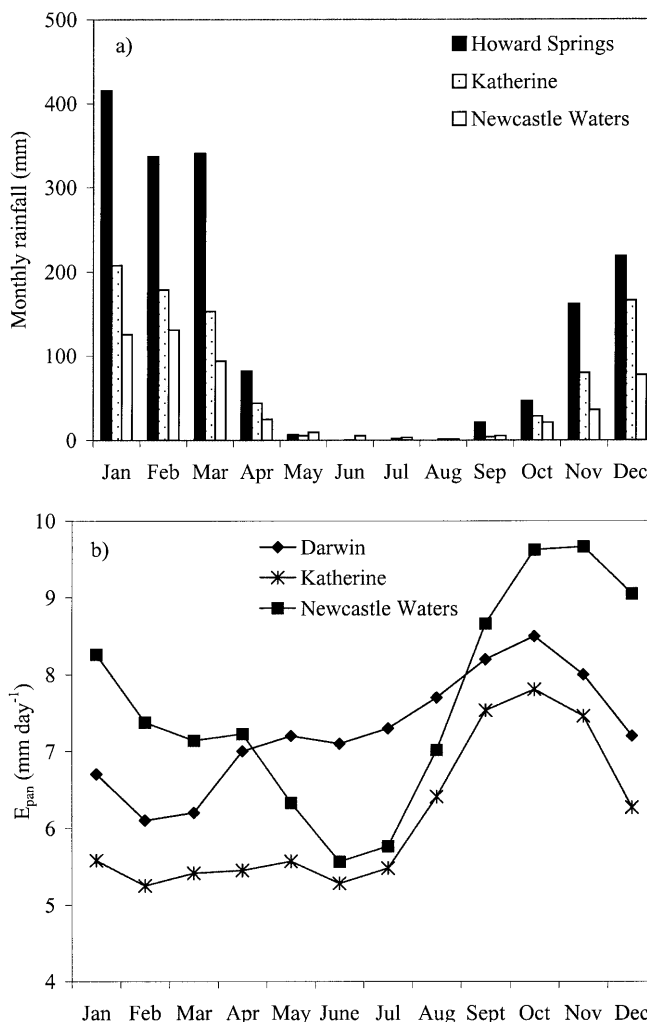


Fig. 1 Mean monthly rainfall (a) and mean daily pan evaporation (E_{pan}) (b) for Darwin Airport (20 km north-west of Howard Springs), Katherine and Newcastle Waters sites. Pan evaporation data for Darwin Airport and Katherine were supplied by the Bureau of Meteorology. E_{pan} data for Newcastle Waters are an interpolation generated by the 'Data Drill', Queensland Department of Natural Resources and Bureau of Meteorology (<http://www.dnr.qld.gov.au/silo/>, SILO site)

days at each location. Eddy covariance and associated instruments were mounted on a pole supported by a tower at a height of 18 m, except at Newcastle Waters, where instruments were installed at 16 m. We used a Campbell Scientific (Logan, Utah, USA) eddy covariance system, consisting of a three-dimensional sonic anemometer (model CSAT3) and a krypton hygrometer (model KH20) interfaced to a 21X datalogger. All data were collected at 10 Hz with latent energy (LE) and sensible heat flux (H) calculated at 30-min intervals. Corrections for oxygen absorption by the krypton hygrometer (Tanner et al. 1993), coordinate rotation and corrections accounting for air density changes (Webb et al. 1980) were applied to raw fluxes. For each day of measurement, 30-min LE estimates were integrated and expressed as evapotranspiration, E_a (mm day⁻¹).

Thirty-minute means of air temperature, relative humidity, wind speed and direction (model 03001-5; RM Young Wind Sentry) and net radiation, R_n (model Q7.1; Radiation and Energy Balance Systems, Seattle, Wash.) were made simultaneously at the same reference height as the eddy covariance instruments. Soil

heat flux was estimated using a combination of four soil heat flux plates (model HFT-3; Radiation and Energy Balance Systems) buried at 8 cm with an averaging soil thermocouple (model TC4V; Campbell Scientific) located at 2- and 6-cm depth in the soil. The heat flux plates were randomly located within a 10-m plot with mean flux calculated from the four plates. Soil samples were also taken for estimates of water content. The complete system provided data on all components of the forest energy balance, with the exception of biomass storage, which was assumed to be small on a diurnal basis.

Heat pulse and LAI measurements

Commercially available sapflow sensors (Greenspan Technology, Warwick, Queensland) were used to estimate heat pulse velocity. These velocities were scaled to tree water use using the weighted-averages technique of Hatton et al. (1990). The area of conducting wood and bark thickness were determined from cores taken from trees; sapwood was distinguished from heartwood by a distinct colour change. These wood cores were used to determine volumetric wood and water fractions and a wound width of 3.1 mm was used to correct velocity estimates. Five trees each of the two dominant eucalypt species at each location were instrumented for 5 days for each measurement period. At the Howard Springs site, individuals of *E. miniata* and *E. tetradonta* were instrumented; at Katherine, *E. umbonata* and *E. tetradonta* and at Newcastle Waters, *E. capricornia* and *E. terminalis*. For each instrumented tree, diameter at breast height (DBH) and leaf area were recorded. Leaf area was estimated using the Adelaide technique which involved estimating leaf area visually by counting the number of leaf modules on a tree (O'Grady et al. 2000). Reference modules were collected in the field and their total area was later determined using a Delta-T leaf area meter (Delta-T Devices, Cambridge, UK). Sap velocity was recorded at 15-min intervals and integrated to provide daily totals. These totals were regressed for each day against DBH (cm) and cross-sectional area (m²). At the Howard Springs and Katherine sites, these relationships were used to express tree water use on an areal basis in three permanent plots (30×30 m). Each plot was surveyed for tree DBH/basal area and leaf area. At Newcastle Waters, these relationships were determined for trees in a 1-ha plot. Plot water use was the sum of all trees within the plot divided by plot area to give area-averaged tree stand water use, E_t (mm day⁻¹). In addition, the plot data were used to calculate stem density per hectare.

At Howard Springs and Katherine sites, understory LAI was estimated by destructively sampling all green leaf area in seven 1 m² plots at three separate locations (21 plots for each site). The distance between locations was approximately 500 m. Leaf area was determined using a Delta-T leaf area meter. Plots containing large amounts of leaf material were sub-sampled and regressions between leaf area and leaf dry weight were developed for each species, with total plot leaf area estimated from leaf dry weights. At Newcastle Waters, the high density of *Acacia* shrubs did not permit direct measurement of LAI and the Adelaide technique was employed. Reference modules were defined for each shrub species in three 30×30 m plots. Leaf area was estimated by counting the number of leaf modules on all shrubs in the plot. Reference modules were collected in the field and their total area later determined.

Pre-dawn leaf water potential

Pre-dawn leaf water potential (ψ_{pd}) was measured using a Scholander-type pressure chamber (Soil Moisture Corp., Santa Barbara, Calif.) and was used as a surrogate of soil water availability (Crombie et al. 1988). For each site and season, leaf ψ_{pd} was measured between 6.30 and 7.00 a.m. on two randomly selected leaves on each of the trees instrumented with a sapflow logger. Data were analysed as a fixed, two-factor analysis of variance with the factors season and location. Species were not included as a factor in the analysis because each species at each location could not be replicated. However, differences in pre-dawn leaf water potential between species of similar phenological guilds within a site have been shown to be non-significant (Duff et al. 1997; Meinzer et al. 1999).

Results

Pre-dawn leaf water potential

Pre-dawn leaf water potentials (ψ_{pd}) for each site and season are given in Table 2. There were significant differences in pre-dawn leaf water potential between seasons and locations as well as a significant season by location interaction (season *df* 1,106, $F=870.2$, $P<0.01$; location *df* 2,106, $F=190.3$, $P<0.01$; season×location *df* 2,106, $F=129.7$, $P<0.01$). There were no differences between sites at the end of the wet season. However, by the end of the dry season, ψ_{pd} was significantly lower and all sites differed. Furthermore, seasonal differences increased with latitude (Table 2).

Energy balance

Fluxes of LE , H and R_n at the three sites are given for typical days at the end of the wet season, March 1999 (Fig. 2) and dry season, August 1998 (Fig. 3). Daily totals of LE have been integrated and converted to a depth equivalence of water in mm day⁻¹ and these are also given on the figures. Energy balance closure ranged from 5 to 15% when integrated over a day. Fluxes during the wet season describe typical diurnal patterns of sensible and latent heat transfer, with LE and H essentially following R_n . At Howard Springs, maximal mid-day fluxes of LE ranged from 400 to 480 W m⁻² during the wet season (Fig. 2). Typical mid-day fluxes of LE at the Katherine site were 350–400 W m⁻², with Newcastle Waters attaining similar rates to Howard Springs. During the dry season, rates of LE at Howard Springs followed a similar diurnal pattern to that of the wet season but maximal rates were 50–75% lower and never exceeded 250 W m⁻². Sensible heat, H , accounted for a larger fraction of R_n during

Table 2 Seasonal changes (means with SE in parentheses) in pre-dawn leaf water potentials (MPa) for dominant *Eucalyptus* tree species at the Howard Springs, Katherine and Newcastle Waters sites

	Howard Springs		Katherine		Newcastle Waters	
	<i>E. miniata</i>	<i>E. tetradonta</i>	<i>E. tetradonta</i>	<i>E. umbonata</i>	<i>E. capricornia</i>	<i>E. terminalis</i>
Wet	-0.23 (0.03)	-0.23 (0.14)	-0.09 (0.02)	-0.21 (0.02)	-0.26 (0.03)	-0.32 (0.05)
Dry	-0.42 (0.03)	-0.58 (0.04)	-1.14 (0.02)	-0.73 (0.04)	-2.23 (0.05)	-2.42 (0.30)

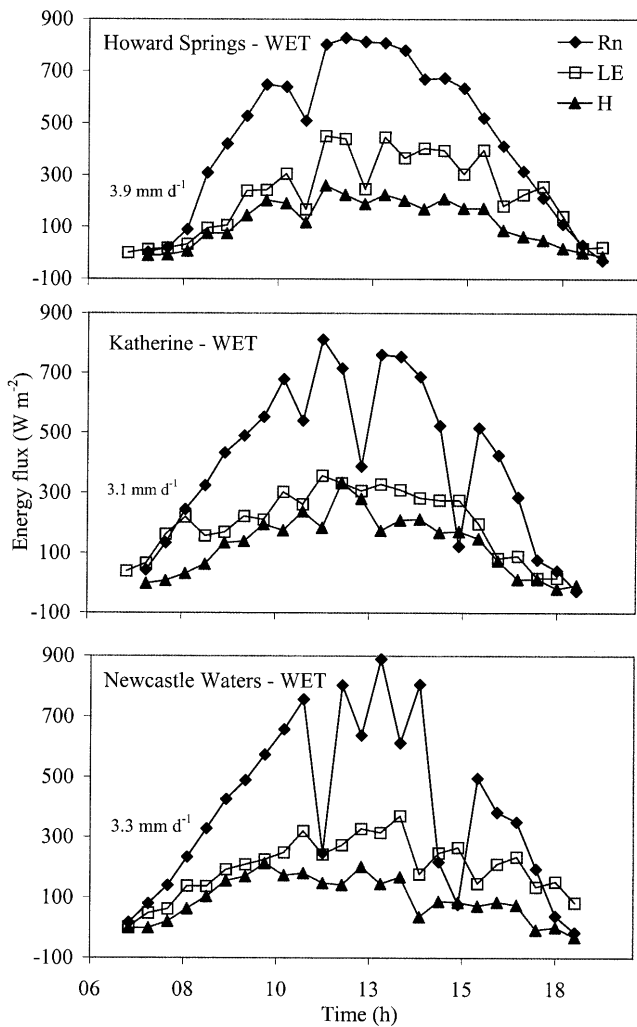


Fig. 2 Typical diurnal patterns of the energy balance components (Rn, LE, H) during the late wet season (March) for Howard Springs, Katherine and Newcastle Waters. Integrated daily totals of actual evapotranspiration (E_a) in millimetres are given on each plot. Time of day is local time

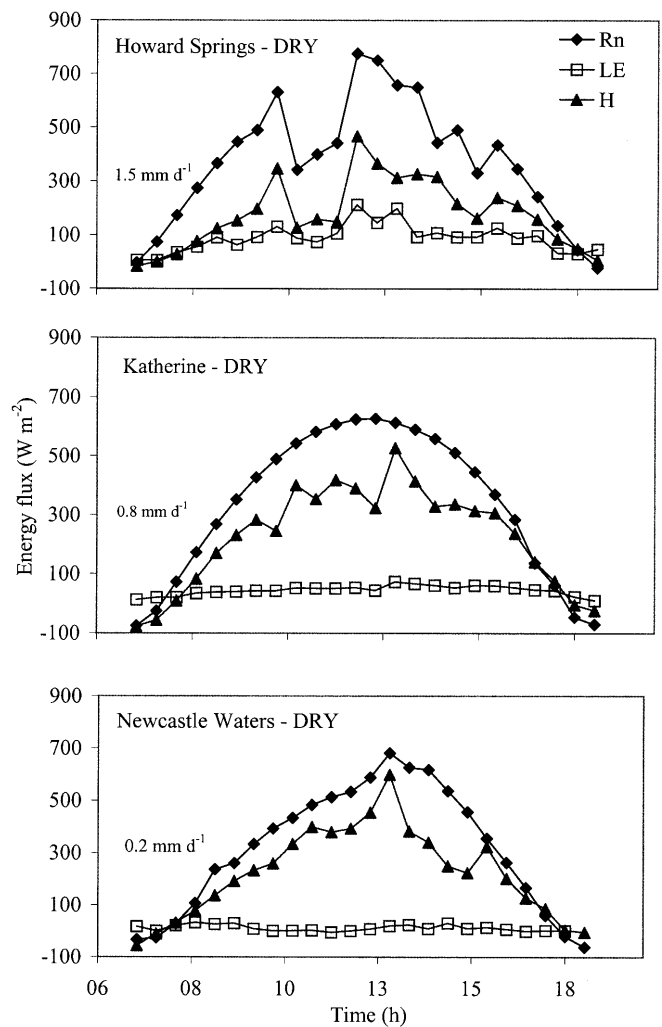


Fig. 3 Typical diurnal patterns of the energy balance components (Rn, LE, H) during the late dry season (September) for Howard Springs, Katherine and Newcastle Waters. Mean values of the daily totals of actual evapotranspiration (E_a) in millimetres are given on each plot. Time of day is local time

Table 3 The Bowen ratio, H/LE (β), decoupling coefficient (Ω), ecosystem surface (G_s) and aerodynamic (G_a) conductance ($\text{mol m}^{-2} \text{s}^{-1}$) for wet and dry season measurements for each NATT site. Values are means taken from half-hourly estimates for 11.00 a.m.

Parameter	Howard Springs		Katherine		Newcastle Waters	
	Wet	Dry	Wet	Dry	Wet	Dry
β	0.40 (0.02)	2.4 (0.11)	0.84 (0.03)	6.5 (0.26)	0.62 (0.02)	34.4 (4.0)
Ω	0.37 (0.09)	0.13 (0.04)	0.32 (0.07)	0.06 (0.01)	0.39 (0.09)	0.02 (0.02)
G_s	0.27 (0.11)	0.07 (0.05)	0.23 (0.09)	0.04 (0.01)	0.24 (0.08)	0.01 (0.01)
G_a	2.2 (0.3)	2.4 (0.1)	2.4 (0.44)	2.9 (0.45)	1.8 (0.7)	1.7 (0.7)
$E_t:E_a$	0.26	0.47	0.13	0.41	0.03	0.38
$E_u:E_a$	0.74	0.53	0.87	0.59	0.97	0.62

the dry season (Fig. 3). Similar patterns were also observed at Katherine, with dry season rates of LE significantly reduced and H dominating the surface energy balance. This dry season pattern was more extreme at Newcastle Waters, with H accounting for up to 90% of Rn

to 3.00 p.m. with the SEs given in parentheses. Seasonal changes to ratios of stand water use, E_t , and understorey evaporation, E_u to actual evapotranspiration, E_a , are also given for each NATT site

during some averaging periods with mid-day fluxes of LE less than 30 W m^{-2} . These seasonal changes in energy balance partitioning can be summarised by calculating the Bowen ratio ($H/LE=\beta$). The ratio was calculated using the 30-min estimates of LE and H between 11.00 a.m.

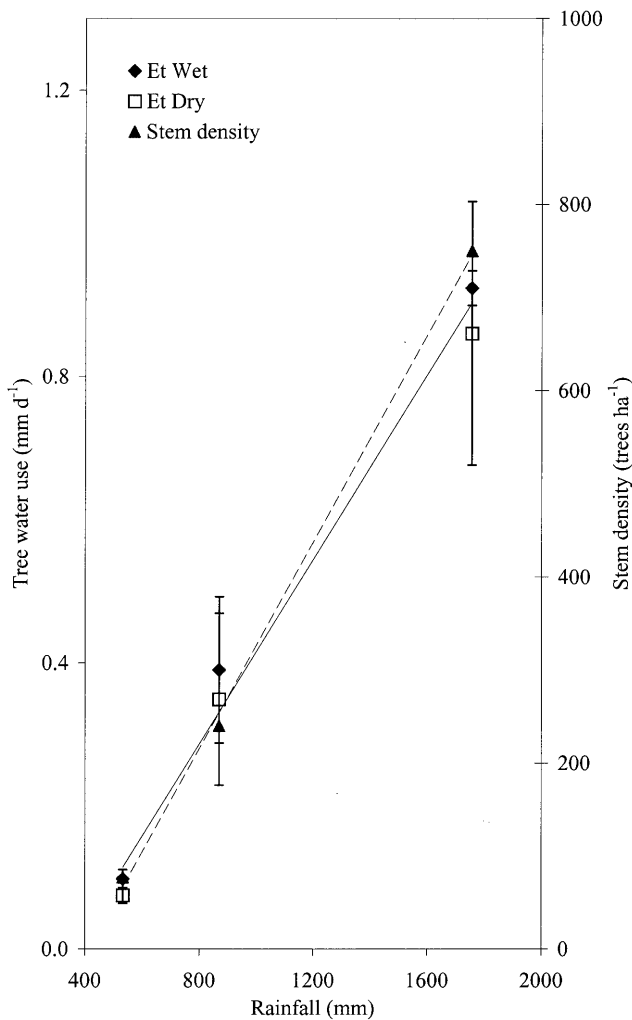


Fig. 4 Patterns of stand water use, E_t (mm day^{-1}), for the Howard Springs, Katherine and Newcastle Waters sites, plotted against annual rainfall (solid line). Also shown is tree density (stems ha^{-1}) for each site (dashed line)

and 3.00 p.m. for each day at each site, and mean values are given in Table 3. The Bowen ratio increased in the dry season compared to the wet season for all sites, and the ratio of dry to wet season β increased with increasing aridity.

Water use

Sapflow ($\text{m}^3 \text{day}^{-1}$) was correlated with DBH (m) at all sites. The relationship was identical for trees at the Howard Springs and Katherine sites and was described by a power curve, $y=0.550x^{2.042}$ ($R^2=0.85$). Trees at the Newcastle Waters site differed, with sapflow rates significantly lower per unit tree size. This relationship was described by $y=0.097x^{1.6486}$ ($R^2=0.59$), which has a lower slope than the curve for the Howard Springs and Katherine sites. There was no seasonal difference in these relationships at any of the sites and the lines of best fit have been calculat-

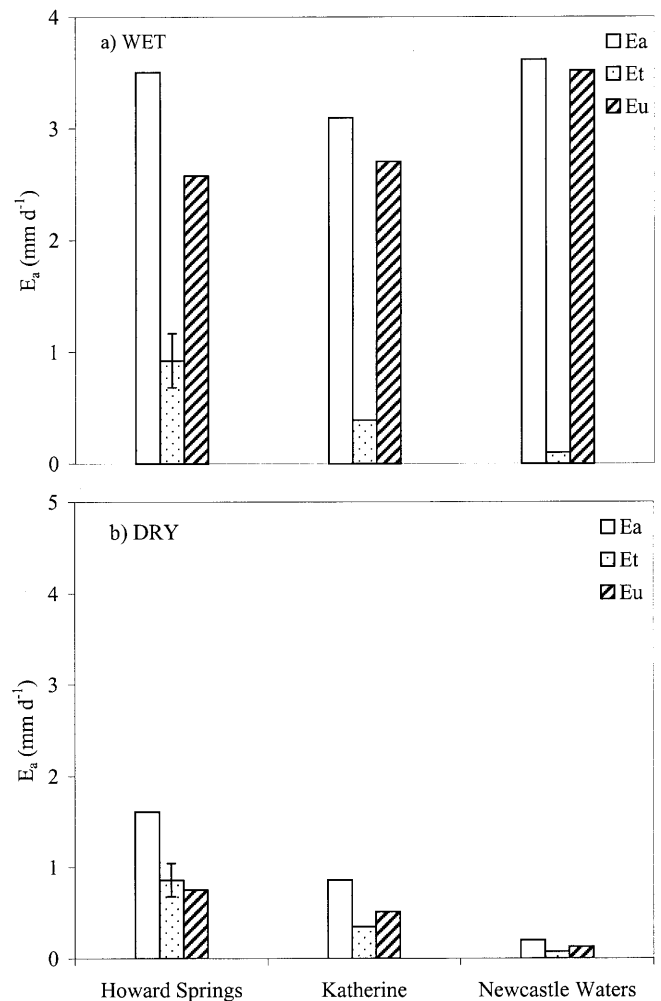


Fig. 5 Daily actual evapotranspiration (E_a) partitioned into stand water use (E_t) and understorey evaporation (E_u) for Howard Springs, Katherine and Newcastle Waters sites during the wet (a) and dry (b) season. Understorey evaporation was calculated as the difference between E_a and E_t

ed from pooled wet and dry season values. Sapflow data were scaled to stand water use, E_t , and these data are plotted against rainfall in Fig. 4. Stand water use increased with increasing annual rainfall and tree density and ranged from a low of 0.08 mm day^{-1} at Newcastle Waters during the dry season to a wet season maximum of 0.9 mm day^{-1} at the high-rainfall Howard Springs site. There was no significant difference between wet and dry season values of E_t at any site (Fig. 4).

Mean daily rates of actual evapotranspiration (E_a) and stand water use (E_t) are given for the three sites for wet (Fig. 5a) and dry (Fig. 5b) seasons. Also shown on Fig. 5 is understorey evapotranspiration, E_u , for each site. Previous work at the Howard Springs site has demonstrated that understorey evaporation can be approximated by subtracting E_t from E_a (Hutley et al. 2000). During wet season measurements, all sites had recent rainfall (approximately 50 mm) and soil moisture contents of the upper 10 cm were high, ranging from $0.26 \text{ m}^3 \text{ m}^{-3}$ at

Newcastle Waters to $0.31 \text{ m}^3 \text{ m}^{-3}$ at Howard Springs. Wet season evapotranspiration was similar at all three sites with mean values of E_a ranging from 3 to 3.6 mm day^{-1} , with E_u contributing $>75\%$ of this flux at all sites (Fig. 5a). The ratio of E_a to Penman potential evaporation, E_o , was similar at each site, being 0.62, 0.57 and 0.61 for the Howard Springs, Katherine and Newcastle Waters sites, respectively. At the low-rainfall site, Newcastle Waters, tree LAI was low (0.05) and more than 90% of the total wet season vapour flux was from E_u (Fig. 5a, Table 3).

The ratio $E_u:E_a$ decreased from Howard Springs to Newcastle Waters with the contribution of E_u increasing (Table 3). During the dry season, mean rates of E_a at Howard Springs were less than 50% those of the wet season. The ratio of wet:dry E_a increased from Howard Springs to Newcastle Waters, such that at Newcastle Waters, dry season E_a was 0.2 mm day^{-1} , or 5% of the wet season value.

For each site, ecosystem surface (G_s) and aerodynamic (G_a) conductance was calculated from an inversion of the Penman-Monteith equation using measured values of E_a , R_n , vapour pressure deficit (VPD) and horizontal wind speed. Miranda et al. (1997) and Gash et al. (1991) provide examples of this technique for savanna vegetation. Using these bulk conductances, the surface decoupling coefficient, Ω , was calculated (Jarvis and McNaughton 1986). Values of Ω , G_s and β are given for each site and season in Table 3. Mean mid-day values of G_a for all sites ranged from 2.4 to $1.8 \text{ mol m}^{-2} \text{ s}^{-1}$ with the maximum ranging from $5.3 \text{ mol m}^{-2} \text{ s}^{-1}$ at Howard Springs to $2.4 \text{ mol m}^{-2} \text{ s}^{-1}$ at Newcastle Waters, reflecting canopy height of each site. Wet season values of Ω were similar at each site, ranging from 0.3 to 0.4. During the dry season, values were reduced and large site differences become apparent. Similar patterns and declines were evident for G_s (Table 3).

Discussion

E_u as a function of site and season

The data presented describe maximum and minimum values for evapotranspiration from savanna vegetation over a 700-km-long rainfall gradient. In terms of biomass, the savannas of northern Australia are dominated by *Eucalyptus* species which form an overstorey canopy with an LAI typically less than 1. This open structure results in a well-ventilated canopy air space with high penetration of solar radiation. Evapotranspiration is dominated by water loss arising from the understorey, E_u . This flux is significantly larger than the contribution from E_t and the observed seasonality of E_a was largely due to shifts in understorey LAI and hence E_u in response to the large seasonal decline in upper-soil water content. At the high- and moderate-rainfall sites, Howard Springs and Katherine, high rates of wet season E_u are due to transpiration of annual C4 grasses (dominated by

Sorghum spp.), which senesce immediately at the end of the wet season. The absence of *Sorghum* spp. from the understorey is largely responsible for the marked decline in E_u and E_a over the wet-dry cycle.

Rainfall decreases with distance from the coast as the monsoonal influence weakens, and tree density, height and LAI decline. Over this gradient, perennial, as opposed to annual, grass species increase in abundance (Ludwig et al. 1999b). *Acacia* species also become more dominant (Bowman and Connors 1996). At the Newcastle Waters site, *Acacia* shrubs formed a large proportion of surface cover which persisted on site all year. By the late dry season, they exhibited very low rates of LE, G_s and a greatly reduced LAI (Fig. 5, Table 1). However, this changed rapidly following rainfall. Two weeks prior to our wet season measurements, Newcastle Waters received 60 mm of rainfall, a significant event for this site, resulting in flushing of new foliage of the understorey *Acacia* species. Under these conditions of non-limiting soil water availability and high ψ_{pd} (Table 2), rates of latent heat flux at the Newcastle Waters site were equivalent to the coastal eucalypt-dominated open-forest savanna of Howard Springs (Figs. 2, 5), despite a total LAI that was fivefold lower. Given the high cover of *Acacia* at the Newcastle Waters site, wet season E_u , and therefore E_a , would be largely due to transpiration from the *Acacia* shrubs. Rapid changes in E_u are characteristically observed in semi-arid savanna following rainfall (Gash et al. 1991; Stannard et al. 1994; Allen and Grime 1995; Ludwig and Tongway 1995). In such systems, E_a is storm driven and strongly related to time since rainfall (Tunstall and Connor 1981).

Tree and stand water use, season and location

In contrast to the understorey vegetation, stand water use (E_t) was constant at all sites, all year (Fig. 5), despite pronounced seasonality of soil and atmospheric water content. At the high- and medium-rainfall sites of Howard Springs and Katherine, rainfall is largely derived from monsoonal weather systems such as tropical depressions (Jackson 1988). Trees from these sites are from a different bioclimatic and biogeographic region (Bowman et al. 1988; Egan and Williams 1996) compared to trees from the Newcastle Waters site. This is reflected in patterns of tree water use, with higher rates of sapflow per unit tree size (DBH) at the wetter, more monsoonal sites of Howard Springs and Katherine than the more arid Newcastle Waters site. However, the large decline in scaled tree water use, E_t , along the NATT was simply due to declines in the tree density able to exploit available soil water at a particular rainfall (Fig. 4) and was not due to large reductions in rates of sap flow of individual trees at each site. A similar pattern of stand water use has been described by Meinzer et al. (1999) for Brazilian cerrado species, where the use of precipitation by woody species was also simply related to density. This is an important finding, because it suggests that re-

gional estimates of stand water use can be based on simple allometric measures, such as stand density, basal or sapwood area (O'Grady et al. 1999).

The seasonally constant E_t suggests that trees may be extracting moisture from the sub-soil (>3 m) and possibly the capillary fringe of the water table as it receded over the dry season. The wet season is typically of 185 and 150 days duration at Howard Springs and Katherine, respectively (G. Cook, personal communication). Soil water storage is in excess of plant requirement for much of this time and the well-drained, sandy soils of the region recharge the sub-soil (>3 m) and surface aquifers in excess of 10% of annual rainfall (Cook et al. 1998). Excavation of tree roots at Howard Springs revealed an extensive development of root biomass in the sandy loams of the top 1 m of soil with some larger-diameter roots (>3 cm) of mature trees able to extend through weaknesses in the duricrust and access water stored in the heavier clay sediments of the sub-soil (Hutley et al. 2000). Roots reached depths of approximately 10 m, the depth of the water table at the end of the dry season (Cook et al. 1998), although the amount of root material at such depths was very low, and extraction is likely to be dominated by the upper 3 m of soil. Given the similarities in monsoon-dominated rainfall, tree species, soil type and parent material, such patterns are likely to be similar at Katherine. Walker and Langridge (1997) found that for 20 savanna sites in the Northern Territory, Queensland and New South Wales, the best predictor of savanna woody biomass was sub-soil water content, underlining the importance of this store in supplying water through the dry season.

Aseasonal patterns of E_t at the Newcastle Waters site are more difficult to explain, given the large decrease in Ψ_{pd} during the dry season (Table 2). At this site, access to a deep water supply is unlikely, given the low rainfall and a short wet season of less than 100 days. Deep drainage and recharge to groundwater or storage of significant soil water reserves will only occur during extreme wet seasons and is generally not a feature of the water balance of such dry savannas (Scholes and Walker 1993; Allen and Grime 1995). At Newcastle Waters, 75% of rainfall events are 15 mm or less, with a mean duration between events of 20 days and in sandy soils such rainfalls will wet dry soil to a depth of 10–15 cm only. Woody species at such sites often have shallow root systems with extensive lateral development (Pressland 1975; Scholes and Walker 1993) which maximise absorption of the sporadic, low-rainfall events. A consequence is that a significant fraction of the root systems will experience very low soil water potentials, resulting in the low Ψ_{pd} , as observed during the dry season at Newcastle Waters.

At the Newcastle Waters site, the aseasonal pattern of E_t may be attributed to a hydraulic limitation of conducting xylem in either the stem or root (Meinzer et al. 1999). Vegetation of northern Australia has evolved in a seasonal climate since at least the late Miocene (Pole and Bowman 1996). Trees are likely to have developed a hy-

draulic architecture that will limit run-away embolism during the extended periods of low water availability (Tyree and Sperry 1989). While this protective mechanism ensures survival, a trade-off is a high resistance to sapflow, especially for trees of semi-arid climates such as Newcastle Waters. During periods of high soil water availability, tree transpiration will be limited to a rate determined by the high resistance of the xylem and the lower limit of leaf water potential that can be sustained whilst maintaining open stomata. Consequently, wet season Ψ_{pd} will respond to increased water availability, but E_t will lack marked seasonality, as has been observed. A similar conclusion has been reached by Meinzer et al. (1999) for woody species of Brazilian cerrado.

Surface conductance and decoupling

Describing the components of total conductance of these savannas is potentially complex, given the two to three overstorey canopy layers which comprise four phenological tree guilds (Williams et al. 1997), an understorey dominated by C4 annual grasses and a contribution from bare soil evaporation. These latter sources are of particular importance when overstorey canopy LAI < 3 (Schulze et al. 1994). Given this complexity, ecosystem surface (G_s) and aerodynamic (G_a) conductances are convenient to examine controls of water vapour exchange, although this obscures the relative contributions from vegetation and soil. However, late dry season estimates will contain little or no contribution from the soil surface. For the eucalypt open forests and woodlands of this study, the maximum and mean values of G_a and G_s (Table 3) are intermediate to values typical of forest (G_a , 8–10 mol m⁻² s⁻¹, G_s 0.9 mol m⁻² s⁻¹) and grassland (G_a , 1 mol m⁻² s⁻¹, G_s 0.9 mol m⁻² s⁻¹) (Shuttleworth 1989; Kelliher et al. 1993). Values of G_s for Howard Springs and Katherine lie within the range for both 'wet and dry savanna' (0.4–0.18 mol m⁻² s⁻¹; Schulze et al. 1994) while values at Newcastle Waters are more similar to those given by Gash et al. (1991) for Sahelian semi-arid savanna.

The high G_a to G_s ratio (one to two orders of magnitude) and resultant low values (less than 0.4) of the decoupling coefficient, Ω , at all sites of this study indicate strong surface and stomatal control of water vapour exchange in response to seasonal changes to atmospheric VPD and soil moisture deficit. Northern Australia experiences one of the most seasonal climates supporting savanna and the long dry season requires a high degree of surface control of water loss. Along the NATT, this is achieved through reductions in tree density and canopy leaf area of both overstorey and understorey (Table 1) plus stomatal regulation of transpiration. Despite being dominated by evergreen eucalypt tree species, overstorey LAI had declined by 30% by the end of the dry season. This canopy adjustment is due to reduced canopy fullness of the evergreen trees and the significant presence of semi-, brevi- and fully deciduous tree species in the

mid-stratum of the canopy. The semi- and brevideciduous species are capable of significant canopy adjustment in response to increasing soil and atmospheric water deficits, which is likely to be an adaptive trait of these tree species to the monsoonal wet-dry tropics. There is an approximately equal representation of these four phenological guilds, a feature of the savannas of northern Australia (Williams et al. 1997; Eamus and Prior, in press). By reducing canopy area, stomata of the remaining leaves can remain significantly open to prevent the internal CO₂ concentration becoming limiting to assimilation. In the absence of canopy loss, stomatal control of transpiration at large values of VPD will result in major reductions in CO₂ supply to the chloroplast and sub-optimal leaf function (Thomas and Eamus 1999).

Conclusions

The use of a sub-continental transect to study community physiology is a convenient method of sampling terrestrial ecosystems. We have presented values for a range of surface energy balance and water use parameters along a steep environmental gradient that spans much of the range of savanna of northern Australia. Our measurements were taken over relatively small durations and represent maximal and minimal fluxes only. However, we have shown that during periods of non-limiting water availability, evapotranspiration from savanna of northern Australia was constant over a wide geographic range. The period for which these high flux rates can be maintained is determined by wet season duration, which is a function of proximity to the coast and the strength of the monsoonal influence. The high- and medium-rainfall savanna sites were structurally and floristically similar, with a rainfall regime strongly influenced by the annual monsoon. In contrast, the rainfall regime of the low-rainfall, semi-arid savanna site was characterised by infrequent storm events and vegetation was able to exploit available moisture resources rapidly.

Transpiration from understorey vegetation and soil evaporation were the most important source of water vapour exchange, and alterations to surface conditions (e.g. fire and grazing impacts) are therefore likely to have significant hydrological consequences (Ludwig and Tongway 1995; Ludwig et al. 1999a). Given the strong canopy coupling, we conclude that savanna water (and carbon) balance will be largely determined by G_s , its response to atmospheric and soil water content, and adjustments to canopy leaf area.

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