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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 (R_n), latent and sensible heat (LE and H), ecosystem surface conductance (G_s) and tree water use (E_t) for three 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 (1873 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 of these parameters were measured at the seasonal extremes of late wet and dry seasons. During the wet season, daily rates of evapotranspiration were 3.0-3.6 mm d^{-1} and were similar for all sites along this rainfall gradient and did not reflect site differences in annual rainfall. However, site differences were very apparent during the dry season, with rates of evapotranspiration declining to 1.6, 0.8 and 0.2 mm d^{-1} at the high, medium and low rainfall sites respectively. Due to low overstorey LAI, more than 80% of water vapour flux was attributed to the understorey. Water use of individual trees did not differ between the wet and dry seasons at any of the three sites and stand water use was a simple function of tree density. 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 quickly exploit available moisture resources. Ecosystem surface conductance (G_s) declined markedly during the dry season at all sites and we conclude that savanna water (and carbon) balance is largely determined by G_s and its response to atmospheric and soil water content and by seasonal adjustments to canopy leaf area.

Keywords: Tropical savanna, evapotranspiration, monsoon climate, ecosystem surface conductance, understorey evaporation

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 2000). Savanna distribution is largely determined by plant available moisture (PAM) and plant available nutrients (PAN) (Huntley and Walker 1982; Ben-Shahar 1991; Scholes and Archer 1997). For savannas of northern Australia, the overriding determinant is PAM. While PAN and fire are also of significance, they are of secondary importance (Williams *et al.* 1996; Walker and Langridge 1997). In recent years there have been a number of studies examining the interactions of savanna vegetation with the environment of northern Australia. These studies have been conducted at a leaf (Myers *et al.* 1997, Duff *et al.* 1997, Fordyce *et al.* 1997, Prior *et al.* 1997 a,b), tree (O'Grady *et al.* 1999) and stand scale (Cook *et al.* 1998, Hutley *et al.* 2000). Such studies have contributed significantly to our understanding of plant communities' interactions with the tropical monsoonal environment. However, these studies have been conducted at the wettest end of the rainfall gradient and we have little knowledge of savanna function at drier, inland sites.

There has been an increasing use of environmental gradients in ecophysiological studies. Examples include Schulze *et al.* (1998), who reported a weak relationship between carbon isotope discrimination, water use efficiency and annual rainfall along the Northern Australia Tropical Transect (NATT, Egan and Williams (1996)). Stewart *et al.* (1995) observed a similar but stronger relationship over a large rainfall gradient in south-east Queensland. 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 as 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 may contribute to our understanding of savanna functioning over a large rainfall gradients.

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 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 characterised surface energy balance, conductance, tree water use and vegetation structure at three savanna sites from 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 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? And what is the relative contributions of the soil, understory and tree canopy to total evapotranspiration in the wet and dry seasons? To achieve this aim high, moderate and low rainfall NATT sites were chosen, each with vegetation representative of the region.

Methods

Sites - Northern Australian Tropical Transect (NATT)

We used three NATT sites which spanned a 700 km and 1350 mm rainfall gradient. These sites were Howard Springs (high annual rainfall site, 1873 mm), Katherine (moderate rainfall site, 870 mm) and the most inland site, Newcastle Waters (low rainfall site, 520 mm) (**Error! Reference source not found.**). Soil type at all three sites was similar, removing the confounding influence of soil hydraulics on interpretations of vegetation water use. Soils were all well drained laterised red earths with a surface texture commonly a 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.

Insert
Table 1

Vegetation

The vegetation of the high rainfall site, Howard Springs, approximately 35 km south-east of Darwin, 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 tetradonta* (F. Muell.) and *E. miniata* (Cunn. Ex Schauer) which form a canopy of about 50% cover and 12-14 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 *brevi*, semi and fully deciduous tree species and LAI typically ranges from 0.6 during the dry to 0.95 during the wet season. (Table). Evergreen canopy fullness varies little seasonally (Williams *et al.* 1997). 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).

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Table 2

The moderate rainfall site, Katherine, approximately 360 km south of Darwin, was broadly similar, structurally and floristically, to the Howard Springs site. The main difference was a reduced abundance of mid-stratum tree species, which was replaced by smaller scattered shrubs. The overstorey was dominated by *E. latifolia* and *E. tetradonta* 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). 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, differed significantly from Howard Springs and Katherine sites by being a low open woodland. The open overstorey consisted of *E. terminalis* and *E. capricornia* and a thick understorey dominated by *Acacia* shrubs. Mean height of the trees was approximately 8 m with a basal area of 4.8 m² ha⁻¹ and an LAI of 0.07, which changed little between the wet and dry season (Table). The dense understorey consisted of shrub species *Acacia lysiphloia*, which grew to a maximum height of 2 m with *A. shirleyi* and *Sorghum* spp also present. Understorey LAI was much more seasonally dynamic than the trees and increased 5-fold between seasons (Table).

Climate

Climate at the high and moderate rainfall sites (Howard Springs and Katherine) is wet-dry tropical, with a strong monsoonal influence with a predictable wet season occurring from December to March. This period accounts for approximately 95% mean annual rainfall (Figure 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 the Darwin, Katherine and Newcastle Waters are 2656, 2279 and 2789 mm respectively (Figure 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 d⁻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. More pronounced seasonality of E_{pan} is evident at the semi-arid Newcastle Waters site (Figure 1).

Insert
Fig 1

Temperature at the high and moderate rainfall sites vary little annually. Mean daily maximum temperatures at the 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 temperature 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 d^{-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 ranging from open forests at high rainfall to low open woodlands at low rainfall (**Error! Reference source not found.**). In addition we 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 total evapotranspiration and tree water use (Hutley et al. 2000). Measurements were made at the seasonal extremes in terms of soil water availability, during the late wet seasons of March 1998 and 1999 and during the late dry season of 1999 (**Error! Reference source not found.**). 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.

Inset
Table 3

Eddy covariance

Each site had adequate (~ 1 km) fetch in all directions with slopes of less than 1° . Measurements were conducted for 5 consecutive 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 minutes intervals. Corrections for oxygen absorption by the krypton

hygrometer (Tanner, Swiatek & Greene 1993), coordinate rotation and corrections accounting for air density changes (Webb, Pearman & Leuning 1980) were applied to raw fluxes. For each day of measurement, 30 minute LE estimates were integrated and expressed as evapotranspiration, E_a (mm d^{-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, Washington) were simultaneously made at the same reference height as the eddy covariance instruments. Soil heat flux, G_S , was estimated using a combination of 4 soil heat flux plates (model HFT-3, Radiation and Energy Balance Systems, Seattle, Washington) buried at 8 cm with an averaging soil thermocouple (model TCAV, Campbell Scientific, Logan, Utah) 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 4 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 for determinations of 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 five days for each measurement period (**Error! Reference source not found.**). At the Howard Springs site individuals of *E. miniata* and *E. tetradonta* were instrumented; at Katherine *E. latifolia* and *E. tetradonta* and Newcastle Waters *E. capricornia* and *E. terminalis* were instrumented. For each instrumented tree, 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 minute 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 x 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 transpiration, E_t , in mm day⁻¹.

At Howard Springs and Katherine sites, understorey LAI was estimated by destructively sampling all green leaf area in seven 1 m² plots at three separate locations (21 plots for each site). Distance between locations was approximately 500 m to 1 km. Leaf area was determined using a Delta-T leaf area meter (Delta-T Devices, Cambridge UK). For plots containing large amounts of leaf material, sub-sampling was undertaken 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 x 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, CA) and was used as a surrogate of soil water availability (Schulz and Hall 1982, Crombie et al. 1988). For each site and season, leaf ψ_{pd} was measured between 6:30 and 7:00 am 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 as it was not possible to have replicates of each species at each location. 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 **Error! Reference source not found.** There were significant differences in pre-dawn leaf water potential between seasons and locations as well as a significant season by location interaction (Season *d.f.* 1,106 $F=870.2$ $p<0.01$, Location *d.f.* 2,106 $F=190.3$ $p<0.01$ Season \times location *d.f.* 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 (**Error! Reference source not found.**).

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Fig 2

Energy Balance

Fluxes of LE, H and Rn at the three sites are given for typical days at the end of the wet season, March 1999 (Figure 2) and dry season, August 1998 (Figure 3). Daily totals of LE have been integrated and converted to a depth equivalence of water in mm d^{-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 Rn. At Howard Springs, maximal mid-day fluxes of LE ranged from 400-480 W m^{-2} during the wet season (Figure 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 Rn (Figure). 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 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 minute estimates of LE and H between 1100 to 1500 h 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.

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Fig 3 &
Fig 4

Water Use

Mean daily rates of total evapotranspiration (E_a) and tree water use (E_t) are given for the 3 sites for wet (Figure a) and dry seasons (Figure b). Tree water use is plotted against rainfall in Figure . Also shown on Figure 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.

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Fig 5

Wet season evapotranspiration was similar at all 3 sites with mean values of E_a ranging from 3 to 3.6 mm d^{-1} , with E_u contributing >75% of this flux at all sites (Figure a). 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 (Figure a, **Error! Reference source not found.3**). The ratio $E_t : E_a$ decreased from Howard Springs to Newcastle Waters with the contribution of E_u increasing (**Error! Reference source not found.3**).

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Table 4

During the dry season mean rates of E_a at Howard Springs were less than 50% that 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 d^{-1} , 5% of the wet season value.

Tree water use, E_t , increased with increasing annual rainfall (Figure 5) and ranged from a low of 0.08 mm d^{-1} at Newcastle Waters during the dry season to a wet season maximum of 0.9

Insert
Fig 6

mm d⁻¹ at the high rainfall Howard Springs site. There was no difference between wet and dry season values of E_t at any site (Figure 5).

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, 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 conductance's, the surface decoupling coefficient, Ω was calculated (Jarvis and McNaughton 1986). This coefficient evaluates the relative importance of surface versus aerodynamic conductance to controlling transpiration with low values of Ω indicate a close coupling of transpiration rates to atmospheric VPD.

Values of the Ω, G_s and β are given for each site and season in Table . Mean mid-day values of G_a for all sites ranged from 2.4 to 1.8 mol m⁻² s⁻¹ with maximal ranged from 5.3 mol m⁻² s⁻¹ at Howard Springs to 2.4 mol m⁻² s⁻¹ at Newcastle Waters, reflecting canopy height of each site. Wet season values of Ω are 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).

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Table 5

Discussion

E_u as a function of site and season

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 a canopy with a 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 tree water use, E_t and the observed seasonality of E_a was largely due to shifts in understorey LAI and 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 is due to transpiration of annual C4 grasses (*Sorghum* spp), which die off 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 declines with distance from the coast as the monsoonal influence weakens, results in a decline tree density declines and understorey vegetation is characterised by an increased abundance of perennial as opposed to annual species (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 persist on site all year. By the late dry season they exhibit very low rates of LE, G_s and reduced leaf area (Figure , Table). However this changes 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} , rates of latent heat flux at the Newcastle Waters site were equivalent to the coastal Eucalypt dominated open-forest savanna of Howard Springs (Figure), despite a total LAI that was 20% of the lower. Given their high cover at this 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 Water Use, Season and Location

In contrast to the behaviour of understorey vegetation, tree water use E_t was constant at all sites all year, despite pronounced seasonality of soil and atmospheric water content.

Transpiration rates measured using Greenspan sapflow sensors were similar at Howard Springs and Katherine for both seasons, but were lower at Newcastle Waters. However, site differences were not large and given the large inter-annual variation of E_t for these savanna on average, tree transpiration per unit leaf area was similar at all sites and between seasons (O'Grady et al 1999). The large decline of scaled estimates of tree water use, E_t , are not due to large differences in tree behaviour between sites but simply reflect the decline tree density with annual rainfall (Figure). 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 as it suggests that regional estimates of stand water use can be based on simple allometric measures such as basal or sapwood area (O'Grady et al. 1999).

The seasonally constant E_t requires that trees were extracting moisture from the sub-soil (> 3 m) and possibly the capillary fringe of the water table as it receded over the dry season. At the high and moderate rainfall sites of Howard Springs and Katherine, rainfall is largely derived from monsoonal weather systems such as tropical depressions (Jackson 1988). The wet season is 185 and 150 days duration for Howard Springs and Katherine respectively (G. Cook, pers comm.). Soil water content 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 suggested that there was an extensive development of root biomass in the sandy loams of the top 1 m of soil. However, large diameter roots (> 3 cm) of mature trees were able to extend through weaknesses in the duricrust and access water stored in the heavier

clay sediments of the sub-soil. Roots reached depths of approximately 10 m, the depth of the water table at the end of the dry season (Cook et al. 1998). 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 the supply of 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 (**Error! Reference source not found.**). At this site, access to deep water supply is unlikely to be occurring 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 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 will often have shallow root systems with extensive lateral development (Scholes and Walker 1993, Pressland 1975) which maximise absorption 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 hydraulic 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 sap flow, 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 the 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 2-3 overstorey canopy layers which comprise four phenological guilds of trees (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, it is convenient to use ecosystem surface (G_s) and aerodynamic (G_a) conductances to examine controls of water vapour exchange, although this obscures the relative contributions from vegetation and soil. However, 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 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 ratio of G_a to G_s (1 to 2 orders of magnitude) and resultant low values of the decoupling coefficient, Ω (less than 0.4) 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. This is achieved through both stomatal regulation of transpiration and through reductions in canopy leaf area. A feature of the savannas of northern Australia is the significant presence of semi-deciduous and brevi-deciduous species, which are generally not a major functional group of other savanna and seasonally dry ecosystems (Eamus and Prior 2000). These species are capable of significant canopy adjustment (50% loss of leaf area) in response to increasing soil water deficits and this is likely to be an adaptive trait of these tree species of the monsoonal wet-dry tropics. By reducing canopy area, stomata of the remaining leaves can remain significantly open to prevent the internal CO_2 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 CO_2 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 that 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. Transpiration from understorey vegetation and soil evaporation was the most important source of water vapour exchange and alterations to surface conditions (eg fire and grazing impacts) are therefore likely to have significant hydrological consequences (Ludwig and Tongway 1995; Ludwig et al. 1999a). Given the high degree of stomatal control and strong 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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Captions

Figure 1 a) Mean monthly rainfall and b) mean daily pan evaporation (E_{pan}) 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 is an interpolation generated by the 'Data Drill', Queensland Department of Natural Resources and Bureau of Meteorology (www.dnr.qld.gov.au/resourcenet/silo/datadril.html, SILO site).

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

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

Figure 4 Actual evapotranspiration (E_a) partitioned into tree water use (E_t) and understory evaporation (E_u) for Howard Springs, Katherine and Newcastle Waters sites during the a) wet season and b) dry season. Understorey evaporation was calculated as the difference between E_a and E_t .

Figure 5 Patterns of tree water use for the Howard Springs, Katherine and Newcastle Waters sites. Data have been expressed as scaled stand water use (E_t) plotted against rainfall. Also shown is tree density (stems per ha^{-1}) for each site.

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

<i>Site</i>	<i>Wet Season</i>			<i>Dry Season</i>		
	Overstorey	Understorey	Total	Overstorey	Understorey	Total
Howard Springs	0.9	0.8	1.7	0.6	0.02	0.62
Katherine	0.75	0.5	1.25	0.42	<0.02	0.44
Newcastle Waters	0.05	0.20	0.25	0.07	0.05	0.12

Table 2: Seasonal mean pre-dawn leaf water potentials (MPa).

	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	-0.23	-0.09	-0.21	-0.26	-0.32
Dry	-0.42	-0.58	-1.14	-0.73	-2.23	-2.42

Table 3 The Bowen Ratio, H/LE (β), decoupling coefficient (Ω) and 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 1100 to 1500 hours with the standard errors given in parenthesis.

<i>Site</i>	<i>Wet season</i>				<i>Dry season</i>			
	β	Ω	G_s	G_a	β	Ω	G_s	G_a
Howard Springs	0.40 (0.02)	0.37 (0.09)	0.27 (0.11)	2.2 (0.3)	2.4 (0.11)	0.13 (0.04)	0.07 (0.05)	2.4 (0.1)
Katherine	0.84 (0.03)	0.32 (0.07)	0.23 (0.09)	2.4 (0.44)	6.5 (0.26)	0.06 (0.01)	0.04 (0.01)	2.9 (0.45)
Newcastle Waters	0.62 (0.02)	0.39 (0.09)	0.24 (0.08)	1.8 (0.7)	34.4 (4.0)	0.02 (0.02)	0.01 (0.01)	1.7 (0.7)

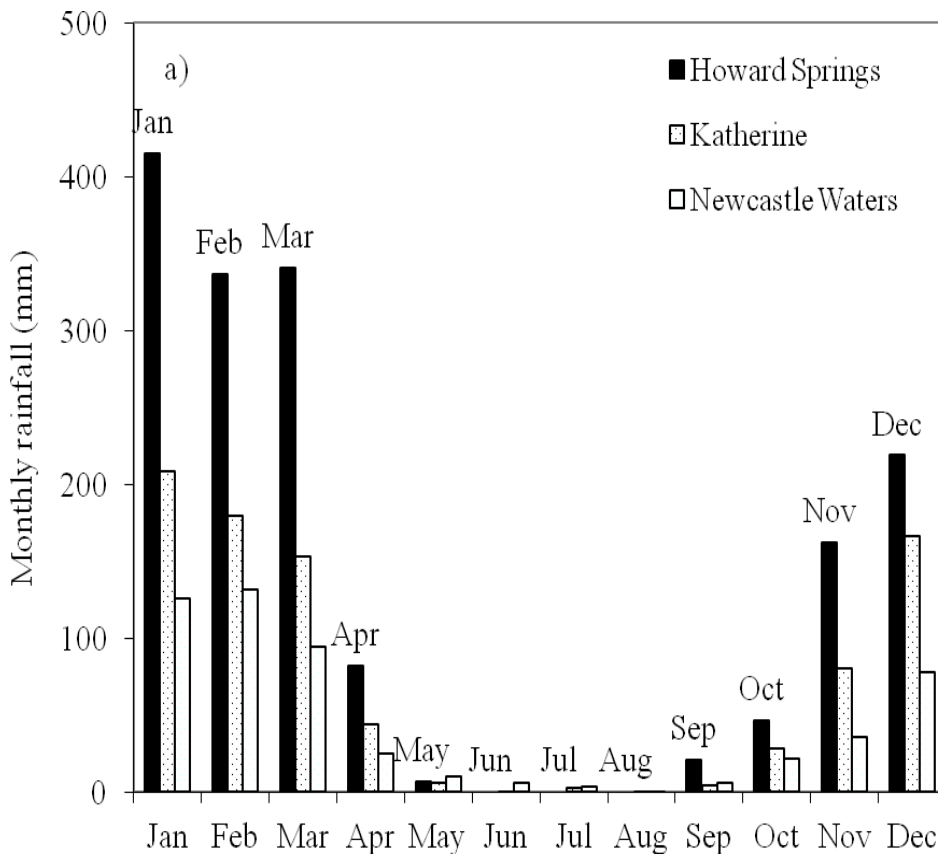


Fig 1a

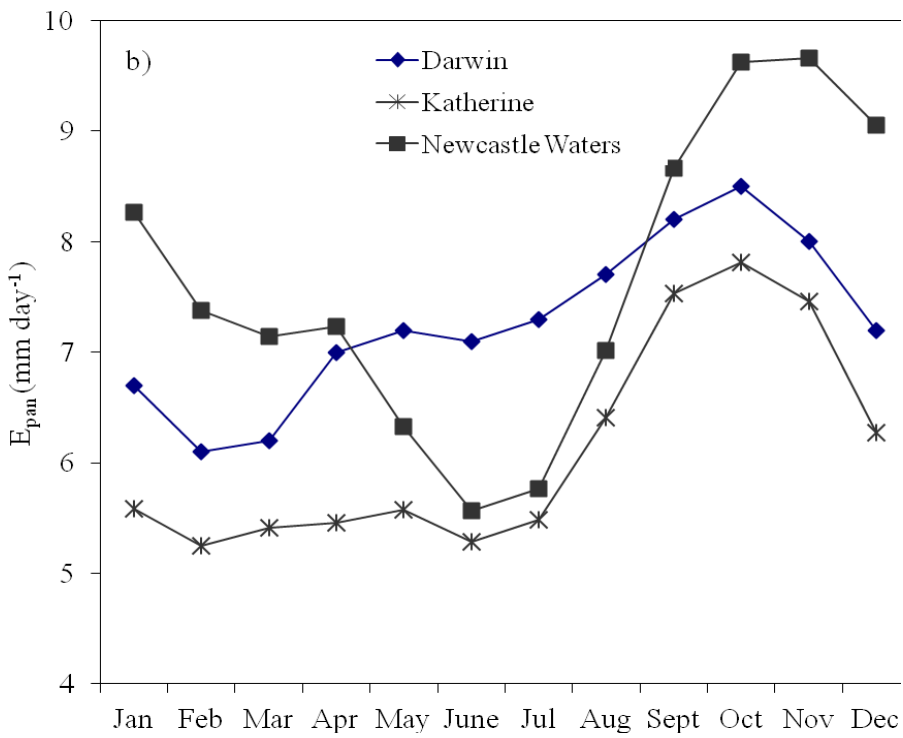


Fig 1b

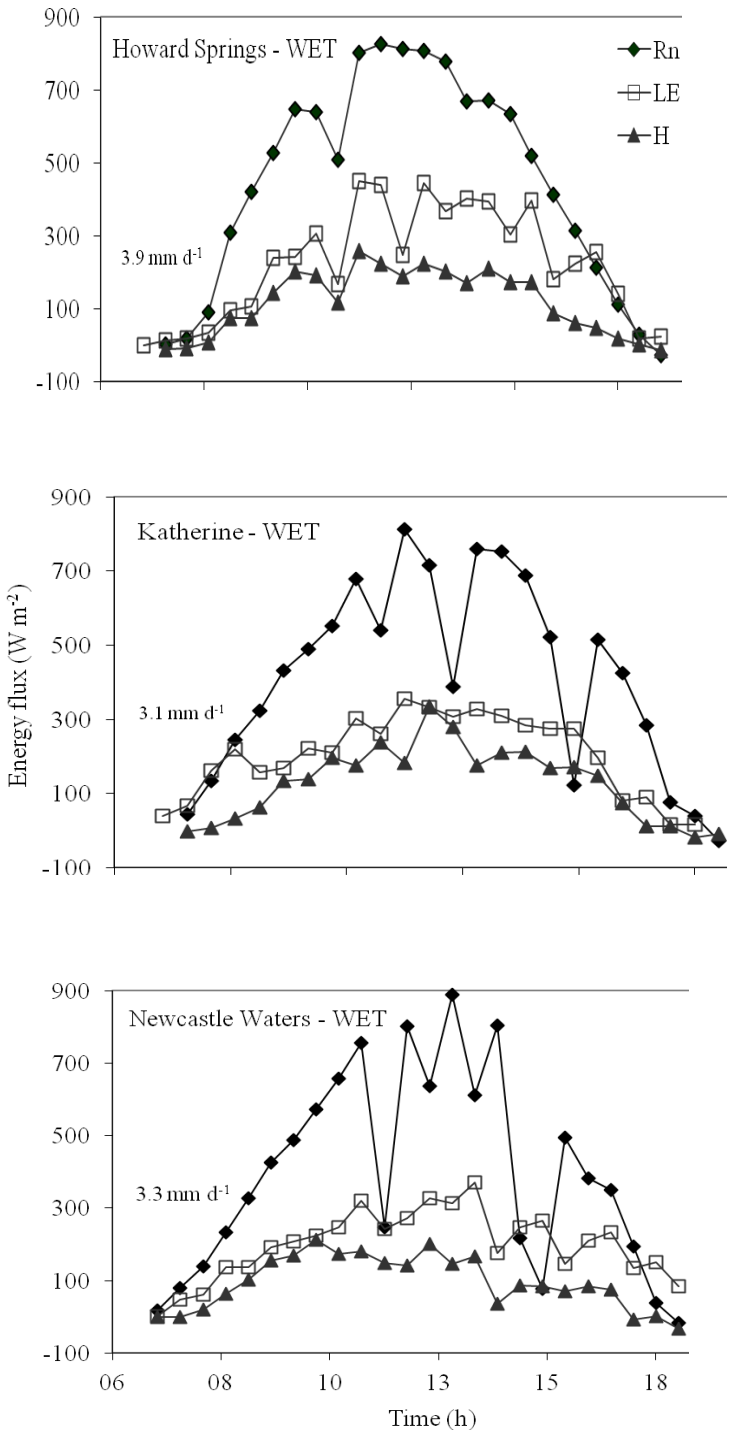


Fig 2

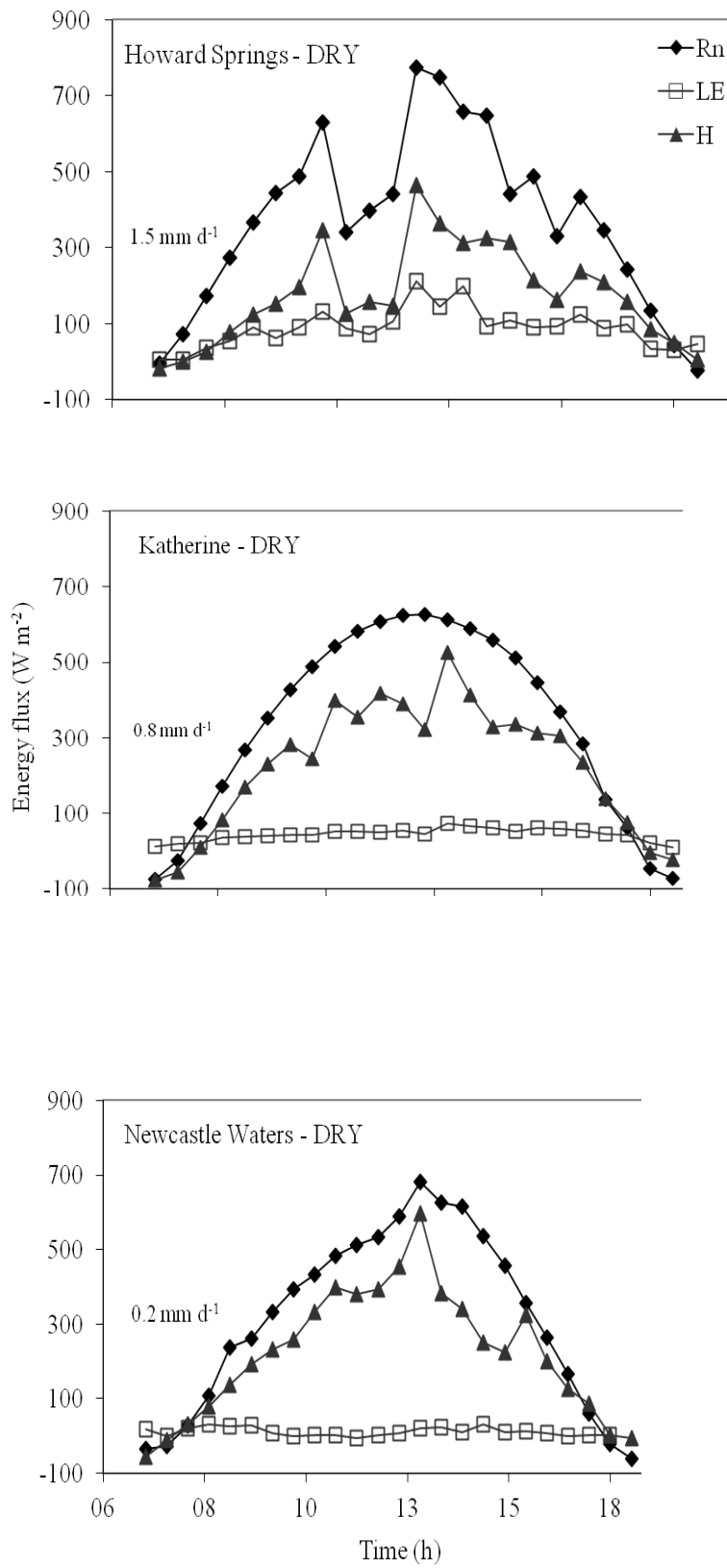


Fig 3

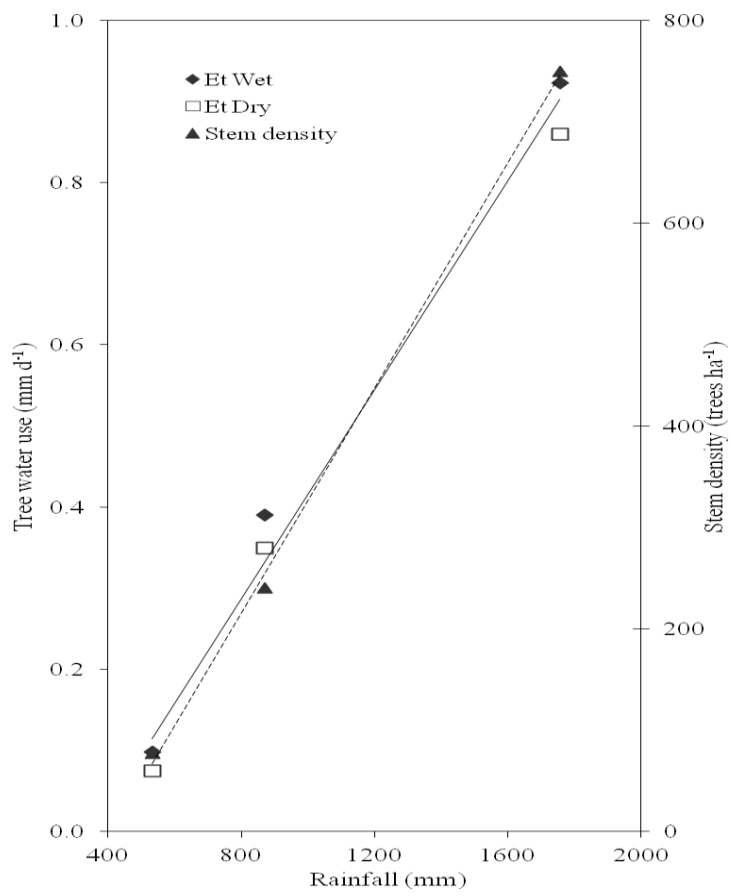


Fig 4

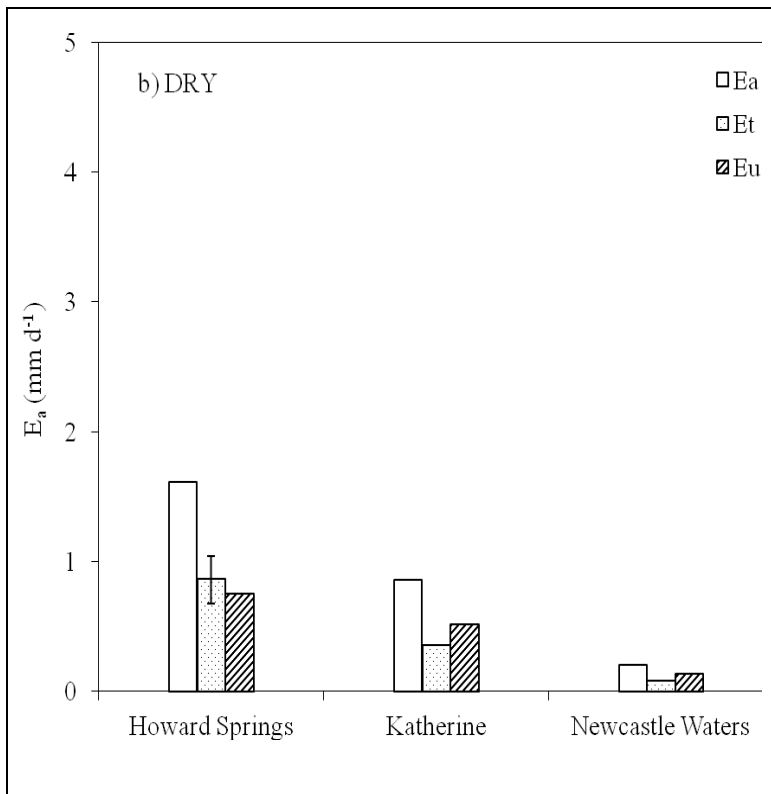
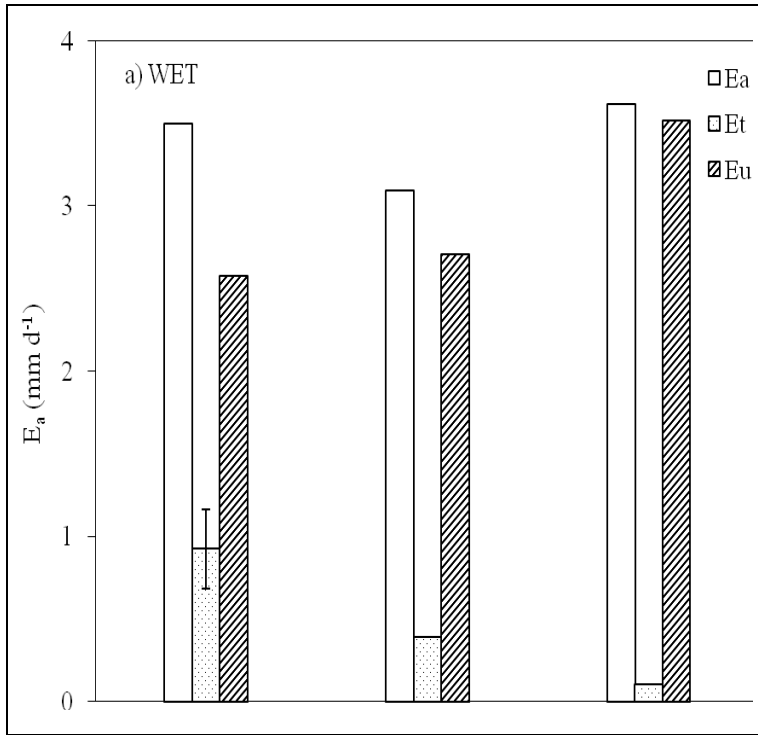


Fig 5