

Net primary production and ecosystem carbon flux of Brazilian tropical savanna ecosystems from eddy covariance and inventory methods

George Louis Vourlitis¹, Osvaldo Borges Pinto Jr.², Higo José Dalmagro³, Paulo Arruda⁴, Francisco de Almeida Lobo², and José de Souza Nogueira²

¹California State University

²Universidade Federal de Mato Grosso

³University of Cuiabá

⁴Unknown

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Abstract

Estimates of net primary (NPP) and ecosystem production (NEP) are needed for tropical savanna, which is structurally diverse but understudied compared to tropical rainforest. Estimates of NPP and NEP are available from eddy covariance and inventory methods, but both approaches have errors and uncertainties. We used both methods to estimate carbon (C) fluxes for an upland mixed grassland and a seasonally flooded forest to determine the correspondence in C cycling components derived from these methods and assess the contribution of the various C cycling components to the overall NEP. Both techniques provided similar estimates of NPP, NEP, and gross primary production (GPP). Belowground NPP accounted for 49-53% of the total NPP for both ecosystems, followed by aboveground litter (26-27%) and wood (16-17%) production. Increases in water availability increased the potential for C storage, but the mechanism was different in the savanna types with an increase in soil moisture causing higher NPP in the mixed grassland but lower ecosystem respiration (R_{eco}) in the Cerrado forest. Compared to other savanna ecosystems, the mixed grassland had a similar rate of R_{eco} but lower productivity and C use efficiency ($CUE = NPP/GPP = 0.28$). The Cerrado forest had a high CUE (0.58) and similar C flux rates to other tropical savanna forests and woodlands. While our measurements are spatially and temporally limited, the agreement in C fluxes estimated using inventory and eddy covariance methods suggest that the C cycle estimates for these savanna ecosystems are robust.

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Net primary production and ecosystem carbon flux of Brazilian tropical savanna ecosystems from eddy covariance and inventory methods

George L Vourlitis^{1*}, Osvaldo Borges Pinto Jr.²; Higo J. Dalmagro²; Paulo Enrique Zanella de Arruda³; Francisco de Almeida Lobo³; and José de Souza Nogueira^{3†}

¹Department of Biological Sciences, California State University, San Marcos, CA, 92096.

²Programa de Pós-Graduação em Ciências Ambiental, Universidade de Cuiabá (UNIC), Cuiabá, Mato Grosso, 78065-900, Brazil.

³Programa de Pós-Graduação em Física Ambiental, Universidade Federal de Mato Grosso (UFMT), Cuiabá, Mato Grosso, Brazil.

*Corresponding author: George L Vourlitis, Department of Biological Sciences, California State University, San Marcos, CA, 92096. Phone: 1-760-750-4119. Email: georgev@csusm.edu.

†This paper is dedicated to the memory of our friend and leader Dr. Prof. Jose de Souza Nogueira (Paraná), who lost his battle with cancer on December 12, 2021. The research described here would not be possible without his vision and leadership. His guidance and friendship will be sorely missed, but his legacy lives on with the research groups that he developed and nurtured throughout his life's work.

Key points

- Estimates of C cycling from inventory and eddy covariance methods were similar for two floristically different tropical savannas of Brazil
- Belowground NPP was 49-53% of the total NPP for both ecosystems, followed by aboveground litter (26-27%) and wood (16-17%) production.
- The grass dominated savanna had a low C use efficiency (CUE = $NPP/GPP = 0.28$) while the Cerrado forest had a CUE = 0.58.

Abstract

Estimates of net primary (NPP) and ecosystem production (NEP) are needed for tropical savanna, which is structurally diverse but understudied compared to tropical rainforest. Estimates of NPP and NEP are available from eddy covariance and inventory methods, but both approaches have errors and uncertainties. We used both methods to estimate carbon (C) fluxes for an upland mixed grassland and a seasonally flooded forest to determine the correspondence in C cycling components derived from these methods and assess the contribution of the various C cycling components to the overall NEP. Both techniques provided similar estimates of NPP, NEP, and gross primary production (GPP). Belowground

NPP accounted for 49-53% of the total NPP for both ecosystems, followed by aboveground litter (26-27%) and wood (16-17%) production. Increases in water availability increased the potential for C storage, but the mechanism was different in the savanna types with an increase in soil moisture causing higher NPP in the mixed grassland but lower ecosystem respiration (R_{eco}) in the Cerrado forest. Compared to other savanna ecosystems, the mixed grassland had a similar rate of R_{eco} but lower productivity and C use efficiency ($\text{CUE} = \text{NPP}/\text{GPP} = 0.28$). The Cerrado forest had a high CUE (0.58) and similar C flux rates to other tropical savanna forests and woodlands. While our measurements are spatially and temporally limited, the agreement in C fluxes estimated using inventory and eddy covariance methods suggest that the C cycle estimates for these savanna ecosystems are robust.

Plain language summary

Estimates of net primary and ecosystem production are needed for tropical savannas, which are highly diverse but understudied compared to tropical forests. Several methods have been used to measure primary and ecosystem production; however, these approaches have errors and uncertainties. We used available methods to estimate the productivity of a grass-dominated savanna in the southern Amazon Basin and a seasonally flooded forest in the northern Pantanal to assess the correspondence in the productivity estimated from these methods and evaluate the contribution of above and belowground processes to the overall ecosystem productivity. Productivity estimates derived from the different techniques were similar. Belowground processes accounted for 49-53% of the productivity followed by leaf (26-27%) and wood (16-17%) production. Increases in water availability increased the productivity for both savanna types, but for different reasons. An increase in soil moisture caused an increase productivity in the mixed grassland but a decline in carbon losses from the seasonally flooded forest. Compared to other savanna ecosystems, the mixed grassland had lower productivity while the forest had high productivity. While our measurements are spatially and temporally limited, the broad agreement in the different methods increases our confidence in the productivity estimates for our savanna ecosystems.

Key words and phrases: Amazon Basin, Cerrado, biometric measurements, climate change, ecosystems ecology, micrometeorology, Pantanal.

1. Introduction

Savanna makes up 15-37 million km² of the global terrestrial surface area (Grace et al. 2006). The wide range associated with this estimate of spatial coverage illustrates the difficulties in defining what constitutes “savanna” due to the high structural complexity of this biome (Hill et al. 2011). For example, Brazilian savanna (known as Cerrado) consists of forests, woodlands, and grass-dominated landcovers, depending on substrate and/or disturbance (fire) regimes, and can be upland or seasonally flooded (Goodland and Pollard 1973; Eiten 1972; Lopes and Cox 1977; Ribeiro and Walter 2008). This structural complexity causes

high plant and animal diversity (Hill et al. 2011) and highly variable estimates of plant and ecosystem production (Grace et al., 2006; Vourlitis and Rocha 2011; Arruda et al. 2016). For example, estimates of net ecosystem CO₂ exchange (NEE) suggest that Cerrado can be a net sink for atmospheric CO₂ (Miranda et al. 1997; Santos et al. 2003), approximately in balance (Rocha et al. 2002), or a net source of CO₂ to the atmosphere (Arruda et al. 2016). The variability in these estimates of NEE is likely due to differences in ecosystem structure, such as tree density, grass cover, leaf area index, climate variability, and hydrology, which influence carbon (C) stocks and C storage capacity (Vourlitis and Rocha 2011; Vourlitis et al. 2013, 2015, 2019).

However, another reason for the high variability in productivity estimates may stem from uncertainties associated with measurement techniques. For example, eddy covariance methods provide continuous measurements of NEE, but localized coverage, differences in sensors, data collection and analysis techniques, and systematic and random errors can increase uncertainty in estimates of ecosystem productivity (Goulden et al. 1996; Miller et al. 2004; Teets et al. 2018). Similarly, rates of net primary production (NPP) and ecosystem production (NEP) can be estimated from field plots using well-known inventory methods (Chen et al. 2003; Grace et al. 2006; Clark et al. 2013), but many components, such as herbivory and below ground production processes, are poorly known and/or rarely measured (Clark et al. 2001a). Furthermore, inventory measurements are time and labor intensive, which severely limits their widespread and/or prolonged use (Teets et al. 2018). Thus, both eddy covariance and inventory measurements of ecosystem production, especially in the floristically diverse tropical savanna, are highly uncertain.

While uncertainties associated with both measurement techniques are increasingly being quantified and reduced (Burba 2013; Chave et al. 2014), simultaneously using both methods can help constrain estimates of NPP and NEP (Miller et al. 2004; Gough et al. 2008; Teets et al. 2018). For example, Miller et al. (2004) used inventory measurements to provide a range of possible net ecosystem productivity estimates for an Amazonian tropical forest to help determine the best frictional velocity (u^*) value for reducing errors in nighttime flux loss from inadequate turbulence. Simultaneous flux and tree growth measurements can also shed light on time lags between canopy gas exchange and stand growth (Gough et al. 2008; Teets et al. 2018). Stand inventory data can also be used to understand C cycle dynamics that are not possible from eddy covariance measurements of gas exchange (Clark et al. 2001b).

Here we report simultaneous eddy covariance and stand inventory measurements for two tropical savanna ecosystems in Brazil, a mixed grassland (*campo sujo*) located in the southern Amazon Basin and a seasonally flooded Cerrado forest (*mata de galaria*) located in the northern Pantanal. Data are limited to two years at each site due to challenges associated with maintaining the eddy covariance infrastructure; however, field inventory measurements made over a longer period of time provided data needed for estimating above and below-

ground NPP and allowing comparisons of C flux estimates derived from eddy covariance and inventory methods. Our objectives were to (1) determine the correspondence between the eddy covariance and inventory measurements, (2) assess the contribution of the various C cycling components to the overall NEP, and (3) to compare the estimates of the C cycling components for our mixed grassland and Cerrado forest to those published in the literature.

2. Methods

2.1. Site descriptions

Eddy covariance and inventory measurements were conducted in 2011-13 in the Cuiabá Basin and 2015-17 in the Pantanal (Fig. 1). Measurements in the Cuiabá Basin were conducted at the Fazenda Miranda, located 15 km SSE of Cuiabá, Mato Grosso, Brazil (15°43'51"S: 56°04'17"W). The eddy covariance site is situated on a flat plain that is 181 m above sea level and covered primarily by a mixed-grassland (*campo sujo*) vegetation (Arruda et al. 2016). Soils are acidic (pH = 4.5), stony, shallow (50-100 cm deep), and nutrient-poor red-yellow latosols (Vourlitis et al. 2013). The vegetation is dominated by the tree species *Curatella americana* and *Pouteria ramiflora* and exotic C_4 grasses, with a tree density of 533 trees/ha and a grass cover of 65% (Vourlitis et al., 2013; Arruda et al. 2016). Measurements in the Pantanal were made at the Baia das Pedras (16°29'53' S; 56°24'46' W), which is 130 km SSW from Cuiabá, Mato Grosso, Brazil (Fig. 1). The tower is located 128 m above sea level on a flat floodplain that is seasonally flooded with approximately 50-100 cm of water between December and July (Dalmagro et al. 2019). Soils are classified as Plinthosols (Couto and Oliveira 2011) that have high clay content (50%) but low organic matter (2.0%) and pH (4.8) (Vourlitis et al. 2014). Vegetation is characteristic of a seasonally flooded forest (*mata galaria*) dominated by *Mouriri elliptica*, *Tabebuia aurea*, *T. heptaphylla*, and *Combretum leprosum* with a tree density of 1,441 trees/ha and little (5%) understory vegetation (Vourlitis et al. 2014; 2022). Neither site has experienced fire for over 35 years due to active fire suppression.

Both sites have similar climate, with a long-term (30 year) average annual rainfall of 1420 mm and a dry season from May-September when < 5% of the annual rainfall occurs (Nunes da Cunha and Junk 2001; Vourlitis and Rocha 2011). Average annual temperature is 26.5°C, and while seasonal variation is minimal (ca. < 2°C), the wet season is slightly warmer than the dry season (Vourlitis and Rocha 2011).

2.2. Eddy covariance measurements

Tower-based eddy covariance instrumentation, and data collection and analysis methods, were extensively reported for the Cuiabá Basin (Arruda et al. 2016) and Pantanal (Dalmagro et al. 2019). Briefly, both sites used an open-path infrared gas analyzer (LI-7500, LI-COR, Inc., Lincoln, NE, USA) to measure mean and fluctuating quantities of CO₂ and H₂O vapor density. Measurements of the orthogonal components of wind velocity (u_x , u_y , u_z) in the Pantanal (WindMaster, Gill, Instruments Ltd., Lymington, UK and a Model 81000, R.M. Young

Company, Traverse City, MI) and Cuiabá Basin (C-SAT3, Campbell Scientific, Inc., Logan, UT, USA) were made using three-dimensional sonic anemometers. Eddy covariance sensors were mounted 10 and 20 m above ground in the Cuiabá Basin and Pantanal, respectively, and measurements were made at 10 Hz.

Raw data were processed at 30-min intervals using EddyPro® software (v.6.1.0) (LI-COR Biosciences, Lincoln, Nebraska) in the Pantanal and Alteddy software (version 3.9) in the Cuiabá Basin. Data were corrected for air density fluctuations (Webb et al. 1980), spectral loss (Moncrieff et al., 2004), sonic air temperature humidity (Van Dijk et al., 2004), and inadequate frequency response (Lee et al. 2004). Data were rejected due to sensor or power failure, warning flags generated by the system software, spikes in the sonic and/or gas analyzer data, nonstationary wind speed conditions, and when flux data were outside plausible ranges (Foken et al. 2005). Data collected in the Pantanal were also screened for low windspeed and turbulence conditions ($u^* < 0.10$ m/s). System failure and data rejection resulted in the retention of 75-83% of all possible data in the Cuiabá Basin and 70% in the Pantanal. Data gaps were filled by the marginal distribution sampling method as described by Reichstein et al. (2005). Energy balance closure, assessed as the slope of the regression with sensible and latent heat flux (H+Le) as the dependent variable and net radiation minus ground heat flux (Rn-G) as the independent variable was on average 0.71-0.74 for both study sites (Arruda et al., 2016; Dalmagro et al., 2019).

Net ecosystem CO₂ exchange (NEE) was calculated from measurements of eddy flux and CO₂ storage in the Pantanal (Dalmagro et al. 2019); however, CO₂ storage was not measured in the Cuiabá Basin because of the open canopy associated with the mixed grassland (Arruda et al. 2016). NEE was partitioned into gross primary production (GPP) and ecosystem respiration (R_{eco}) for both sites (Table 1) using the “REddyProc” online tool (Reichstein et al. 2005). These methods assume that nighttime NEE = R_{eco} (i.e., GPP = 0). R_{eco} is calculated by (1) estimating the temperature sensitivity of R_{eco} for the entire data set, (2) calculating a seasonal reference respiration rate ($R_{\text{eco,ref}}$) for each week using a 4 day moving window, and (3) calculating R_{eco} as a function of temperature using the temperature sensitivity and $R_{\text{eco,ref}}$ for all 30-minute periods (Arruda et al., 2016). GPP was then calculated from the measured NEE and estimated R_{eco} values and integrated over an annual basis (Table 1). Autotrophic respiration (R_{Aut}) was estimated as 63% of R_{eco} based on measurements from other tropical forest (Malhi et al. 2009), and heterotrophic respiration ($R_{\text{Het}} = R_{\text{eco}} - R_{\text{A}}$) (Table 1).

2.3. Meteorological measurements

Meteorological sensors and measurement methods were discussed in detail by Arruda et al. (2016) for the Cuiabá Basin and Dalmagro et al. (2019) for the Pantanal. Air temperature and relative humidity were measured 10 m (Cuiabá Basin) and 20 m (Pantanal) above ground level using a thermohygrometer (HMP45AC, Vaisala Inc., Woburn, MA, USA). These data were used to calculate the vapor pressure deficit (VPD), which was calculated as the dif-

ference between the atmospheric saturation vapor pressure minus the actual atmospheric vapor pressure. Solar radiation (R_s) was measured 5 m (Cuiabá Basin) and 20 m (Pantanal) above ground level using a pyranometer (LI200X, LI-COR Biosciences, Inc., Lincoln, NE, USA). Soil moisture was measured using time domain reflectometry probes ($n = 2$ probes/site) installed 20 cm below the soil surface (CS616-L50, Campbell Scientific, Inc., Logan, UT, USA). Micrometeorological variables were measured every 30 s and stored and processed using a data logger (CR1000, Campbell Scientific, Inc., Logan, UT). Precipitation was measured at both sites; however, the data were not consistently reliable. Thus, precipitation data were obtained for the Cuiabá station (Station No. 83361) from Brazilian Instituto Nacional de Meteorologia (INMET; <https://bdmep.inmet.gov.br/>; accessed on 1 December, 2021), which is located between both research sites.

2.4. Inventory measurements

Woody C storage measurements (P_W ; Table 1) were described in detail by Vourlitis et al., (2019, 2022). Briefly, annual measurements of stem density and circumference were made during the dry season (July-August) in 2011-13 for the Cuiabá Basin and 2015-17 for the Pantanal when variations in stem diameter due to trunk water-storage were small (Vourlitis et al. 2022). Tree density was measured at each site using the point-quarter method (Vourlitis et al. 2013) every 5 m along a randomly placed 100 m transect. The four closest trees to each 5 m sample point with a diameter > 3 cm were tagged ($n = 80$ trees/transect), identified to genus and species, and measured for circumference at breast height (1.3 m aboveground level). All stems were measured for multi-stemmed trees; however, most trees were single stemmed at breast height. Tagged trees that died were noted, and new trees (> 3 cm in diameter) that were closest to the sample point were tagged and identified as above.

Circumference was converted to diameter at breast height (DBH) and aboveground woody biomass was calculated using measured values of DBH and wood density and estimated values of tree height calculated from DBH using established equations for tropical forest trees (Chave et al. 2014; Vourlitis et al. 2019). Annual changes in stem circumference were calculated from annual measurements of circumference at breast height for the Cuiabá Basin and from plastic spring-loaded dendrometer bands in the Pantanal (Vourlitis et al., 2019; 2022). Wood density was measured from tree cores obtained at breast height using an increment borer ($n = 146$ trees in the Cuiabá Basin and 129 trees in the Pantanal), and wood C concentration was measured from the dried cores using a wet combustion (Walkley-Black) method (Vourlitis et al. 2015). Wood biomass (kg/tree) was converted to C units (kgC/tree) by multiplying aboveground woody biomass by the wood C concentration, and the aboveground woody C pool was calculated by multiplying woody C by the average stand density (kgC/ha). The annual change in the wood C increment (P_W) was calculated as the difference in the woody C pool between two consecutive years (Vourlitis et al. 2019).

Aboveground litter production (P_{AL} ; Table 1) was measured at each site between 2014-2018 from 6-8, randomly located 1 m² tall litterfall traps constructed from metal frames and 1 mm nylon mesh (Pinto Jr. et al. 2020). Litterfall was collected monthly, dried at 70°C for 72 hours, and separated into leaves, stems, and reproductive structures. Litter was analyzed for C concentration by wet combustion methods described above (Pinto Jr. et al. 2020), and litter dry mass per unit area was converted to C units by multiplying the dry mass by the C concentration. Annual P_{AL} was calculated as the sum of the monthly litter produced each year. Measured values of P_{AL} for the Cerrado forest (Pinto Jr. et al. 2020) were used to estimate P_{AL} for the study period (2015-17). However, P_{AL} as not measured in the mixed grassland in 2011-13 and was estimated to be 0.46 MgC m⁻² y⁻¹ based on the site average measured in 2014-17 (Table 1).

Estimates of residual productivity (P_{resid}) correspond to the sum of herbaceous productivity (P_H) and the amount of leaf production lost to herbivores and emission of volatile organic compounds (VOC). P_H was considered as a residual productivity because it was a minor component of the overall productivity for each site (Vallejo 2020). P_H was measured from each site in 2019 by Vallejo (2020) as the difference between the maximum and minimum herbaceous C pool size, but because these measurements did not correspond to the 2011-13 and 2015-17 study periods, P_H was estimated for both sites as the ratio of P_W and P_H calculated in 2019 by Vallejo (2020) (Table 1). The leaf production was estimated from the litterfall data assuming that leaf litter accounted for nearly all (ca. 80%) of the of the annual P_{AL} (Pinto Jr. et al. 2018; 2020). Measurements of leaf herbivore damage made from two of the most common species found at each study site (*Curatella americana* and *Vochysia divergens*) indicate that herbivores consume on average 25% of the biomass from 28% of the leaves produced at 75% of the biomass from an additional 6% of leaves produced (Dalmolin et al., 2015). VOC emissions were estimated at 2% of annual leaf production (Clark et al. 2001a).

Root biomass was measured in 2013 from both sites in the upper 50 cm soil layer from soil cores collected every 20 m along each randomly selected 100 m transect. Collected roots (> 2 mm fragments) were removed by wet sieving, cleaned of debris, and dried at 72°C. Root density was calculated as the dry root mass per unit core area (g dry weight/m²). Roots were measured for C concentration as described for wood and litter above, and root biomass pool sizes were converted to a C pool sizes by multiplying biomass per unit area by the root C concentration. Because these root C pools were only measured once, annual estimates of root biomass production (P_R ; Table 1) were obtained from surface (0-10 cm) core samples obtained monthly from the Cerrado forest site in 2014-15 (n = 6 cores/site/month; Pinto Jr. et al., 2018). Root biomass per unit area were converted to C pools using the root C concentration measured for surface roots as above, and the P_R was calculated as the difference between the maximum and minimum root C pool size over the 2014-15 study period. These estimates of P_R resulted in a root turnover rate of 0.80 y⁻¹, which is consistent with that reported for tropical forests worldwide (Gill and Jackson,

2000). Because P_R was not measured for either site during the study period, P_R had to be estimated from an existing measured value. We chose P_w , since it was the most consistently measured C cycle component and there was enough information from our own field measurements and already published studies to provide a justifiable estimate of P_R . Published results from tropical forests indicated that the ratio of P_R (coarse and fine) to P_w was between 0.8 and 1.25 (Chambers et al. 2004; Malhi et al. 2009); however, Pinto Jr. et al. (unpublished) and Taques (2020) found a ratio of 1.9 for the seasonally flooded Cerrado forest studied here and Chen et al. (2003) reported a ratio of 4.4 for a eucalypt forest-savanna. We chose an average of 1.7 from these studies (Table 1), which suggests a higher C allocation below ground, as is indicated by our measurements and those of Chen et al. (2003). Belowground litter production (P_{BL}) was estimated from P_R using the mean turnover rate of 0.80 y^{-1} calculated for the Cerrado forest described above (Table 1).

2.5. Data analysis

Estimates of total NPP (TNPP), NEE, and GPP were estimated for both eddy covariance and inventory-based methods (Table 1). For eddy covariance methods, annual estimates of NEE and GPP were derived from the eddy covariance measurements as described in section 2.2, while TNPP was calculated as $GPP - R_{Aut}$.

For inventory methods, TNPP was calculated as the sum of aboveground NPP ($P_W + P_{AL} + P_{resid}$) and belowground NPP ($P_R + P_{BL}$), $NEE = TNPP - R_{Het}$, and $GPP = TNPP + R_{Aut}$ (Table 1). The annual change in the soil organic C pool (SOC) was estimated as the sum of the above and belowground litter inputs ($P_{AL} + P_{BL}$) minus heterotrophic respiration (R_{Het}). Annual changes in above- and belowground C pools (AGC and BGC, respectively) were estimated as the residual of the eddy derived NEE and SOC (NEE - SOC).

This residual was partitioned into AGC and BGC pools based on their fraction of the total plant C pool, which is consistent with measurements made in Amazonian tropical forests (Malhi and Grace 2000).

Confidence intervals (95%) were calculated for fluxes based on levels of replication where multiple, independent, randomly samples were available (e.g., P_{AL} , P_R). For unreplicated data (e.g., P_W ; eddy fluxes), 95% confidence intervals were calculated using bootstrapping randomization techniques as described in Arruda et al. (2016), Dalmagro et al., (2019), and Vourlitis et al. (2019).

3. Results

3.1. Meteorological conditions during the study period

Annual precipitation was on average 1467 mm over the 2011-13 study period (Fig. 2a), which was slightly higher than the long-term average, and 1420 mm over the 2015-16 study period (Fig. 2b), which is identical to the long-term average. However, interannual variations were large, with 2011-12 registering about 200 mm more precipitation than 2012-13 for the Cuiabá Basin and 2015-16 recording nearly 700 mm less rainfall than 2016-17 for the Pantanal. For the Cuiabá Basin, 2011-12 had significantly higher solar radiation than 2011-

13 (Fig. 2c) while 2012-13 had significantly higher soil moisture than 2011-12 (Fig. 2i). These patterns contrast the interannual variations in precipitation and suggest that the wetter year (2011-12) had higher solar radiation and lower soil moisture. However, the reason for the higher precipitation in 2011-12 was due to extremely high rainfall in May 2012 (ca. 264 mm vs. 20 mm in May 2013), which is normally the beginning of the dry season in this region.

For the Pantanal, 2015-16 was significantly warmer (Fig. 2f) and drier, with a significantly higher vapor pressure deficit (VPD; Fig. 2h) and lower soil moisture (Fig. 2j) than 2016-17. These differences can be attributed to the strong El Niño that occurred in 2015-16, which normally cause warmer and drier than average conditions for this region, and the subsequent La Niña that occurred the following year, which normally cause cooler and wetter conditions for the northern Pantanal (Panisset et al., 2018).

3.2. Correspondence between eddy covariance and inventory estimates of C cycling

Estimates of total NPP (TNPP), gross primary production (GPP), and net ecosystem CO₂ exchange (NEE) were similar for inventory and eddy covariance methods with no significant differences (Fig. 3). For both sites, estimates of TNPP were consistently higher for the inventory-based approach than those derived from eddy covariance; however, these differences were not statistically significant (Fig. 3a and b). Inventory methods tended to underestimate the net ecosystem C loss of the mixed grassland in 2012-13 (Fig. 3c) and overestimate the net ecosystem C uptake for the Cerrado forest in 2015-16 (Fig. 3d), but again there were no significant differences between the eddy and inventory estimates. Correspondence between GPP derived from inventory and eddy measurement techniques was qualitatively similar to that observed for TNPP, with slightly higher rates of GPP estimated from inventory methods (Fig 3e and f). However, none of the differences between the GPP estimated from inventory and eddy covariance methods were statistically significant.

3.3. Interannual variations in C cycle

The mixed grassland in the Cuiabá Basin was a consistent net C source to the atmosphere of 2.75-3.30 MgC ha⁻¹ y⁻¹ during the 2011-13 study period, while the Cerrado forest in the Pantanal was in balance in 2015-16 and a net sink of approximately 4.75 MgC ha⁻¹ y⁻¹ in 2016-17 (Fig. 4a and b; Table 1). Interannual variations in ecosystem respiration (R_{eco}) and GPP were minimal for the mixed grassland (Fig. 4c and d; Table 1), but for the Pantanal, the warmer and drier conditions in 2015-16 year caused a significant increase in R_{eco} than in 2016-17 which was wetter and cooler (Fig. 4f).

In contrast, aboveground NPP (ANPP) was nearly 2-times higher for the mixed grassland in 2012-13 than in 2011-12 while ANPP for the Pantanal was slightly higher (ca. 0.60 MgC ha⁻¹ y⁻¹) in 2015-16 than in 2016-17 (Fig. 5a and b; Table 1). ANPP was 0.74 and 1.21 MgC ha⁻¹ y⁻¹ for the mixed grassland in 2011-12 and 2012-13, respectively and 4.70 and 4.09 MgC ha⁻¹ y⁻¹ for the Cerrado

forest in 2015-16 and 2016-17, respectively (Fig. 5a and b; Table 1). ANPP made up on average 51% of the TNPP for the mixed grassland (Fig. 5e) and 47% for the Cerrado forest (Fig. 5f) depending on year. Belowground net primary production (BNPP) exhibited similar trends as ANPP for the mixed grassland (Fig. 5c), but BNPP for the Cerrado forest was approximately $1.7 \text{ MgC ha}^{-1} \text{ y}^{-1}$ higher in 2016-17 than in 2015-16 (Fig. 5d). BNPP was between 0.50 and $1.59 \text{ MgC ha}^{-1} \text{ y}^{-1}$ for the mixed grassland and 4.28 and $5.95 \text{ MgC ha}^{-1} \text{ y}^{-1}$ for the Cerrado forest (Fig. 5c and d; Table 1), and on average, BNPP accounted for 49 and 53% of the TNPP for the mixed grassland and Cerrado forest, respectively (Fig. 5e and f). In the mixed grassland, root production (P_R) and aboveground litter production (P_{AL}) were the dominant terms in TNPP (ca. 27%; Fig. 5e), while in the Cerrado forest, P_R accounted for 30% of TNPP followed closely by P_{AL} (26%; Fig. 5f). After that, belowground litter production (P_{BL}) accounted for 22% of the TNPP for the mixed grassland and 24% for the Cerrado forest, wood production (P_W) 16% in the mixed grassland and 17% in the Cerrado forest), and residual production (P_{Resid}) was 8% in the mixed grassland and 3% for the Cerrado forest (Fig. 3e and f).

3.4. Mixed grassland and Cerrado forest C cycle

The average GPP for the Cerrado forest from eddy covariance was $16.3 \text{ MgC ha}^{-1} \text{ y}^{-1}$ for the two year study period, while the TNPP from inventory measurements was on average $10.8 \text{ MgC ha}^{-1} \text{ y}^{-1}$, resulting in a C use efficiency (CUE = NPP/GPP) of 0.58 (Fig. 6). The NEE from eddy covariance ($2.3 \text{ MgC ha}^{-1} \text{ y}^{-1}$) was partitioned into the above, below, and soil organic C (SOC) pools to estimate the instantaneous change in the soil and above and belowground vegetation C pools. First, the change in the SOC pool was calculated as $[P_{AL} + P_{BL}] - R_{Het}$, and given these fluxes, the instantaneous change in the SOC pool was estimated to be $-0.5 \text{ MgC ha}^{-1} \text{ y}^{-1}$ (Fig. 6). Next, the remaining NEE was partitioned into the above and belowground C pools by assuming that the change in the pool size is a function of the fractional size of each C pool (Malhi and Grace, 2000). Thus, given the fraction of the aboveground C pool to the total plant C pool $[AGC/(AGC+BGC)] = 0.73$, the change in the aboveground C pool (ΔAGC) would be $2.1 \text{ MgC ha}^{-1} \text{ y}^{-1}$ and the change in the belowground C pool (ΔBGC) would be $0.7 \text{ MgC ha}^{-1} \text{ y}^{-1}$ (Fig. 6). Thus, while the SOC pool is estimated to be declining given the instantaneous rate of R_{Het} , the vegetation C pools must be accumulating C given the rate of NEE measured by the eddy covariance tower. These instantaneous rates of vegetation C storage would be larger if the estimate of NEE derived from the inventory methods (ca. $4.3 \text{ MgC ha}^{-1} \text{ y}^{-1}$; Table 2) was used.

In contrast, the GPP for the mixed grassland was $7.5 \text{ MgC ha}^{-1} \text{ y}^{-1}$ from eddy covariance and the TNPP from inventory measurements was $2.1 \text{ MgC ha}^{-1} \text{ y}^{-1}$, resulting in a CUE of 0.28 (Fig. 6). Using the eddy covariance NEE as the reference value, SOC was $-2.9 \text{ MgC ha}^{-1} \text{ y}^{-1}$, accounting for nearly all of the net ecosystem C loss, and both ΔAGC and ΔBGC were $-0.1 \text{ MgC ha}^{-1} \text{ y}^{-1}$ (Fig. 6).

4. Discussion

4.1. Correspondence between the eddy covariance and inventory estimates and other studies

The C flux values calculated from inventory methods agreed well to those estimated from eddy covariance (Fig. 3), and while small, differences between inventory and eddy covariance methods are expected given the inherent measurement errors and uncertainties associated with both methods and time lags between rates of CO₂ exchange and growth (Gough et al. 2008; Teets et al. 2018).

Our estimates of the key C cycle variables for the Cerrado forest were similar to those published in the literature (Table 2). For example, estimates of NEE from other savanna forests and woodlands ranged between 0.1 to 3.8 MgC ha⁻¹ y⁻¹, which agrees with the Cerrado forest estimates derived from both methods (Table 2). However, our mixed grassland was consistently less productive than other comparable grass-dominated tropical savannas during the study period and was losing C (Fig. 6; Table 2). There are undoubtedly many reasons for these differences, but soils associated with our mixed-grassland are shallow, stony, with low water-holding capacity and fertility (Vourlitis et al. 2013), and it is likely that these conditions promote low productivity. Furthermore, fire has been suppressed at this site for decades, and periodic fire can stimulate gross productivity in campo forms of Cerrado (Santos et al. 2003). Interestingly, the only C cycle variable for the mixed-grassland that agreed well with other grass-dominated savannas was R_{eco}, which was 10.6 MgC ha⁻¹ y⁻¹ for our mixed-grassland compared to 9.8 MgC ha⁻¹ y⁻¹ for other grass-dominated savanna in Brazil (Table 2).

Estimates of GPP for the Cerrado forest studied here ranged between 16.3 and 18.4 MgC ha⁻¹ y⁻¹ based on eddy covariance and inventory estimates, respectively, which is slightly lower than the estimate reported for a eucalypt forest-savanna in Australia (Table 3). However, the estimate of R_{eco} for our Cerrado forest is well lower than that reported for the same forest (Table 3), which is probably related to the seasonally flooded hydrology of our forest (Dalmagro et al. 2019). However, rates of ANPP, BNPP, and TNPP for our Cerrado forest are well within the range of values reported for other forest- and woodland-savanna (Table 3), which provides confidence in the values estimated here.

4.2. Carbon storage and cycling of Cerrado mixed-grasslands and forests

Carbon use efficiency was on average 0.58 for the Cerrado forest and 0.28 for the mixed grassland, compared to CUE values reported for tropical forests (0.30-0.51; Malhi et al. 1999, 2009; Chambers et al. 2004) and savanna (0.53; Chen et al. 2003). The lower value for the mixed grassland presumably reflects the relatively low growth rates of the C4 grasses and dominant tree species (*Curatella americana*), which has a lower RGR than many other tree species observed the Cuiabá Basin and Pantanal (Vourlitis et al. 2022). In contrast, the high value for the Cerrado forest reflects a greater proportion of GPP that is allocated to growth (Chambers et al. 2004), and dominant tree species within the tower

footprint (e.g., *Mouriri elliptica* Mart., *Eugenia florida* DC., *Vochysia divergens*, and *Erythroxylum anguifugum*) have high relative growth rates (Vourlitis et al. 2022). Many of these species are also considered to be pioneer or secondary species, suggesting that the Cerrado forest is recovering from a disturbance that happened in the past.

TNPP was roughly equally partitioned into ANPP and BNPP for both ecosystems studied, which is similar to that reported for other savanna ecosystem worldwide (Table 2). Most of the TNPP was composed of P_R , which reflects the relatively higher belowground C allocation for both arboreal and grass-dominated savanna (Chen et al., 2003; Mokany et al. 2006), followed by P_{AL} , P_{BL} , P_W , and P_{Resid} accounting for the lowest fraction of TNPP (Fig. 5). P_{AL} was also an important component of TNPP, exceeding P_W by 9-11%, and since the majority of P_{AL} is leaf litter (80%; Pinto Jr. et al. 2018; 2020), these results imply an important contribution of leaf production to the total forest NPP. The NPP of tropical forests is typically dominated by leaf production (Clark et al. 2001b; Chambers et al. 2004) reflecting the high leaf area index of these forests. P_W accounted for 16-17% of the TNPP, but 30-39% of the ANPP for the savanna ecosystems studied here, which is similar to that reported for other tropical forests (Clark et al., 2001b) and savannas (Chen et al. 2003). This C allocation to wood represents a stable, long-term C storage pool (Malhi et al. 2004).

Our data suggest that losses of NPP from herbivory and grazing are a minor component of the TNPP for these systems, but unfortunately, we are unable to reduce the potential uncertainty in our estimates of herbivore pressure on NPP. ANPP lost to herbivores has been shown to be an important avenue of C loss for some of the tree species studied here (Dalmolin et al. 2015), and grazing losses for pastures in the Pantanal-Cerrado transition of Mato Grosso account for around 15% of annual NEE (Dalmagro et al. in prep.). In contrast, Wilsey et al. (2002) found that aboveground biomass production was positively correlated with grazing intensity even though annual NEE was not significantly affected by grazing.

Given the NEE and productivity estimates for each ecosystem type, instantaneous rates of C storage were positive for the above- (AGC) and belowground (BGC) and soil C (SOC) pool for the forest but not for the mixed grassland (Fig. 6). For the forest, inputs of C from above and belowground litter production are apparently not enough to balance C losses from heterotrophic respiration, and as a result, we estimate an instantaneous loss of C from the SOC pool (Fig. 6). To balance the NEE, the largest increase was observed for the AGC pool (+1.6 MgC ha⁻¹ y⁻¹), based on the ratio of above and below ground pool size, followed by the BGC pool. For the grassland, the largest loss was estimated for the SOC pool (-2.9 MgC ha⁻¹ y⁻¹), which almost completely accounted for the net ecosystem loss (Fig. 6). This result, while surprising, may be reasonable in light of the high R_{eco} (ca. 10.6 MgC ha⁻¹ y⁻¹) estimated for the mixed grassland (Fig. 6), which is about 0.8 MgC ha⁻¹ y⁻¹ higher than estimates reported for

other grass-dominated topical savannas (Table 2).

4.3. Interannual patterns of C fluxes

Admittedly, the two-year study period associated with each savanna landcover type limits our ability to assess climatic controls on C cycling. However, some trends emerged that are consistent with what is known about how climate variation affects C cycling in these ecosystems. TNPP was higher in 2012-13 for the mixed grassland, due to higher ANPP and BNPP, while NEE was trending higher in 2012-13 because of increases in GPP. While 2012-13 had lower rainfall and solar radiation than 2011-12, soil moisture was significantly higher in 2012-13, which presumably increased water availability. Increases in water availability typically increase leaf photosynthesis (Dalmagro et al. 2014; Dalmolin et al., 2018), NEE (Arruda et al. 2016), tree growth (Vourlitis et al. 2022) and wood C storage (Vourlitis et al. 2019) for Cerrado of the Cuiabá Basin. The interannual variations in NEE and NPP for the Pantanal forest are perhaps more interesting, as net ecosystem CO₂ uptake increased significantly in 2016-17, which was a cooler and wetter year than 2015-17. However, the increase in NEE appeared to be due more to a decline in R_{eco} than an increase in productivity (i.e. GPP or NPP). Growth rates for many of the tree species in the study area have been shown to be sensitive to variations in rainfall dry season length, and temperature (Vourlitis et al., 2022), so it is not clear why ANPP, and thus, TNPP did not increase in 2016-17, which was significantly wetter and cooler. Apparently, the increase in rainfall and soil moisture caused an increase in the duration of the anaerobic period, which reduced R_{eco} (Dalmagro et al. 2019).

4.4. Caveats and limitations

Our estimates of C fluxes are broadly consistent with those reported for similar tropical savanna ecosystems. However, there are several limitations associated with our data that warrant consideration. First, the eddy covariance and inventory measurements only overlapped for two years at each study site, which is probably not enough time to robustly assess temporal trends in the eddy and inventory C fluxes, and especially, climatic controls on these variables (Clark et al. 2013). This is especially true for the inventory methods, which require estimation of litter production for both above and below ground NPP, which were either not measured at either site (P_{BL}) or not measured when other inventory measurements were conducted (P_{AL} in the mixed grassland). The lack of such important data required their estimation from averages measured during other time periods or from other measurements, which have their own uncertainties and errors. Because P_{AL} was a dominant component for ANPP, the lack of measured data for the mixed grassland presumably increases the uncertainty in the inventory estimates of TNPP and NEE for this landcover type. The same can be said for P_R, which was estimated empirically from P_W because comparable data of both sites were lacking. Given the presumed importance of P_R for both sites, the lack of actual measurements during the study period adds uncertainty to the estimates of BNPP and TNPP.

Estimates of C cycling variables also required assumptions that were highly uncertain. As mentioned above, assumptions of herbivore pressure on NPP were highly uncertain, and estimates of root litter production were based on measured rates of root turnover for the Cerrado forest only. While these estimates of root turnover were consistent with those reported for other tropical forests (Gill and Jackson, 2000), it is unclear whether these values are representative of the mixed grassland and/or whether they adequately characterize belowground litter production.

Finally, our scaled estimates of NEE and GPP from the inventory measurements assumed that the tower footprints were dominated by mixed grassland vegetation (Cuiabá Basin) and seasonally flooded Cerrado forest (Pantanal) because detailed analyses of the tower footprints were not conducted. We feel that the lack of a detailed footprint assessment is not likely to significantly increase the uncertainty of our inventory estimates because both Arruda et al. (2016) and Dalmagro et al. (2019) indicated that ca. 80% of the eddy flux originated within 250 m upwind of the flux towers, which consisted of relatively uniform mixed grassland or Cerrado forest vegetation. However, variations in the composition of trees and herbaceous plant species, cover, soil type, and/or C stocks are unknown and may contribute to scaling errors for the inventory data.

5. Conclusions

We estimated C fluxes for two tropical savanna ecosystems in the southern Amazon Basin and northern Pantanal using eddy covariance and inventory measurements. Both techniques provided similar estimates of NPP, NEE, and GPP, which increases the level of confidence in the C fluxes estimated for these land-cover types. Belowground NPP accounted for approximately half of the total NPP for both ecosystems, followed by aboveground litter and wood production. Carbon fluxes for both savanna types increased with higher water availability but for different reasons; an increase in soil moisture stimulated above and below ground NPP in the mixed grassland but caused a decrease in R_{eco} in the seasonally flooded Cerrado forest. Compared to other savanna ecosystems, the mixed grassland had low productivity and low C use efficiency ($\text{CUE} = 0.28$) but had similar rates of R_{eco} . In contrast, the Cerrado forest had a high CUE (0.58), and C flux rates estimated for the Cerrado forest were similar to other savanna forests and woodlands. While our measurements are limited and potentially uncertain, the broad agreement in the C fluxes estimated using inventory and eddy covariance methods, coupled with those reported in the literature, indicate that our estimates of C flux for these savanna ecosystems are robust. Furthermore, the sensitivity of these ecosystems to variations in water availability suggests that warming and drying associated with climate change will likely alter the C productivity and C balance of savanna ecosystems in the southern Amazon Basin and northern Pantanal.

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Author contributions

Conceptualization: George Vourlitis

Data curation: George Vourlitis, Osvaldo Borges Pinto Jr., Higo J. Dalmagro, Paulo Enrique Zanella de Arruda

Formal Analysis: George Vourlitis, Osvaldo Borges Pinto Jr., Higo J. Dalmagro, Paulo Enrique Zanella de Arruda

Funding acquisition: George Vourlitis

Investigation: George Vourlitis, Osvaldo Borges Pinto Jr., Higo J. Dalmagro, Paulo Enrique Zanella de Arruda, Francisco de Almeida Lobo; and José de Souza Nogueira

Methodology: George Vourlitis, Osvaldo Borges Pinto Jr., Higo J. Dalmagro, Paulo Enrique Zanella de Arruda

Project administration: George Vourlitis, José de Souza Nogueira

Resources: Osvaldo Borges Pinto Jr., José de Souza Nogueira

Visualization: George Vourlitis,

Writing – original draft: George Vourlitis, Osvaldo Borges Pinto Jr., Higo J. Dalmagro, Paulo Enrique Zanella de Arruda

Writing – review & editing: Osvaldo Borges Pinto Jr., Higo J. Dalmagro, Francisco de Almeida Lobo

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Figure legends

Fig. 1. Location of the study sites in the Cuiabá Basin (Fazenda Miranda) and the northern Pantanal (Baia das Pedras) (main image) and the location of the study region with respect to Brazil and the South America (small image in the lower right-hand corner). The light-green shaped portion of the main image displays the boundary of the Pantanal. Modified from Justica Ambiental (www.justicaambiental.org.br).

Fig. 2. Meteorological conditions for the Cuiabá Basin (left-panels) and the Pantanal (right-panels). Data are for total annual rainfall (a and b) and mean (\pm 95% confidence interval) solar radiation (c and d), air temperature (e and f), vapor pressure deficit (g and h), and soil moisture (I and j). Precipitation data were obtained from INMET for Cuiabá station (Station No. 83361). All other data are from the tower sites. Confidence intervals were obtained by bootstrapping randomization techniques calculated over 1000 iterations. Asterix indicate significant ($p < 0.05$) differences between years.

Fig. 3. Mean (\pm 95% confidence interval) (a and b) total net primary production (TNPP), (c and d) net ecosystem CO_2 exchange (NEE), and (e and f) gross primary production (GPP) derived from eddy covariance and increment measurement techniques for the mixed grassland in the Cuiabá Basin (left-panels) and the Cerrado forest in the Pantanal (right-panels).

Fig. 4. Mean (\pm 95% confidence interval) net ecosystem CO_2 exchange (NEE: a and b), gross primary production (GPP: c and d), and ecosystems respiration (e and f) for the Cuiabá Basin (left-panels) and the Pantanal (right-panels). Positive values indicate net CO_2 gain by the ecosystem. Confidence intervals were obtained by bootstrapping randomization techniques calculated over 1000 iterations. Asterix indicate significant ($p < 0.05$) differences between years.

Fig. 5. Net primary production (NPP) components for aboveground NPP (ANPP: a and b), belowground NPP (BNPP: c and d), and the of wood (P_W), aboveground litter (P_{al}), residual (P_{resid}), root (P_r), and belowground litter (Pbl) production to TNPP for mixed-grasslands of the Cuiabá Basin (left-panels) and Cerrado forests of the Pantanal (right-panels). P_W = wood production; P_{al} = aboveground litter production; P_{resid} = residual production (herbaceous production + production losses to herbivory and volatile organic C emission); P_r = root production; P_{bl} = belowground litter production.

Fig. 6. Conceptual carbon balance for the Cerrado forest in the Pantanal (left-panel) and the mixed grassland in the Cuiabá Basin (right-panel) based on a combination of stand increment and eddy covariance measurements for 2011-13 (Cuiabá Basin) and 2015-17 (Pantanal). Fluxes ($\text{MgC ha}^{-1} \text{ y}^{-1}$) are displayed as arrows, with gains to the ecosystem as green arrows and losses as red arrows. Pools (boxes: MgC/ha) are based on data published by Pinto Jr. et al. (2020), Vourlitis et al. (2013, 2015, and 2019), and from unpublished data. Data are averages of those displayed in Table 1. The change in soil organic C (SOC) is estimated as the sum of the above and belowground litter inputs minus heterotrophic respiration. The change in above- and belowground C pools (AGC and BGC, respectively) are estimated as $\text{NEE} - \text{SOC}$ and are partitioned into AGC and BGC pools based on their fraction of the total plant C pool. Positive values of net ecosystem CO_2 exchange (NEE) depict net uptake by the ecosystem.

Table 1. Data sources and rationale for calculating net ecosystem exchange (NEE), gross primary production (GPP), ecosystem respiration (R_{eco}), wood

production (P_W), above (P_{AL}) and belowground litter (P_{BL}) production, herbaceous production (P_H), carbon losses from herbivory and volatile organic carbon (VOC) emissions, aboveground net primary production (ANPP), root production (P_R), total net primary production (TNPP) derived from inventory (I) or eddy covariance (E) methods, autotrophic respiration (R_{Aut}), and the estimated NEE derived from inventory methods (NEE_I). All values are in $MgC\ ha^{-1}\ y^{-1}$. NEE data with a negative sign indicates net loss from the ecosystem to the atmosphere. See Methods for a detailed explanation of calculation procedures and rationale.

Variable		Cuiabá Basin	Pantanal		
($MgC\ ha^{-1}\ y^{-1}$)	Data source or calculation	2011-12	2012-13	2015-16	2016-17
NEE_E	CB: Arruda et al. (2016) PAN: Dalmagro et al (2019)				
GPP_E	CB: Arruda et al. (2016) PAN: Dalmagro et al (2019)				
R_{eco}	CB: Arruda et al. (2016) PAN: Dalmagro et al (2019)				
R_{Aut}	% of R_{eco} (Mahli et al. (2009)				
R_{Het}	Reco - R_{Aut}				
P_W	Vourlitis et al. (2019a and b)				

Variable	Cuiabá Basin	Pantanal
P_{AL}	CB: average from 2014-2017	
P_H	PAN: Pinto Jr. et al. (2020) Vallejo (2020)	
Herbivory	Assumes 28% of leaves = 25% loss and 6% of leaves = 75% loss (Dalmolin et al. 2016)	
VOC	% of leaf production (Clark et al. 2001a)	
P_{Resid}	$P_H +$ Herbivory $+ VOC$	
ANPP	$P_W + P_{AL}$ $+ P_{Resid}$	
P_R	$P_R = 1.7$ $\times P_W$ (Tagues 2020)	
P_{BL}	Assumes a P_R turnover = 0.8 y^{-1} (Gill and Jackson 2000); (Tagues 2020)	
BNPP	$P_R = P_{BL}$	

Variable	Cuiabá Basin	Pantanal
TNPP _I	ANPP + BNPP	
TNPP _E	GPP R _{Aut}	
NEE _I	TNPP	
GPP _I	R _{Het} TNPP + R _{Aut}	

Table 2. Summary of published estimates of net ecosystem CO₂ exchange (NEE), gross primary production (GPP), ecosystem respiration (R_{eco}), above-ground net primary production (ANPP), belowground NPP (BNPP), and total NPP (TNPP) for various savanna ecosystems. Estimates of NEE < 0 indicate net C loss from the ecosystem to the atmosphere. E = eddy covariance; I = inventory or harvest methods.

Variable	MgC ha ⁻¹ y ⁻¹	Ecosystem type	Method	Location	Reference
NEE	2.3	Cerrado forest	E	Brazil	This study
	4.3	Cerrado forest	I	Brazil	This study
	-3	Mixed grassland	E	Brazil	This study
	-1.9	Mixed grassland	I	Brazil	This study
	2.8	Mesic savanna forest	E	Australia	Eamus et al. (2001)
	3.8	Eucalypt forest-savanna	I	Australia	Chen et al. (2003)
	2.9	Mixed grassland	E	Brazil	Santos et al. (2003)
	0.1	Woodland savanna	E	Brazil	Rocha et al. (2002)
GPP	16.3	Cerrado forest	E	Brazil	This study
	18.4	Cerrado forest	I	Brazil	This study
	7.5	Mixed grassland	E	Brazil	This study
	8.7	Mixed grassland	I	Brazil	This study
	20.2	Eucalypt forest-savanna	I	Australia	Chen et al. (2003)
R_{eco}	12.7	Mixed grassland	E	Brazil	Santos et al. (2003)
	14.1	Cerrado forest	E	Brazil	This study
	10.6	Mixed grassland	E	Brazil	This study
ANPP	17	Eucalypt forest-savanna	I	Australia	Chen et al. (2003)
	9.8	Mixed grassland	E	Brazil	Santos et al. (2003)
	4.4	Cerrado forest	I	Brazil	This study
BNPP	1.0	Mixed grassland	I	Brazil	This study
	3.0	Eucalypt forest-savanna	I	Australia	Chen et al. (2003)
	6.6±2.7 ^{†‡}	Savanna	I	Various	House and Hall (2001) (n =
	5.1	Cerrado forest	I	Brazil	This study
	1.0	Mixed grassland	I	Brazil	This study
	8.0	Eucalypt forest-savanna	I	Australia	Chen et al. (2003)
	4.6±2.4 ^{†‡}	Savanna	I	Various	House and Hall (2001) (n =

Variable	MgC ha ⁻¹ y ⁻¹	Ecosystem type	Method	Location	Reference
TNPP	7.5	Cerrado forest	E	Brazil	This study
	9.5	Cerrado forest	I	Brazil	This study
	0.9	Mixed grassland	E	Brazil	This study
	2.0	Mixed grassland	I	Brazil	This study
	10.5 [‡]	Forest/shrub woodland	I	Various	Atjay et al. (1979)
	11.5 [‡]	Savanna	I	Various	Atjay et al. (1979)
	6.4 [‡]	Dry forest	I	Various	Olson et al. (1983)
	5.5 [‡]	Savanna	I	Various	Olson et al. (1983)
	6.3 [‡]	Woodlands	I	Africa	Scholes and Hall (1996)
	7.1 [‡]	Savanna	I	Africa	Scholes and Hall (1996)
	11.2 _{+4.4} ^{‡†}	Savanna	I	Various	House and Hall (2001) (n = 10)
	11.0	Eucalypt forest-savanna	I	Australia	Chen et al. (2003)
	10.2 _{+5.9} [†]	Forest/woodland	I	Various	Grace et al. (2006) (n = 10)
	5.9 _{+3.6} [†]	Savanna	I	Various	Grace et al. (2006) (n = 12)

[†]Mean \pm standard deviation

[‡]Data reported as dry mass. Converted to C units assuming the dry mass is 50% C.

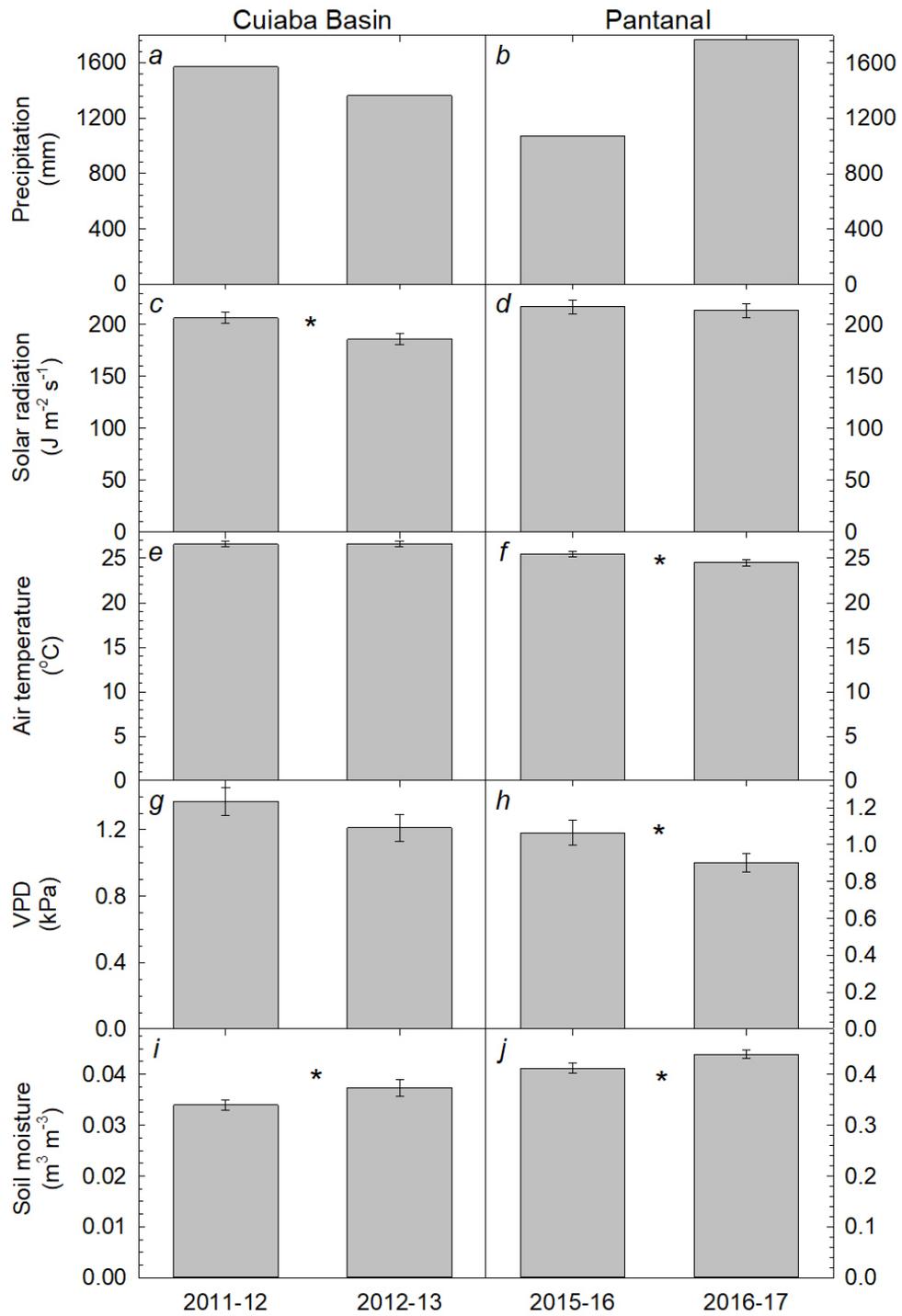


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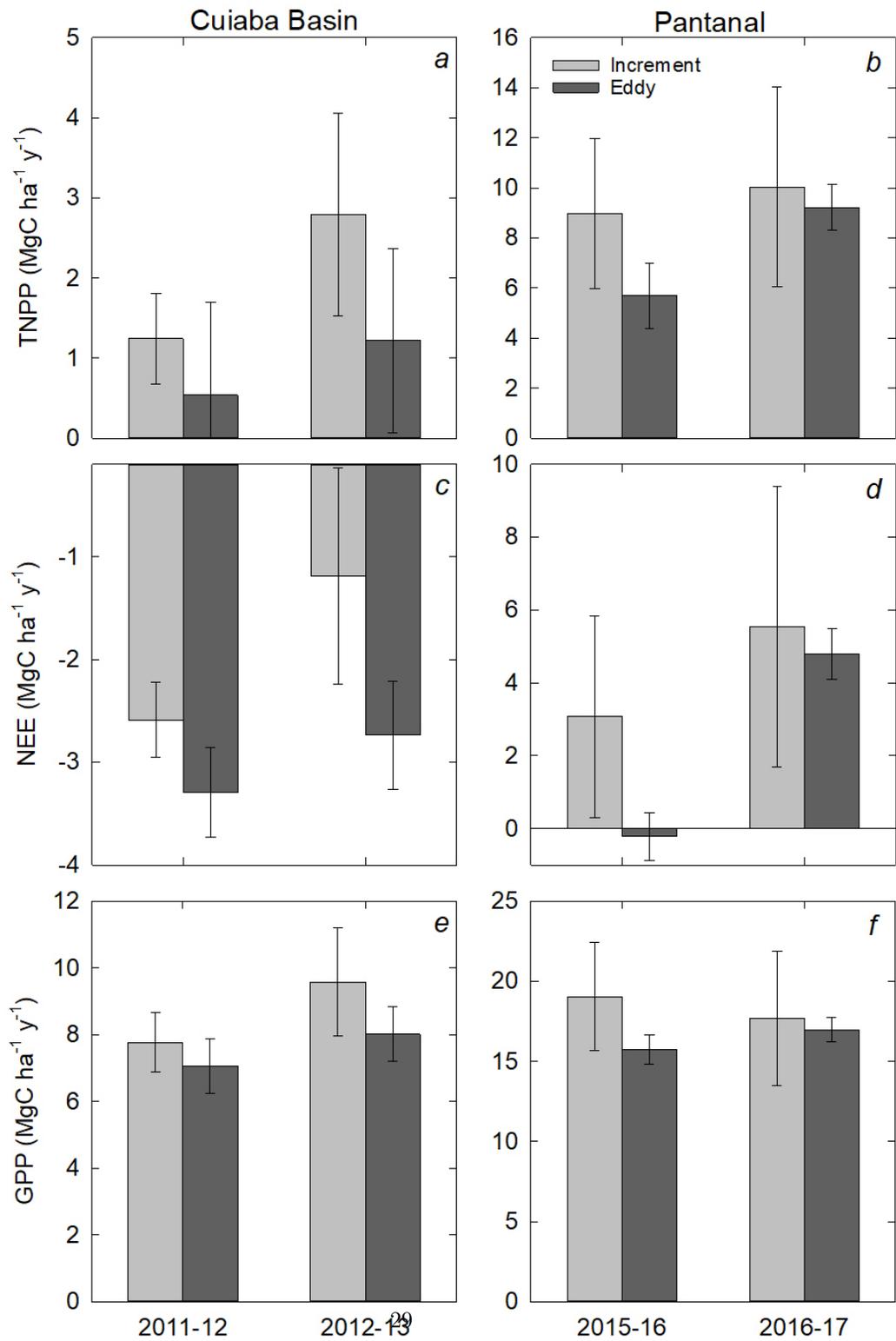


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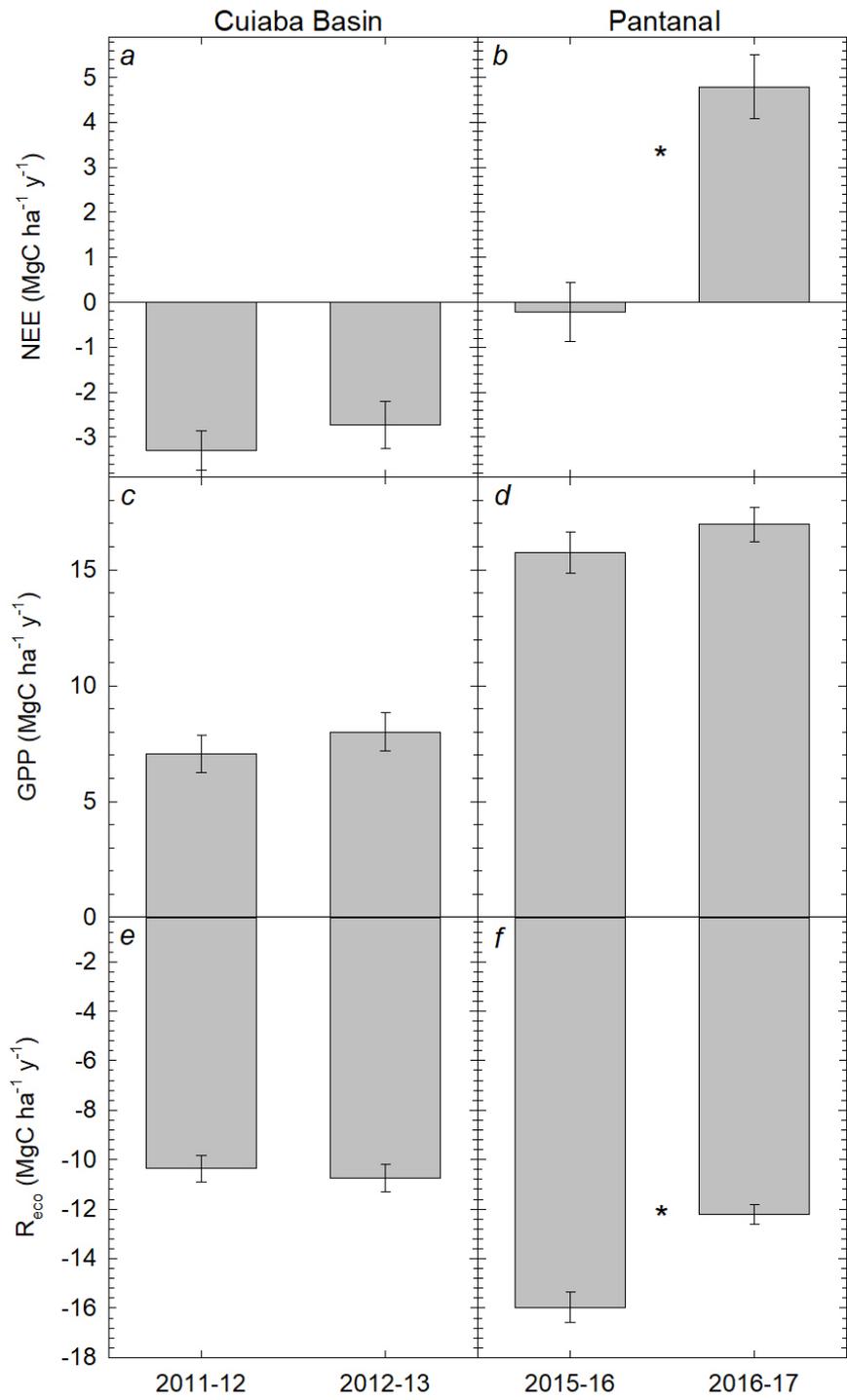


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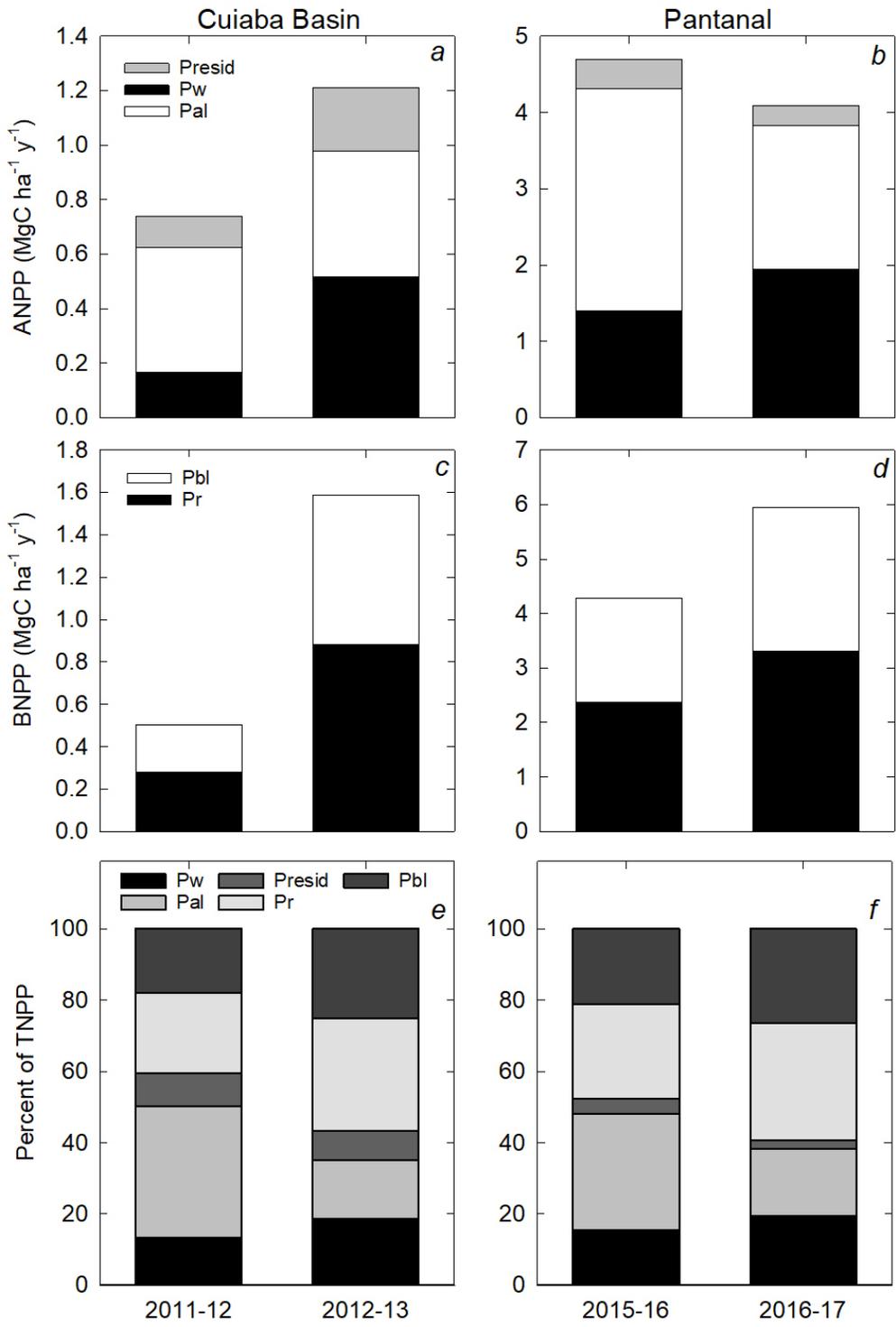


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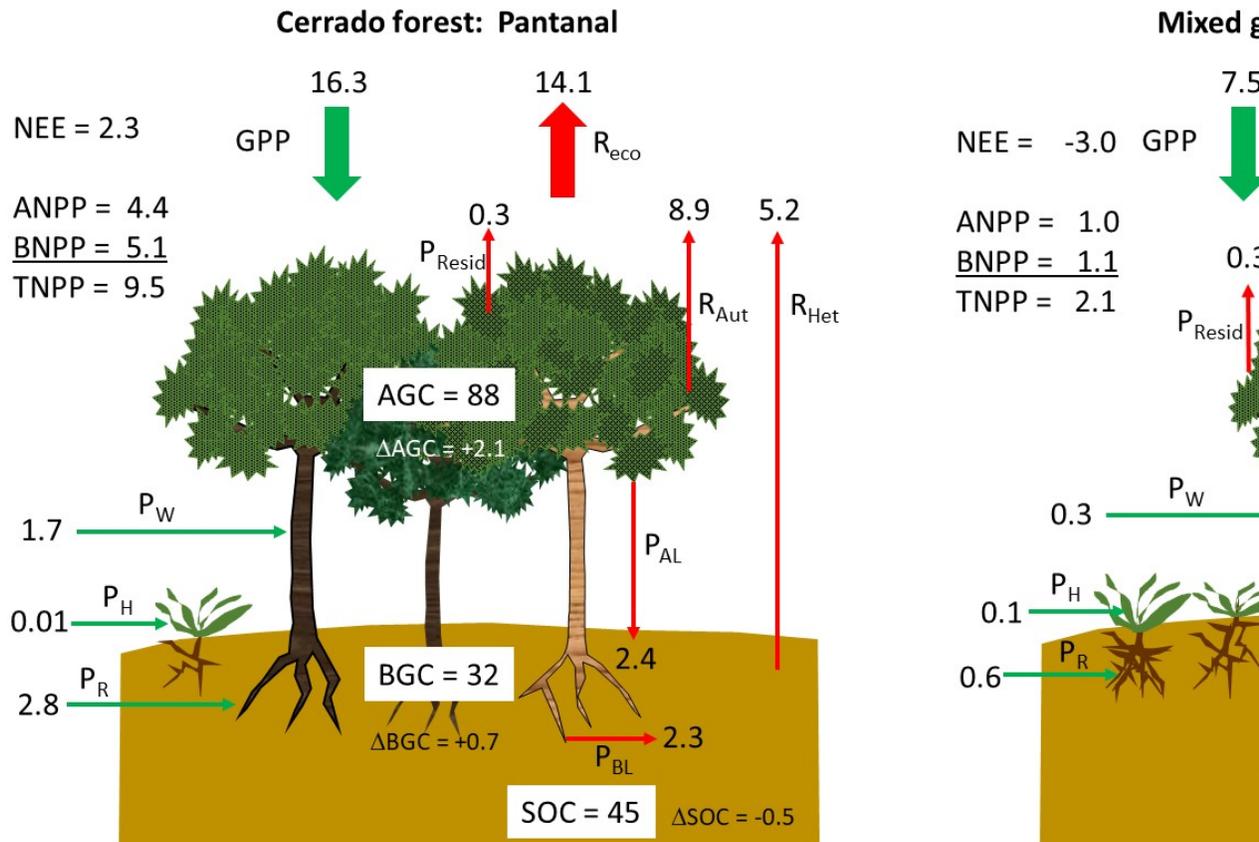


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