

A sub-continental scale living laboratory: Spatial patterns of savanna vegetation over a rainfall gradient in northern Australia

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ABSTRACT

Savanna landscapes across north Australia are characterised by limited topographic variation, and in the Northern Territory, by a relatively constant decline in rainfall with distance inland. The North Australian Tropical Transect (NATT) traverses this 1000 km gradient of largely intact vegetation which provides an ideal 'living laboratory' and framework to investigate the influence of vegetation structural and floristic change and climate drivers on land–atmosphere exchange at a regional scale. We conducted a multidisciplinary program examining carbon, water and energy fluxes as a function of climate and vegetation change along a sub-continental environmental gradient. Initial findings are reported in this Special Issue. During the program, an intensive field campaign was undertaken during the dry season to characterise vegetation and soil properties of eight flux tower sites used to describe spatial and temporal dynamics of fluxes across this gradient. This paper provides an overview of the savanna landscapes of north Australia detailing vegetation structural and physiological change along this gradient. Above-ground woody biomass, stem density, overstorey LAI and canopy height declined along sites that spanned an 1100 mm annual rainfall gradient. Biomass ranged from 35 to 5 t C ha⁻¹ with dry season LAI ranging from ~1 to 0.05 across savanna sites both intact and cleared for grazing. Across open-forest and woodland savanna, basal area ranged from 9.7 to 5.3 m² ha⁻¹. While structural change was significant and correlated with rainfall, leaf scale physiological properties (maximal photosynthesis, V_{cmax} , C_i/C_a , light use efficiency) of the dominant woody species showed little variation, despite the significant environmental gradient. It is likely that changes in structural properties dominate spatial patterns of flux as opposed to physiological plasticity or species differences along this gradient.

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1. Introduction

The use of transects is a standard ecological method that has been adopted by the global change research community over the last two decades to examine spatial patterns of biogeochemical processes that have both regional and global scale influences (Koch et al., 1995). Such gradients can be used to examine the impact of future environmental and climate change by substituting observations made over space to changes that may occur over time (Cook et al., 2002). Such an approach was undertaken during the 'Savanna Patterns of Energy and Carbon Integrated Across the Landscape' (SPECIAL), an international experimental program aimed at understanding climate and vegetation drivers of carbon, water and energy fluxes from north Australian savanna. Beringer et al.

(1995, 2007, 2011) provide an overview of this multidisciplinary program as part of the Special Issue in this journal, with this paper describing the landscape features of the North Australian Tropical Transect (NATT, Williams et al., 1995) where the study was conducted. This 1000 km transect spans a systematic decline in rainfall with distance from the northern coast of the Northern Territory, Australia. The NATT is one of three transects established in savannas as part of the IGBP in the mid 1990s (Koch et al., 1995), the others being located in western Africa (Savannas in the Long Term (SALT), Menaut et al., 1995) and the Kalahari Transect (KT) of sub-Saharan Africa (Scholes and Parsons, 1997; Ringrose et al., 1998). These transect all feature strong precipitation gradients, appropriate for savanna process studies given the importance of available moisture as a determinant of savanna physiognomy (Scholes and Archer, 1997).

Australian savanna occurs across the northern third of the continent (Fig. 1), essentially the wet–dry tropical climate zone, and feature a high degree of canopy intactness and relatively low levels of fragmentation when compared to South America and Africa savanna (Woinarski et al., 2007). The NATT runs north–south along

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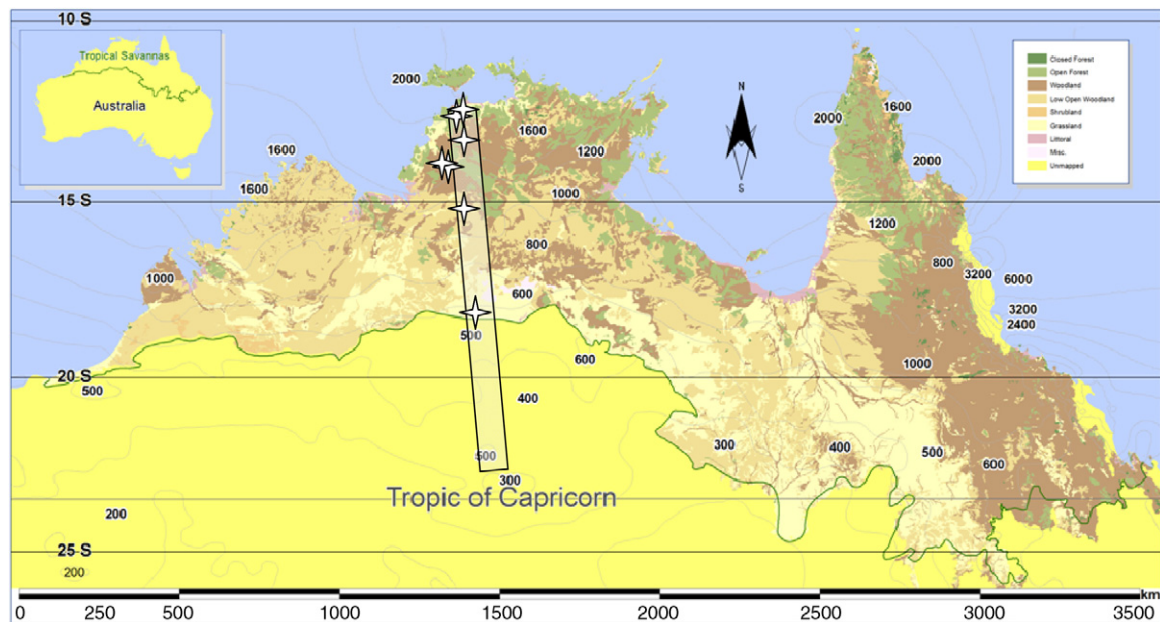


Fig. 1. The savanna biome of northern Australia as defined by Fox et al. (2001). The approximate area of the NATT transect and SPECIAL intensive observation sites are marked.

a rainfall gradient that is relatively constant, with a ~ 1 mm decline in annual rainfall per km inland (Cook and Heerdegen, 2001). The savanna vegetation occupies vast undulating sandy to sandy clay loam plains interspersed with cracking clay plains. Given the relatively constant rainfall gradient, an extensive and largely intact vegetation cover across flat landscapes of similar soil types, the NATT provides us with an ideal 'living laboratory' in which to investigate the influence of vegetation structural and floristic change and climate drivers on land–atmosphere exchange at a regional scale.

Tropical savanna is a large biome, occupying some ~ 27.6 million km^2 of Australia, South America, Asia and Africa (Hutley and Setterfield, 2008). Savannas consist of a mixture of C3 trees and C4 grasses and are distinct from grasslands (near absence of woody plants) and closed forests (tree dominant). The competitive tree:grass balance is highly variable spatially and temporally and the competitive balance between tree and grass components is critical to fuel production and flammability, productivity and carbon balance (House et al., 2003; Hutley and Beringer, 2010). Savannas account for a third of global terrestrial primary productivity (Grace et al., 2006), largely due to their size, and a significant fraction of this carbon uptake can be lost via savanna burning (van Der Werf et al., 2003). Emissions from savanna fires have a major impact on atmospheric chemistry (Andreae, 1991) and may contribute to climate forcings (Hoffmann et al., 2002; Lynch et al., 2007; Luhar et al., 2008).

Given the size and importance of the savanna biome, there is a need for well calibrated land surface models (LSM) and dynamic global vegetation models (DGVM) to predict shifts in savanna distributions, fire regime, carbon storage and feedbacks to regional and global climate. However, savannas are poorly described in current global vegetation and climate models, making predictions of their future distribution and carbon and water balance difficult (Scheiter and Higgins, 2009). As a result, well designed, multidisciplinary field measurement campaigns are required to provide data for the continued development of LSM and DGVMs to better capture savanna dynamics. This is a major goal of the SPECIAL program.

The role of this paper is to provide background on the nature of the landscape under investigation for the SPECIAL campaign. This includes, (1) an overview of the soils and vegetation of the NATT, (2) a review of previous studies utilising the transect, (3) description

of the tower sites, their distribution and measurement protocols used to characterise structural and physiological properties, (4) an analysis of observed vegetation properties along the transect and (5) a discussion of observed trends.

2. Vegetation and soils of the North Australian Tropical Transect

The NATT extends ~ 1000 km south from Darwin (12.5°S) on the northern coast of the Northern Territory (NT) to south of Tennant Creek (22°S), traversing the mesic (>1200 mm annual rainfall) to semi-arid savanna and into the arid zone, eight bioregions zones in all (IBRA, 2006). Fox et al. (2001) defined the area of the Australian tropical savannas using the 500–600 mm rainfall isohyet, although this is somewhat arbitrary since the boundary between savanna and semi-arid shrubland is gradational. North of this isohyet the dominant vegetation is tropical savanna, featuring a woody overstorey strata dominated by evergreen *Eucalyptus* and *Corymbia* tree species and an understorey dominated by annual and perennial C4 grasses and other forb and shrub species (Egan and Williams, 1996). In meridional extent, the savanna extends from north Queensland, across the northern half of the Northern Territory to the Kimberly region of north-west Western Australia (Fig. 1). Below the 400–500 mm isohyet, the dominance of *Eucalypt* and *Corymbia* savanna woodlands tends to decline, with *Acacia* woodlands and shrublands and hummock grasslands becoming increasingly prominent with inland aridity (Bowman and Connors, 1996). Within this vast savanna landscape, small closed forest patches occur in fire protected, rocky outcrops or in riparian, spring-fed habitats.

A key feature of this landscape is the regular occurrence of fire due to the annual dry season. The 4–6 months dry season results in the curing of C4 grasses and accumulated litter and fire occurs across 30–50% of this region each year (Russell-Smith and Yates, 2007). Fire frequency increases with higher rainfall due to higher fuel production and higher human population density with mesic savanna (>1000 mm annual rainfall) burning two in every 3 years. Fire severity increases through the dry season as fuels cure and fire weather is more extreme (Williams et al., 1998).

Soils are dominated by Kandosols of sandy to sandy-clay loam texture, with a mosaic of Vertosols or cracking clays, with limited woody plant growth (Isbell, 2002; Williams et al., 1996). These Kandosols tend to form extensive, gently undulating plains and are ancient, leached and relatively infertile (McKenzie et al., 2004). Alternating wet and dry seasons and the oxidation and reduction of metal-rich soils produce duricrusts of variable depths that present difficult habitats for vegetation and have a tendency to erode when cleared (Dilshad et al., 1996).

3. Previous studies utilising the NATT

A number of studies covering a range of disciplines including biogeography, entomology, soil science, ecophysiology, meteorology and land-atmosphere exchange have been undertaken along the NATT and at other sites located over this gradient (Table 1). These studies informed planning for the SPECIAL campaign and are an important background for interpreting observed patterns of leaf (Cernusak et al., 2011) to canopy and regional scale fluxes (Kanniah et al., 2009, 2010, 2011). Because of the key role this work has played in framing the SPECIAL program, a summary and synthesis of previous work along the NATT is provided below.

3.1. Biogeographical studies

Core vegetation descriptions along the NATT are provided by Williams et al. (1995, 1996) and Egan and Williams (1996), with findings summarised in Table 1. Egan and Williams (1996) and Williams et al. (1996) describe a systematic change to vegetation structure (canopy height, cover, basal area), floristics, phenology and reproductive strategies across 54 sites with sampling on sand, loams and clay soils. Prior to these studies, Bowman et al. (1988) provided an examination of floristic assemblages across the NT and found that rainfall is a key driver of species change, with soils and fire regime determining floristics at finer scales.

A floristic dichotomy at 17–18°S was identified, with a northern phytogeographic zone distinct from flora south of this latitude (an Eremaean zone, after Burbidge, 1960). Williams et al. (1996) and Bowman and Connors (1996) focussed on woody structural change as a function of climate, with rainfall the strongest determinant of woody basal area, canopy height and cover along the NATT. Soil type and texture modified the slope of these relationships, with the best developed stands occurring on deep, well drained sands. Between 18 and 21.5°S Bowman and Connors (1996) documented a shift from *Eucalyptus* to *Acacia* dominated woodlands and shrublands, attributing this to increasing elevation with latitude south and declining minimum winter temperatures limiting *Eucalyptus* regeneration.

3.2. Ecophysiological studies

These biogeographical and ecological studies all suggested further ecophysiological investigations at finer scales (leaf, stand) were required to understand mechanisms controlling structural and floristic change. Schulze et al. (1998) and Miller et al. (2001) both sampled leaf carbon isotope discrimination (Δ), nitrogen isotope ratios, N-concentrations and specific leaf area (SLA) along the NATT to examine patterns of leaf scale water use efficiency (WUE) and N cycling. This approach enabled comparison of physiological attributes across distributions of replacement woody species with increasing aridity. Both studies observed a near constant value of community averaged Δ of ~19‰ between 1600 and 400 mm annual rainfall (~12.5–19.5°S) despite sampling differing species along the transect.

These analyses suggest replaced species had an ability to maintain stomatal conductance (g_s) relative to photosynthetic capacity

as rainfall declined (Miller et al., 2001). Physiological boundaries identified from shifts in isotopic signature were apparent at 16 and 19°S along the NATT, and matched those found from biogeographical studies of Bowman et al., and Williams et al. (dominance of *Acacia* over *Eucalyptus*). The decline in Δ below a rainfall threshold of ~450 mm may be a function of both low species diversity (Bowman and Connors, 1996) and an increasingly aseasonal and unpredictable rainfall pattern as the monsoonal influence declines (Cook and Heerdegen, 2001). While Schulze et al. (1998) argued that systematic variation in grazing pressure was responsible for the variation in $\delta^{15}\text{N}$ down the rainfall gradient, Cook (2001) argued that differences in fire frequency were a more likely cause.

Cook et al. (2002) examined vegetation water use at a stand scale along the NATT using relationships between tree size and water use, rainfall and simple soil water balance modelling. They concluded exploitation of deep soil moisture reserves was critical to maintaining the observed aseasonal pattern of tree transpiration down the NATT (Hutley et al., 2001) and limited leaf scale shifts in Δ (Miller et al., 2001). Extraction from depths of up to ~5 m of soil is required at the high rainfall end (>1000 mm annual rainfall) of the NATT to support higher woody plant cover when compared to lower rainfall sections of the NATT. At the arid end of the transect (~450 mm and below), tree populations with shallower root systems would be favoured to maximise root uptake of small, isolated rainfall events associated with a storm driven rainfall distribution (Cook et al., 2002).

3.3. Flux studies

There have been few studies of mass and energy fluxes along the NATT (Table 1). Hutley et al. (2001) used EC and sapflow methods at three NATT sites (1750, 870 and 520 mm annual rainfall) and estimated evapotranspiration (ET) and tree water use at seasonal extremes. During the wet season, rates of ET were similar across the three sites, with fluxes from the tall grasses and shrubs of the understorey accounting for 70–80% of the total ecosystem flux. Tree transpiration rates per unit ground area were similar in both wet and dry seasons, although understorey ET declined significantly in the dry season and site differences were apparent.

Two previous airborne based eddy covariance campaigns measuring latent (LE) and sensible heat (H) fluxes have been conducted along the NATT. Matthews (1999) and Matthews et al. (2000) estimated fluxes along flight paths traversing the NATT from the northern coastline (Arafura Sea) to Tennant Creek, NT. Early dry season (April) fluxes showed a dramatic change in Bowen ratio ($\beta = H/LE$) from the LE-dominated energy balance for mesic savanna (north of 13.5°S), shifting to an H -dominant energy balance below 600 mm annual rainfall (16.5°S). Airborne fluxes of LE and H were also measured during the peak wet season of 2006 during the Tropical Warm Pool International Cloud Experiment (May et al., 2008). The observations were carried out over the northern end of the NATT (Hacker, 2007).

Planning for the SPECIAL program drew on these previous studies. Hutley et al. (2001) observed limited differences in ET across three NATT sites during the wet season. Previous airborne flux studies (Matthews et al., 2000) demonstrated significant and rapid shifts surface energy balance during dry season flights, but no detailed ground sampling was undertaken to link flux observations with vegetation attributes. Consequently, the intensive observation campaign was undertaken in the late dry season to explicitly examine differences in structure, physiological attributes and flux along the transect at a time when the spatial variability in these quantities was expected to be greatest.

Previous physiological studies had focussed on isotopic analysis, with little data available for basic leaf physiological variables, especially for the lower rainfall end of the transect (<800 mm annual

rainfall). No previous studies had linked leaf, canopy and aircraft fluxes (Beringer et al., in press). Distribution of vegetation and established relationships between rainfall, cover and the influence of soil type (sand, loam or clays, after Williams et al., 1996) on struc-

ture played a part in site selection, and five of the eight towers sites located on common soil types along the rainfall gradient. The selected SPECIAL sites are characterised below with methods used for structural measurements and analysis between sites given.

Table 1

Previous studies using the NATT and other associated sites across NT savanna ecosystems. Site characteristics, methods and key findings are provided for each study. Studies cover aspects of biogeography and ecology, ecophysiology, flux studies and remote sensing.

Sites	Methods	Key findings	Source
Biogeographical studies 1:100 000 vegetation mapping sheets, herbarium records	Assess species richness and distribution across NT and along rainfall gradient, ordination methods, comparison of floristic affinities across north Australia nationally and globally	Definition of floristic regions across NT rainfall gradient. Floristic dichotomy at 17–18°S following 650 mm isohyet. Rainfall most significant determinant with soil type and landform also significantly influencing floristic assemblages at finer scales	Bowman et al. (1988)
Ground-truthing sites with contrasting vegetation and soils representative of three regions of increasing aridity along transect; sub-tropical (King river, 1050 mm annual rainfall), semi-arid (Tennant Creek, 422 mm annual rf) and arid (Alice Springs, 275 mm annual rf)	Remote sensing, Landsat-MSS, NDVI	Quantified variability of spectral response of savanna vegetation for across rainfall and soils gradients. Vegetation classification, canopy cover estimates across rainfall gradient, separation of soil and vegetation spectra	Matheson and Ringrose (1994)
NATT sites established, 18 plots, 1–5 ha from Darwin (1650 mm annual rf) to Tennant Creek (400 mm annual rf) on massive red sands and loam soils. Sites grouped into five foci; Darwin, Katherine, Daly Waters, Newcastle Waters and Tennant Creek	Morphological classification of vegetation into six lifeform categories (forb, shrub or sub-shrub, tree, vine, graminoid and epiphyte). Reproductive classification into seven 'replacement strategies' (annual vs. seasonal and year round perennial). Site similarities using above variables assessed using Sorensen's Index of Similarity	Distribution of lifeforms and replacement strategies along rainfall gradient. Biogeographical boundary at approximately 16°S. Storage-roots become more prominent feature of vegetation north of this boundary, possibly due to increasing fire frequency. Fraction of annual species constant along NATT, woody deciduous species decline along transect	Egan and Williams (1996)
Transect of 15 contiguous cells (width 3.5° of longitude, length 1° of latitude), from NT coast (11°S) to South Australian border (26°S)	Floristic survey, using 20 × 20 m quadrats sampled within each cell of transect, ~2000+ quadrats sampled. Ordination and regression methods to correlate diversity indices with rainfall and elevation	Alpha (quadrat species richness) and beta (turnover of species) diversity declined with rainfall along transect, correlated with rainfall, elevation and topographic diversity	Bowman (1996)
As per Bowman (1996)	Quadrats sampled for basal area, % cover in addition to floristic and richness indices along transect. Landform and soils described in terms of slope, % gravel, rock cover and soil texture. Simple regression models used to correlate vegetation attributes with meteorological data (rainfall, temperatures)	Canopy height and basal area decline with rainfall to a minimum at 18.5°S latitude, the southern limit of monsoon rainfall along NATT. <i>Acacia</i> richness increases at this latitude with <i>Eucalypt</i> richness and basal area declining to minima at 21.5°S. Change in dominance of <i>Eucalyptus</i> to <i>Acacia</i> southwards attributed to minimum temperature of southern latitudes limiting <i>Eucalyptus</i> regeneration	Bowman and Connors (1996)
Approximately 2000 quadrats of 20 × 20 m sampled along 18 NATT sites, Darwin to Tennant Creek, NT	Quadrats established at NATT sites in savanna ecosystems north of 18°S. Texture used as a surrogate for PAM and PAN. Structural (tree height, basal area and cover), floristic and environmental variables measured (rainfall, soil texture, slope, gravel, % bare ground). Regression and ordination techniques used	Variation in structural (tree height, basal area, cover) and compositional (woody species richness, deciduous tree species richness) attributes described as a function of annual rainfall and soil texture. Predictive, empirical models developed describing height and basal area declines with rainfall, with slope of relationships modified by soil texture (sand, loam, clay substrates)	Williams et al. (1996)
Sampling at 17 NATT sites of Williams et al. (1996) plus the Howard Springs flux site, giving nine sand and nine loam sites. Three 30 × 30 m plots sampled within each 1 ha NATT site	Tree height and basal area from DBH and Bitterlich wedge measures, SLA of all dominant woody species along NATT, overstorey LAI using a non-destructive method (Adelaide technique after Andrew et al., 1979; O'Grady et al., 2000)	Provided mid dry season o/s LAI and relationship with basal area on sand and loam soils along the NATT. Basal and leaf area relations for top 10 <i>Eucalyptus</i> species	Hoogerwerf and van Wieringen (1999)
Climate records examined for eight long-term BoM [†] stations along the NATT	Statistical definition of rainy, monsoon and dry seasons with examination of onset timing of each season along NATT. Analysis undertaken during impact of ENSO and La Nina effected years for the Katherine station	Timing of extra-monsoonal rainfall events determinant of many important ecological processes for savanna vegetation (germination of grasses, woody species phenology). Relative contribution and importance of isolated rainfall events increases with latitude south. The Australian monsoon is affected by ENSO cycles	Cook and Heerdegen (2001)

Table 1 (Continued)

Sites	Methods	Key findings	Source
Integration of a range of data sources from studies across north Australian savanna. Data included tree growth rates and demographics, tree and grass water use, soil moisture data, grass productivity and observations of fire intensity, rate of spread and impacts on tree survival	Developed a process-based model (FLAMES) to examine the processes operating on the eucalypt dominated tree component of the northern Australian savannas, focussing on the interaction of water availability and fire. Tree population dynamics were simulated over time and space using differing fire and climate regimes	FLAMES simulated stand basal area along the NATT with good agreement between model output and measurements. Seasonal variability and inter-annual variability in rainfall is the critical driver of structure and density of tree stands in these savannas. Fire removes very young and old trees, and frequent fronting fires will lead to ongoing reductions in tree population density and thus carbon storage. Simulation of carbon fluxes associated with the tree population dynamics for different rainfalls were undertaken. Low fire frequency (1 in 10y) resulted in a carbon sink 85% of the simulation period at high rf sites (1600 mm). Reducing rainfall resulted in a higher probability of the site shifting to a carbon source. Fire impacts on tree populations at a sub-continental scale are secondary to rainfall variability as a driver of stand dynamics	Liedloff and Cook (2007, 2010)
Ecophysiological studies Leaves from dominant woody and herbaceous species sampled at 20 locations from Melville Island ~100 km north of Darwin (1801 annual rf) to Uluru, NT (310 mm annual rf)	C isotope discrimination (Δ), N isotope ratios ($\delta^{15}\text{N}$), foliar N and SLA measured in 50 tree species along NATT. Between 1 and 14 species sampled per site, with 3–5 leaves sampled for isotopic and N content analysis. Species partition into N fixing and non-N fixing species. Tree height and DBH also measured	Community averaged Δ for woody species was ~ constant for rainfalls above 475 mm annual rf (mean Δ $19.4 \pm 1.2\%$), likely due to replacement of functional type and species along gradient. Below this threshold, Δ decreased to 17‰ at 220 annual rf mm. Increasing foliar $\delta^{15}\text{N}$ values observed with decreasing rainfall along NATT, reaching maxima at ~16°S. South of 16°S tended decrease to with aridity. $\delta^{15}\text{N}$ values indicated N_2 fixation only at high rainfall	Schulze et al. (1998)
NATT sampled ~50 km intervals for 1750 km, Darwin to southern NT border giving 97 sampling locations	C isotope discrimination (Δ) used to infer distribution of dominant <i>Eucalyptus</i> species along NATT. Late dry season sampling of leaf and wood tissues from five replicate trees per dominate species of within each of 97 locations of the NATT	Non-linear response of the multispecies average leaf and wood Δ to decreasing rainfall. No change in Δ between 1400 and 400 annual rf mm along NATT, ~3‰ decrease by 200 mm annual rf zone. Patterns of Δ did not provide a simple measure of the physiological limits of woody species	Miller et al. (2001)
Dominant woody and grasses sampled at mesic savanna (Darwin region, 1650 mm annual rf and semi-arid sites (VRD Research Station, 435 mm annual rf)	Impact of grazing pressure and fire frequency on soil and foliar $\delta^{15}\text{N}$ of woody and grass species examined. Soil and tissue samples taken from grazed and ungrazed and burnt/unburnt sites at mesic vs. semi-arid savanna sites. Monsoon vine forest species also sampled	Limited response of $\delta^{15}\text{N}$ due to grazing pressure, fire regime and rainfall more significant drivers of savanna N dynamics.	Cook (2001)
Three sites along NATT, from Darwin region to south of Katherine used, at ~1560, 1200 and 990 mm annual rf. Leaf thickness and mass per area (LMA) were sampled at sites every ~20 km from Darwin to most southern site used (Cutta Cutta caves, NT)	Attributes of four woody savanna species common to three sites of increasing aridity were assessed during wet and dry seasons. Leaf attributes included LMA, thickness, N and chlorophyll content, leaf assimilation rates and stomatal conductance in saturating light in wet and dry seasons. Stand attributes included basal area, stem increment over 1 year plus monthly phenology. Soil N and P and gravel content determined for each site	Leaves at drier sites were thicker with higher mass per area compared to the mesic site. Assimilation rates per unit leaf mass were similar at all three sites, but were higher at the drier sites when expressed on a per unit leaf area basis. Results suggest lower LAI and stem density as rainfall declines enables maintenance of similar rates of assimilation per unit mass invested in leaves along transect	Prior et al. (2005)
Five sites along the NATT from 1370 to 640 mm rainfall used. Tree, shrub and grass cover measured and tree, shrub, grass foliage plus soil sampled for isotopic analysis. Savanna sites in Brazil and Ghana also sampled using the same sampling protocols	Relative contributions of tree and grass to savanna productivity assessed using $^{13}\text{C}/^{12}\text{C}$ isotopic ratios of woody and grass foliage and soil carbon. Comparisons made with south American and African savanna sites. A mixing model used to relate soil $\delta^{13}\text{C}$ to the relative abundances of C3 trees and C4 grasses	The model suggested that foliar projected cover of trees and grasses described relative contribution of each lifeform to NPP. Using maps of savanna woodiness, scaling suggested 60% of global savanna NPP attributed to C4 grasses, despite their short growing season. For the NATT sites this 70% of NPP was from grasses	Lloyd et al. (2008)
Flux studies Airborne flux measurements of ET and H along 1000 km transect, Arafura Sea to Tennant Creek during two field campaigns in the late dry season (September 1995) and early dry season (April 1997)	Repeated low-level N–S transects flights (~500 km) flown at ~25 m AGL, plus several short E–W transects over key habitats using airborne EC. Continuous video coverage of the landscape along the flight lines	Spatial variation of LE and H dynamic along NATT. Small-scale patterns in vegetation, surface water, fire activity, soils and geology correlated with H . The Bowen ratio was observed to increase with surface temperature	Matthews (1999), Matthews et al. (2000)

Table 1 (Continued)

Sites	Methods	Key findings	Source
Three NATT sites used, Howard Springs (1750 mm), south of Katherine (870 mm), Newcastle Waters (520 mm annual rf). All sites located on sand soils	Wet and late dry season measurements of surface energy balance (LE, H, G, R _n , surface conductance) made at all three sites using eddy covariance (EC) methods. Stand scale transpiration measured using heat pulse methods. Stand structure (canopy height, basal area, tree and grass LAI) also assessed at all sites during wet and dry seasons	Wet season LE was similar at all sites (~3.1–3.6 mm d ⁻¹) and did not reflect site differences in rainfall. Approximately 80% of flux was attributed to the understorey in the wet season. Dry season rates 2–18 times lower than wet, with site differences significant. Canopy water use determined by surface conductance and its response to atmospheric and soil water content and by seasonal adjustment to LAI	Hutley et al. (2001)
Modelling study using published NATT data describing tree water use and stand structure on sandy soils	Published relationships of tree water use and DBH at 3 NATT sites (O'Grady et al., 1999; O'Grady et al., 2000; Eamus et al., 2001) were combined with NATT basal area data along all 18 NATT sites. A simple bucket model of stand water use for the NATT was developed.	Simple water balance modelling suggests a minimum depth of sandy soil that needs to be exploited by trees declines with increasing aridity along the NATT from ~5 to <1 m at low rainfall sites. This is consistent with observations of shallow rooting in semi-arid savannas to maximise moisture uptake from small rainfall events	Cook et al. (2002)
Airborne flux measurements (ET, H, CO ₂) over northern NATT during TWP-ICE field campaigns in the late wet season (February 2006)	Repeated low-level transects (10–40 km long) flown at ~25 m AGL, plus several short transects over key habitats using airborne eddy-correlation method. Continuous imaging coverage of the landscape along the flight lines	When composited onto a 1 × 1 km 25 × 40 km grid, the influence of the vegetation structure on LE, H and CO ₂ flux was significant	Hacker (2007)

* Refers to abbreviation of BoM which stands for Australian Bureau of Meteorology.

4. SPECIAL site characterisation

4.1. Site distribution

The SPECIAL program consisted of long-term flux, meteorological and soil moisture monitoring from five flux tower sites distributed along the NATT, plus an intensive field campaign during 1–15 September 2008 detailed by Beringer et al. (in press). Three additional tower sites were established at the start of the intensive campaign. During the intensive campaign, measurements were taken of vegetation structure and floristics, leaf area index (LAI), leaf scale physiological properties (gas exchange, leaf isotope ratios, N and chlorophyll concentrations), vegetation and soil reflectance properties and soil physical properties. The flux towers were established across common vegetation types of the NATT and included a coastal wetland, four open-forest/woodland savanna sites, cleared sites and a semi-arid grassland (Mitchell grassland) on cracking clay at the low rainfall end of the transect (Table 2).

A considerable area of the northern coast of the NT is occupied by wetlands and floodplain communities associated with the large, meandering rivers that drain into the Arafura Sea. To quantify fluxes from this extensive land surface, a flux tower was established at Fogg Dam, a seasonal wetland ~50 km south of Darwin.

Fluxes from the dominant savanna vegetation were quantified using four tower sites spanning a 1200 mm rainfall gradient along the NATT. Observations were made at two open-forest savanna sites (Howard Springs, Daly River Uncleared) and a woodland savanna site (Dry River) as described in Table 2. These three sites span the range of *Eucalyptus tetrodonta*/*Eucalyptus miniata* dominated savanna communities, a widely distributed savanna type that occurs across the northern Australia. It and savannas of similar floristic assemblages occupy about 350 000 km² and occur above ~800 mm annual rainfall (Fox et al., 2001). These systems occur on the well drained and widely distributed red Kandosol (after Isbell, 2002) sands and sandy loams.

The fourth savanna tower site at Adelaide River and featured a savanna type that is distinct from the more common *E. tetrodonta*/*E. miniata* savanna. The dominant canopy species at this site were *Eucalyptus tectifera* and *Corymbia latifolia*, an assemblage that typically occurs on less well drained and heavier textured soils (hydrosols). This and other similar savanna woodlands dominated

by *E. tectifera* occupy ~96 000 km² across the savanna region (Fox et al., 2001).

The Daly River sites include an uncleared open-forest savanna site (Daly River Uncleared), an adjacent regenerating savanna site (Daly River Regrowth) and a long-term improved pasture site some 10 km from the uncleared and regrowth sites (Daly River Pasture). These three sites provide data on mass and energy exchanges across contrasting land uses (Weinmann et al., 2009).

At the semi-arid region of the NATT (~500 mm rainfall, 17°S), two further sites were established, an *Acacia* dominated woodland (Sturt Plains Woodland) and a Mitchell grassland site (Sturt Plains Grassland, Table 2), with a flux tower installed at the Mitchell grassland site. Mitchell grasslands are an extensive tussock grassland ecosystem that occur on heavy cracking clay soils, covering 93 782 km² across the Barkley Tablelands of the NT and extend into western Queensland.

4.2. Structural characterisation

Vegetation structure and floristics were characterised at each SPECIAL tower site using a 1 ha plot that was sub-divided into 20 m × 20 m grids and centred on the flux tower. Within the 1 ha plot, vegetation was assessed via measurements of; (1) woody plant diameter at breast height (DBH), (2) tree/shrub height, (3) species identification and (4) understorey biomass (vegetation below 2 m in height). Soil texture, surface moisture and bulk density measurements at 10 cm depth (five replicates per site) were also taken. Vegetation measurements were used to estimate mean canopy height, stem density and plot basal area (Fig. 2). Tree height and DBH measures were combined with allometric equations developed for the dominant savanna tree species of this region (Chen et al., 2003; Williams et al., 2005) to estimate above-ground woody biomass at each site. A differential GPS was employed to geo-reference each tree to enable precise mapping and linking to airborne LiDAR returns (Beringer et al., in press).

LAI is a critical variable in ecosystem studies but accurate measurement can be problematic (Macfarlane et al., 2007). During the September 2008 campaign, LAI estimates from three methods were averaged to give robust overstorey LAI values for the SPECIAL sites. The three LAI estimates were obtained from; (1) eight day composited MODIS collection 5 data, (2) the basal area of trees within the

Table 2

Vegetation structural attributes, classification and soil characteristics for the eight flux tower sites as used in the intensive observation period of the SPECIAL campaign. Common and plant species are given with vegetation classified using the 1:2 000 000 using Fox et al. (2001), the vegetation of the Australian tropical savanna. The spatial extent of each mapping unit as represented by the tower sites is given in km². Site soil orders are given as per the classification of Australian soils by Isbell (1996). Basal area is provided for woody stems >2 cm DBH. Mean \pm stand error for site LAI as estimated during the September 2008 ground campaign. Means were calculated from MODIS Collection 5 estimate and regressions against basal area and rainfall, see text for details. Mean annual rainfall is from 2000 to 2007 from SILO (Bureau of Meteorology) interpolated rainfall surfaces or nearby climate stations.

Site	Lat/Long	Vegetation characteristics	Annual rainfall (mm)	Canopy ht (m)	Stem density (ha ⁻¹)	Basal area (m ² ha ⁻¹)	Biomass (t ha ⁻¹)	LAI
Fogg Dam	12°32'42.79"S 131°18'25.86"E	Seasonally flooded wetland Veg unit C19 <i>Oryza rufipogon</i> , <i>Pseudoraphis spinescens</i> , <i>Eleocharis dulcis</i> Map unit area: 19 536 km ² Soil: black vertosol, cracking clay Land use: conservation	1401	0.5–1.5	–	–	~3–5	1.1
Howard Springs	12°29'39.12"S 131°09'09"E	Open-forest savanna Veg unit D4 <i>E. miniata</i> , <i>E. tetradonta</i> , <i>Erythrophleum chlorostachys</i> , <i>Cycas armstrongii</i> , <i>Sorghum</i> spp., <i>Heteropogon triticeus</i> Map unit extent: 59 986 km ² Soil: red kandosol with ironstone gravels Land use: vacant crown land, water management area	1714	18.0	661	9.7	62.4	1.04 \pm 0.07
Adelaide River	13°04'36.84"S 131°07'04.08"E	Woodland savanna Veg unit D10 <i>E. tectifera</i> , <i>C. latifolia</i> , <i>Planchonia careya</i> , <i>Sorghum</i> spp., <i>Chrysopogon fallax</i> Map unit area: 49 811 km ² Soil: yellow hydrosol, shallow, loamy sand with coarse gravel Land use: seasonal grazing, native pastures	1460	12.5	365	5.1	27.6	0.68 \pm 0.07
Daly River Uncleared	14°09'33.12"S 131°23'17.16"E	Woodland savanna Veg unit D4 <i>E. tetradonta</i> , <i>C. latifolia</i> , <i>Terminalia grandiflora</i> <i>Sorghum</i> sp., <i>Heteropogon triticeus</i> Map unit area: 59 986 km ² Soil: red kandosol, deep sand Land use: grazing, native pastures, low stocking density	1170	16.4	330	8.3	63.5	0.80 \pm 0.12
Daly River Regrowth	14°7'50.16"S 131°22'58.08"E	Regenerating woodland savanna Veg unit D4 <i>E. tetradonta</i> , <i>C. latifolia</i> , <i>Sorghum</i> sp., <i>Heteropogon</i> spp. Map unit area: 59 986 km ² Soil: red kandosol soil, deep sand Land use: grazing, native and introduced pastures, low stocking density	1170	3.3	410	1.3	2.8	0.11 \pm 0.01
Daly River Pasture	14°3'47.88"S 131°19'5.16"E	Tropical pasture <i>Chamaecrista rotundifolia</i> (Round-leaf cassia cv. Wynn), <i>Digitaria milijiana</i> (Jarra grass), <i>Aristida</i> sp. Soil: red kandosol, deep sand Land use: grazing, introduced pastures, low stocking density	1170	0.3	–	–	~2–5	~0.05
Dry River	15°15'31.62"S 132°22'14.04"E	Woodland savanna Veg unit D5 <i>E. tetradonta</i> , <i>E. dichromophloia</i> , <i>C. terminalis</i> , <i>Sorghum intrans</i> , <i>S. plumosum</i> , <i>Themeda triandra</i> , <i>Chrysopogon fallax</i> Map unit area: 32 583 km ² Soils: red kandosol with ironstone gravels Land use: grazing, native pastures, low stocking density	850	12.3	582	5.4	26.4	0.58 \pm 0.11
Sturt Plains (Woodland)*	17°10'58.44"S 133°21'9.36"E	Low woodland Veg unit E1 <i>Acacia cowleana</i> , <i>E. dichromophloia</i> , <i>Lysophyllum cunninghamii</i> Map unit area: 48 037 km ² Soils: red kandosol Land use: ungrazed, on managed property	535	5.9	438	5.2	3.9	0.39 \pm 0.11
Sturt Plains (Grassland)	17°09'2.76"S 133°21'1.14"E	Mitchell grassland Veg unit C17 <i>Astrebla</i> spp. Map unit area: 93 782 km ² Soils: grey vertosol, cracking clay Land use: grazing on native pastures, low stocking density	535	0.2				0

* No flux tower installed at this site.

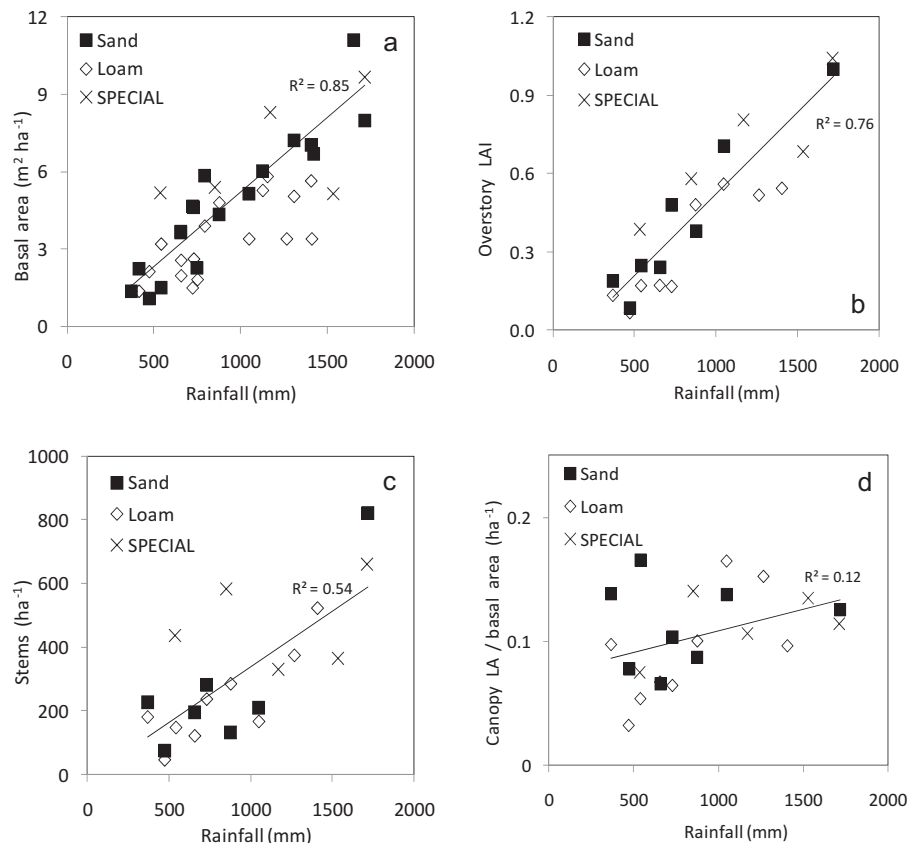


Fig. 2. Vegetation structural attributes of NATT and SPECIAL sites plotted against annual rainfall for each site. Data for basal area (a) and dry season overstorey LAI (b) for NATT sites were taken from Hoogerwerf and van Wieringen (1999). LAI from SPECIAL sites are estimated from regressions of basal area, site rainfall and MODIS Collection 5 (see Sea et al., 2011). Stem density (c) and canopy leaf area per unit basal area is also plotted (d). The SPECIAL sites for this plot are the open-forest/woodland savanna sites where flux towers were installed.

1 ha plots and (3) the mean annual rainfall at each site. As these estimates are for the late dry season, when understorey LAI is near zero, the MODIS estimates can be compared with data from the allometric methods.

For the allometric methods, Hoogerwerf and van Wieringen (1999) showed a high degree of correlation between basal area, mean annual rainfall and overstorey LAI ($R^2 = 0.79$ and 0.82 respectively) for 18 sites along the NATT on sand and loam soils. These regressions were applied to the basal area and annual rainfall data for each of the SPECIAL tower sites to provide estimates of dry season, overstorey LAI. The LAI values given in Table 2 for the woody savanna sites are the mean of the LAI values derived from the MODIS data, from the basal area measured over the 1 ha plots at each site and from the mean annual rainfall. LAI estimates for the wetland and grassland sites were obtained from Sea et al. (2011).

The representativeness of the SPECIAL tower sites in terms of capturing structural, and to a lesser extent, floristic change along the NATT, was assessed by comparing tower site data with the more comprehensive biogeographical studies that focussed on structural and floristic change (Table 1). This provides a measure of confidence in the spatial extrapolation of point-based fluxes to landscape and regional scales (e.g. Kanniah et al., 2011).

Tree population structure at each woody site was compared by constructing histograms of DBH across size/age classes. Frequency data were plotted on a semi-log plot against stem DBH and a negative exponential function fitted to enable comparison between tree populations. The slope of this relationship for a given site is determined by factors such as rainfall, soil attributes (available moisture and nutrients) plus fire and disturbance regimes that affect tree

growth, recruitment and mortality rates (Lehmann et al., 2008). Tree size class distributions from the SPECIAL sites were also compared to distributions from a large savanna tree population data base consisting of 4100 trees sampled across 133 sites over a 15 year period from three national parks in the NT (Russell-Smith et al., 2010). This extensive '3 Parks' database sampled across a range of savanna communities provides a reference stand structure with which to compare the SPECIAL tower plots and to assess their structural representativeness (Fig. 3).

4.3. Physiological characterisation

Leaf photosynthetic capacity is an important scalar for modelling canopy to landscape scale carbon and water exchanges (Baldocchi and Amthor, 2001). Stomatal conductance (g_s), maximum Rubisco carboxylation velocity (V_{cmax}), maximum photosynthetic rate (A_{max}) and light use efficiency (α) are key variables that require parameterisation for accurate modelling (Groenendijk et al., 2011).

Cernusak et al. (2006) reports on a detailed study of leaf characteristics as part of the intensive field campaign in September 2008 that targeted physiological attributes across all woody savanna dominant tower sites. Instantaneous leaf gas exchange measurements, leaf carbon isotope discrimination ($\Delta^{13}C$) and foliar N concentration were sampled for two common woody species at each flux tower site. An additional site, Boulia in the Barkly Table 1 and in south-west Queensland ($22^\circ 59' 40''S$, $139^\circ 56' 43''E$, Cernusak et al., 2006) was also used. This was the lowest rainfall site (~ 290 mm annual rainfall), with sandy soils and a mixture of *Aca-*

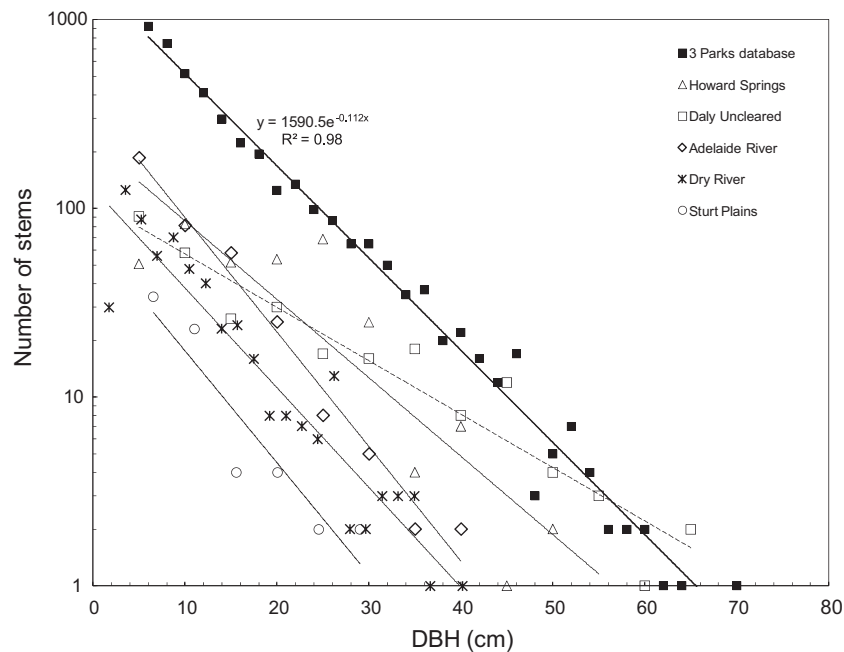


Fig. 3. Semi-log plot of the number of stems per DBH size class for all trees within the 1 ha plots sampled at each flux tower site. Also plotted is data from the '3 Parks' dataset of Russell-Smith et al. (2010). Fitted lines are negative exponential functions with the regression equation and R^2 given for the 3 Parks data set.

cia and *Corymbia* woody shrubs and small tree species present. Two *Corymbia* species were sampled. Leaf scale data presented here focus on variables frequently used in LSMs and compare maximal leaf (g_{smx}) and canopy (G_{cmx}) conductances (as opposed to daily means).

Portable photosynthesis systems (LiCor 6400, Licor Inc., USA) were used to develop $A-c_i$ and light use curves for six replicate leaves from each of two dominant overstorey tree or shrub species at each site. Leaf scale values of mean A_{max} , V_{cmax} , α and c_i/c_a for each species at each site are given in Fig. 4. Mean maximal leaf conductance was calculated from the initial conductance values taken under ambient CO_2 concentration and saturated radiation ($\sim 2000 \mu mol m^{-2} s^{-1}$ PFD) as part of the $A-c_i$ routine. Mean g_{smx} is also given in Fig. 4 for each species and site. Details of these and other leaf scale observations are given in Cernusak et al. (2006). To match g_{smx} estimates, canopy conductance was derived from flux tower measurements for a similar period to that of the field campaign, 1 September–14 October 2008, the late dry season. An inversion of the Penman–Monteith equation was used with measured values of LE available energy, VPD and wind speed to estimate canopy scale conductance. Values between 9 and 11 am local time were used to estimate G_{cmx} . Details of eddy covariance instrumentation and data analysis are given by Isaac et al.

4.4. Trends in vegetation structure and function

Fig. 2 compares basal area, stem density and overstorey LAI across the five woody savanna SPECIAL sites and 18 NATT sites as used by Hoogerwerf and Wieringen (1999). Basal area ranged from 2 to $10 m^2 ha^{-1}$ and overstorey LAI from 0.2 to ~ 1 over a 1200 mm rainfall gradient. A tight coupling of woody basal area, stem density and overstorey LAI with rainfall is evident, with the SPECIAL sites (sands) similar to the NATT sites (Fig. 2a–c). The ratio of overstorey leaf area per unit basal area across all sites is given in Fig. 2d. Tree canopy leaf area supported per unit basal area is approximately constant across the SPECIAL and NATT sites, with a regression with rainfall not significant ($P = 0.06$, $df = 21$). The distribution of tree size classes at each of the SPECIAL sites was similar (Fig. 3), with the line of best fit between the sites and between the '3 Parks' data set

not significant different (GLM, $P = 0.13$), except for the Daly River Uncleared site which differed from all other sites. This site had a lower slope and a distribution skewed towards larger tree sizes. The drier sites had lower stem density and smaller trees (left-shifted on the semi-log plot, Fig. 3), consistent with basal area data.

Fig. 4a–b gives values for physiological variables A_{max} , V_{cmax} , α , and the ratio of intercellular to atmospheric CO_2 concentrations during photosynthesis (c_i/c_a) plotted against mean annual rainfall for the SPECIAL sites. Mean values for two dominant species at each site are given and two-way ANOVA and post hoc tests suggested there were no differences between species and annual rainfall (except for *Corymbia terminalis* at the Boulia site). Maximal canopy conductance (g_{smx}) ranged between 0.10 and $0.15 mol m^{-2} s^{-1}$ across the sites with differences between sites marginal but evident (one-way ANOVA, $P = 0.045$, $df = 74$). Maximal canopy conductance (G_{cmx}) ranged from 0.1 to $0.035 mol m^{-2} s^{-1}$. A weak trend with site rainfall is evident (one-way ANOVA, $P = 0.01$, $df = 281$), with the high rainfall site, Howard Springs, different from all other sites. Site differences were still apparent after normalising G_{cmx} by site LAI (Fig. 4c), with Howard Springs and Adelaide River being significantly different from the drier sites Daly Driver and Dry River ($P = 0.01$, $df = 281$).

5. Discussion

The monsoon tropics of Australia is a largely intact region and as such is a unique landscape for linking vegetation structure to function by integrating with remote sensing and modelling tools. Over a decade ago, Bowman and Connors (1996) and others suggested ecophysiological and climatological studies were required to fully understand biogeographical patterns across this region. The SPECIAL program contributes to this broad aim.

Attempting to capture vegetation change over such a large gradient with only eight observational sites is problematic, however the sites used are broadly representative of environmental and vegetation gradients as observed along the NATT (Fig. 2). At this spatial scale, annual rainfall explained 80% of the variation of stand basal area and LAI, with fire regime, land use (grazing), soil characteristics and other climate factors (such as changes to VPD) contributing to

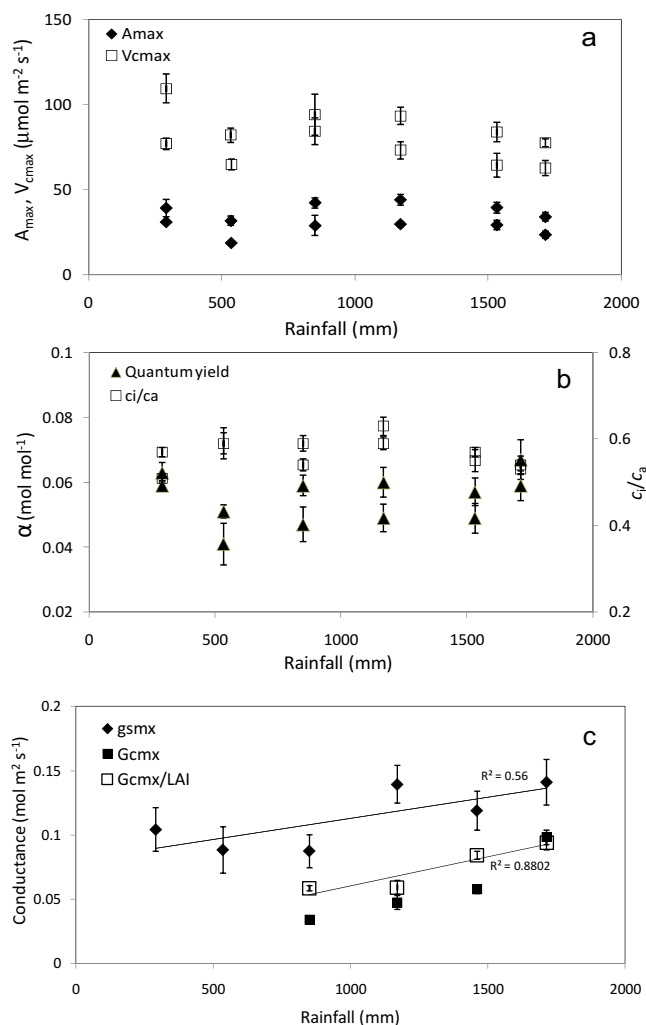


Fig. 4. (a, b) Mean values for physiological variables A_{max} , V_{cmax} , α , and the ratio of intercellular to atmospheric CO_2 concentrations during photosynthesis (c_i/c_a) plotted against rainfall for each flux tower site. Data taken from Cernusak et al. (2006). Error bars are standard errors of the mean, with values given for the two dominant woody species measured at each site. Daily mean maximal stomatal and mean maximal canopy conductance for each SPECIAL site is given in panel c) and is plotted against rainfall. Error bars are standard error of the mean. See text for data sources used.

the residual variance. The strength of this relationship is of note, given confounding factors such as the decline in fire frequency down the gradient, which will also influence productivity and stand structure (Lehmann et al., 2009). Grazing pressure was another variable not controlled for across the SPECIAL sites, with four of sites subjected grazing (Adelaide River, Daly River Uncleared, Daly River Regrowth and Dry River), although grazing pressures were typically low.

Comparison of tree size classes across the woody SPECIAL sites with the '3 Parks' data set suggested the SPECIAL sites have typical rates of growth, recruitment and mortality given the similarity of slopes evident in Fig. 3. The Daly River Uncleared site differed and has either higher growth and/or lower mortality rates and is more productive as a consequence, given the shift in tree size class to larger tree sizes. This may reflect grazing and fire suppression, as this site was situated on a managed property with deep sandy loam soils, or site quality (soil depth).

Privette et al. (2004) and Scholes et al. (2004) also report on savanna vegetation change along the rainfall gradient of the KT as part of the SAFARI 2000 program. As with this study, LAI was esti-

mated at five sites down a 650 mm gradient using several methods and a degree of within-site variability was found due to the differing methods used (Scholes et al., 2004). Woody LAI was also strong function of annual rainfall along the KT and ranged from ~ 2.0 at a broad-leaved deciduous savanna woodland (1000 mm annual rainfall) to 0.8 at a fine-leaved savanna/shrubland site (350 mm annual rainfall, Scholes et al., 2004). The ratio of LAI per unit rainfall along this gradient was approximately double that of the NATT. Overstorey LAI during the wet season at a 1000 mm annual rainfall on the NATT is ~ 1.25 (Hutley et al., 2001) and at 350 mm annual rainfall, NATT woody LAI is ~ 0.1 as compared to 0.8 as observed on the KT at this rainfall.

Despite significantly lower LAI along the NATT, basal area was comparable for a given rainfall suggesting the Eucalyptus and Corymbia species produce significantly more biomass per unit canopy leaf area than woody vegetation of the KT. Such comparisons between these savanna transects suggest functional differences in productivity efficiencies, potentially determined by differences in herbivory and nutrient cycling, fire regime and/or climate factors (e.g. temperature and VPD, given the altitude of the KT at ~ 1000 m asl compared to the NATT between 30 and 300 m asl, Cernusak et al., 2006).

Changes to key leaf scale physiological variables along the NATT are modest (Fig. 4), with limited or no site/species differences observed (although only two species were sampled per site). Maximum canopy conductance showed a decline with rainfall, suggesting available soil moisture was limiting gas exchange as rainfall declined. These observations are from the late dry season when available moisture is at its lowest. Differences in site LAI account for some of this variation (G_{cmx}/LAI) but the relationship was still significant (Fig. 4c) and suggests a feedback to soil moisture. Hutley et al. (2001) also reported a decline in canopy conductance during the late dry season at the three NATT sites used in that study, although there were no site differences during the wet season.

Spatial variation in the fluxes of carbon and water are likely to be explained by structural variation as opposed to species change, a similar conclusion to that of Miller et al. (2001) and Cernusak et al. (2006). Tight coupling of basal area and LAI with rainfall suggests canopy leaf area and stem density are optimised for a given rainfall and soil type. The ratio of canopy area to basal area was constant (Fig. 2d), a similar finding to that of Scholes et al. (2004), who reported a similar mean tree leaf area index along the KT, with stem density determining stand scale LAI.

Seasonal adjustment of canopy LAI and high rates of leaf turnover are also evident in these savannas, despite the dominance of evergreen species (Williams et al., 1997; O'Grady et al., 2000; Prior et al., 2005). Both spatial and temporal regulation of canopy gas exchange may be dominated by structural adjustment and leaf turnover in response to (1) the reduction in available moisture along gradient and, (2) the annual drought. There is little evidence of leaf scale physiological differences along the NATT and leaves of the evergreen canopy at any period of the seasonal cycle or location will consist of leaves that are adequately hydrated and physiologically efficient (Cernusak et al., 2006). This would explain the limited variation in observed wood and leaf $\Delta^{13}\text{C}$ (Miller et al., 2001).

Tight coupling of fluxes with structure may also explain why an optimality approach to modelling fluxes of CO_2 and water for these savannas is successful (Vegetation Optimisation Model, Schymanski et al., 2007, 2008). In this approach, respiration and construction costs of leaves, roots, trunks and branches are included in a calculation of the net carbon profit (NCP). An optimisation approach makes no assumptions about the particular vegetation or site characteristics and is based on the concept that vegetation adapts optimally to its environment. Schymanski et al. (2007) applied this model to the Howard Springs flux tower site and predicted canopy and root system properties, as well as the dynamics

of water use and CO₂ flux without constraining the model by nutrient availability or site-specific vegetation properties.

6. Conclusions

Of the world's savannas, the Australian savanna is something of an anomaly, given the dominance of evergreen species over deciduous (Bowman and Prior, 2005). Over the last 2–3 million years, north Australian climates have become more seasonal and thus fire prone, with Eucalypt and Corymbia species evolving fire and drought tolerances (Bowman et al., 2010). Fire and annual drought constraint productivity of these Eucalypt savannas (Hutley and Beringer, 2010), requiring resprouting and rapid turn-over of canopies post-fire. Canopy adjustment may confer a mechanism of optimising NCP (Schymanski et al., 2007), enabling Eucalypts to dominate one of the most seasonally extreme savanna climates in the world (Bowman and Prior, 2005; Liedloff and Cook, 2010).

Outputs from the SPECIAL campaign include estimates for key modelling parameters (e.g. V_{cmax} , A_{max}), which are significantly different when compared to default values used for savanna or 'seasonal vegetation' functional types in LSM or DGVMs (Beringer et al., in press). Regional modelling of savanna carbon and water fluxes will require integration of these revised parameters estimates and precise estimates of structural variables and soil moisture dynamics from remote sensing products. Observational campaigns such as this program and SAFARI play an important role in improving global modelling of terrestrial carbon and water cycling.

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References

- Andrew, M.H., Noble, I.R., Lange, R.T., 1979. A non-destructive method for estimating the weight of forage on shrubs. *Australian Rangelands Journal* 1, 225–231.
- Andreae, M.O., 1991. Biomass burning: its history, use and distribution and its impact on environmental quality and global climate. In: Levine, J.S. (Ed.), *Global Biomass Burning: Atmospheric, Climatic and Biospheric Implications*. MIT Press, Cambridge, Massachusetts, pp. 3–21.
- Baldocchi, D.D., Amthor, J.C., 2001. Canopy photosynthesis: history, measurements and models. In: Saugier, B., Mooney, H.A. (Eds.), *Terrestrial Global Productivity*. Academic Press, San Diego, USA, pp. 9–32.
- Beringer, J., Packham, D., Tapper, N.J., 1995. Biomass burning and resulting emissions in the Northern Territory, Australia. *International Journal of Wildland Fire* 5, 229–235.
- Beringer, J., Hutley, L.B., Tapper, N.J., Cernusak, L.A., 2007. Savanna fires and their impact on net ecosystem productivity in North Australia. *Global Change Biology* 13, 990–1004.
- Beringer, J., Hacker, J., Hutley, L.B., Leuning, R., Arndt, S.K., Amiri, R., Bannehr, L., Cernusak, L.A., Grover, S., Hensley, C., Hocking, D., Isaac, P., Jamali, H., Kas-turi, K., Livesley, S., Neininger, B., Paw U, K.T., Sea, W., Straten, D., Tapper, N.J., Weinmann, R., Wood, S., Zegelin, S. SPECIAL – The savanna patterns of energy and carbon integrated across the landscape campaign. *Bulletin of the American Meteorological Society*, in press.
- Beringer, J., Hutley, L.B., Hacker, J.M., Neininger, B., Paw, U.K.T., 2011. Patterns and processes of carbon, water and energy cycles across northern Australian landscapes: From point to region. *Agricultural and Forest Meteorology* 151, 1409–1416.
- Bowman, D.M.J.S., Wilson, B.A., Dunlop, C.R., 1988. Preliminary biogeographic analysis of the Northern Territory vascular flora. *Australian Journal of Botany* 36, 503–517.
- Bowman, D.M.J.S., 1996. Diversity patterns of woody species on a latitudinal transect from the monsoon tropics to desert in the Northern Territory, Australia. *Australian Journal of Botany* 44, 571–580.
- Bowman, D.M.J.S., Connors, G.T., 1996. Does low temperature cause the dominance of Acacia on the central Australian mountains? Evidence from a latitudinal gradient from 11° to 26° South in the Northern Territory, Australia. *Journal of Biogeography* 23, 245–256.
- Bowman, D.M.J.S., Prior, L.D., 2005. Turner review no. 10. Why do evergreen trees dominate the Australian seasonal tropics? *Australian Journal of Botany* 53, 379–399.
- Bowman, D.M., Brown, G.K., Braby, M.F., Brown, J.R., Cook, L., Crisp, M.D., Ford, F., Haberle, S., Hughes, J., Isagi, Y., Joseph, L., McBride, J., Nelson, G., Ladiges, P.Y., 2010. Biogeography of the Australian monsoon tropics. *Journal of Biogeography* 37, 201–216.
- Burbidge, N.T., 1960. The phytogeography of the Australian region. *Australian Journal of Botany* 8, 75–211.
- Cernusak, L.A., Hutley, L.B., Beringer, B., Tapper, N.J., 2006. Stem and leaf gas exchange and their responses to fire in a north-Australian tropical savanna. *Plant, Cell and Environment* 29, 632–646.
- Cernusak, L.A., Hutley, L.B., Beringer, J., Holtum, J.A.M., Turner, B.L., 2011. Photosynthetic physiology of eucalypts along a sub-continental rainfall gradient in northern Australia. *Agricultural and Forest Meteorology* 151, 1462–1470.
- Chen, X., Hutley, L.B., Eamus, D., 2003. Carbon balance of a tropical savanna in northern Australia. *Oecologia* 137, 405–416.
- Cook, G.D., 2001. Effects of frequent fires and grazing on stable nitrogen isotope ratios of vegetation in northern Australia. *Austral Ecology* 26, 630–636.
- Cook, G.D., Williams, R.J., Hutley, L.B., O'Grady, A.P., 2002. Variation in vegetative water use in the savannas of the North Australian Tropical Transect. *Journal of Vegetation Science* 13, 413–418.
- Cook, G.D., Heerdegen, R.G., 2001. Spatial variation in the duration of the rainy season in monsoonal Australia. *Journal of Climatology* 21, 1723–1732.
- Dilshad, M., Motha, J.A., Peel, L.J., 1996. Surface runoff, soil and nutrient losses from farming systems in the Australian semi-arid tropics. *Australian Journal of Experimental Agriculture* 36, 1003–1012.
- Eamus, D., Hutley, L.B., O'Grady, A.P., 2001. Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. *Tree Physiology* 21, 977–988.
- Egan, J.L., Williams, R.J., 1996. Lifeform distribution of woodland plant species along a moisture availability gradient in Australia's monsoonal tropics. *Australian Systematic Botany* 9, 205–217.
- Fox, I.D., Neldner, V.J., Wilson, G.W., Bannink, P.J., 2001. The Vegetation of the Australian Tropical Savannas. Environmental Protection Agency, Queensland Government, Brisbane.
- Grace, J., San, J.J., Meir, P., Miranda, H.S., Montes, R.A., 2006. Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography* 33, 387–400.
- Groenendijk, M., Dolman, A.J., van der Molen, M.K., Leuning, R., Arneeth, A., Delpierre, N., Gash, J.H.C., Lindroth, A., Richardson, A.D., Verbeeck, H., Wohlfahrt, G., 2011. Assessing parameter variability in a photosynthesis model within and between plant functional types using global Fluxnet eddy covariance data. *Agricultural and Forest Meteorology* 151, 22–38.
- Hacker, J.M., 2007. Airborne measurements of the atmospheric structure, evaporation and heat fluxes over the Arafura Sea and the Northern Australian savanna during the TWP-ICE field experiment. In: *Proceedings of the 14th National AMOS Conference*, 5–8 Feb 2007, Adelaide.
- Hoffmann, W.A., Schroeder, W., Jackson, R.B., 2002. Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. *Geophysical Research Letters* 29, doi:10.1029/2002GL015424.
- Hoogerwerf, C.G., van Wieringen, S.M., 1999. Leaf area index in the savannas of northern Australia: research along the North Australian Tropical Transect. BSc Thesis, Wageningen Agricultural University, Wageningen and CSIRO Terrestrial Ecosystem Research Centre, Darwin, NT, 72 pp.
- House, J.I., Archer, S., Breshears, D.D., Scholes, R., 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography* 30, 1763–1777.
- Hutley, L.B., O'Grady, A.P., Eamus, D., 2001. Monsoonal influences on evapotranspiration of savanna vegetation of northern Australia. *Oecologia* 126, 434–443.
- Hutley, L.B., Setterfield, S.A., 2008. Savannas. In: Jorgensen, S.E., Faith, B.D. (Eds.), *Encyclopaedia of Ecology*, vol. 4, 1st ed. Elsevier B.V., Oxford, pp. 3143–3154.
- Hutley, L.B., Beringer, J., 2010. Disturbance and climatic drivers of carbon dynamics of a north Australian tropical savanna. In: Hill, M.J., Hanan, N.P. (Eds.), *Ecosystem Function in Savannas: Measurement and Modeling at Landscape to Global Scales*. CRC Press, Boca Raton, pp. 57–75.
- Interim Biogeographic Regionalisation of Australia (IBRA), 2006. Department of the Environment, Water, Heritage and the Arts, Canberra.
- Isbell, R.F., 2002. Australian Soil Classification. CSIRO Publishing, Melbourne.
- Kanniah, K.D., Beringer, J., Hutley, L.B., Tapper, N.J., Zhu, X., 2009. Evaluation of collections 4 and 5 of the MODIS gross primary productivity product and algorithm improvement at a tropical savanna site in northern Australia. *Remote Sensing of Environment* 113, 1808–1822.
- Kanniah, K.D., Beringer, J., Hutley, L.B., 2010. A review of the environmental determinants of the spatio-temporal variability of north Australian savanna productivity. *Progress in Physical Geography* 34, 459–490.
- Kanniah, K.D., Beringer, J., Hutley, L.B., 2011. Environmental controls on the spatial variability of savanna productivity in the Northern Territory. *Australia Agricultural and Forest Meteorology* 151, 1429–1439.

- Koch, G.W., Vitousek, P.M., Steffen, W.L., Walker, B.H., 1995. Terrestrial transects for global change research. *Vegetation* 121, 53–65.
- Lehmann, C.E.R., Prior, L.D., Williams, R.J., Bowman, D.M.J.S., 2008. Spatio-temporal trends in savanna tree cover is driven by landscape disturbance. *Journal of Applied Ecology* 45, 1304–1311.
- Lehmann, C.E.R., Prior, L.D., Bowman, D.M.J.S., 2009. Fire controls population structure in four dominant tree species in a tropical savanna. *Oecologia* 161, 505–515.
- Liedloff, A., Cook, G.D., 2007. Modelling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the Flames simulation model. *Ecological Modelling* 200, 269–282.
- Liedloff, A., Cook, G.D., 2010. The interaction of fire and rainfall variability on tree structure and carbon fluxes in savannas: application of the Flames model. In: Hill, M.J., Hanan, N.P. (Eds.), *Ecosystem Function in Savannas: Measurement and Modeling at Landscape to Global Scales*. CRC/Taylor and Francis, Boca Raton, pp. 293–308.
- Luhar, A.K., Mitchell, R.M., Meyer, C.P., Qin, Y., Campbell, S., Gras, J.L., Parry, D., 2008. Biomass burning emissions over northern Australia constrained by aerosol measurements: II model validation, and impacts on air quality and radiative forcing. *Atmospheric Environment* 42, 1647–1664.
- Lloyd, J., Bird, M.I., Vellen, L., Miranda, A.C., Veenendaal, E.M., Djagbletey, G., Miranda, H.S., Cook, G., Farquhar, G.D., 2008. Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate. *Tree Physiology* 28, 451–468.
- Lynch, A.H., Abramson, D., Görden, K., Beringer, J., Uotila, P., 2007. Influence of savanna fire on Australian monsoon season precipitation and circulation as simulated using a distributed computing environment. *Geophysical Research Letters* 34, L20801, doi:10.1029/2007GL030879.
- Matthews, S., 1999. Turbulent heat fluxes over Australia's wet-dry tropics. Honours Thesis, Flinders University, 98 pp.
- Matthews, S., Hacker, J.M., Williams, A., Hutley, L.B., 2000. Heat fluxes over Northern Australia: results from aircraft measurements during the NATT experiment. In: *Proceedings of the AMOS 2000 Conference*, February 2000, Melbourne, Australia.
- Matheson, W., Ringrose, S., 1994. The development of image processing techniques to assess changes in green vegetation cover along a climatic gradient through Northern Territory, Australia. *International Journal of Remote Sensing* 15, 17–47.
- May, P.T., Mather, J.H., Vaughan, G., Jakob, C., McFarquhar, G.M., Bower, K.N., Mace, G.G., 2008. The tropical warm pool international cloud experiment. *Bulletin of the American Meteorological Society* 89, 629–649.
- Macfarlane, C., Arndt, S.K., Livesley, S.J., Edgar, A.C., White, D.A., Adams, M.A., Eamus, D., 2007. Estimation of leaf area index in eucalypt forest with vertical foliage, using cover and fullframe fisheye photography. *Forest Ecology and Management* 242, 756–763.
- McKenzie, N., Jacquier, D., Isbell, R., Brown, K., 2004. *Australian Soils and Landscapes: An Illustrated Compendium*. CSIRO Publishing, Melbourne, 416 pp.
- Menaut, J.C., Flouzat, G., Valentin, C., 1995. Modeling, mapping and remote sensing – the SALT project (CNRS, OSTOM and CNES). *Ecosystems and Global Change* 8, 261–279.
- Miller, J.M., Williams, R.J., Farquhar, G.D., 2001. Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia. *Functional Ecology* 15, 222–232.
- O'Grady, A.P., Eamus, D., Hutley, L.B., 1999. Transpiration increases during the dry season: patterns of tree water use in Eucalypt open-forests of Northern Australia. *Tree Physiology* 19, 591–597.
- O'Grady, A.P., Chen, X., Eamus, D., Hutley, L.B., 2000. Composition, structure, leaf area index and standing biomass of eucalypt open forests near Darwin in the Northern Territory, Australia. *Australian Journal of Botany* 48, 629–638.
- Privette, J.L., Tian, Y., Roberts, G., Scholes, R.J., Wang, Y., Caylor, K.K., Frost, P., Muke-labai, M., 2004. Vegetation structure characteristics and relationships of Kalahari woodlands and savannas. *Global Change Biology* 10, 281–291.
- Prior, L.D., Bowman, D.M.J.S., Eamus, D., 2005. Intra-specific variation in leaf attributes of four savanna tree species across a rainfall gradient in tropical Australia. *Australian Journal of Botany* 53, 323–335.
- Ringrose, S., Matheson, W., Vanderpost, C., 1998. Analysis of soil organic carbon and vegetation cover trends along the Botswana Kalahari Transect. *Journal of Arid Environments* 38, 379–396.
- Russell-Smith, J., Yates, C.P., 2007. Australian savanna fire regimes: context, scales, patchiness. *Fire Ecology* 3, 48–63.
- Russell-Smith, J., Price, O.F., Murphy, B.P., 2010. Managing the matrix: decadal responses of eucalypt-dominated mesic savanna to ambient fire regimes in three north Australian conservation reserves. *Ecological Applications* 20, 1615–1632.
- Scholes, R.J., Archer, S.R., 1997. Tree and grass interactions in savanna. *Annual Review of Ecology and Systematics* 28, 517–544.
- Scholes, R.J., Parsons, D.A.B., 1997. *The Kalahari Transect: Research on Global Change and Sustainable Development in Southern Africa*. International Geosphere-Biosphere Programme (IGBP) Report No. 42, Stockholm, 62 pp.
- Scholes, R.J., Frost, P.G.H., Tian, Y., 2004. Canopy structure in savannas along a moisture gradient on Kalahari sands. *Global Change Biology* 10, 292–302.
- Schulze, E.-D., Williams, R.J., Farquhar, G.D., Schulze, W., Langridge, J., Miller, J.M., Walker, B.H., 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* 25, 413–425.
- Scheiter, S., Higgins, S.I., 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach (aDGVm). *Global Change Biology* 15, 2224–2246.
- Schymanski, S.J., Roderick, M.L., Sivapalan, M., Hutley, L.B., Beringer, J., 2007. A test of the optimality approach to modelling canopy properties and CO₂ uptake by natural vegetation. *Plant, Cell and Environment* 30, 1586–1598.
- Schymanski, S.J., Roderick, M.L., Sivapalan, M., Hutley, L.B., Beringer, J., 2008. A canopy scale test of the optimal water use hypothesis. *Plant, Cell and Environment* 31, 97–111.
- Sea, W.B., Choler, P., Beringer, J., Weinmann, R.A., Hutley, L.B., Leuning, R., 2011. Documenting improvement in leaf area index estimates from MODIS using hemispherical photos for Australian savannas. *Agricultural and Forest Meteorology* 151, 1453–1461.
- van Der Werf, G.R., Randerson, J.T., Collatz, G.J., Giglio, L., 2003. Carbon emissions from fires in tropical and subtropical ecosystems. *Global Change Biology* 9, 547–562.
- Weinmann, R.A., Isaac, P.R., Hutley, L.B., Beringer, J., Grover, S., 2009. Surface energy balance from three land cover classes in a tropical savanna of the Daly River catchment, Northern Territory. *iLEAPS Science Conference*, Melbourne, 24–28 August 2009.
- Williams, R.J., Cook, G.D., Braithwaite, R.W., Andersen, A.N., Corbett, L.K., 1995. *Impact of Climate Change on Ecosystems and Species: Terrestrial Ecosystems*. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, 99 pp.
- Williams, R.J., Duff, G.A., Bowman, D.M.J.S., Cook, G.D., 1996. Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *Journal of Biogeography* 23, 747–756.
- Williams, R.J., Myers, B.A., Muller, M.J., Duff, G.A., Eamus, D., 1997. Leaf phenology of woody species in a northern Australian tropical savanna. *Ecology* 78, 2542–2558.
- Williams, R.J., Gill, A.M., Moore, P.H.R., 1998. Seasonal changes in fire behaviour in a tropical savanna in northern Australia. *International Journal of Wildland Fire* 8, 227–239.
- Williams, R.J., Zerihun, A., Montagu, K., Hoffman, M., Hutley, L.B., Chen, X., 2005. Allometry for estimating aboveground tree biomass in tropical and subtropical eucalypt woodlands: towards general predictive equations. *Australian Journal of Botany* 53, 607–619.
- Woinarski, J.C.Z.R., Mackey, B.G., Nix, H., Trail, B., 2007. *The Nature of Northern Australia: its Natural Values, Ecology, and Future Prospects*. ANU Electronic Press, Canberra.