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Land use change and the impact on greenhouse gas exchange in north Australian savanna soils

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Abstract

Savanna ecosystems are subject to accelerating land use change as human demand for food and forest products increases. Land use change has been shown to both increase and decrease greenhouse gas fluxes from savannas and considerable uncertainty exists about the non-CO_2 fluxes from the soil. We measured methane (CH_4), nitrous oxide (N_2O), and carbon dioxide (CO_2) over a complete wet-dry seasonal cycle at three replicated sites of each of three land uses: savanna, young pasture and old pasture (converted from savanna 5–7 and 25–30 yr ago, respectively) in the Douglas Daly region of northern Australia. The effect of break of season rains at the end of the dry season was investigated with two irrigation experiments.

Land use change from savanna to pasture increased net greenhouse gas fluxes from the soil. Pasture sites were a weaker sink for CH_4 than savanna sites and, under wet conditions, old pastures turned from being sinks to a significant source of CH_4. Nitrous oxide emissions were generally very low, in the range of 0 to 5 μg N_2O-N m^{-2} h^{-1}, and under dry conditions soil uptake of N_2O was apparent. Break of season rains produced a small, short lived pulse of N_2O up to 20 μg N_2O-N m^{-2} h^{-1}, most evident in pasture soil. Annual cumulative soil CO_2 fluxes increased after clearing, with savanna (14.6 t CO_2-C ha^{-1} yr^{-1}) having the lowest fluxes compared to old pasture (18.5 t CO_2-C ha^{-1} yr^{-1}) and young pasture (20.0 t CO_2-C ha^{-1} yr^{-1}). Clearing savanna increased soil-based greenhouse gas emissions from 53 to ~70 t CO_2-equivalents, a 30 % increase dominated by an increase in soil CO_2 emissions and shift from soil CH_4 sink to source. Seasonal variation was clearly driven by soil water content, supporting the emerging view that soil water content is a more important driver of soil gas fluxes than soil temperature in tropical ecosystems where temperature varies little among seasons.

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1 Introduction

It is widely accepted that the increasing atmospheric concentrations of the greenhouse gases carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) are warming the earth's climate (IPCC, 2007). Fossil fuel use and land use are the two key processes driving the increase in concentration of these three greenhouse gases (Houghton, 2007). While fossil fuel use and resultant emissions are relatively easy to measure and model, fluxes of greenhouse gases from land use, either modified agricultural systems or natural ecosystems, are more difficult due to their spatial and temporal variability and our limited understanding of the processes controlling these fluxes. Considerable progress has been made with regards to CO_2, but CH_4 and N_2O have only just begun to be incorporated into global climate models (Arneth et al., 2010). While CH_4 and N_2O are present in the atmosphere in smaller concentrations than CO_2, their greenhouse warming potentials are much greater (CH_4 25 times, N_2O 296 times) (IPCC, 2007).

Changes in land use are occurring continuously, all over the earth. A change in land use will often result in a change in the greenhouse gas fluxes from the land. Afforestation of improved pastures in Western Australia, significantly decreased soil N_2O emissions and increased soil CH_4 uptake (Livesley et al., 2009). Conversely, it may be anticipated that deforestation might increase soil N_2O emissions and decrease the capacity of soils to oxidize atmospheric CH_4. Deforestation is likely to increase in the tropical savanna woodlands of northern Australia, as prolonged drought in the south prompts agricultural producers to look north in search of water and soil resources (Petheram and Bristow, 2008; Bowman et al., 2010). In a review of N_2O and CH_4 fluxes from savanna soils under different land uses world-wide, Castaldi et al. (2006) found that, compared to natural systems, in managed systems the soils' ability to act as a CH_4 sink was decreased, while no statistically significant effect upon N_2O fluxes could be found. Both land use and rainfall affected N_2O fluxes from savanna soils in Senegal (Dick et al., 2006), with increased N_2O emissions associated with heavy (simulated) rainfall and the presence of N-fixing tree species.

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Savannas cover one sixth of the earth's surface and are subject to accelerating land use change (Grace et al., 2006). However, data on greenhouse gas fluxes from savannas is scarce in comparison with other ecosystems. In Australia, savanna covers a quarter of the country, and this is the most intact savanna ecosystem left in the world (Woinarski et al., 2007). A number of studies have described the carbon dynamics of Australian savannas (Chen et al., 2002, 2003; Eamus et al., 2001; Beringer et al., 2003, 2007), and the greenhouse gas emissions from burning these ecosystems have also been quantified (Russell-Smith et al., 2009). However, there is a lack of data on non-CO_2 greenhouse gas fluxes from these soils, and soil is the main source/sink of CH_4 and N_2O. The first objective of this study was to describe the soil fluxes of CH_4, N_2O and CO_2 over an entire wet-dry seasonal cycle in uncleared tropical savanna woodland (savanna) and from improved pastures. Measurements were made at sites cleared between 5 and 7 yr ago ("young pasture") and between 25 and 30 yr ago ("old pasture"). The second objective of this study was to assess the impact of "break of season" rains on N_2O and CH_4 fluxes, speculating here that these rainfall events were linked to significant pulse emissions (Borken and Matzner, 2008). The third objective was to investigate the environmental drivers that influence greenhouse gas fluxes from savanna soils, with the aim of developing relationships that can be used to model greenhouse gas fluxes across the savanna biome as a function of land use and environmental conditions.

2 Methods

To address these objectives, we took an integrated approach combining a number of different methods. Manual chambers were used to measure greenhouse gas fluxes over the entire wet dry cycle (September 2007–November 2008), at three replicate sites for each land use (savanna, young and old pasture). This spatially replicated but temporally coarse data set was augmented by two experiments. The first experiment utilised an automated chamber system, which has a temporal resolution of 4 h, and an artificial irrigation simulating break of season rains. The second experiment utilised the inert tracer gas SF_6 for studying soil gas diffusion, and two artificial rainfall treatments. These experiments addressed the second objective, and justified the manual chamber re-sampling period of 6 weeks. The third objective involved recording potential environmental drivers during the manual and automated chamber sampling and statistical analysis. Continuous recording of some potential environmental drivers of soil greenhouse gas fluxes also occurred at nearby flux tower sites.

2.1 Site description

The Douglas Daly region of the Northern Territory was chosen for this study, as this catchment is dominated by savanna but due to suitable climate and soil conditions – is also the focus for expanding agriculture (Bowman et al., 2010) and forestry. Land clearing for agriculture in the region began shortly after the Northern Territory became self-governing in 1978 (Chapman et al., 1996). The Agricultural Development and Marketing Authority (ADMA) cleared land and allocated farms of 4000–6000 ha to six farmers in 1980. The past two decades have seen numerous subdivisions and significant further land clearing and, recently, the addition of small areas of irrigated cropping and plantation forestry.

The climate of the Douglas Daly region is typical of the wet-dry tropics. The mean annual maximum and minimum temperatures are 34.2 °C and 19.6 °C. At 09:00 a.m., the annual mean relative humidity is 70 %. The area receives an annual average of 1177 mm of rain, which falls on just 66 days, predominantly between December and March (Bureau of Meteorology). The dominant vegetation of the region is savanna, an ecosystem consisting of a continuous or near continuous C4 grass dominated understorey, with a discontinuous woody overstorey (Hutley and Setterfield, 2008). Savanna vegetation is adapted to frequent fire and a highly seasonal rainfall distribution, with rapid growth during the 5 month wet season and low growth or dormancy during the dry season (Bowman et al., 2010). The vegetation at the savanna site is dominated by the tree species *Eucalyptus tetrodonta, Corymbia latifolia* and *Terminalia grandiflora*,

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with the understorey vegetation dominated by the grasses *Sorghum* spp. and *Heteropogon contortus*.

Nine sites were chosen to provide three replicates of each land use: savanna, young pasture and old pasture. The sites were all on the same soil type; Red Kandosol (Isbell, 2002), and originally supported the same vegetation community. At six of the sites, the savanna was cleared (vegetation felled by chains, then burnt) and pasture was sown between 25 and 30 yr ago (old pasture) or between 5 and 7 yr ago (young pasture). The pastures have all been grazed by beef cattle at low stocking rates and sporadically fertilized. The pastures now support a range of grasses including *H. contortus*, *Digitaria eriantha, Pennisetum pedicellatum*, *Chloris* spp., and *Eragrostis* spp. and leguminous species including *Senna obtusifolia*. For site locations see Fig. 1, and for further site details see Table 1.

2.2 Seasonal and spatial variation in soil gas exchange

The manual closed chamber method (Hutchinson and Mosier, 1981) was used to quantify the spatial and seasonal variation in soil-atmosphere exchange of CO_2, CH_4 and N_2O in the three land uses: savanna, young pasture and old pasture (at three replicate sites for each land use). Manual chambers were made up of a dark PVC pipe (diameter 25 cm, height 24.5 cm, volume 12.0 l, basal area 0.049 m^2) with a twist-lid (PVC) incorporating a butyl-rubber septum and a rubber O-ring to form a gas tight seal. Manual chamber bases were installed at least one hour before lid closure. Five chambers were installed at each site, on each measurement occasion. The litter layer was cut around the circumference of each chamber base and the chambers were inserted 2 cm into the soil surface. Grass was avoided where possible, but some chambers did contain small amounts of grass foliage. The internal height of each manual chamber was carefully measured so as to calculate the headspace volume of each chamber. Once the manual chamber lids were attached and twist-sealed, 15 ml headspace gas samples were taken at 0, 20, 40 and 60 min after closure using a 20 ml syringe (Terumo™ USA) and

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a one-way stopcock. Gas samples were stored in pressurized exetainers (Labco Ltd., UK) which were usually analysed within 20 days for N_2O and CH_4 by gas chromatography (Schimadzu GC17A). Previous work demonstrated no change in concentrations with storage over this time. Injection of a single gas sample filled two 2.0 ml sample loops, one leading to a flame ionisation detector for determination of CH_4 concentration and one leading to an electron capture detector for determination of N_2O concentration. Exetainers were stored in a cool, dark container and over-pressurised (20 ml in 12 ml container volume) to ensure any minor leaks were from the exetainers to the bulk air. Soil N_2O and CH_4 fluxes were calculated from the linear increase or decrease in concentration with time, since a linear regression was suited best to describe temporal changes in chamber head space concentrations. Soil CO_2 emission rates were measured after headspace gas sample collection was complete, using an Infra-red gas analyser (IRGA) (EGM, PP-Systems™, UK). The individual manual chamber lids were removed and the chambers vented. A two port chamber lid was then attached and the linear increase in CO_2 concentration instantaneously measured between 90 and 180 s after lid closure using the IRGA in a closed dynamic setup. Soil temperature (3 cm) and soil water content were measured at each chamber.

2.3 Environmental drivers: soil sampling and measurements

Soil was sampled from each chamber using soil cores (Ø 72 mm) to determine bulk density (0–5 cm). Soil samples were transferred immediately to an ice box and then stored refrigerated for 1 to 4 days prior to analysis. The soil samples were weighed, and subsamples were removed for analysis of gravimetric water content and soil NO_3^- and NH_4^+. Soil samples were extracted with 1M KCl (1:4, soil:KCl) and shaken for one hour on a wrist shaker, then filtered (Whatman 42) and frozen prior to analysis of NO_3^- and NH_4^+ on a Technicon™ Auto-analyser. Gravimetric water content was determined through oven drying at 105 °C for 48 h. The remaining soil was air-dried and stored for

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C and N measurements. A sub-sample of each air-dried soil sample was analysed for total C and N content as above.

2.4 Environmental drivers: soil N mineralisation

Soil nitrification and ammonification were estimated by direct incubation of nylon mesh bags containing 4 g of ion exchange resin beads (MTO-Dowex Marathon MR-3) at a depth of ∼5 cm. Three replicate resin bags were buried at each of the 9 sites on 6 occasions. The resin bags were collected after 45 to 142 days and stored refrigerated until extraction. Total exchangeable ions were extracted from the resin with four repeat 1M KCl washes (1:25, resin:KCl), that were frozen prior to analysis for NO_3^- and NH_4^+ concentration on a Technicon™ segmented flow auto-analyser.

2.5 Break of season rains Experiment 1: continuous soil trace gas exchange measurements

Trace gas flux was measured continuously for twelve days between 12 and 26 September 2007 (the end of the dry season) using an automated trace gas measurement system (Breuer et al., 2002) , consisting of a gas chromatograph (GC, SRI™, Torrance, CA, USA) linked to ten clear acrylic chambers (six 30.4 l chambers, two 37.5 l chambers and two 21.6 l chambers) with lids that open and close automatically through pneumatic piston control. Five chambers were installed in the savanna and the other five chambers were installed in the adjacent young pasture. Chamber bases were driven approximately 5 cm into the soil several days before measurements began. Chambers were attached to a frame using clamps and closed cell foam.

To measure trace gas flux, five of the ten chambers would close for 2 h, then these chambers (1–5) would open and the other chambers (6–10) would close. During chamber closure, four air samples (∼0.5 l each) were withdrawn at equal time intervals from each closed chamber. Each air sample took four minutes to withdraw. Towards the end of each four minute air sample withdrawal, two 3 ml sub-samples of the sample air were

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collected and passed into the GC for measurement of N_2O concentration using a ^{63}Ni electron capture detector (ECD) and CH_4 concentration using a flame ionisation detector (FID). The GC was calibrated with certified standard gas (Air Liquide™, USA) every 30 min. From the four N_2O and CH_4 concentration measurements during a 2 h period of closure, a linear regression and therefore flux rate was calculated. For each chamber, six flux rate measurements were made during a 24 h period, one every 4 h. CO_2 was measured during the experiment but not recorded due to instrument malfunction. Soil water content (0–6 cm) and soil temperature (at 5 cm depth) were continually measured using "standing wave" soil moisture probes (MP406) and temperature sensors attached to a weather station (Tain™ electronics) in the savanna and in the pasture (data not shown). Soil water content was also measured manually by taking soil cores.

The minimum detectable limit (MDL) for this automated trace gas system was calculated as:

$$\mathrm{MDL} = 2 \cdot \mathrm{SD} \cdot V \cdot A \cdot T \quad (1)$$

where SD is the standard deviation of the gas concentration in ambient air, V is the volume of the chamber (l), A is the area of soil under the chamber (m^2) and T is the time for incubation (h). The MDL for N_2O was 0.77 $\mu g\,N\,m^{-2}\,h^{-1}$ and for CH_4 was 1.64 $\mu g\,C\,m^{-2}\,h^{-1}$.

On 21 September 2007 all chambers were irrigated with 40 mm of water over 20 min, to simulate break-of-season rains. One meter square quadrats were also irrigated, in both the savanna and the pasture, from which soils cores were collected to measure soil water content 1, 3 and 5 days after the irrigation event. Two soil pits were dug to 50 cm depth in the savanna and the pasture, adjacent to the chambers. Soil cores were taken to measure bulk density and soil water content (5 cm cores at 5, 15, 30 and 45 cm depth).

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2.6 Break of season rains Experiment 2: soil gas diffusivity

In the dry season of 2009, soil gas diffusion was measured at contrasting water contents. The method followed von Fischer et al. (2009) and uses sulphur hexa fluoride (SF_6) as a tracer to estimate soil gas diffusion. A 12 ml volume of SF_6 was injected into a manual chamber headspace and the decrease in concentration monitored over 30 min. Three contrasting soil moisture contents were established: (i) dry soil (not irrigated), (ii) medium soil moisture (50 l m^{-2} added one day before) and (iii) wet soil moisture (50 l m^{-2} added one day before and 20 l m^{-2} added in the hour before). Three replicate gas flux and diffusion measurements were made in each water treatment (dry, medium, wet) at each of the three land uses (savanna, young pasture, old pasture). The 20 ml gas samples were taken from the chamber headspace at 2, 12, 22 and 32 min after chamber closure using a 20 ml syringe (Terumo, USA) and a one-way stopcock. No sampling in the initial two minutes enabled equilibration and good mixing of SF_6. Gas samples were immediately transferred and stored in pre-evacuated exetainers and analysed for CH_4 and N_2O concentration as described in Sect. 2.2 for manual chamber measurements.

2.7 Data analysis and presentation

Continuous flux rates are the average values from 5 chambers. Manual flux rates are the average of 15 chambers (5 chambers at each of three replicate sites). Data from the manual chamber measurements were not normally distributed, so the following transformations were applied to normalise their distribution: CO_2 LN(value), CH_4 LN(LN(value + 100), N_2O LN(LN value + 10). Statistical significance was defined as difference at the 95 % level (i.e. $p \leq 0.05$). Differences between land uses and the effect of seasonality were investigated for each gas and environmental properties by a two way analysis of variance (ANOVA), with LSD post hoc analysis where appropriate. Data from the break of season rains Experiment 2 were normally distributed, except for CH_4 diffusivity, which was LN transformed to normalise distribution. The effect of water

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treatment was investigated using ANOVA to compare diffusivity and fluxes of CH_4 and N_2O. The effect of land use was investigated using ANOVA to compare diffusivity and fluxes of CH_4 and N_2O, for each water treatment. Seasonal mean flux rates (mass $CO_2/CH_4/N_2O$ ha^{-1} d^{-1}) were estimated from the chamber data for savanna, young pasture and old pasture soils. Seasonal mean flux were multiplied by the days in each season and summed to provide an estimate of annual CO_2, CH_4 and N_2O flux for each land use. Annual flux expressed as CO_2 equivalents was estimated for each GHG based on global warming potentials (GWP) of 1 (CO_2), 25 (CH_4) and 296 (N_2O).

3 Results

3.1 Site properties

The properties of the nine sites are described in Table 1. All sites were located on the same soil type, red kandosols, Blain sub-order (after Lucas et al., 1985). The soils are slightly acidic, with very low levels of soil organic C (0.5 to 0.9 %) and total N (0.02 to 0.06 %). The pasture soils, particularly the old pastures, tended to have higher levels of C and N, higher CEC and lower soil pH than the savanna soils (Table 1), although phosphorous levels were elevated in the pastures when compared to the savanna sites, reflecting the fertilisation of some of the pasture sites.

3.2 Variation in soil gas fluxes with season and land use

Over a complete wet-dry seasonal cycle at the savanna sites, higher (or less negative) fluxes of all three gas species were recorded when the soil water content was above ~0.10 cm^3 cm^{-3} (Fig. 2). Mean CO_2 emissions ranged from 44 to 390 mg C m^{-2} h^{-1}, with the highest fluxes occurring during the early wet season (March). Mean CH_4 uptake ranged from −24 to −7 µg C m^{-2} h^{-1}, while mean N_2O fluxes ranged from −1.0 to 1.5 µg N m^{-2} h^{-1} over the seasonal cycle. The seasonal patterns of fluxes observed at the young pasture sites were similar to those at the savanna sites. However, the range of values recorded was greater at the young pasture sites: mean fluxes of CO_2 ranged between 32 to 560 $mg\,C\,m^{-2}\,h^{-1}$; CH_4 −18 to −5 $\mu g\,C\,m^{-2}\,h^{-1}$, N_2O −0.3 to 1.8 $\mu g\,N\,m^{-2}\,h^{-1}$. Fluxes of CH_4 and N_2O recorded at the old pasture sites were an order of magnitude greater than fluxes measured at the other sites with peak fluxes during February when the soil water content was ~0.3 $cm^3\,cm^{-3}$. Over the seasonal cycle, mean CH_4 fluxes ranged from −14 to +116 $\mu g\,C\,m^{-2}\,h^{-1}$, and mean N_2O fluxes ranged from −0.7 to +6 $\mu g\,N\,m^{-2}\,h^{-1}$. Mean CO_2 emissions were comparable with those at the savanna and young pasture sites.

3.3 Variation in plant available N across season and land use

Seasonal patterns of plant available N were assessed across land uses using soil extractions of NO_3^- and NH_4^+ and incubated resin bags. In extracts from the soil, NH_4^+ tended to be present in higher concentrations than NO_3^- at all sites at all times of year (Fig. 2). Concentrations of both nutrients pools across season increased in the following order: savanna < young pasture < old pasture. The amount of nitrate and ammonia extracted from resin bags was highest in the old pasture sites, followed by the young pasture sites and lowest in the savanna sites (Fig. 3). The highest values at all sites were recorded in the wet season, November 2007 and January 2008. Land use and seasonality both had a statistically significant effect upon soil-extracted NH_4^+ but not upon soil-extracted NO_3^- (Table 2).

3.4 Break of season rains: the response of trace gas fluxes

The irrigation event, which simulated break-of-season rains, affected the fluxes of both CH_4 and N_2O (Fig. 4). Under the low soil moisture conditions of the late dry season (September) and prior to the wetting event, N_2O at both land use sites fluctuated around 0 $\mu g\,N\,m^{-2}\,h^{-1}$. Follow the irrigation event of 40 mm equivalent rainfall, fluxes increased from ~0 $\mu g\,N\,m^{-2}\,h^{-1}$ to a maximum of 19 $\mu g\,N\,m^{-2}\,h^{-1}$ in the pasture site the day after irrigation. Emissions after irrigation of the savanna soil were more moderate, reaching a maximum of 8.3 $\mu g\, N\, m^{-2}\, h^{-1}$ immediately after the event. Only four days after irrigation, N_2O fluxes had returned to their pre-irrigation levels at both sites. This occurred despite soil water content remaining well above the initial dry soil moisture values >5 days after irrigation (Fig. 4).

Both the pasture soil ($-5.8 \pm 0.2\, \mu g\, C\, m^{-2}\, h^{-1}$) and the savanna soil ($-7.8 \pm 0.3\, \mu g\, C\, m^{-2}\, h^{-1}$) were sinks for CH_4 under dry soil conditions. After the irrigation event, both soils became much weaker sinks (pasture average $-1.1 \pm 0.4\, \mu g\, C\, m^{-2}\, h^{-1}$, savanna average $-2.3 \pm 0.3\, \mu g\, C\, m^{-2}\, h^{-1}$) and for short periods, sources of CH_4 (maximum values of 2.2 $\mu g\, C\, m^{-2}\, h^{-1}$ pasture, 1.1 $\mu g\, C\, m^{-2}\, h^{-1}$ savanna). Unlike N_2O fluxes, which quickly returned to pre-irrigation values, CH_4 fluxes remained at their new "wet soil" values for the duration of the experiment (i.e. greater than 5 days post irrigation).

3.5 Break of season rains: diffusivity and soil water content

Gas diffusivity decreased as water content increased in all three land uses (Fig. 5). Fluxes of CH_4 were negative under dry soil conditions at all land uses, and became positive as the soil was wetted up (Fig. 5). Fluxes of N_2O also generally increased with increasing water content. Land use also had a significant effect on gas diffusivity and CH_4 and N_2O flux with an interaction with different soil water conditions (Table 3). Under dry conditions, land use had a significant effect upon CH_4 flux, with savanna having the largest rate (net sink) when compared to the pastures. When the soil was wettest, land use significantly affected only N_2O flux, with rates at the old pasture site reaching 25 $\mu g\, N\, m^{-2}\, h^{-1}$ compared to less than 5 $\mu g\, N\, m^{-2}\, h^{-1}$ at the savanna (Fig. 5). Under medium soil wetness, land use significantly affected diffusivity and N_2O.

3.6 Relationships between gas fluxes and environmental drivers

Given the large seasonality in fluxes as described above, analysis of land use change was undertaken within each seasonal period, namely wet, dry and dry-wet season transition. Statistical analysis of fluxes for each season and land use is given in Table 2. Land use had a statistically significant effect upon the fluxes of all three gases and upon soil temperature, soil water content and bulk density (Table 2). Seasonality had a statistically significant effect upon CO_2, CH_4, soil temperature and soil water content and the interaction between land use and seasonality was only significant for CO_2 (Table 2). Relationships between soil fluxes and environmental drivers (soil water content, soil temperature, soil NO_3^- and NH_4^+, available NO_3^- and NH_4^+) were investigated across all land use sites and seasons using step-wise multiple regression. For all gases and all land uses, stepwise multiple regression yielded only one significant driving factor ($p < 0.01$) and for most treatment combinations this was soil water content. The exceptions were: soil NH_4^+ was the significant driving factor affecting CH_4 fluxes in the young pasture, and soil NO_3^- was the significant driving factor affecting N_2O fluxes in the old pasture. The ability of these regression relationships to describe the variation in gas fluxes (as quantified by r^2) ranged from 0.29 to 0.69. The relationship between gas flux and soil moisture was strongest at the savanna site and is given in Fig. 6. Over the observed range of soil moisture, N_2O flux was negative (net uptake by the soil) until a threshold moisture content of $0.06\,m^3\,m^{-3}$ was reached. Moisture levels above this value resulted in emission, with a maximal rate of $5\,\mu g\,N\,m^{-2}\,h^{-1}$ at $\sim 0.2\,m^3\,m^{-3}$ soil water content (Fig. 6). Methane and CO_2 fluxes were both positively related to soil water content, with moisture content alone explaining 70 % of the observed variation in soil CO_2 efflux.

3.7 Cumulative flux estimates

Fluxes of N_2O were positive for all land uses in the wet season and the dry-wet transition, but in the dry season, there was a net uptake of N_2O by the soil in the savanna and the old pasture sites (Table 4). Methane was absorbed by the soil all year in the savanna and the young pasture, but CH_4 was emitted from the old pasture in the dry-wet transition and, particularly, in the wet season. Comparison of seasonal fluxes

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demonstrated that the wet season was when the largest positive rates occurred, i.e. net emission of GHG. This held true across all land uses and all gases. The annual fluxes indicate that the conversion from savanna to pasture has increased greenhouse gas emissions from the soil by 17.36 t CO_2-equivalent ha^{-1} yr^{-1} , and decreased the ability of the soil to act as a sink for CH_4 (Table 4). When all gas fluxes are converted to CO_2-equivalent units, CO_2 was the dominant flux from these land use types, despite the greater warming potentials of CH_4 and N_2O.

4 Discussion

This study focused on quantifying fluxes of CH_4, N_2O and CO_2 from soils of contrasting land use types in the Douglas-Daly River basin in the NT. This region has been identified as a catchment for potential intensification of horticulture, plantation forestry and cattle grazing. Soil types sampled in this study are from the Blain and Oolloo sub-orders (Lucas et al., 1985) of the red kandosol group and are the soil types targeted for agricultural development, occupying >200 000 ha within the catchment. Understanding of greenhouse gas emissions associated with differing land use decision making is now essential for national greenhouse gas inventory reporting (Cook et al., 2010). This is the first comprehensive study in northern Australia to investigate the effect of savanna clearing on soil based greenhouse gas fluxes. Our results clearly show that conversion of savanna ecosystems to grazed pastures increases the overall greenhouse gas flux to the atmosphere, with increases in N_2O and CO_2 fluxes and decreases in soil CH_4 uptake.

4.1 Effect of land use change on N_2O flux

The change in land use from native savanna woodland to grazed pasture significantly increased N_2O flux from the soil. Generally, fluxes of N_2O fluctuated around zero, however in the old pasture, N_2O emissions of up to 20 µg N m^{-2} h^{-1} occurred when

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the soil was wet. While this was a maximal rate observed during this measurement program, when compared with other savanna ecosystems, these N_2O fluxes are well below the global average emissions for natural savannas ($0.95\,kg\,N_2O\,h^{-1}\,yr^{-1}$) (Dalal and Allen, 2008). N_2O fluxes from pasture and both primary and secondary wet forest in subtropical Puerto Rico were of a similarly low magnitude as in our study (below $2\,\mu g\,N\,m^{-2}\,h^{-1}$), except where the forest was fertilized or dominated by leguminous N fixing species (Erickson et al., 2001). The low N_2O fluxes observed in our study are likely due to the low N content of the soils (0.02–0.07 % N). In such a low N system, N is tightly cycled and this is reflected in the low levels of soil nitrate and ammonia (Fig. 2) as was also found for a pine forest in the Mediterranean region (Rosenkranz et al., 2006). Dry conditions and low atmospheric N deposition also play a role in situations with low N_2O fluxes (Dalal and Allen, 2008). The negative N_2O fluxes (net soil uptake) observed were all associated with dry soil conditions and likely occur in low N systems when sufficient air can diffuse through soil pores to allow N-starved microbes to use gaseous N_2O as an N source (Rosenkranz et al., 2006). N_2O uptake has been observed in savanna soils in West Africa and in dry tropical forest soils in Puerto Rico or in sandy soils stocked with Pine in the Mediterranean region (Brümmer et al., 2008; Erickson et al., 2002; Rosenkranz et al., 2006). However, the processes involved are, as yet, poorly understood (Dalal and Allen, 2008).

The N_2O emissions recorded in the old pasture occurred at the end of the dry season- with the first rain of the dry-wet transition. Our manual chamber results show some evidence of a build up of soil nitrate and ammonia during the dry season, with a small pulse of N_2O emission with the first rain of the dry-wet transition. This phenomenon is more clearly demonstrated in the break of season rains, Experiment 1. N_2O emissions are often a result of denitrification and increase as the soil becomes wetter (Dalal and Allen, 2008). However, when the soil was wettest in our study there was little soil nitrate or ammonia present and thus N_2O fluxes remained low.

The land use change in our study was from native savanna vegetation to grazed pasture, and this increased N_2O flux from the soil. Compaction by grazing can increase

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bulk density in pasture soils (as seen in Table 2), decreasing pore space and limiting gas diffusion. Gas diffusivity was lowest in the old pasture and highest in the savanna under all water treatments, in the break of season rains Experiment 2. Tropical forest soils converted to pasture initially emitted more N_2O than the forest soils, but from 10 to 35 yr N_2O fluxes decreased as pasture age increased, to values 1/2 to 1/3 lower than the original forest soil emissions (Keller et al., 1993). In dry tropical forest in Puerto Rico, an increase in leguminous N_2 fixing tree species brought about by prior agricultural use lead to greater N_2O fluxes from the post-agricultural forest than from old forest sites (Erickson et al., 2002). Land use change from native vegetation to cropping decreased N_2O flux from savanna soils in West Africa and also from semiarid Mallee soils in south-eastern Australia (Brümmer et al., 2008; Galbally et al., 2010). Cropping may increase gas diffusion through the soil as soil structure is opened up by tillage. The effect of land use change on soil structure and N cycling will influence the outcome of this change on soil N_2O fluxes.

4.2 Seasonal changes in N_2O flux

Seasonality did not have a significant effect upon N_2O fluxes. The N_2O fluxes were generally very low in all ecosystems and did not change significantly with changes in the environmental conditions. The only exception were the break of season rains, that resulted in sizable (though still small in comparison with other ecosystems) emissions of N_2O (15–25 $\mu g\,N\,m^{-2}\,h^{-1}$) the day after the irrigation. This effect, however, was transient and four days after the break of season rain experiment, the soil was still wet but N_2O emissions had returned to near zero (Fig. 3). Brümmer et al. (2008) also observed a pulse of N_2O when the first rains fell after the dry season, in savanna in Burkina Faso, West Africa. Ongoing wet soil conditions did not yield continuing high N_2O fluxes, likely because the soil nitrate and ammonia that built up in the dry season had been used up.

This lack of seasonality was also observed in other studies, such as a near-continuous 16 month study of N_2O fluxes from savanna soils at Howard Springs in

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northern Australia (Livesley et al., 2011) or in N_2O fluxes from pasture or forest soils in tropical Puerto Rico (Erickson et al., 2001). The most likely explanation for the lack of seasonality is the low nitrogen levels of the system. Even when soil was near field capacity, i.e. favourable for denitrification and production of N_2O, all the N present is efficiently immobilized by plants and soil microbes. The sand fraction of the top 50 cm depth in these soils tends to range from 80 to 90 % sand which may also prevent anaerobic microsites where denitrification would take place. In times when mineralisation and nitrification occurs (i.e. in the transition period between wet and dry, Fig. 5) most of the available NO_3^- is probably taken up by plants or immobilised by microbes and not lost as N_2O via nitrification.

4.3 Effect of land use change upon CH_4 flux

Conversion of savanna woodland to pasture decreased the CH_4 sink strength of the soils. Under the environmental conditions encountered during the manual chamber measurements, the young pasture soils remained weak sinks for CH_4, while the old pastures became substantial sources of CH_4 under wet conditions. This is consistent with a review of global patterns of CH_4 flux from natural and managed savannas by Castaldi et al. (2006), which found that land use change dramatically decreased the CH_4 sink strength of soils, and conversion to pasture resulted in the soil becoming a CH_4 source in the wet season (Castaldi et al., 2006). The magnitude of fluxes that we measured is within the standard deviation of the global mean value as given by Castaldi et al. (2006) for savanna and seasonally dry ecosystems (annual daily mean $-0.48 \pm 0.96\,\mathrm{mg\,CH_4\,m^{-2}\,d^{-1}}$). In the break of season rains experiments, conducted under wetter conditions than were encountered in the manual chamber measurements, both the young pasture and the old pasture became net sources of CH_4. Methane is produced under anaerobic conditions by methanogenic bacteria. When soil is aerobic, CH_4 is consumed by methanotrophic bacteria (Dalal and Allen, 2008) and the change from CH_4 sink to CH_4 source observed with conversion to pasture is likely to be related

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to the increase in bulk density associated with grazing. Compaction by grazing animals decreases the pore space in soils, thus the volumetric water content in pasture soils will be higher for a given rain fall than in adjacent savanna woodland soils. This can be seen in the soil water content data from the break of season rains Experiment 1. Consequently anaerobic microsites, being locations of net CH_4 production, will be more prevalent in pasture soils compared to natural savanna soils.

Land use change from native vegetation to pasture has decreased the CH_4 sink strength of soils in a variety of ecosystems. Conversion of tropical forest to pasture decreased CH_4 consumption by soils in the dry season, and altered the system from a CH_4 sink to a CH_4 source in the wet season. Pasture age did not affect CH_4 fluxes (Keller et al., 1993). Land use change from native forest to pasture decreased the CH_4 sink strength of soils in south west Western Australia (Livesley et al., 2009). In contrast, reafforestation of the pasture with *Pinus radiata* and *Eucalyptus globulus* improved the ability of the soils to remove CH_4 from the atmosphere but not back to the levels of the original forest (Livesley et al., 2009). In contrast, when native vegetation is replaced by cropping, the CH_4 sink strength of the soil can increase, likely because cultivation can decrease bulk density and increase the air-filled porosity of the soil and thus the soil gas diffusivity. In contrast to this study, Brümmer et al. (2009) found that savanna soils converted to cropping were stronger sinks of CH_4 when compared to native savanna soils. Galbally et al. (2010) also found that soils converted to wheat cropping were a stronger sink for CH_4 than the native mallee vegetation in semiarid south-eastern Australia. A positive correlation between CH_4 sink strength and time since cropping was abandoned and afforestation began was found in soils in Scotland and Denmark (Prieme et al., 1997). These varied results emphasise that rainfall distribution, soil type and both current and past land use and their affect upon soil structure and water holding capacity need to be considered in the management of CH_4 fluxes from soils.

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4.4 Seasonal changes in CH_4 flux

Season had a statistically significant effect upon CH_4 flux from the soil, due to the large seasonal differences in soil water content between seasons typical of the wet-dry tropics. During the dry season, soil water content declined to between 0.02 and 0.05 $cm^3\,cm^{-3}$ and the soils were a sink for CH_4 under these conditions. As soil moisture increased through the dry-wet transition and into the wet season, the soil became a weaker sink and sometimes a source of CH_4 to the atmosphere. Methanotrophy is limited by gas diffusion into the soil as diffusion controls the movement of CH_4 from the bulk air to the microbes in the soil. Diffusion occurs through air filled pores. Water filled pores limit gas diffusion, clearly demonstrated in the break of season rains Experiment 2. Methanogenesis occurs when soils are sufficiently waterlogged, leading to O_2 depletion in the soil and prevailing anaerobiosis. This occurred at the old pasture sites under the environmental conditions encountered during the manual chamber measurements and in all soils during the break of season rains experiments. Our results concur with a synthesis of CH_4 fluxes from savannas which found that there was a statistically significant difference between wet season and dry season fluxes (Castaldi et al., 2006). Brümmer et al. (2009) found that both cropped and intact savanna soils were CH_4 sources when wet and CH_4 sinks when dry. Dry season CH_4 consumption was 2 to 3 times greater than wet season CH_4 consumption in tropical forest soils in Costa Rica (Keller et al., 1993). In contrast, the CH_4 fluxes at a savanna woodland in northern Australia showed no seasonal pattern at the Howard Springs savanna flux tower site, a higher rainfall savanna site (1700 mm annual rainfall) near Darwin, NT (Livesley et al., 2011).

4.5 Effect of land use change upon CO_2 flux

The change in land use from native savanna woodland to pasture increased emissions of CO_2 from the soil. The highest CO_2 emissions occurred in the young pasture. This may be explained by the hotter and wetter conditions in the pasture soils, which had

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less shading and insulation by vegetation than the savanna soils. Substrate availability likely also played a role in the higher CO_2 fluxes from the pasture soils, similarly the presence of dense, fibrous grass roots beneath the soil surface and occasional grass foliage within a chamber. Table 2 indicates that the pasture soils had higher carbon contents than the savanna soils (savanna 0.56 % C, young pasture 0.73 % C, old pasture 0.85 % C). The magnitude of CO_2 fluxes in our study is similar to those of a savanna open-forest in north Australia (Livesley et al., 2011). In contrast to our results, pasture soils emitted less CO_2 than primary and secondary forest soils on an annual basis in the wet dry tropics of the eastern Amazon Basin (Davidson et al., 2000). However, the highest and lowest monthly measurements were recorded at pasture sites. Brümmer et al. (2009) found that natural savanna soils produced more CO_2 than cropped savanna soils. This may be because cropping tends to reduce levels of C in the soil due to tillage.

4.6 Seasonal changes in CO_2 flux

Season had a significant effect upon the flux of CO_2 from the soil. CO_2 fluxes increased dry < dry-wet transition < wet. The change in CO_2 flux with season has been well documented in many different ecosystems, and is generally attributed to the increase in temperature in summer (Dalal and Allen, 2008). However, in the wet dry tropics of northern Australia, there is little change in temperature with season. Rather, it is water content that changes and our data show that water content, rather than soil temperature, drives the change in CO_2 efflux with season. Other north Australia measures of soil CO_2 efflux found similar seasonal dynamics with both Chen et al. (2002) and Livesley et al. (2011) reporting a five-fold seasonal difference in CO_2 flux from the soil over a complete seasonal cycle at the Howard Springs flux site largely driven by soil moisture, although Chen et al. (2002) observed an interaction between soil temperature and soil water content with a relationship between CO_2 efflux and soil temperature evident but only in wet soils. Davidson et al. (2000) measured soil CO_2 efflux in the wet dry tropics of the eastern Amazon Basin where there is also little variation in soil

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temperature, in order to investigate the effect of seasonal change in soil water content. They found that soil water content, in the absence of a confounding temperature effect, had a significant effect upon CO_2 flux. Brümmer et al. (2009) also found that soil water content, rather than soil temperature, controlled CO_2 flux from savanna soils.

This research and the studies mentioned above add to a growing body of evidence which suggests that global climate models need to account for the dominant effect of soil water content on CO_2 efflux in systems which experience little annual change in temperature and which are water limited for part or most of the year. Such ecosystems (seasonally dry forests, tropical, semi-arid and temperate savannas) occupy approximately 20 % of the earth land surface (Hutley and Setterfield 2008). Chen et al. (2002) estimated that predicting soil CO_2 emissions from savannas based on temperature alone would result in errors in both the seasonality and magnitude of fluxes. Soil respiration of these savannas is typically >70 % of ecosystem respiration (Chen et al., 2003) and is between 10 to 15 t C ha^{-1} yr^{-1}: a significant flux of CO_2 to the atmosphere when extrapolated across the seasonal tropics.

4.7 Annual budget

Conversion of savanna woodland to pasture decreases the CH_4 sink strength of the soil and may, under wet conditions, result in emissions of both CH_4 and N_2O. Pasture soils consistently emit more CO_2 than savanna soils and thus, the net effect of this land use change is an increase in greenhouse gas emissions from soil. However, the net effect on the whole ecosystem also includes the contribution of plants to CO_2 uptake and C sequestration, and thus measurements of net ecosystem exchange are required to fully understand the greenhouse gas impacts of converting savanna to pasture. Methane production by termites was found to offset 21 % of the soil CH_4 sink in similar savanna types in north Australia (Jamali et al., 2011). Brümmer et al. (2009) found that converting savanna to cropping decreased the abundance of termite mounds, and thus reduced the CH_4 producing potential of the ecosystem. Termites in our savanna live in mounds, in trees and below the ground, and it is not clear whether their abundance is

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reduced by conversion of savanna to pasture. The annual GHG emission from each land use type in CO_2 equivalent units was 53.31, 73.19 and 67.95 t CO_2-e ha^{-1} yr^{-1} for the savanna, young and old pasture respectively (Table 2). These estimates demonstrate that CH_4 and N_2O make up only a small proportion of the overall greenhouse gas flux from these systems, which is dominated by CO_2. Our estimate of annual CO_2 emissions from the savanna soil (14.55 t CO_2-C ha^{-1} yr^{-1}) is in close agreement with the results from savanna woodland in a higher rainfall area of northern Australia (Chen et al., 2002) (14.3 t ha^{-1} yr^{-1}) and (Livesley et al., 2011) (13.26 t ha^{-1} yr^{-1}). Across land uses, clearing essentially increased GHG by 30 %, largely driven by increased CO_2 soil fluxes.

5 Conclusions

This study clearly demonstrated that land use change from savanna to pasture increased the greenhouse gas flux from the soil. More importantly, savanna clearing led to increases in fluxes to the atmosphere of all three greenhouse gases. Nitrous oxide and CO_2 fluxes increased after conversion of savannas to pastures and soil CH_4 uptake decreased and some pastures were even a CH_4 source. Most of these changes can be explained by the structural changes of the ecosystems – pastures were exposed to greater fluctuations in soil moisture and greater soil temperature and generally showed a lower soil diffusivity. This led to greater rates of denitrification and increased nitrification and subsequent increases in N_2O fluxes but also to significant decreases in CH_4 uptake. The CO_2 fluxes also increased as soil water content increased, and the pasture soils consistently produced more CO_2 than the savanna soils. A conversion of savannas to pastures in northern Australia means therefore that there may be a significant increase in greenhouse gas emissions in CO_2 equivalents from the soil ecosystem and our study highlights that soil greenhouse gas exchange processes need to be considered to inform land use decision making in this least-developed part of Australia.

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Table 1. Site details from the manual chamber sites. Soil samples were taken from 0–10 cm, values are the average of triplicate samples.

Site	Land use	Vegetation	Soil type	BD ($g\,cm^{-3}$)	pH	EC ($\mu S\,cm^{-1}$)	C %	N %	CEC ($mg\,l^{-1}$)	Bray P ($mg\,l^{-1}$)
A	savanna	*Eucalyptus tetrodonta, Corymbia latifolia, Erythrophleum, chlorostachys* woodland with a sparse mid stratum of *E. chlorostachys, E. tetradonta, Terminalia canescens* and *Acacia* sp. over a mid to tall tussock grassland of *Sorghum* spp. and *Heteropogon* spp.	Red Kandosol	1.52	6.67	0.01	0.48	0.02	41.3	0.28
D	savanna	*Eucalyptus tetradonta, Eucalyptus miniata, Sorghum* spp., *Heteropogon contortus*	Red Kandosol	1.45	6.34	0.01	0.66	0.04	41.3	0.15
G	savanna	*Eucalyptus tetradonta, Eucalyptus miniata, Sorghum* spp., *Heteropogon contortus*	Red Kandosol	1.34	7.02	0.02	0.53	0.04	54.8	0.21
	average savanna			1.44	6.68	0.01	0.56	0.03	45.8	0.21
B	young pasture	mixed tussock grassland of perennial and annual species including *Sorghum* spp., *Heteropogon contortus* and *Chrysopogon* fallax with regrowth of cleared *Eucalyptus tetradonta*, *Eucalyptus miniata* and a shrubby mid-stratum of *Terminalia sp.* and *Acacia* spp.	Red Kandosol	1.50	6.51	0.01	0.65	0.03	51.2	0.66
E	young pasture	*Jarrah grass, wincassia*	Red Kandosol	1.54	6.22	0.02	0.67	0.04	42.4	0.29
H	young pasture	*Heteropogan contortus, pennisetum pedicellum, sesamum indicum* with regrowth of cleared *Eucalyptus tetradonta*, *Eucalyptus miniata*	Red Kandosol	1.51	6.65	0.02	0.87	0.06	86.4	1.45
	average young pasture			1.52	6.46	0.02	0.73	0.04	60.0	0.80
C	old pasture	*Heteropogon contortus, Aristida* spp. and other tussock grasses	Red Kandosol	1.55	6.12	0.02	0.82	0.05	54.2	0.49
F	old pasture	*Eragrostis* spp., *heteropogan contortus*	Red Kandosol	1.59	6.25	0.02	0.74	0.05	44.7	0.29
I	old pasture	*Senna obtusifolia, Digitaria eriantha*	Red Kandosol	1.48	5.71	0.02	0.98	0.07	51.0	0.30
	average old pasture			1.54	6.03	0.02	0.85	0.06	50.0	0.36

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Table 2. The effect of land use and seasonality on soil gas fluxes and environmental properties, as determined by 2-way ANOVA with LSD post-hoc analysis. Values followed by different letters are significantly different from one another. Non-normally distributed data were transformed as indicated.

		Land Use				Season			Interaction
		Savanna	Young Pasture	Old Pasture		Dry	Dry-wet transition	Wet	Season × LU
	P-value	Mean (se)	Mean (se)	Mean (se)	P-value	Mean (se)	Mean (se)	Mean (se)	P-value
LN CO_2	0.000	4.74 (0.55)a	4.81 (0.56) a	5.15 (0.55) b	0.000	4.09 (0.48) a	4.75 (0.59) b	5.86 (0.59) c	0.013
LN N_2O+10	0.009	0.825(0.009)a	0.859(0.009)b	0.828(0.009)a	n.s.	0.839 (0.007)	0.832 (0.009)	0.841(0.009)	n.s.
LN LN CH_4+100	0.040	1.495(0.006)a	1.527(0.006)b	1.485(0.006)a	0.040	1.510 (0.005)a	1.490 (0.006)b	1.506(.006)ab	n.s.
Temperature	0.000	32.4 (0.51)a	34.6 (0.49)b	31.6 (0.54)a	0.000	30.7 (0.43)a	37.1 (0.58)b	30.7 (0.52)a	n.s.
LN Soil Water	0.000	−3.53(0.074)a	−3.47(0.074)a	−2.88(0.074)b	0.000	−4.48 (0.064)a	−3.55 (0.078)b	−1.85(0.079)c	n.s.
LN NO_3+5	n.s.	1.773(0.041)	1.704(0.041)	1.807(0.041)	n.s.	1.769 (0.035)	1.750 (0.050)	1.765(0.035)	n.s.
LN NH_4+5	0.001	1.976(0.048)a	2.182(0.048)b	2.216(0.048)b	0.007	2.094 (0.042)a	2.257 (0.059)b	2.024(0.042)a	n.s.
LN BD	0.000	0.330(0.009)a	0.406(0.009)b	0.419(0.009)b					n.s.

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Table 3. The effect of water content and land use on gas diffusivity, CH_4 and N_2O fluxes, as determined by ANOVA. Diffusivity data were LN transformed to improve the normality of their distribution. The p-value is reported for significant results, non-significant results are indicated by "n.s.", and post hoc tests (Tukey's) were used to determine how the three water contents differed. Different letters indicate where results were significantly different from one another.

	p-value	Dry	Medium	Wet
		Effect of water content pooled across all land uses		
Diffusivity	0.001	a	b	b
CH_4	0.006	a	b	ab
N_2O	0.02	a	b	ab
		Effect of land use		
Diffusivity		n.s.	0.002	n.s.
CH_4		0.000	n.s.	n.s.
N_2O		n.s.	0.004	0.008

Table 4. Seasonal and annual cumulative fluxes of CO_2, N_2O and CH_4 for each land use, calculated from manual chamber flux data. Note that CO_2 is in tonnes (t CO_2-C ha^{-1} yr^{-1}) while N_2O and CH_4 are in kilograms (kg N_2O-N ha^{-1} yr^{-1}, kg CH_4-C ha^{-1} yr^{-1}). The final row is in CO_2-equivalent units (t ha^{-1} yr^{-1}).

	CO_2			N_2O			CH_4		
Season	Savanna	Young pasture	Old pasture	Savanna	Young pasture	old pasture	Savanna	Young pasture	Old pasture
Dry-wet transition	3.34	4.53	5.95	0.00	0.01	0.06	−0.42	−0.25	0.09
Wet	8.54	12.28	8.76	0.03	0.03	0.03	−0.16	−0.11	2.55
Dry	2.66	3.15	3.79	−0.02	0.00	−0.02	−0.97	−0.70	−0.12
Annual sums	14.55	19.96	18.50	0.02	0.05	0.07	−1.55	−1.06	2.52
Annual CO_2-e	53.35	73.19	67.84	0.01	0.02	0.03	−0.05	−0.03	0.08

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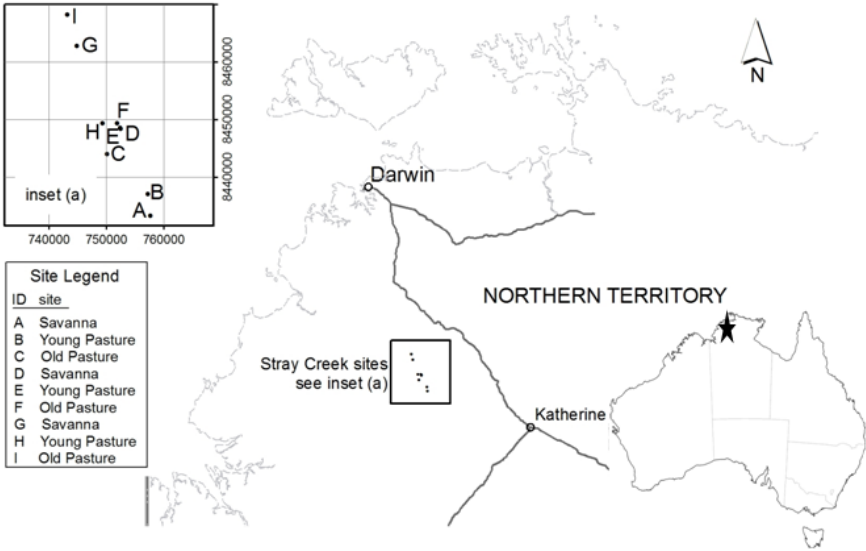

Fig. 1. Regional map of the Douglas-Daly region in the Northern Territory of Australia, showing the locality of the nine field sites; three savanna woodlands, three young pastures and three old pastures. The star shows the location on the continental map of Australia.

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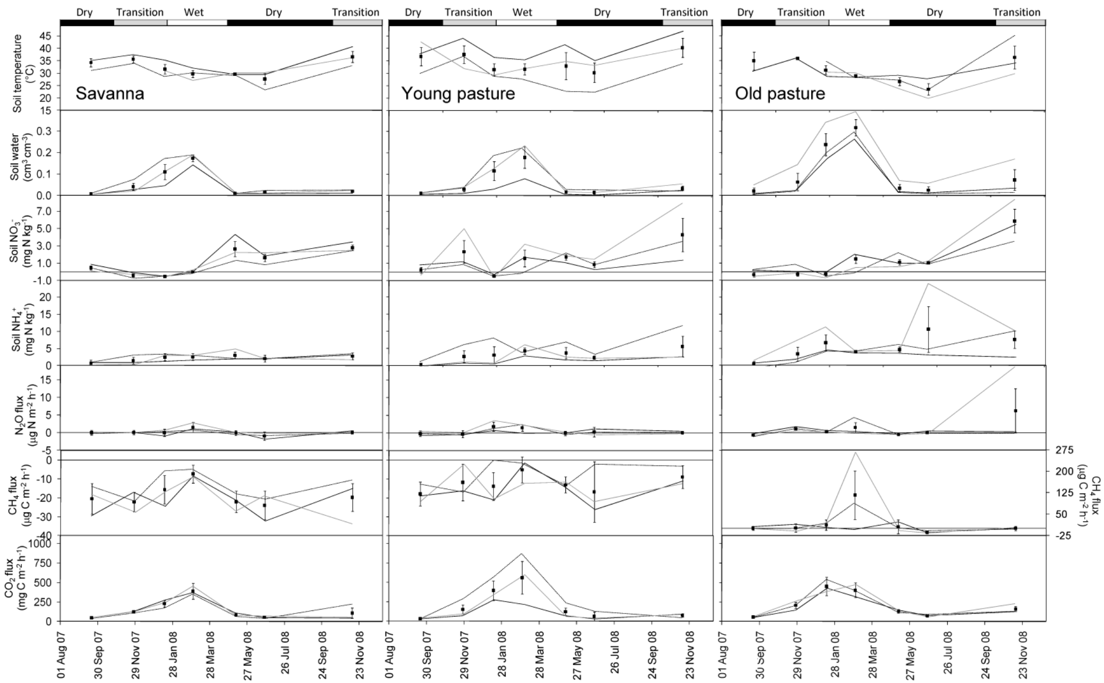

Fig. 2. Seasonal patterns of soil gas fluxes and environmental properties at savanna woodland, young pasture and old pasture sites as measured by static manual chambers on seven separate measurement events. Solid data points with standard error bars are the average of three replicate sites, as indicated by solid line, grey line and dashed line. Five measurements of flux and soil properties were made at each site.

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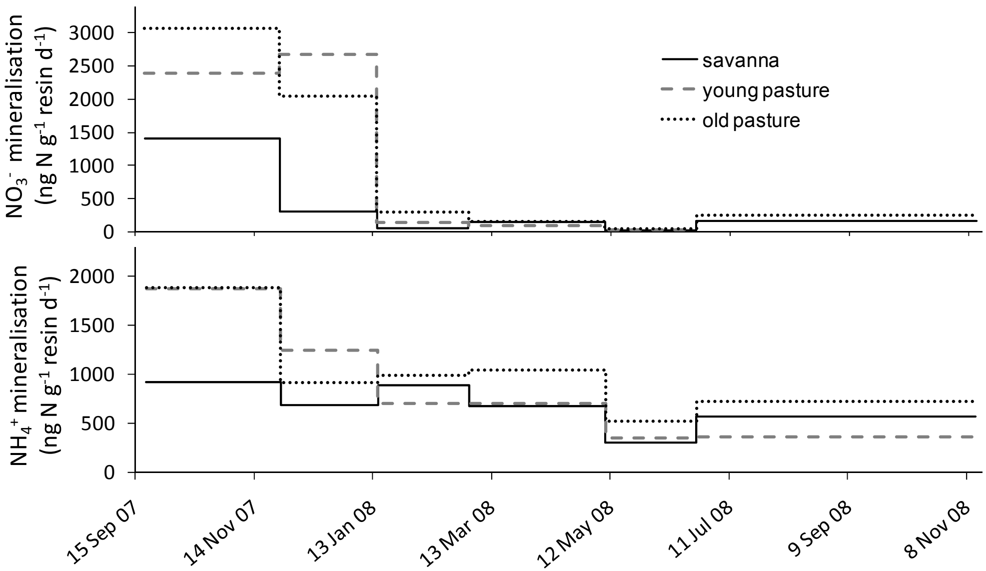

Fig. 3. Net nitrate and ammonia mineralisation rates as measured with shallow buried (~5 cm) resin bags in savanna woodland, young pasture and old pasture sites. Means and standard error bars are from three replicate sites for each land use. At each site three resin bags were buried.

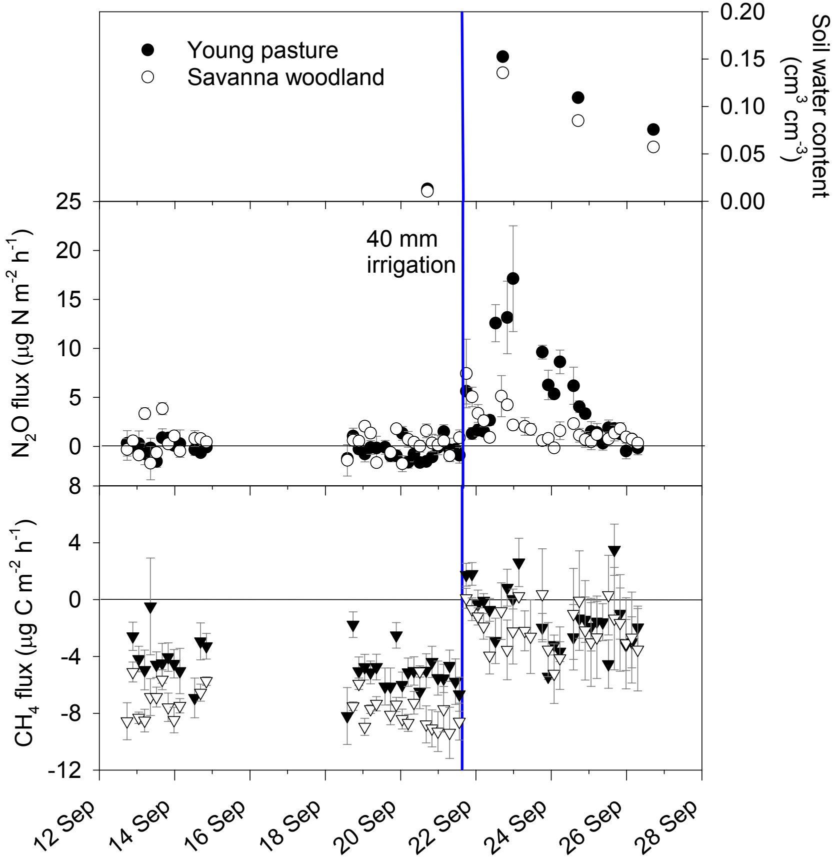

Fig. 4. Methane and nitrous oxide fluxes from soil in a savanna woodland (closed circles) and adjacent young pasture (triangles), before and after a 40 mm irrigation event. Error bars are the standard errors from five replicate chambers. Soil water content was measured before and during the irrigation experiment (young pasture closed circles, savanna open circles).

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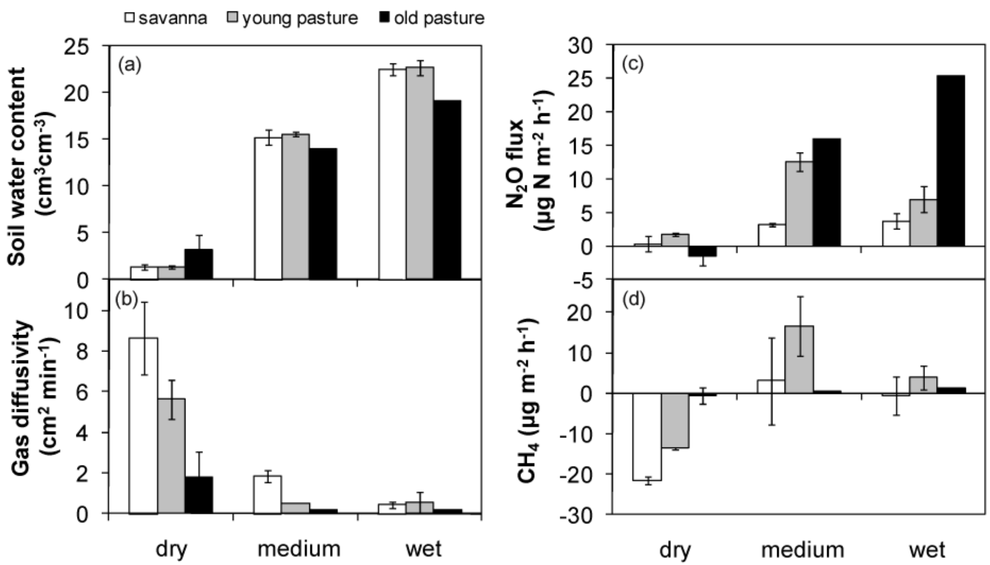

Fig. 5. The effect of artificially increased soil water contents **(a)** upon soil gas diffusivity **(b)** and soil CH_4 **(d)** and N_2O **(c)** fluxes. White bars are savanna woodland, grey bars are young pasture and black bars are old pasture. Standard error bars ($n \leq 3$) are indicated.

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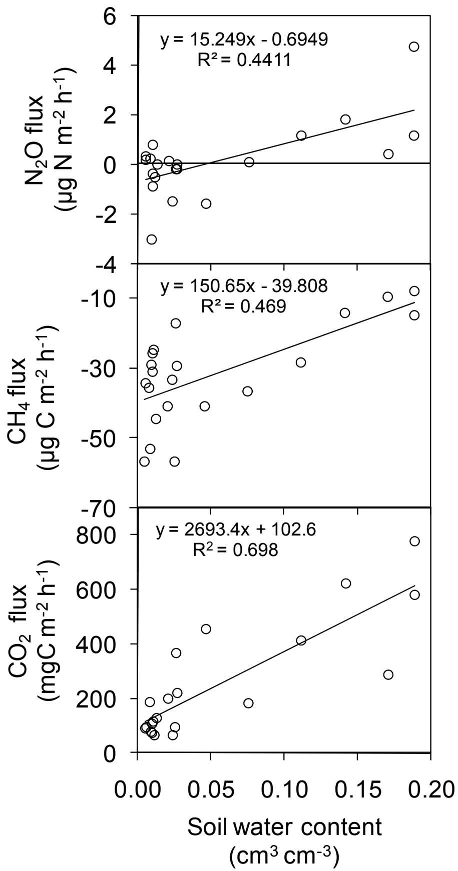

Fig. 6. The relationships between soil water content and CO_2, CH_4 and N_2O fluxes from savanna soils in the Douglas Daly region. Each point is the average value from five replicate chambers as measured at woodland, young pasture and old pasture sites on seven occasions through a 14 month period.

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