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Environmental controls on the spatial variability of savanna productivity in the Northern Territory, Australia

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ABSTRACT

Gross Primary Productivity (GPP) is a critical measure of the health and sustainability of natural ecosystems. Understanding the magnitude, spatial patterns and processes of GPP will underpin predictions of the impact of climate change on the carbon cycle. In Australia, savannas account for one third of the terrestrial carbon stores and therefore, estimating the magnitude of savanna GPP and studying the spatial relationship between GPP and environmental determinants at the regional scale is essential in understanding ecosystem responses to increasing atmospheric CO_2 concentrations and climate change. In this study we employed an integrated approach combining in situ measurements, eddy covariance based flux tower data and remote sensing techniques to examine the role of environmental drivers in controlling the spatial variation in GPP of savannas in the Northern Territory (NT), Australia. We used field based light use efficiency (LUE), regional specific meteorology and Moderate Resolution Imaging Spectro-radiometer (MODIS) based fraction of absorbed Photosynthetically Active Radiation (fPAR) data to estimate GPP. The estimated GPP agreed quite well (only a 6% error) with GPP estimated from flux tower at the Howard Springs site. The spatial pattern of GPP along the Northern Australian Tropical Transect (NATT) was calculated and showed a strong gradient in GPP from the coast (12.50°S where rainfall was 1622 mm $year^{-1}$) to inland (17.73°S where mean rainfall was 643 mm $year^{-1}$) with a decrease of 77%. A decreasing trend in GPP with rainfall is noticed especially at the dry end of the transect studied. However, in the wet end and middle part of the transect (e.g. dominated by different *Eucalyptus* species), the response of GPP to changes in rainfall is reduced. This finding suggests that the influence of rainfall on various *Eucalyptus* species may be dampened by biotic factors. Our results suggest that future changes in precipitation driven by climate change may affect the future distribution and dynamics of GPP in northern Australia.

1. Introduction

Although savannas account for 33% of the terrestrial carbon stores in Australia (Williams et al., 2004), the patterns and processes of the fluxes of carbon into (photosynthesis) and out of (respiration and combustion) this ecosystem are still uncertain (Barrett et al., 2005; Hutley et al., 2005). The photosynthetic assimilation (gross primary productivity or GPP) is not well quantified yet it is a critical flux because the partitioning of carbon into the different ecosystem components depends on the initial quantity entering the system. Thus, estimating the correct magnitude of savanna GPP, describing its spatial and temporal patterns and analysing its dependency on environmental factors at the regional scale is essential in understanding ecosystem responses to increased atmospheric CO_2 concentrations and climate change. For northern Australia, elucidating the patterns of savanna productivity and understanding its driving mechanisms is important to identify 'hot spots' that need greater attention and management strategies to avoid fire. Improved management of savanna ecosystem is also critical in national and global policy decision making for combating global climate change and global warming (IPCC, 2007).

Recently, patch scale studies have quantified carbon pools and fluxes for mesic savanna in the Northern Territory (NT), Australia (Eamus et al., 2001; Chen et al., 2003; Beringer et al., 2003, 2007). These studies indicate that the savanna is a net biome production of 2.0 tC ha^{-1} $year^{-1}$, a significant carbon sink (Beringer et al., 2007) that may decline over time as other factors will limit productivity, such as competition for light, available nutrients, moisture and cyclonic disturbances (Hutley and Beringer, 2010). However, these

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patch scale estimates cannot be assumed to represent the entire region because the savanna biome varies widely in its vegetation structure and composition. For example, savannas are dominated by over storey trees with an under storey layer of grasses that form a continuum of vegetation types within the biome (Scholes and Archer, 1997). Each of the vegetation types differ in canopy cover, height, leaf area and thereby the capacity to exchange CO_2 with the atmosphere. Therefore, the estimation of savanna productivity over the entire region or sub-regions that cover different vegetation types is necessary when identifying locations of potential sinks or sources of carbon. Moreover, analyzing the influence of environmental factors on the spatial pattern of savanna productivity is indispensable to assess and predict the response of savannas to changing environmental conditions. Therefore, the 'Savanna Patterns of Energy and Carbon Integrated Across the Landscape' (SPECIAL), experimental program was undertaken to understand vegetation drivers of carbon, water and energy fluxes from north Australian savanna covering different vegetation types (see Beringer et al. in this issue). The current study uses a remote sensing approach to estimate gross primary productivity (GPP) of different vegetation types and analyzes the influence of environmental drivers on GPP at a sub continental scale (12°S to ~18°S) which also encompasses the six sites considered in SPECIAL campaign.

Numerous ecological studies have established that the overall spatial and temporal patterns of savanna structure and productivity are determined by mean annual rainfall, soil nutrient availability, CO_2 fertilization, herbivory, and fire (see Kanniah et al., 2010 for a review). For instance, the influence of precipitation gradients on savannas' ecosystem structure, function and biogeochemistry was studied during the Southern African regional science initiative – Kalahari transect wet season campaign (Midgley et al., 2004; Scanlon and Albertson, 2004; Scholes et al., 2004; Shugart et al., 2004). Similar studies were also conducted on above ground net primary productivity dynamics across a natural precipitation gradient in South America (Austin and Sala, 2002). In Australia, the influence of rainfall in determining savanna vegetation structure, composition, surface energy balance, conductance and tree water use have been established before (Egan and Williams, 1996; Williams et al., 1996; Ludwig et al., 1999; Hutley et al., 2001; Cook et al., 2002) along the North Australian tropical transect (NATT). Hutley et al. (in this issue) review previous researches along the NATT and provide the framework for study along this living laboratory. However, the influence of rainfall on productivity has not been studied in Australian savannas at the regional or multi temporal scale. This is the first study to analyze the spatial variation and environmental controls for the variation of GPP at the sub-regional scale in Australian savannas.

Studying large scale spatial patterns of savanna productivity continuously is most feasible using remote sensing techniques (Caylor and Shugart, 2004). Remote sensing has the potential to capture the highly heterogeneous savanna landscape over large spatial scales as well as the temporal dynamics such as the seasonal variability. Satellite based method for mapping GPP utilizes a light use efficiency (LUE) approach that takes advantage of remote sensing data (vegetation), meteorological inputs and relies on empirical relationships or constants such as LUE (Running et al., 2000). One major source of uncertainty for such models is the use of globally gridded meteorological fields to represent local meteorology because weather data is not available at every point across the land surface (Zhao et al., 2005). This can result in about 20% difference between estimated and simulated GPP (Zhao et al., 2006; Jung et al., 2007). Nevertheless, there are still many good remote sensing based LUE models that provide reasonably good estimation of GPP (Xiao et al., 2005a,b; Maselli et al., 2006; Yuan et al., 2007). These studies have illustrated that reliable estimates of satellite based vegetation indices and local meteorological data can realistically reproduce ecosystem GPP patterns and magnitudes. In a previous study, Kanniah et al. (2009) showed that accurate estimates of meteorological inputs, vegetation indices and LUE can produce reliable estimate of GPP for a woodland savanna site in northern Australia. The current study is an extension of the previous study that aims to:

(i) quantify the monthly GPP across the entire savanna region of the Northern Territory (NT) using remotely sensed vegetation indices (i.e. fPAR), regional specific meteorological data and vegetation specific LUE.
(ii) analyze the spatial pattern of GPP along the major rainfall gradient (NATT) in the NT.

Although there is a systematic variation in climate and vegetation along the NATT, the spatial pattern of GPP and the influence of rainfall as an environmental driver of GPP has not been analyzed in this region. Thus, in this study we seek to answer if there is any distinct spatial pattern in terms of productivity along the rainfall gradient and if rainfall is a major driver of GPP in this region. Vegetation productivity is an important environmental property because it is a result of an interaction between plants and their environment. Any changes in productivity therefore can alter a variety of environmental variables such as temperature, light, water, nutrients and CO_2 (Austin and Gaywood, 1994). Productivity can be considered as a collective property of the vegetation with potentially different responses to different gradients.

2. Study region

Northern Australian savannas are found in four major regions namely Kimberley, the Gulf country, Cape York peninsular and Northern Territory (Woinarski et al., 2007). The Northern Territory (NT) savannas occupy much of the north-central region (Inset in Fig. 1) and comprise ~32.6% of the total savanna cover in northern Australia (based on classification by Fox et al., 2001). Across the huge extent of savannas in the NT, there is significant spatial and temporal variability in climatic drivers such as rainfall, temperature and vapor pressure deficit (VPD) resulting in a highly varied distribution, composition, structure and function of savannas over plant successional timescales (see Beringer et al., in this issue) for a description of climatology along major sites down the NATT). Within the savanna region of the NT Fox et al. (2001) have identified 19 vegetation types which were then regrouped into 8 classes based on structural and plant functional types (Kanniah, 2009) (Fig. 1). These vegetation types form a continuum from the wet coastal landscapes to the arid inland regions across the strong rainfall gradient which is 1622 mm $year^{-1}$ at latitude 12.50°S and 643 mm $year^{-1}$ at 17.73°S. A total of 31 sites were established in NATT under an IGBP (International Geosphere – Biosphere Programme) transect. From these, a total of 21 sites that represent different rainfall regimes and savanna types across the same gradient and region were chosen in this study (Fig. 1). A subset of the sites were used in the larger study (SPECIAL) that examine the Patterns and processes of carbon, water and energy cycles across northern Australian landscapes (see Beringer et al., in this issue).

In addition to the spatial variability, there is a large temporal variability that results from the two distinct seasons that dominate this ecosystem: the wet (December to April) and dry (May to November). An extended and predictable period of monsoon activity brings extensive rain in the northern parts of the NT in the wet season months (Taylor and Tulloch, 1985 in Hutley et al., 2001). The large spatial and seasonal changes in precipitation directly control

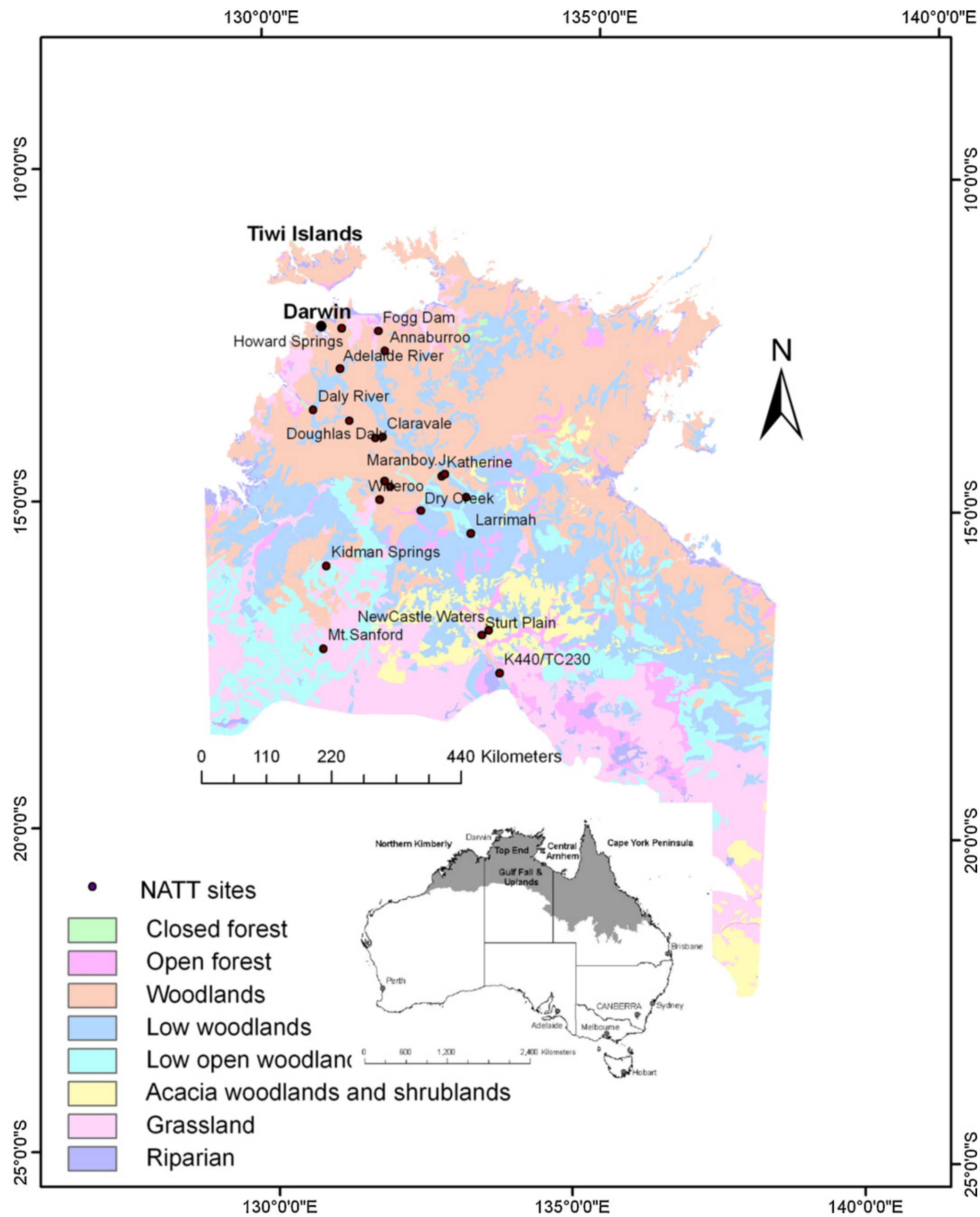

Fig. 1. Savanna vegetation classes that were aggregated into eight structural/functional classes in the Northern Territory, Australia (source: Fox et al., 2001) and the Northern Australian Tropical Transect (NATT) sites used to study the spatial variation in savanna GPP. Refer to Table 1 for details on the NATT sites.

soil water content (Cook and Heerdegen, 2001) and hence the vegetations' structure, composition and function. Generally, the coastal site (Howard Springs – Fig. 1) receives ∼1600 mm rainfall in the wet season (December to April) than Newcastle Waters (600 mm) located further south (Kanniah, 2009). High rainfall and humidity in the wet season causes the VPD to be lower in Howard Springs (1.5 kPa) compared to Newcastle Waters (2.6 kPa) (Kanniah, 2009). In contrast, the dry season (May to November) is characterized by prevailing dry south east trade winds. As a result, little or no rainfall is received during this time of the year and the VPD is high and ranges between 2.3 and 3.1 kPa among sites (Kanniah, 2009). Regions south of the coast receive rainfall from small, isolated convective storms (Cook and Heerdegen, 2001). In the far south, rainfall also comes from Southern cold fronts (Beringer and Tapper, 2000).

Unlike rainfall and VPD, solar radiation and temperature do not exhibit a clear distinction between sites along the NATT. The difference in the wet season radiation is 13% among these sites which decreases to only 4% in the dry season (Kanniah, 2009). High cloud cover in the wet season in coastal regions is responsible for the relatively large difference in radiation in the wet season. The difference in temperature in the wet season is minimal among the sites (ranging between 28 °C and 29 °C). However, inland temperature is lower in the dry season (winter). For example in Newcastle Waters (−17.07°S, Fig. 1) the monthly temperature is lowest in July with 19.6 °C, whereas in Howard Springs the lowest monthly temperature is 23.9 °C (Kanniah, 2009).

Like many other savanna systems, savannas in the NT are also adapted to highly weathered landscapes with relatively low relief and low nutrient soils. Weathering, and leaching of nutrients in a stable high temperature landscape is the main reason for the low nutrient soils (Gillison, 1983) (see Hutley et al., in this issue). The distinct seasonal climate, along with the strong north-south gradient in annual rainfall and variability in soil types across NT modulate the structure and spatial distribution of vegetation types in this region (see Hutley et al., in this issue). The major savanna type found in wetter areas in the NT is woodland (Fig. 1) dominated by *Eucalyptus miniata* and *Eucalyptus tetrodonta*. The under storey is predominantly vegetated by annual grasses, i.e. annual *Sorghum* (Egan and Williams, 1996; Williams et al., 1996). As rainfall decreases inland towards the south, low and sparse vegetation (low open woodlands and grasslands) are abundant (Fig. 1) and perennial grasses become more abundant in the under storey. This shows that savannas in northern Australia exhibit a spatial variation in vegetation structure, composition and possibly productivity that change gradually over hundreds of kilometers (Egan and Williams, 1996; Williams et al., 1996). Therefore, the spatial variation of savanna productivity and its environmental determinants were analyzed in this study using the specific datasets and methods as detailed in the following section.

We also selected four sites (Howard Springs, Daly River, Katherine and Newcastle Waters) that represent different rainfall regimes and vegetation structure along the NATT to describe the temporal and spatial patterns of fPAR. These sites were chosen also due to the availability of field data (i.e. LAI) that were used to describe the patterns of fPAR in these sites.

3. Data and methodology

To determine GPP for the savannas of the NT region, a simple light use efficiency (LUE) model was used along with gridded satellite remote sensing (MODIS) fPAR (fraction of absorbed photosynthetically active radiation) and gridded meteorological data. The LUE approach was originally formulated by Monteith (1972) and has been subsequently modified for remote-sensing by the MODIS land science team (Heinsch et al., 2003) as:

$$GPP = APAR \times LUE \times T_{MIN}\ \ scalar \times VPD\ \ scalar \quad (1)$$

where, GPP is the gross primary productivity ($g\,C\,m^{-2}\,day^{-1}$), APAR (MJ) is the total PAR (Photosynthetically Absorbed Radiation) absorbed by a canopy (estimated as APAR = fPAR × PAR) and fPAR is the fraction of PAR absorbed by canopy. LUE is the maximum potential LUE ($g\,C\,MJ^{-1}$) of a particular vegetation type that is constrained by environmental stress i.e. daytime vapor pressure deficit (VPD) and daily minimum temperature, T_{MIN} (LUE = maximum LUE × VPDscalar[1] × T_{MIN}scalar[2]). The scalars vary from 0 to 1. The inputs used to estimate MODIS GPP and the overall methodology adopted to estimate GPP at the regional scale in the NT are shown in Fig. 2 and the elements are described in the subsections below.

3.1. MODIS fPAR data

MODIS Collection 5 fPAR data (MOD15) from the Terra sensor were used in this study since it has been previously validated against field data and shown to be of acceptable accuracy (Kanniah et al., 2009). Similarly, MODIS LAI (Collection 5) was also found to be in good agreement with ground-based LAI estimates from hemispherical photos along NATT (see Sea et al., in this issue). The spatial

[1] VPD scalar = $\frac{(VPD_{max} - \text{daytime average VPD})}{(VPD_{max} - VPD_{min})}$ where VPD_{min} is the minimum VPD at which LUE is maximum, VPD_{max} is the maximum VPD at which LUE = 0.

[2] TMIN scalar = $\frac{T_{MIN} - T_{MIN\,min}}{T_{MIN\,max} - T_{MIN\,min}}$ where, $T_{MIN\,min}$ is the daily minimum temperature at which LUE = 0, $T_{MIN\,max}$ is the daily minimum temperature at which LUE is maximum.

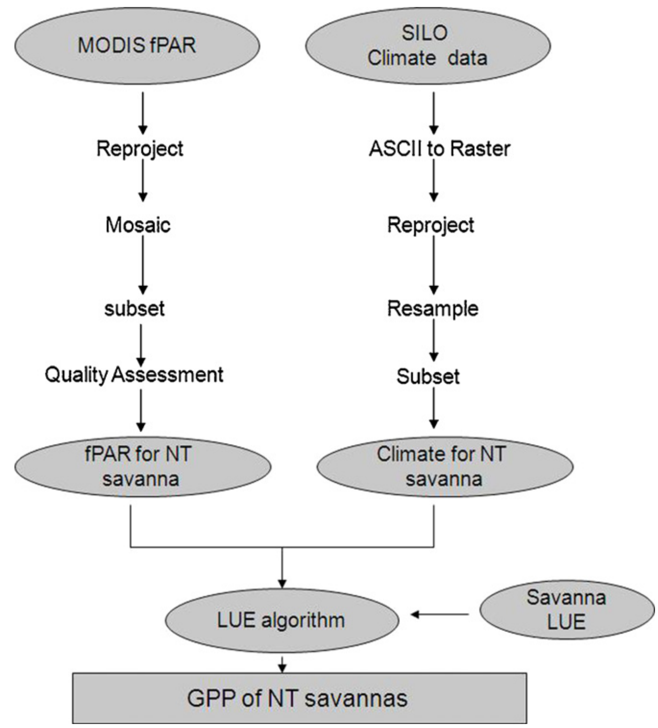

Fig. 2. Flow chart showing datasets and methodology adopted to estimate GPP (gross primary productivity) for the Northern Territory (NT) savanna region using a LUE (light use efficiency) algorithm. ASCII represents American Standard Code for Information Interchange.

resolution of MODIS LAI/fPAR data is ~1 km and is aggregated into 8 day composites. MODIS LAI/fPAR data were acquired for the whole NT region of Australia which included MODIS tiles h29 v10, h30 v10, h31 v10 and h30 v11 for the period February 2000 to December 2007 and were obtained from the NASA EOS Data Gateway website (http://edcimswww.cr.usgs.gov/pub/imswelcome/).

Good quality MODIS LAI/fPAR data were selected based on the quality control information stored in layer 3 of MOD15 product. Each MODIS tile contains LAI, fPAR and QA (quality assessment) variable data sets. The QA variable data sets contain information about retrieval status such as the overall quality of input data, cloud condition, and the algorithm used to retrieve LAI and fPAR. LAI and fPAR derived by the MRT (main radiative transfer) algorithm under cloudless conditions (QC = 0) are most reliable (Myneni et al., 2002) and these values were used to estimate GPP in NT in this study.

3.2. SILO Climate data

MODIS fPAR are spatially gridded datasets and therefore to calculate GPP over the NT savanna region, meteorological data needs to spatially match the MODIS data. Gridded meteorological data (SILO) from the Department of Natural Resources and Water, Queensland (DNRW) were obtained using the 'SILO Data Drill' service, which supplies long term daily meteorological data such as rainfall, solar radiation, vapor pressure, daily minimum and maximum temperature and relative humidity (http://www.longpaddock.qld.gov.au/silo/). These datasets were created specifically to provide spatially and temporally continuous climate data for spatial modeling purposes at 0.05° (5 km) resolution. SILO data were constructed for the continent using the Australian weather station observations at point locations collected by the Bureau of Meteorology (Jeffrey et al., 2001).

Climate data were provided by the DNRW in ASCII format and were converted into raster in ARCGIS (a geographical information system) software version 9.2 (ESRI, http://www.esri.com/). The climate data were composited into 8- day averages (average for temperature and VPD and 8 day sum for radiation) to match MODIS 8 day composite fPAR data. They were also reprojected into lambert conformal conic projection, and resampled from ~5 km^2 to 1 km^2 to match the MODIS fPAR. The incident shortwave radiation (MJ day^{-1}) was converted into PAR by multiplying with a factor of 0.47 (Kanniah, 2009). From the datasets: rainfall, minimum and maximum temperature, minimum and maximum relative humidity and solar radiation were used in this study. Daytime VPD (Jeffrey et al., 2001) was calculated in this study using the formula of Allen et al. (1998).

With these meteorological datasets and fPAR; GPP was estimated for each cell across the savanna region in the NT. Spatially explicit information on LUE is not available and in MODIS, maximum LUE is assigned as a constant for each biome type. The MODIS LUE value for the savanna biome was found to be inappropriate for Australian savannas and in this study we used a maximum LUE value of 1.26 g C MJ^{-1} calculated specifically for Australian savannas (Kanniah et al., 2009). This value was calculated using GPP derived from flux tower at Howard Springs and fPAR estimated from field based LAI (Kanniah et al., 2009). We used a constant LUE across the NATT sites because other studies have shown little variation in leaf and canopy LUE for different sites and different savanna species within a site along the NATT (Cernusak et al., in this issue; Issac et al., in this issue). In the MODIS algorithm the maximum LUE is downscaled by daytime VPD and daily T_{MIN} factors (Heinsch et al., 2003 – Eq. (1)). These VPD and T_{MIN} scalars were calculated spatially for each of the grid cells for each 8 day composite for the NT (Eq. (1)). GPP estimated with a LUE algorithm for the savanna region in the NT was analyzed for the NATT sites as described in Section 2.

4. Results and discussion

4.1. fPAR

Howard Springs flux tower site was chosen for the validation of fPAR and GPP (Section 4.3) due to the availability of long term observational data of plant physiology, GPP and meteorology. The quality controlled MODIS fPAR data (derived by MRT under cloudless sky) was used to examine the temporal and spatial patterns of fPAR values at four sites (Howard Springs, Daly River, Katherine and Newcastle Waters). MODIS provided plausible temporal patterns in fPAR over the sites chosen across the north-south rainfall gradient (Fig. 3). This gives some confidence in using MODIS Collection 5 fPAR data to estimate regional GPP in this study. Decreases in MODIS fPAR values coincided with decreasing rainfall and a decline in basal area (see Hutley et al., in this issue) and Leaf Area Index (see Sea et al., in this issue) along the NATT transect (Fig. 3 and Table 1). For example, woodlands, low woodlands and low open woodlands dominate areas with intermediate levels of rainfall (~600–1000 mm year^{-1}) and Acacia and open grasslands are found predominantly in the driest parts (<400 mm year^{-1}). FPAR also generally increases with increasing canopy cover (represented by LAI-Table 1) and vegetation height (Spessa et al., 2005; Hutley et al., in this issue). Seasonal mean fPAR (2000–2007) at Howard Springs was 52.21% ± 1.17 (mean ± SE) (Fig. 3a), but this value reduced to 38.71% ± 1.12 at Daly River (Fig. 3b), 35.71% ± 0.62 at Katherine (Fig. 3c) and 27.70% ± 0.74 at Newcastle Waters (Fig. 3d), which receives relatively low rainfall.

Howard Springs and Daly River had a large SE of fPAR, indicating a large seasonal variability due to the presence of dense annual grass species (*Sorghum* spp.) that dominate the under storey in the wet season, but senescence in the dry season. The seasonal changes in total LAI is quite large at these sites. For instance, at Howard Springs, the maximum LAI can reach 2.30 in the wet season, but drop to 0.8 in the dry season (O'grady et al., 2000). In contrast, Katherine and Newcastle Waters had wet season maximum total LAI of only 1.14 and 0.49 respectively (Hoogerwerf and Van Wieringen, 2000; Hutley et al., 2001). In these sites, the under storey is co-dominated by grasses and shrubs. For example, in Newcastle Waters, as the rainfall decreases, shrub species (*Acacia lysiphloia*) dominate the under storey besides *A. shirleyi* and *Sorghum* spp., whilst the over storey consists of low open woodland trees i.e. *E. terminalis* and *E. Capricornia* (Hutley et al., 2001). This may explain the reduced fPAR values and lower variability at low rainfall sites compared to the wetter sites located near coast (Egan and Williams, 1996).

Large inter-annual variations of fPAR were found in the drier sites (Newcastle Waters – SE of 1.19) compared to the wetter sites such as Howard Springs or Daly River (SE of 0.82 and 0.45, respectively). This may be due to consistent inter-annual wet season (monsoon) rainfall in the northern (mesic) part of the NT, compared to the more highly variable rainfall in the drier sites (Cook and Heerdegen, 2001) that are on the fringes of the monsoonal rain belt. For example, in the drier sites of the NT (e.g. Katherine and Newcastle Waters); rainfall is highly variable and dependent on either monsoon incursion from the north or weak frontal systems from the south, thus, making it hard to predict the onset of the rainy season. In Howard Springs and Daly Rivers, the rainy season is more predictable (December to April) and therefore, the inter-annual variation of fPAR is much smaller (Cook and Heerdegen, 2001).

4.2. Meteorological variables

Meteorological variables from SILO including rainfall, PAR, temperature, and VPD were validated against data that were measured at the flux tower to gain some confidence in using these datasets. Results (Kanniah, 2009) showed that PAR and daily average temperature from the spatially gridded SILO matched quite well with flux tower data. Overall, from 2001 to 2006 (period for available tower data) PAR, and daily average temperature only slightly overestimated tower data (2.4% and 3.8%, respectively). In contrast, the daytime VPD scalar (Eq. (1)) calculated using SILO data was considerably lower (17%) compared to VPD scalar calculated using tower data. Similarly, rainfall from SILO was also lower (14%) compared to tower data.

4.3. Performance of the LUE model

GPP calculated using MODIS Collection 5 fPAR data and climate data from DNRW were extracted for a single pixel at the Howard Springs site by making an assumption that the fetch of the tower was approximately 1 km^2 (Beringer et al., 2007), following the methods of Maselli et al. (2006) and Coops et al. (2007). The estimated GPP was validated against GPP estimated using flux tower measurements at the Howard Springs woody savanna site. A *t*-test for independent samples showed that GPP calculated using the best QC fPAR values were not significantly different from tower GPP ($t_{115,63} = 0.90$, $p = 0.37$). This was further indicated by high index of agreement (IOA) (0.93), low RMSE (0.80 g C m^{-2} day^{-1}) and RPE (−6.3%) values. Overall (2001 to 2006), GPP estimated in this study (average GPP for 6 years) was lower than tower derived GPP by only 6%.

Quantification of the spatial variability in productivity across an environmental gradient affords an opportunity to evaluate plant–environment interactions and plant responses to environ-

Table 1

Details of the sites used in this study that include sites from the SPECIAL campaign (Beringer et al., in this issue) (asterixed*) as well as the Northern Australian Tropical Transect (NATT) (Anon, 1994 in Williams et al., 1996). Annual GPP (gross primary productivity), fPAR (fraction of absorbed Photosynthetically Active Radiation), LAI (leaf area index), PAR (Photosynthetically Active Radiation), VPD (vapor pressure deficit), temperature and rainfall along the transect are shown. Annual rainfall was extracted from SILO datasets for period from 2000 to 2007. Data source for fPAR and LAI: MODIS (Collection 5) and for meteorology (SILO). Daily average temperature was calculated as the average of daily minimum and maximum temperature. Data are shown as annual values ± SE from 2000 to 2007.

Sites	Location (Latitude, Longitude)	Soil type	Savanna Vegetation Groups (Fox et al., 2001)	Dominant Species	Annual rainfall ± SE (mm)	GPP ± SE (gC m^{-2} $year^{-1}$)	Fpar ± SE (%)	LAI ± SE (m^2 m^{-2})	PAR ± SE (MJ)	Daytime VPD ± SE (kPa)	Daily average temperature ± SE (°C)
*Howard Springs	−12.50, 131.15	Sand	Woodlands	*Eucalyptus miniata Erythrophleum chlorostachys Terminalia ferdinandiana*	1621 ± 130	1364.71 ± 33.51	52.21 ± 1.17	1.55 ± 0.04	3464.31 ± 30.12	1.95 ± 0.0.3	27.25 ± 0.20
*Fogg Dam	−12.54, 131.71	Wetland, black soil	Grasslands	In the dry season grasses *Oryzarufipogon* and *Pseudoraphis spinescens*, and sedges *Eleocharisdulcis*	1447 ± 100	1047.41 ± 43.24	49.46 ± 1.27	1.49 ± 0.03	3430.94 ± 39.76	2.13 ± 0.03	27.66 ± 0.21
Annaburroo	−12.84, 131.81	Sand	Woodlands		1489 ± 102	977.41 ± 24.99	48.4 ± 0.88	1.39 ± 0.03	3387.94 ± 50.39	2.20 ± 0.03	27.49 ± 0.23
*Adelaide River	−13.10, 131.12	–	Woodlands	*Eucalyptus tectifica,Planchonia careya* and *Buchanania obovata*	1531 ± 122	834.06 ± 110.96	35.21 ± 0.85	1.42 ± 0.30	3402.45 ± 41.91	2.20 ± 0.05	27.25 ± 0.25
Daly River	−13.72, 130.70	Sand	Low woodlands	*Terminalia grand flora,Eucalyptus tetrodonta* & *Eucalyptus latifolia*	1393 ± 141	841.86 ± 31.49	38.71 ± 1.12	0.98 ± 0.03	3391.99 ± 38.52	2.17 ± 0.03	26.74 ± 0.27
Douglas Daly	−13.89, 131.27	Sand	Woodlands		1105 ± 88	782.06 ± 41.14	43.54 ± 0.89	1.18 ± 0.03	3353.10 ± 58.56	2.35 ± 0.03	26.94 ± 0.30
Claravale	−14.14, 131.77	Sand	Woodlands		1189 ± 91	831.81 ± 37.35	38.99 ± 1.02	0.98 ± 0.02	3317.02 ± 75.47	2.32 ± 0.03	26.84 ± 0.31
*Daly River flux site	−14.16, 131.66	Sand	Woodlands		1206 ± 92	789.41 ± 34.86	44.67 ± 0.82	1.19 ± 0.02	3328.54 ± 72.61	2.36 ± 0.03	27.01 ± 0.31
Maranboy Junction	−14.70, 132.74	Sand	Low woodlands		1111 ± 110	694.45 ± 26.43	38.17 ± 0.85	0.97 ± 0.02	3406.62 ± 62.11	2.34. ± 0.03	26.51 ± 0.36
Katherine Flux site	−14.73, 132.70	Sand	Woodlands		1113.50 ± 108	646.76 ± 26.04	35.71 ± 0.62	0.86 ± 0.01	3399.45 ± 61.42	2.34 ± 0.03	26.25 ± 0.37
Scott Crk KZH site	−14.81, 131.81	Sand	Woodlands		999 ± 83	611.53 ± 33.03	38.91 ± 0.89	1.00 ± 0.02	3419.01 ± 58.57	2.55 ± 0.03	27.24 ± 0.35
Scott Creek	−14.90, 131.89	Sand	Woodlands		991 ± 85	682.73 ± 39.47	42.09 ± 1.04	1.11 ± 0.03	3421.13 ± 57.51	2.52 ± 0.03	27.01 ± 0.35
TC550 Stuart Hwy Kath-TC	−15.05, 133.08	Sand	Low woodlands		943 ± 102	681.23 ± 36.56	41.44 ± 0.87	1.09 ± 0.02	3445.75 ± 57.15	2.50 ± 0.04	26.69 ± 0.38
Willeroo	−15.09, 131.72	Sand	Woodlands		940 ± 86	631.84 ± 27.14	40.67 ± 0.98	1.08 ± 0.02	3434.64 ± 52.70	2.56 ± 0.04	26.99 ± 0.36
*Dry Creek	−15.26, 132.37	–	Low woodlands	*Eucalyptus tetrodonta, Eucalyptus terminalis & Eucalyptus dichromophloia*	957 ± 98	590.89 ± 79.92	39.87 ± 1.3	1.30 ± 0.02	3456.01 ± 54.66	2.56 ± 0.06	26.83 ± 0.37
Larrimah	−15.60, 133.16	Sand	Low woodlands		969 ± 110	620.59 ± 36.49	41.69 ± 0.61	1.05 ± 0.01	3470.30 ± 57.50	2.56 ± 0.04	26.31 ± 0.39
Kidman Springs	−16.09, 130.89	Sand	Grasslands	*Eucalyptus terminalis* & *Eucalyptus brevifolia*	826 ± 75	476.74 ± 43.36	38.97 ± 0.95	0.98 ± 0.02	3564.66 ± 45.20	2.83 ± 0.04	27.13 ± 0.42
Newcastle Waters	−17.07, 133.46	Sand	Acacia woodlands & shrublands		681 ± 76	357.26 ± 39.95	27.70 ± 0.74	0.53 ± 0.01	3661.42 ± 41.40	2.90 ± 0.05	26.16 ± 0.44
*Sturt Plain	−17.15, 133.35	–	Grasslands	Mitchell grass (*Astrebla spp.*)	671 ± 77	357.60 ± 134.85	28.13 ± 0.62	1.03 ± 0.01	3681.00 ± 40.90	2.95 ± 0.11	26.24 ± 0.45
Mt Sanford	−17.36, 130.83	Sand	Low open woodlands		701 ± 77	319.27 ± 37.22	25.92 ± 0.68	0.43 ± 0.01	3754.89 ± 26.89	2.94 ± 0.05	26.09 ± 0.47
K440/TC230 Stuart Hwy Kath-TC	−17.73, 133.63	Sand	Low woodlands		643 ± 92	307.83 ± 55.76	25.14 ± 0.81	0.43 ± 0.01	3724.22 ± 41.17	2.98 ± 0.05	26.06 ± 0.46

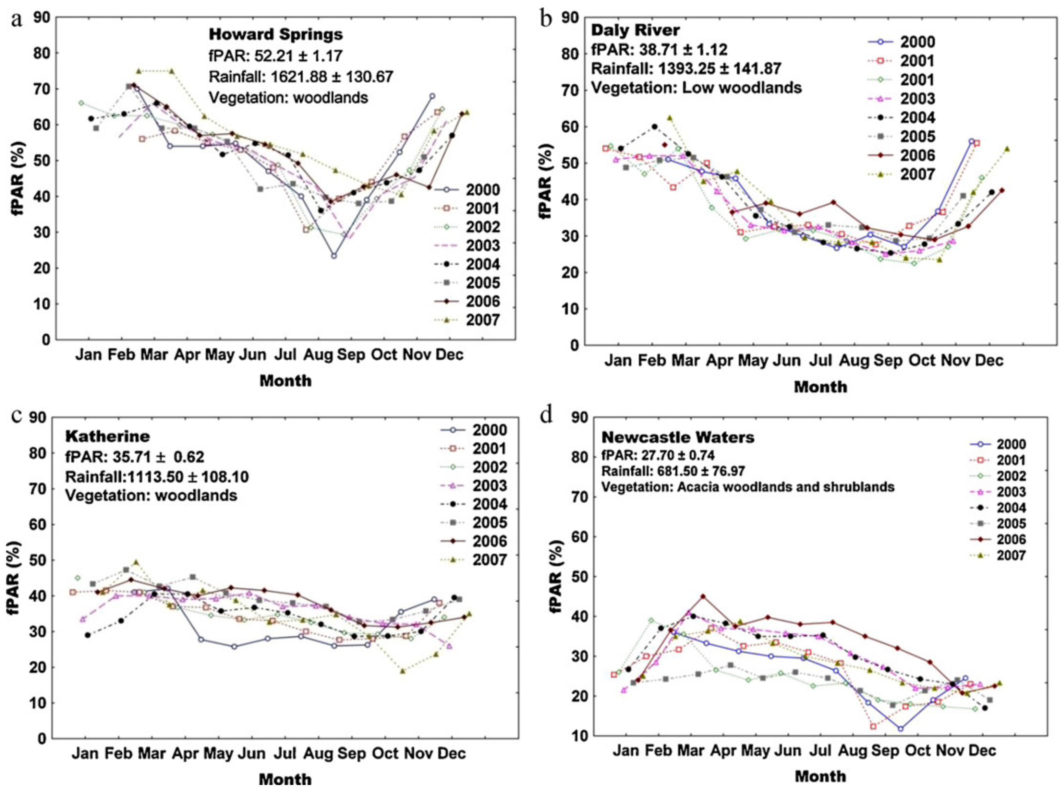

Fig. 3. Spatial and temporal patterns of monthly composite MODIS fPAR (fraction of absorbed Photosynthetically Active Radiation) Collection 5 at four Northern Australian Tropical Transect (NATT) sites: Howard Springs, Daly River, Katherine and Newcastle Waters. Data shows fPAR values derived by the Main Radiative Transfer (MRT) algorithm under cloudless conditions (QC = 0) and cover the period from 2000 to 2007.

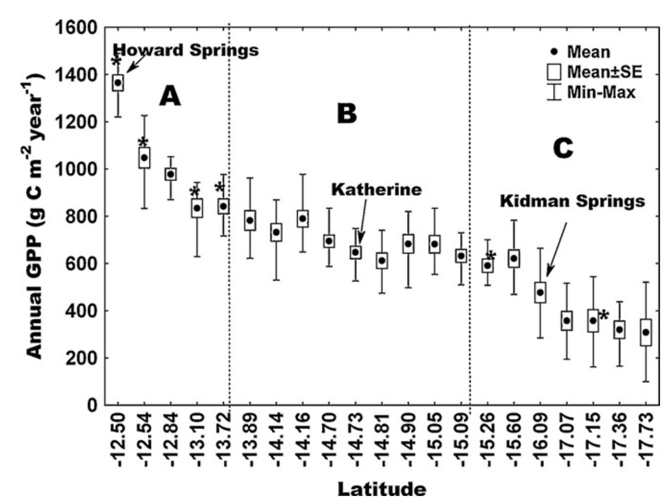

Fig. 4. Annual GPP along a major rainfall gradient in the Northern Australian Tropical Transect (NATT). The mid -point in each of the boxes is the mean, the boxes are ± standard error and the whiskers are the minimum and maximum values. Zones A, B and C represent the wet, middle and dry end of the NATT. Data represent GPP from 2000 to 2007. Locations marked with asterisk are the six sites investigated during SPECIAL Campaign.

mental change (Bai et al., 2008). Results showed that the total GPP accumulated by woody savanna near the coast at Howard Springs (12.50°S) was about 77% more (1365 g C m^{-2} $year^{-1}$) than GPP (308 g C m^{-2} $year^{-1}$) at the most southern arid site along the NATT at latitude 17.73°S (Table 1, Fig. 4). We divided NATT transect from 12.50 to 17.73° into 3 zones (zones A–C) based on our results of fPAR and GPP as shown in Figs. 4 and 5. We also found that such divisions match Miller et al. (2001) who show that the relationship between carbon isotopes of savanna leaf and wood (measure of the stomatal and photosynthetic responses to water shortage) and rainfall are highly non-linear and Egan and Williams (1996) who found a floristic boundary at 16°S.

There was a gradient in total GPP from the coast (12.50°S) to latitude about 13.72°S (zone A – wet end of the transect, Fig. 4), where total annual GPP decreased from 1365 g C m^{-2} $year^{-1}$ to 842 g C m^{-2} $year^{-1}$ (38%) across a change in latitude of ~1.2°. Further south (Zone B, Fig. 4), GPP from 13.89° to ~15.60°S did not vary much (21%), but still showed a decreasing trend and ranged between 782 and 621 g C m^{-2} $year^{-1}$. Another fall in GPP from latitude 16.09° to 17.7° (zone C – dry end of the transect, Fig. 4) was observed, where GPP dropped nearly 35% from 477 g C m^{-2} $year^{-1}$ to 308 g C m^{-2} $year^{-1}$. The average annual GPP as estimated in this study may be lower/higher than the true amount because as discussed in Section 4.2, the VPD scalar calculated from SILO data is lower than the tower measured VPD, especially in the dry season or in drier environments. The true GPP may be higher in arid vegetation such as grasslands and low open woodlands than calculated in this study.

Changes in GPP along the NATT (Fig. 4, Table 1) are influenced by the interaction among four major environmental variables: fPAR (R^2 = 0.85), VPD (R^2 = 0.85), rainfall (R^2 = 0.96) and LAI (R^2 = 0.96). It was found that daily average temperature was only moderately correlated to GPP (R^2 = 0.51). The T_{MIN} scalar calculated for these sites (data not shown) show values ranging between 0.97 and 1.00 (annual average), indicating GPP in this environment is not limited by temperature. However, it should be noted that the fPAR and VPD used to examine the relationship with GPP are in fact the same variables that were used to estimate GPP. Therefore, a relationship between fPAR, VPD and GPP is expected. FPAR, VPD, temperature and rainfall also co-vary which makes it difficult to partition their individual effects on GPP and is beyond the scope of this particular study. Annual rainfall totals are likely to set a limit to maximum LAI to be supported at a given site, which in turn determines transpiration with feedbacks to VPD. Hence these factors co-vary across multiple timescales.

High rainfall in the monsoonal north of the NT for example, causes less radiation (annual rainfall regressed against PAR, $R^2 = -0.50$, $p < 0.05$) to reach the surface (due to high cloud cover), which subsequently reduces the temperature ($R^2 = 0.52$, $p < 0.05$) and VPD ($R^2 = -0.93$, $p < 0.05$) (see Beringer et al., in this issue). The reduced influence of monsoon in the southern part of the NT can result in drought, which can increase the VPD. As a result, a strong relationship was found between GPP and environmental variables that actually reflect the patterns of rainfall as examined in this study. Rainfall controls productivity by changing the structure and composition of vegetation over long timescales as discussed below (Egan and Williams, 1996; Williams et al., 1996; Ludwig et al., 1999).

4.4. Controls on productivity

Since the primary environmental gradient along the NATT is rainfall (Cook et al., 2002), the influence of rainfall on GPP was further analyzed in detail. Vegetation structure (i.e. tree height, stem density and leaf area index) over NATT has adapted to the available water, nutrient and fire regime over plants successional timescales (Cook et al., 2002). These structural and compositional elements determine fPAR and LUE that essentially regulates the maximum modelled GPP. This is then down regulated by environmental factors (PAR, VPD and temperature) operating on short timescales of minutes to days (Prior et al., 1997; Eamus et al., 2001). The response of fPAR to rainfall (RF) is best depicted by a polynomial function with $R^2 = 0.75$ (Fig. 5).

$$\mathrm{fPAR} = 0.0000001 * \mathrm{RF}^3 - 0.0004 * \mathrm{RF}^2 + 0.50 * \mathrm{RF} - 151.21$$

This result suggests that rainfall is a critical factor in defining maximum fPAR and hence GPP along the NATT through the long term influence of rainfall on vegetation structure and composition. GPP is a function of fPAR and as a result of that GPP is also correlated with rainfall on a polynomial fashion ($R^2 = 0.96$)

$$\mathrm{GPP} = 0.000003 * \mathrm{RF}^3 - 0.009 * \mathrm{RF}^2 + 10.12 * \mathrm{RF} - 3280.8$$

There is a clear non-linear relationship between rainfall, fPAR and GPP along the NATT (Figs. 4 and 5). Results of this study show a

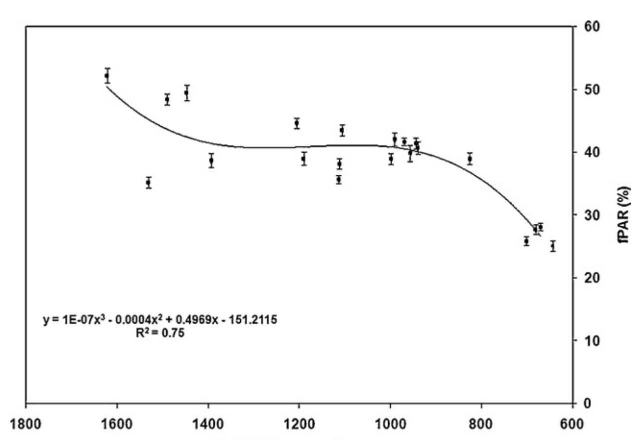

Fig. 5. Influence of rainfall on savanna fPAR (fraction of absorbed Photosynthetically Active Radiation) along the Northern Australian Tropical Transect. Note the plateau in fPAR values to increasing rainfall in the middle part of the transect.

much steeper gradient in GPP and fPAR at the wet and dry ends of the transect (zones A and C in Figs. 4 and 5) compared to a much flatter response in zone B. Interestingly, the shape of this curve is almost identical to that presented by Miller et al. (2001). This can be associated with the morphological characteristics or species replacement strategies of savanna in the NT as studied by Schulze et al. (1998), Miller et al. (2001) and Cernusak et al. (in this issue). In the wetter end of the transect (zone A in Fig. 4), *Eucalyptus* species such as *E. tetrodonta* and *E. miniata* are abundant and co-dominate many of the vegetation types in the NT (Williams et al., 1996) (Table 1). These species were found to adapt to the increasing aridity from north to south (about 15°) by increasing its water use efficiency, thereby influencing the leaf and wood isotope (indicating the response of stomata and photosynthesis to water stress – Farquhar, 1983) composition as was found by Miller et al. (2001) and the fPAR and GPP (this study). Although we found a steep fall in GPP with respect to decrease in rainfall in this zone, the correlation in not significant for both fPAR ($R^2 = 0.14$, $p = 0.53$) and GPP ($R^2 = 0.52$, $p = 0.17$), indicating savanna species at this wet end of the transect is less sensitive to decrease in rainfall.

However, at certain environmental conditions, these species are replaced by others. Thus, we found less response of fPAR ($R^2 = 0$, $p = 0.97$ – Fig. 5) to decreased rainfall in the middle section of the transect, i.e. zone B (Fig. 4). In this zone *E. miniata* and *E. tetrodonta* can be replaced by *E. tectificia* (Schulze et al., 1998 and see Beringer et al., in this issue for figures showing vegetation pattern along the NATT sites). Under the semi arid conditions in this zone, these plants cope with water limitations by having high root-shoot ratios, leaf shedding and osmotic adjustments (Bai et al., 2008; Miller et al., 2001). Lengthy roots for example enable the species to exploit deeper soil water, which may dampen the GPP response to variations in rainfall (Fig. 4). This adaptation strategies of *Eucalyptus* species may have resulted in a weak response of fPAR (Fig. 5) and hence GPP to decreasing rainfall. Similar to this study, Miller et al. (2001) also found that savanna species occurring near the mid point of the rainfall zone they sampled along the NATT transect (1600 mm to about 700 mm annual rainfall) only show a minor change in carbon isotope ratio in relation to decreasing rainfall. In a very recent study Cernusak et al. (in this issue) also found insignificant variations in ecosystem level gas exchange during the dry season in north Australian savannas (region ranging between annual rainfall 1700 mm and 300 mm). They associated the observed pattern with changes in leaf area index of the sites in response to increasing aridity.

At the drier end of the transect (zone C, Fig. 4), a further environmental condition driven by water availability creates a new equilibrium by replacing species again (Table 1). For example, at Kidman Springs (latitude 16.09°, Fig. 4), Schulze et al. (1998) found that *E. tectificia* was replaced by *E. terminalis* and *E. brevifolia* that can withstand much drier conditions. Acacia dominated woodland and shrublands and Mitchell grassland (extensive hummock and tussock grassland ecosystem which is a feature of the Australian arid environment) are also found here around 17° (Table 1, Cook and Heerdegen, 2001). These plants have shallow root systems with extensive lateral development (Scholes and Walker, 1993) to maximise absorption of small rainfall events of only ∼15 mm (Hutley et al., 2001). Consequently, our study showed a steep decrease in fPAR ($R^2 = 0.90$, $p < 0.05$) and GPP ($R^2 = 0.86$, $p < 0.05$) in zone C (Fig. 4) as rainfall decreases. The results that we obtained in this study support other findings such as that of Egan and Williams (1996) and Miller et al. (2001). They identified a floristic boundary around 16–17°S. However, Bowman et al. (1988) found a floristic boundary at 17–18°S when he considered various habitat diversities in NT. At this latitude, greatest change in family and species representation occur in the *Eucalypt* savanna habitats, where deciduous species which is constant between Darwin and Katherine

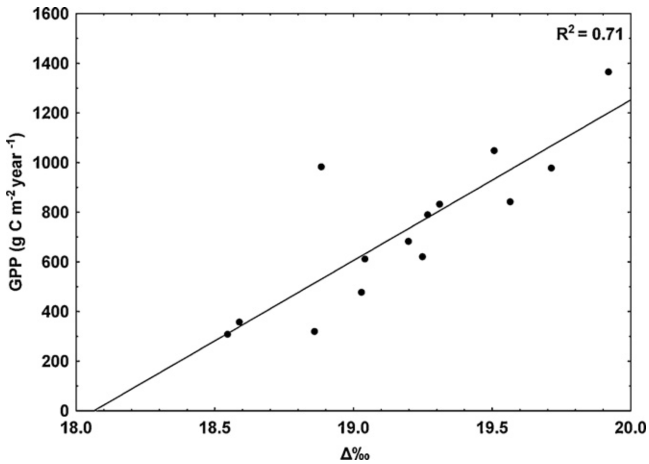

Fig. 6. Relationship between mean leaf carbon isotope values of Miller et al. (2001), page 228 (*x* axis) with GPP estimated in this study along the Northern Australian Tropical Transect (*y* axis).

decreased by 50% in this semi arid zone (Egan and Williams, 1996). Carbon isotope studies conducted along the NATT by Miller et al. (2001) showed that *Eucalyptus* species in this environment exhibited increased stomatal limitation to photosynthesis as rainfall decreased to conserve water and thereby better withstand drought although the species have high leaf nitrogen concentration that can support enhanced photosynthesis rates relative to conductance. Therefore, we confirm/validate our findings with leaf carbon isotope values of Miller et al. (2001) for several locations along the NATT and the results are presented in Fig. 6. GPP estimated in this study correlates well with the leaf carbon isotope values ($R^2 = 0.71$, $p < 0.05$) showing that the influence of rainfall/moisture on various *Eucalyptus* species is also determined by their ability to deal with water limitations. Results from this study also confirm Zhang and Marshall (1995) theory that different species may have varying sensitivity of stomatal conductance or photosynthesis to water availability.

Primary productivity of savannas at regional scale was generally found to be largely controlled by rainfall and the availability of soil moisture (Eamus, 2003; Nemani et al., 2003; Shugart et al., 2004; Woodward and Lomas, 2004; Merbold et al., 2009; Weber et al., 2009). Similar patterns were also obtained by several researchers who investigated the influence of rainfall on savanna structure, composition and water use along NATT (see Hutley et al., in this issue). They have established a strong influence of rainfall on savanna structure, composition and water use only at a few points but have not considered regional scale measurement or prediction as it was done in this study. GPP estimated using remotely sensed fPAR and regional meteorological data has allowed us to explore the relationship across the entire transect within the savanna boundary. We have found that the GPP of savannas were strongly driven by rainfall, only at the dry ends of the transect studied. However, in the wet end and middle part of the transect (e.g. dominated by different *Eucalyptus* species), a decrease in the response of savanna fPAR and GPP to rainfall was noticed. Using these information, we identified a transition zone in savanna vegetation at ∼16°S. These results (non linear response of savanna productivity to rainfall in northern Australia) have important implications to guiding ecosystem and climate modelers to predict the impact of climate change on savanna productivity in this region. For example, decreases in rainfall over arid ecosystems that are vegetated by Acacia and grasslands may respond by decreasing GPP. However, decreases in rainfall in latitudes between 12° and 16° will not substantially reduce the GPP in these ecosystems.

5. Conclusion

The results from regional scale analysis in this study show that the spatial variability of GPP in the savanna region is strongly correlated with rainfall. Rainfall influences savanna vegetation structure, composition and function on plant successional timescales which alters fPAR and LUE that essentially regulates the productivity of savannas. Then, the maximum GPP is down regulated by environmental drivers (PAR, VPD and temperature) operating on minutes to days timescales. However the response of GPP to rainfall is non-linear and our findings suggest that the influence of rainfall on various *Eucalyptus* species may be dampened by biotic factors; such as the rooting depth of species to cope with water limitations. Floristic changes at the drier end of the transect could be due to a threshold in annual rainfall which becomes too low to support vegetation productivity (even deep rooted) due to the soil moisture zone reaching critical (wilting) point. However, over larger spatial areas (e.g. savanna region of the NT) that are covered by different vegetation types; ranging from tropical rainforest to arid grasslands, rainfall may still play a critical role in determining the spatial and temporal distribution of GPP (Kanniah, 2009).

These results have important implications for our understanding of the fundamental nature of Australian savanna systems and for our ability to predict their responses to changes in environmental drivers. Future increases of atmospheric CO_2 (between 525 and 705 ppm by 2070, Hennessy et al., 2004) are predicted to result in climate change with rainfall totals for the NT projected to change between −16% and +8% by 2030 and −40% to +20% by 2070 in the wet season (November to April). Most of the NT is generally projected to become drier during the wet season (Hennessy et al., 2004). With these long term climate forecasts in mind, results from this study allow for future predictions of productivity to be made. However, a detailed knowledge of the response of ecosystems and transitions in vegetation types is required to underpin regional projections of carbon and climate. The "SPECIAL" field campaign has provided a robust data set on the spatial variation in vegetation structure, composition and function (see Hutley et al., in this issue) that can be used to calibrate and/or validate remote sensing based carbon or climate models to describe and predict the response of savannas to changing global climate at regional/global scales.

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