

## Article

# Suitability Evaluation of Three Tropical Pasture Species (Mulato II, Gatton Panic, and Rhodes Grass) for Cultivation under a Subtropical Climate of Australia

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**Abstract:** Exploring improved tropical forages is considered to be an important approach in delivering quality and consistent feed options for dairy cattle in tropical and subtropical regions. The present study aimed to study the suitability of three improved tropical grasses, *Chloris gayana* ‘Rhodes grass cv. Reclaimer’ (RR), *Megathyrsus maximus* ‘Gatton Panic’ (GP), and *Brachiaria ruziziensis* x *B. decumbens* x *B. brizantha* ‘*Brachiaria* Mulato II’ (BM) evaluating their carbon assimilation, canopy structure, herbage plant-part accumulation and quality parameters under irrigated conditions. An experiment was conducted at Gatton Research Dairy (27°54′ S, 152°33′ E, 89 m asl) Queensland, Australia, which has a predominantly subtropical climate. Photosynthesis biochemistry, canopy structure, herbage accumulation, plant part composition, and nutritive value were evaluated. Photosynthesis biochemistry differed between pasture species. Efficiency of CO<sub>2</sub> assimilation was highest for GP and quantum efficiency was highest for BM. Pasture canopy structure was significantly affected by an interaction between pasture species and harvest. Forage biomass accumulation was highest in GP, while BM produced more leaf and less stem compared to both GP and RR. A greater leafy stratum and lower stemmy stratum depth were observed in the vertical sward structure of BM. *Brachiaria* Mulato II showed greater carbon partitioning to leaves, leaf: stem ratio, canopy, and leaf bulk density. It also demonstrated greater nutritive value (Total digestible nutrients (TDN), acid detergent fibre (ADF), neutral detergent fibre (NDF), neutral detergent insoluble protein (NDICP), Starch, nonfibre carbohydrates (NFC), metabolisable energy (ME), mineral profile (Mg, P, K, Fe, Zn) and dietary cation–anion difference (DCAD) for leaf, stem, and the whole plant. Greater quantum efficiency, leaf accumulation, and nutritive value of BM observed in the present study suggest BM as an attractive forage option for dairying that warrants further research in pasture-based systems in tropical and subtropical climates.

**Keywords:** *Brachiaria* Mulato II; canopy structure; carbon assimilation; Gatton panic; nutritive value; Rhodes grass reclaimer; tropical pastures



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## 1. Introduction

Globally, warm-season (C<sub>4</sub>) grasses predominate in the tropical and subtropical climates and are the primary source of feed for grazing livestock including dairy cattle [1,2]. These tropical grasses are well adapted to warm and dry regions and are considered resilient under adverse climatic conditions, which is attributed to a combination of morphological and physiological mechanisms [2–4]. In addition, increasing atmospheric temperatures

may favour the dominance of  $C_4$  species in different ecosystems where they are not currently present [5]. Consequently, these pastures constitute a key resource to fulfil livestock nutritional requirements and increase dairy production in tropical and subtropical regions [6,7]. Despite the importance of tropical grasses in dairying, it is well known that the volume of dairy production associated with tropical pastures is consistently lower compared to temperate pastures, due to poorer nutritive value of herbage [8,9]. In addition, scarcity of quality feed on a consistent basis is often reported as a major constraint to dairy production [7]. Seasonal variation in weather conditions leads to seasonality in forage production, which affects the output from forage-dependent dairy systems. To overcome these constraints, efforts are therefore needed to explore improved perennial tropical forage options to satisfy long-term feed requirements. These improved tropical forages include a wide variety of perennial pasture species that are well adapted to a wider edaphoclimatic conditions, have improved nutritive value, and used for either grazing or mechanical harvest [2,7].

Grasses of the genus *Brachiaria* (syn. *Urochloa*) are widely used across the tropics and subtropics [2,6]. *Brachiaria* Mulato II (BM) is a recently introduced *Brachiaria* hybrid cultivar of Centro Internacional de Agricultura Tropical produced from three-generation hybridization of tetraploidized ruzigrass (clone 44-6) and tetraploid apomictic signalgrass [*Brachiaria decumbens* (Stapf) R. D. Webster (syn. *Urochloa decumbens* (Stapf) R. D. Webster)] (cv. Basilisk) and *B. brizantha*, including cv. Marandu [10]. It grows well in poor, acid soils with high aluminium contents and has shown adaptation to a wide range of soils, climate, and growing conditions in both the tropics and subtropics [10,11]. Guinea grass [*Panicum maximum* (Jacq.) syn. *Megathyrsus maximus* (Jacq.)] is well known for higher forage yield potential making the genus an attractive forage option in the tropics [12]. *Megathyrsus maximus* ‘Gatton Panic’ (GP) is an improved cultivar of genus *megathyrsus*, which is well adapted to a wide range of edaphoclimatic environments, moderately tolerant of drought and exhibits rapid growth response following rainfall [2,8]. Rhodes grass (*Chloris gayana*) is a long-leaved grass broadly used in grazing systems in warm areas [2]. *Chloris gayana* ‘Rhodes grass cv. Reclaimer’ (RR) is a diploid type and a selection from Finecut Rhodes grass for improved plant growth, drought tolerance, and survival under saline conditions, which also exhibits improved agronomic characteristics like fine stems, and a leafy growth habit [2,8].

The fundamental basis of pasture growth is carbon assimilation by photosynthesis [13]. Tropical forage grasses have long been recognised for their high photosynthetic potential [2,3,14], although detailed species-specific descriptions related to carbon assimilation are scarce, especially for recently developed pasture cultivars [15,16]. Understanding the carbon assimilation process of tropical pastures allows for better understanding of the species-specific physiological adaptation and yield potential [15].

Forage growth and nutritive value are ultimately the expression of the response of plants to environmental and management factors. Pasture canopy structure has an important effect on sward productivity (herbage mass), and herbage nutritive value [17,18]. The sward productivity and nutritive value in pastures can be described in a two-dimensional way (vertical and horizontal) in the pasture profile. For a similar herbage mass, swards with a higher leaf: stem ratio result in a higher herbage utilisation by grazing cattle than swards with a higher pseudostem (sheath) or stem: leaf ratio [19]. Length, vertical orientation, and horizontal dispersion of produced pseudostems or stems of the grass determine the sward structure and partly the accessibility of herbage to defoliation by grazing [20]. In addition, maximum daily herbage intake of cattle is related to tiller size, the vertical profile of bulk density, which depends on tiller density, and sheath length [21]. It is well known that the nutritive value of the sward components (leaf and stem) of tropical pastures are substantially different; leaves are superior to the stems, having a higher crude protein (CP), digestibility and ME, and a lower NDF, ADF, and tensile fracture [22]. Meantime, the nutritive value of the sward is expected to be reduced vertically from the top leafy stratum (high leaf: stem ratio) to the bottom stemmy stratum (low leaf: stem ratio) [23–26]. Although it is recognized that the sward structure plays a major role in the capacity of tropical pasture

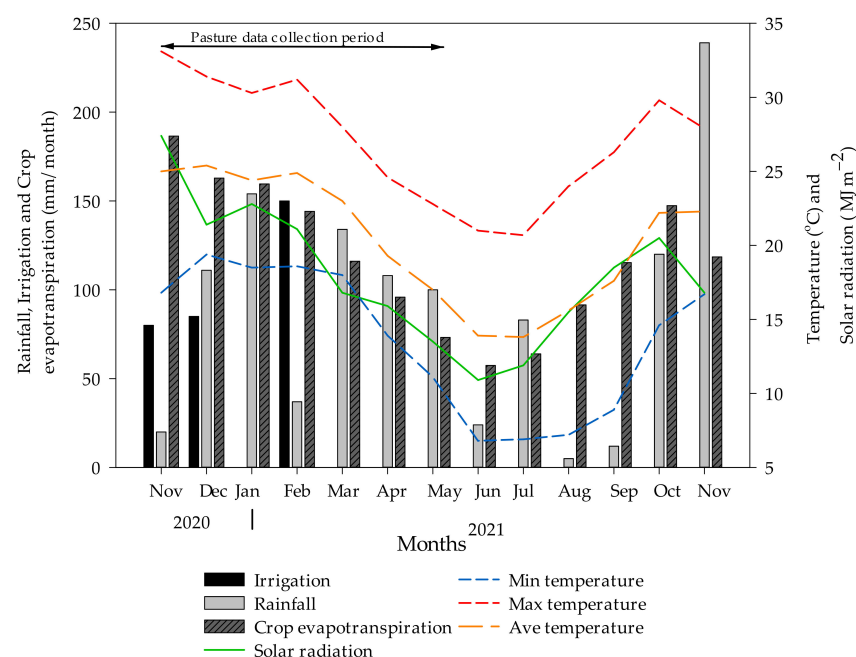
production, composition, and nutritive value, the comparative knowledge of plasticity between species, especially for the improved tropical forages, is still to be understood.

To improve the productivity of dairying in the tropics, the choice of appropriate species and cultivars plays a key role in how well they adapt to the farm environment to achieve the right balance between quantity and nutritive value. Given that BM is a relatively new pasture to the Australian subtropical environment, no attempts have yet been made to compare it with RR and GP. In this context, the aim of the current research was to study the suitability of three tropical pasture species for cultivation under a subtropical climate in Australia by evaluating their carbon assimilation, canopy structure, herbage accumulation, plant-parts composition and nutritive value parameters. We hypothesised that BM can provide (i) greater carbon assimilation, (ii) greater forage and plant-parts accumulation, and iii) better nutritive value parameters than GP and RR.

## 2. Methodology

### 2.1. Experimental Site, Plot Establishment, and Management

This research was conducted at the Gatton Research Dairy (27°54' S, 152°33' E, 89 m asl) Queensland, Australia. The climate at this location is subhumid and subtropical with long hot summers (28–33 °C) and short mild winters (6.3–20.8 °C) with an annual average rainfall of 763 mm (Figure 1). At this location, tropical pastures actively grow between spring to autumn. The soil of the experimental site was characterized as a black vertosol, self-mulching, seasonally cracking clay soil (clay > 35%) [27]. Soil characteristics for the experimental area (depth 0–30 cm) in September 2019 were pH (CaCl<sub>2</sub>) 7.6; organic matter (Walkley black) 1.33%; nitrate (NO<sub>3</sub><sup>-</sup>) 28 mg kg<sup>-1</sup>; ammonium (NH<sub>4</sub><sup>+</sup>) 3.5 mg kg<sup>-1</sup>; phosphorus (P) (Colwell) 58.5 mg kg<sup>-1</sup>, bulk density 1.35 t m<sup>-3</sup>; clay content 48%. Tropical pastures RR, GP, and BM were established on 0.04 ha plots (13 × 31 m) by sowing seeds at the seed company recommended rate of 8, 10 and 8 kg ha<sup>-1</sup> pure viable seeds, respectively, in October 2019. Plots were arranged in a randomized complete block design, replicated four times. Data collection was carried out from 19 November 2020 to 6 May 2021. Subsequently, sampling was terminated due to poor regrowth caused by the minimum daily temperatures dropping below the lower threshold required to support the growth of C<sub>4</sub> grasses.



**Figure 1.** Monthly average weather data at the Gatton Research Dairy, Queensland, Australia from November 2020 to November 2021. Rainfall, irrigation, and temperature data were collated from an automatic weather station at the experimental site and evapotranspiration and solar radiation data were collated from the University of Queensland, Gatton, located 0.9 km from the experimental site.

All plots were supplementary irrigated during the experimental period using hand shift irrigation. Irrigation was applied to restore the 100% crop evapotranspiration (ETc) based on the standardized Penman–Monteith method [28]. A fertiliser blend (CK77) consisting of 13.3% nitrogen (N), 2.2% P, 13.5% potassium (K) and 19.6% sulphur (S) was applied on 23 November 2020 before starting the measurements at a rate of 40 kg N ha<sup>-1</sup>, 6.6 kg P ha<sup>-1</sup>, 40.5 kg K ha<sup>-1</sup> and 58.8 kg S ha<sup>-1</sup>. Urea (46% N) and CK77 were applied on 18 January 2021 and 19 February 2021 at a rate of 69 N kg ha<sup>-1</sup> and 26 N, 4.4 P, 27 K and 39.2 S kg ha<sup>-1</sup> respectively. Plots were spot sprayed with Titan Glyphosate 450 (450 g L<sup>-1</sup> Glyphosate present as Isopropylamine salt) for weeds (*Sorghum halepense*) at a rate of 2 kg ha<sup>-1</sup> on 11 December 2020 and 7 January 2021.

### 2.2. Forage Accumulation and Plant Composition

Following a baseline sampling and defoliation on 19 November 2020, herbage mass was quantified at 33 ± 5 days harvest intervals using quadrats (0.5 m × 0.5 m) clipped with hand shears to 150 mm and 100 mm (except for the first defoliation in BM plots) residual heights from 15 December 2020 to 06 May 2021. A lower residual height was used for BM than GP and RR due to its relatively lower canopy height [2,13]. Harvested herbage samples from each plot were weighed for the fresh weight and subsampled (~500 g) for compositional analysis. The residual stubble (tiller base) from the same quadrat location was destructively sampled using hand shears to ground level after each defoliation to determine the mass and composition. Areas previously sampled to ground level were deliberately avoided for all subsequent quadrat samplings. The subsamples of forage above harvested height and the residual stubble (below residual height) were separated into their morphological components (leaf (lamina only), stem and pseudostem (leaf sheath), dead material and inflorescence) for compositional analysis. Hand-dissected components of the above harvested and residual samplings were dried separately at 60 °C for 48 h to determine their dry weight. The dry weights of the subsampled components were used to calculate total, leaf, stem, dead material, and inflorescence weights on an area basis (kg DM ha<sup>-1</sup>). After each harvesting, RR and GP plots were mown to a 150 mm residual height and BM plots were mown to a 100 mm residual height to achieve the same initial defoliation heights for the subsequent sampling.

### 2.3. Sward Structure and Canopy Bulk Density

The total canopy height and stem height were measured to characterise the sward vertical structure. To reduce edge effects, measurements were taken from the plot center only. Canopy height was measured with a calibrated ruler at four randomly selected locations per plot at the end of the regrowth cycle (just prior to every harvest). Stem height was measured at the same location and defined as the height from ground level to the base of the lamina (ligula) of the top fully expanded leaf. For each harvest event, randomly selected tillers were categorized as vegetative or reproductive depending on the phenological stage of the tiller (presence or absence of seed head) and the number of live leaves per tiller was recorded. The averages of total sward height, stem height, and number of leaves per tiller were then calculated and the number of leaves per tiller was used to calculate the leaf appearance rate. Sward canopy bulk density was determined as total above ground preharvesting herbage mass divided by average sward height. Stem and leaf bulk density were calculated by dividing the stem and leaf mass by stem and leaf height, respectively.

### 2.4. Canopy Light Interception, Carbon Assimilation

The spatial average of photosynthetically active radiation (PAR) transmitted through the canopy was measured immediately before each harvest using a MQ-301 light meter (Apogee Instruments, Inc., Logan, UT, USA). In each plot, 2 readings of incoming PAR (PAR<sub>i</sub>) above the canopy level and 8 readings of transmitted PAR (PAR<sub>t</sub>) at ground level (placing the quantum sensor bar closer to the soil between the pasture plants) were taken.

Net carbon exchange measurements were completed on 11 and 12 February 2021 at the preharvest stage with a portable photosynthesis meter, model LI-6400XT with broad leaf chamber and LED light source (LI-COR Biosciences, USA). All the readings were taken representing the middle portion of the youngest fully expanded leaves. Using preset auto programs, leaf net carbon and water exchange were recorded once per plot ( $n = 4$ ) at a series of PAR levels (2000, 1500, 1000, 500, 250, 120, 60, 30, 15, 0  $\text{PPF}\mu\text{mol}^{-1}\text{mol}^{-1}\text{m}^{-2}$ ) with a reference  $\text{CO}_2$  concentration of 400 ppm. Similarly, carbon and water exchange of leaves in two plots ( $n = 2$ ) were measured under a range of  $\text{CO}_2$  concentrations (400, 300, 200, 100, 50, 100, 200, 300, 400, 700, 800, 1200, 1500, 1700 ppm) at a reference light condition of 1000  $\text{PPF}\mu\text{mol}^{-1}\text{mol}^{-1}\text{m}^{-2}$ . All carbon exchange measurements were taken at 30 °C leaf temperature inside the chamber (reflective of the ambient temperature at the trial site).

### 2.5. Leaf Area Index and Specific Leaf Area

Randomly selected subsamples of fresh leaves ( $n = 8$ ) were scanned for leaf area using a flatbed scanner and analysed using the ImageJ software Version 1.53 [29]. Leaves were dried separately at 60 °C for 48 h to determine the dry weight to calculate the specific leaf area (SLA) of each sample. Subsequently, total dry weights of the leaf fraction harvested inside the quadrat area of each sample were used to calculate the leaf area index (LAI).

### 2.6. Nutritive Value

Subsamples of stem and leaf from each block were separately pooled. Pooled leaf and stem samples of each harvest date were separately analysed at Dairy One Laboratory (Ithaca, NY, USA) using wet chemistry analysis [30] for dry matter (DM), CP, NDICP, ADF, NDF, lignin, nonfibre carbohydrates (NFC), starch, water-soluble carbohydrates (WSC), ethanol-soluble carbohydrates (ESC), crude fat/ether extract (EE), ash, TDN, in vitro true digestibility (IVTD), in vitro NDF digestibility (NDFD) and minerals. Energy values were calculated from a multiple component summative approach used in the Dairy One laboratory [30] using NRC equations [31]. Subsequently, whole plant nutritive values were calculated based on DM proportion.

$$\text{ME (KJ kg}^{-1}\text{ DM)} = [(1.01 \times (\text{DE}) - 0.45) + 0.0046 \times (\text{EE} - 3)] \times 4.184 \quad (1)$$

where, DE is the digestible energy ( $\text{KJ kg}^{-1}\text{ DM}$ )

$$\text{DE (KJ kg}^{-1}\text{ DM)} = [(\text{NFC}\% \times 4.2) + (\text{NDF}\% \times 4.2) + (\text{CP}\% \times 5.6) + ((\text{EE}\% - 1) \times 9.4) - 0.3] \times 4.184 \quad (2)$$

### 2.7. Calculations and Statistical Analyses

#### 2.7.1. Fitting Light Response Curve

All model fittings and statistical analyses were performed using the R (version 4.0.5) statistical computing software [32]. Significant effects and differences were accepted when  $p \leq 0.05$ .

Photosynthetic light response curves were fitted using a nonrectangular hyperbolic model framework (Equation (3)) [33,34]. A fit was made for each pasture species separately and parameters were determined.

$$A(I) = \frac{\varphi I + A_{max} - \sqrt{(\varphi I + A_{max})^2 - 4\theta\varphi I A_{max}} - R_d}{2\theta} \quad (3)$$

where  $A$  = photosynthesis rate,  $I$  = light intensity,  $A_{max}$  = maximum leaf photosynthetic rate,  $\varphi$  = quantum yield,  $R_d$  = dark respiration and  $\theta$  = convexity constant. According to the Equation (3),  $I_c$  is set as the light compensation point, where the value of  $I$  when  $A(I) = 0$ ,  $I_s$  is the light saturation point where the value of  $I$  when  $A'(I) = 0$ , and  $A'(I)$  is the first derivative of the function  $A(I)$ .

### 2.7.2. Fitting the CO<sub>2</sub> Response Curve (A/C<sub>i</sub> Curve)

Nonrectangular hypobaric function (Equation (4)) was fitted to the internal leaf CO<sub>2</sub> concentration and photosynthetic data to derive the A/C<sub>i</sub> curve [35]. Maximum carboxylation rate ( $V_{cmax}$ ) (represented by  $A_c$  in Equation (5)) and maximum electron transfer rate ( $J_{max}$ ) (represented by  $A_j$  in Equation (5)) were calculated using Equation (5) [36,37].

$$A(C) = \frac{\beta C + P_a - \sqrt{(\beta C + P_a)^2 - 4\theta\beta C P_a} - R_c}{2\theta} \quad (4)$$

$$A_m = \frac{A_c + A_j - \sqrt{(A_c + A_j)^2 - 4\theta A_c A_j} - R_c}{2\theta} \quad (5)$$

where  $A_m$  = hyperbolic minimum of  $A_c$  and  $A_j$ , and  $A_c$  = gross photosynthetic rate when the Rubisco activity is limiting,  $A_j$  = gross photosynthetic rate when RUBP regeneration is limiting,  $R_c$  = respiratory rate, and  $\theta$  = convexity constant.

The Linear mixed-effect model (LME) approach was used to analyse the forage yield, canopy structure data using the 'lme4' package [38] in R. Pasture species, harvesting date and interaction of pasture and harvesting date were considered as fixed effects and the effects of plots within replicated blocks were included as random effects of the model. Harvesting dates were included as repeated measures as they were measured from the same plot. Mean comparisons of the effect were performed using the 'lsmeans' package [39] in R. Photosynthetic characteristics were separately analysed using one-way ANOVA for the significant difference among the pasture species. Pasture nutritive value parameters were analysed using one-way ANOVA for the significant difference among the pasture species and plant parts (leaf, stem, and whole plant). Tukey's honestly significant difference post hoc test was used to separate significant differences between pasture species and plant parts.

## 3. Results

### 3.1. Carbon Exchange Characteristics and Photosynthesis Biochemistry

Leaf photosynthetic light response parameters were affected by the pasture species (Table 1). *Brachiaria* Mulato II had the highest maximum carbon exchange rate ( $A_{max}$ ), whereas RR had the lowest  $A_{max}$ . Photosynthetic efficiency of BM reported the highest value indicating that BM has a greater photosynthetic efficiency under low light conditions, followed by GP and RR. Dark respiration ( $R_d$ ) was significantly greater in BM whereas RR and GP had lower values (Table 1). Light compensation point ( $I_c$ ) was lower in GP followed by RR and BM whereas  $I_s$  was highest in GP followed by RR and BM.

**Table 1.** Pasture species effects of photosynthetic light response parameters of tropical pastures (means of four plots) measured on 11 February 2021 at Gatton Research Dairy, Queensland, Australia. Rhodes grass Reclaimer (RR), *Brachiaria* Mulato II (BM), Gatton panic (GP).

Photosynthetic Parameters	Pastures		
	RR	BM	GP
Maximum photosynthesis rate ( $A_{max}$ ) ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	15.79 ± 0.4 <sup>c</sup>	28.95 ± 0.98 <sup>a</sup>	25.04 ± 1.34 <sup>b</sup>
Photosynthetic efficiency ( $\varphi$ ) ( $\mu\text{mol CO}_2 \text{ photon}^{-1}$ )	0.026 ± 0.001 <sup>c</sup>	0.056 ± 0.004 <sup>a</sup>	0.031 ± 0.002 <sup>b</sup>
Dark respiration ( $R_d$ ) ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	0.79 ± 0.1 <sup>c</sup>	2.41 ± 0.3 <sup>a</sup>	0.91 ± 0.3 <sup>b</sup>
Curvature parameter ( $\theta$ )	0.86 ± 0.04 <sup>a</sup>	0.84 ± 0.06 <sup>a</sup>	0.87 ± 0.07 <sup>a</sup>
Light compensation point ( $I_c$ ) ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	30.70 <sup>b</sup>	43.70 <sup>a</sup>	29.01 <sup>c</sup>
Light saturation point ( $I_s$ ) ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	1242.46 <sup>b</sup>	1208.22 <sup>b</sup>	1538.66 <sup>a</sup>

Different superscripts letters in the same row denote significant difference ( $p < 0.05$ ).

The effect of pasture species on photosynthetic CO<sub>2</sub> response parameters is summarised in Table 2. Maximum photosynthetic capacity ( $P_a$ ) was reported to be the highest in GP followed by BM and RR. There was no significant difference between the  $A_c$  of GP and

BM. Gatton panic had greater efficiency for CO<sub>2</sub> (0.24 μmol CO<sub>2</sub> photon<sup>-1</sup>), indicating that GP is photosynthetically efficient under low CO<sub>2</sub> concentrations. Gatton panic (4.23 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) and BM (4.42 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) showed higher R<sub>c</sub> than RR. These high P<sub>a</sub> and R<sub>c</sub> values indicate the potential of GP and BM to produce higher biomass compared to RR. According to the model fitting results, maximum carboxylation rate (V<sub>cmax</sub>) was higher in GP followed by RR and BM, whereas maximum electron transfer rate (J<sub>max</sub>) was highest in BM followed by RR and GP.

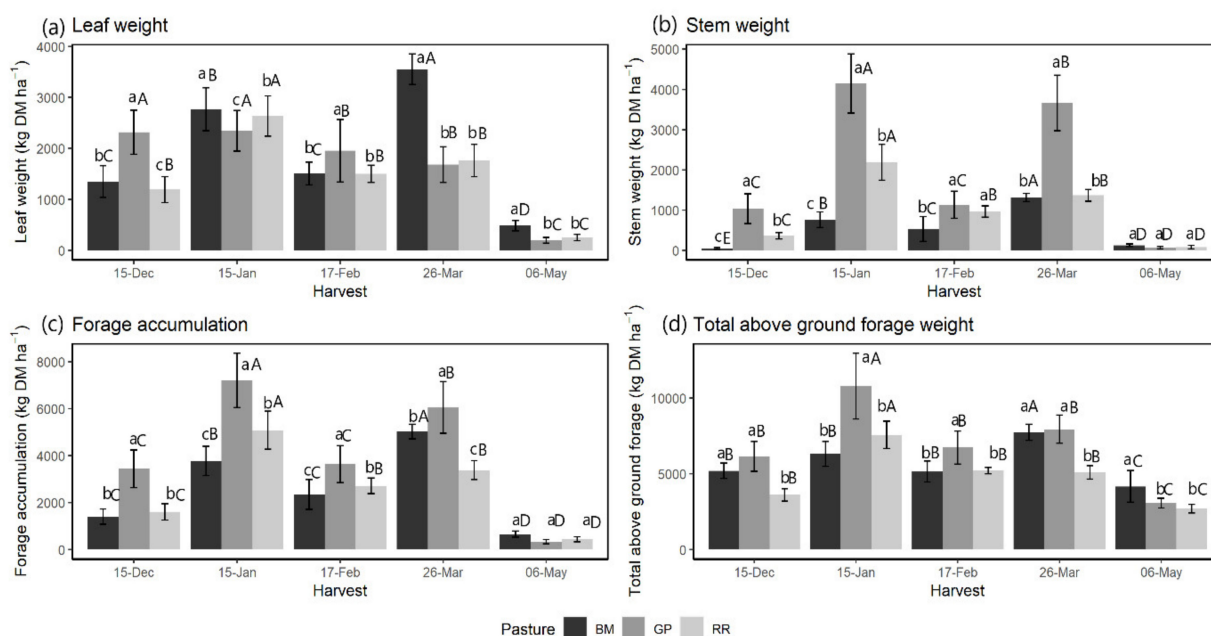
**Table 2.** Pasture species effects of photosynthetic CO<sub>2</sub> response parameters of tropical pastures (means of four plots) measured on 12 February 2021 at Gatton Research Dairy, Queensland, Australia. Rhodes grass Reclaimer (RR), *Brachiaria Mulato II* (BM), Gatton panic (GP).

Photosynthetic Parameters	Pastures		
	RR	BM	GP
Photosynthetic capacity (P <sub>a</sub> ) (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	15.79 ± 0.4 <sup>b</sup>	33.54 ± 1.7 <sup>a</sup>	34.27 ± 4.4 <sup>a</sup>
Photosynthetic efficiency (β) (μmol CO <sub>2</sub> photon <sup>-1</sup> )	0.02 ± 0.001 <sup>c</sup>	0.13 ± 0.02 <sup>b</sup>	0.24 ± 0.11 <sup>a</sup>
Respiration rate (R <sub>c</sub> ) (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	2.04 ± 3.5 <sup>b</sup>	4.42 ± 0.93 <sup>a</sup>	4.23 ± 4.05 <sup>a</sup>
Curvature parameter (θ)	0.86 ± 0.04 <sup>a</sup>	0.83 ± 0.06 <sup>a</sup>	0.65 ± 0.18 <sup>b</sup>
Maximum carboxylation rate (V <sub>cmax</sub> ) (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	83.51 ± 41.23 <sup>b</sup>	71.00 ± 4.33 <sup>c</sup>	92.60 ± 17.90 <sup>a</sup>
Maximum electron transfer rate (J <sub>max</sub> ) (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	118.24 ± 16.48 <sup>b</sup>	122.56 ± 4.60 <sup>a</sup>	106.35 ± 10.93 <sup>c</sup>

Different superscripts letters in the same row denote significant difference (p < 0.05).

### 3.2. Forage Accumulation and Plant Part Composition

There was a significant (p < 0.001) pasture × harvest interaction for the leaf weight, stem weight and forage accumulation (Figure 2a,c). Total above-ground forage yield was significantly affected by pasture species and harvest time (p < 0.001) and had no pasture species × harvest interaction (p = 0.124) (Figure 2d). Dead material accumulation was significantly affected by the harvest time.



**Figure 2.** Leaf weight (a), stem weight (b), forage accumulation (c) and total above-ground forage yield (d) of *Brachiaria Mulato II* (BM), Gatton panic (GP), Rhodes grass Reclaimer (RR) measured in five harvests at Gatton Research Dairy, Queensland, Australia from 2020 November to 2021 May. Error bars represent the standard error of means (kg DM ha<sup>-1</sup>). Different lowercase letters denote the significant difference of pasture species within same harvest and different uppercase letters denote the significant difference of pasture species between harvest at p < 0.05.

The total above-ground biomass was significantly different between the three grasses, with GP recording the highest value (34,725 kg DM ha<sup>-1</sup>), followed by BM (28,590 kg DM ha<sup>-1</sup>) and RR (24,210 kg DM ha<sup>-1</sup>). Total forage accumulation over the experimental period was 36% greater in GP (20,655 kg DM ha<sup>-1</sup>) and there was no significant difference between BM and RR ( $p = 0.0289$ ). (Table 3). Total leaf weight was highest (9660 kg DM ha<sup>-1</sup>) in BM, and lowest (7335 kg DM ha<sup>-1</sup>) in RR. Stem production was significantly different between the three pasture species (Table 3), with GP having 72% greater stem production (10,040 kg DM ha<sup>-1</sup>) than BM which produced the lowest value (2775 kg DM ha<sup>-1</sup>). Dead material accumulation was not affected by pasture species; however, the total dead matter was greatest (1200 kg DM ha<sup>-1</sup>) in GP.

**Table 3.** Effect of pasture species on total forage mass, forage accumulation and plant part composition (kg ha<sup>-1</sup>) DM measured in five harvests at Gatton Research Dairy, Queensland, Australia from November 2020 to May 2021. *Brachiaria* Mulato II (BM), Gatton panic (GP), Rhodes grass Reclaimer (RR).

Pastures	Total above Ground	Total Forage Accumulation	(kg ha <sup>-1</sup> ) DM		
			Total Leaf Mass	Total Stem Mass	Total Dead Mass
BM	28,590 <sup>b</sup>	13,200 <sup>b</sup>	9660 <sup>a</sup>	2775 <sup>c</sup>	732
GP	34,725 <sup>a</sup>	20,655 <sup>a</sup>	8495 <sup>b</sup>	10,040 <sup>a</sup>	1200
RR	24,210 <sup>b</sup>	13,220 <sup>b</sup>	7335 <sup>b</sup>	4955 <sup>b</sup>	690
SEM	1971.8	2008.6	794.5	956.9	222.7

SEM: Standard error of the mean. Means in columns followed by different superscripts are significantly different ( $p < 0.05$ ).

### 3.3. Sward Structural Parameters

Leaf appearance rate was affected by pasture species ( $p < 0.001$ ), harvest time ( $p < 0.001$ ) and pasture species  $\times$  harvest interactions ( $p < 0.001$ ), where the highest leaf appearance rate was reported for GP (0.17 leaf day<sup>-1</sup>) and varied from 0.09–0.17 leaf day<sup>-1</sup>. The leaf appearance rate varied for BM and RR from 0.08–0.10 leaf day<sup>-1</sup> and 0.09–0.16 leaf day<sup>-1</sup>, respectively. There was a pasture species  $\times$  harvest interaction ( $p < 0.001$ ) for canopy height, stem height and proportion of stem height to canopy height. The highest canopy height (98.9 cm), stem height (69.5 cm) and proportion of stem to total canopy (0.7) were reported for GP in the second harvest (Table 4), whereas those parameters were the lowest (43.1 cm, 17.8 cm and 0.4) for BM in the same harvest. Leaf area index and SLA were affected by pasture species ( $p < 0.001$ ), harvest time ( $p < 0.001$ ) and pasture species  $\times$  harvest interactions ( $p < 0.001$ ). Given that BM produced the highest leaf weight, BM had greater average leaf-associated sward parameters, including LAI (6.1 m<sup>2</sup> m<sup>-2</sup>), and leaf: stem ratio (4.3). Specific leaf area was lowest in RR, indicating the production of thicker leaves, whereas the SLA of BM and GP had average values with no significant differences between species. Canopy bulk density was only affected by pasture species and harvest, whereas stem bulk density and leaf bulk density were affected by pasture species ( $p < 0.001$ ), harvest ( $p < 0.001$ ) and their interaction. Mean total bulk density was highest in BM (171.8 kg ha<sup>-1</sup> cm<sup>-1</sup>) followed by GP and RR. Leaf bulk density was highest in BM (139.2 kg ha<sup>-1</sup> cm<sup>-1</sup>) followed by RR; however, it was lowest in GP (70.1 kg ha<sup>-1</sup> cm<sup>-1</sup>) due to the higher stem accumulation (Figure 2, Table 3). Light interception was not affected by pasture species ( $p = 0.53$ ) nor the interaction between pasture species and harvest ( $p = 0.12$ ), but was affected by harvest alone ( $p < 0.001$ ).



**Table 4.** Effect of pasture species and harvest on sward structural parameters measured in five harvests at Gatton Research Dairy, Queensland, Australia from November 2020 to May 2021. *Brachiaria* Mulato II (BM), Gatton panic (GP), Rhodes grass Reclaimer (RR).

Sward Structural Parameters	Leaf Appearance Rate (Leaf Day <sup>-1</sup> )	Canopy Height (cm)	Stem Height (cm)	Stem: Canopy Height	Leaf: Stem Ratio	LAI (m <sup>2</sup> m <sup>-2</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	Canopy Light Interception (%)	Canopy Bulk Density (kg ha <sup>-1</sup> cm <sup>-1</sup> )	Stem Bulk Density (kg ha <sup>-1</sup> cm <sup>-1</sup> )	Leaf Bulk Density (kg ha <sup>-1</sup> cm <sup>-1</sup> )
Harvest	BM										
1	0.08 aB	29.8 bC	11.8 bB	0.4 aA	23.5 aA	2.9 bB	21.6 aA	95.7 aA	175 bA	*	*
2	0.10 aB	43.1 aC	17.8 bC	0.4 aB	3.9 cA	7.9 aA	25.0 aA	94.9 aA	145 cA	74 bA	124 cA
3	0.08 aA	25.6 bB	10.3 bB	0.4 aA	6.1 bA	3.0 bA	16.9 bA	78.7 cB	203 aA	128 aA	159 bA
4	0.10 aB	46.9 aB	24.9 aB	0.5 aB	2.7 cA	9.1 aA	22.9 aA	97.5 aA	165 bA	91 bA	182 aA
5	0.08 aB	23.8 bA	12.5 bA	0.5 aA	4.2 cB	9.1 aA	22.4 aB	81.3 bA	169 bA	80 bA	90 dA
Harvest	GP										
1	0.11 bA	60.5 cA	27.3 cA	0.4 bA	2.8 bB	4.6 bA	19.9 bA	96.3 aA	102 bB	*	*
2	0.17 aA	98.9 aA	69.5 aA	0.7 aA	0.5 dC	5.7 aB	23.3 bA	94.4 aA	109 bB	80 aA	86 aB
3	0.09 cA	50.0 dA	21.6 cA	0.4 bA	1.7 cB	3.5 cA	15.2 cA	91.6 aA	134 aB	88 aB	78 aB
4	0.14 bA	75.9 bA	51.5 bA	0.7 aA	0.4 dC	4.1 bB	22.4 bA	95.7 aA	104 bB	80 aA	75 aB
5	0.09 cB	24.6 eA	12.9 dA	0.5 aA	4.9 aB	4.1 bB	34.0 aA	75.0 bB	125 aB	90 aA	41 bB
Harvest	RR										
1	0.09 cB	41.7 bB	21.4 bA	0.3 bA	3.3 bB	1.8 cC	16.9 bB	91.0 aA	86 bC	*	*
2	0.16 aA	84.2 aB	54.0 aB	0.6 aA	1.2 cB	5.0 aB	17.0 bB	95.0 aA	88 bC	63 bA	96 aB
3	0.09 cA	46.1 bA	21.3 bA	0.5 aA	1.6 cB	2.8 bA	14.7 bA	89.7 aA	114 aB	82 aB	78 aB
4	0.15 aA	79.6 aA	57.0 aA	0.7 aA	1.3 cB	2.8 bC	15.3 bB	93.8 aA	64 cC	34 cB	86 aB
5	0.12 bA	23.6 cA	10.1 cA	0.4 bA	7.6 aA	2.8 bC	22.9 aB	71.5 bC	115 aB	83 aB	42 bB
SEM	0.1	3.0	2.3	0.04	1.3	0.8	1.4	3.3	16.5	10.7	14.6

Harvest; 1; 15 December 2020, 2; 15 January 2021, 3; 17 February 2021, 4; 26 March 2021, 5; 6 May 2021, SEM: Standard error of mean. Means in columns followed by different superscripts are significantly different ( $p < 0.05$ ). Lowercase letters compare the same pasture species within different harvest and uppercase letters compare different pasture species between the same harvest at  $p < 0.05$ . \* Residual plant part compositions of the first harvest were not performed; therefore, total canopy leaf and stem were not calculated.

### 3.4. Nutritive Composition

Nutritive composition values changed between pasture species (Table 5). Between species, CP, WSC, ESC, lignin, ash, IVTD were not significantly different. However, the majority of nutritive value parameters estimated (TDN, ADF, NDF, NDICP, starch, CF, NFC, NDFD and ME) showed significant difference between pasture species. Overall, BM showed greater nutritive value comprising higher TDN, Starch, NFC, and ME and lower ADF, NDF, NDICP.

**Table 5.** Effect of pasture species on the nutritive value measured in leaf and stem fractions of five harvests at Gatton Research Dairy, Queensland, Australia from November 2020 to May 2021. Crude protein (CP), acid detergent fibre (ADF), neutral detergent fibre (NDF), neutral detergent insoluble protein (NDICP), water-soluble carbohydrates (WSC), nonfibre carbohydrates (NFC), crude fat (CF), ethanol-soluble carbohydrates (ESC) total digestible nutrients (TDN), in vitro true digestibility 24 h (IVTD), in vitro NDF digestibility 24 h as % of NDF (NDFD) are presented as g kg<sup>-1</sup>. Metabolisable energy (ME) is given in MJ kg<sup>-1</sup> DM. *Brachiaria* Mulato II (BM), Gatton panic (GP), Rhodes grass Reclaimer (RR).

Pastures	Nutritive Value Parameters														
	TDN	CP	ADF	NDF	NDICP	Starch	WSC	ESC	NFC	Lignin	CF	Ash	IVTD	NDFD	ME
Leaf															
BM	688 <sup>a</sup>	163	282 <sup>b</sup>	504 <sup>b</sup>	26 <sup>b</sup>	15 <sup>a</sup>	72	63	167 <sup>a</sup>	35	51	115	776	560 <sup>b</sup>	10.4 <sup>a</sup>
GP	678 <sup>ab</sup>	172	327 <sup>a</sup>	553 <sup>a</sup>	67 <sup>a</sup>	11 <sup>b</sup>	64	48	105 <sup>b</sup>	40	52	118	814	666 <sup>a</sup>	10.2 <sup>a</sup>
RR	646 <sup>bc</sup>	145	334 <sup>a</sup>	607 <sup>a</sup>	58 <sup>a</sup>	07 <sup>b</sup>	63	50	80 <sup>b</sup>	37	43	124	764	618 <sup>a</sup>	9.5 <sup>b</sup>
SEM	10	16	13	25	05	01	05	05	07	04	02	08	21	27	0.2
Stem															
BM	605	96	380	641 <sup>b</sup>	18	10 <sup>a</sup>	53	51	121 <sup>a</sup>	49	29 <sup>a</sup>	113	722	562	8.4
GP	598	68	432	677 <sup>ab</sup>	19	07 <sup>ab</sup>	51	37	127 <sup>a</sup>	48	19 <sup>b</sup>	109	546	434	7.9
RR	554	83	407	709 <sup>a</sup>	25	05 <sup>bc</sup>	47	31	72 <sup>b</sup>	48	20 <sup>bc</sup>	114	648	512	7.8
SEM	20	10	20	19	03	0.8	07	06	7.2	05	01	07	90	78	0.1
Whole plant															
BM	674 <sup>a</sup>	151 <sup>a</sup>	300 <sup>b</sup>	527 <sup>b</sup>	25 <sup>b</sup>	14 <sup>a</sup>	69	61	158 <sup>a</sup>	37	47	115	766	560	10.0 <sup>a</sup>
GP	629 <sup>ab</sup>	127 <sup>b</sup>	375 <sup>a</sup>	608 <sup>ab</sup>	45 <sup>a</sup>	09 <sup>ab</sup>	58	45	113 <sup>b</sup>	44	37	113	710	570	9.2 <sup>ab</sup>
RR	616 <sup>b</sup>	124 <sup>b</sup>	360 <sup>a</sup>	641 <sup>a</sup>	46 <sup>a</sup>	07 <sup>b</sup>	59	45	77 <sup>c</sup>	42	35	121	729	589	8.9 <sup>b</sup>
SEM	14	17	19	07	06	01	05	05	06	04	03	07	24	25	0.2

SEM: Standard error of the mean. Means in columns followed by different superscripts are significantly different ( $p < 0.05$ ).

Nutritive composition values changed between plant parts (leaf, stem, and whole plant) (Table 5). Leaf and whole plant TDN were affected by pasture species, and while they did not significantly differ between BM and GP, RR had the lowest TDN for leaf and whole plant (64.6% and 61.6%). *Brachiaria* Mulato II had the lowest leaf ADF (28.2%) and NDF (50.4%) whereas RR reported the highest values of 33.4% and 60.7%, respectively. Stem and whole plant ADF and NDF were affected by pasture species where BM produced the lowest stem and whole plant ADF (38.0% and 30.0%) and NDF (64.1% and 52.7%). Leaf, stem, and whole plant CP were not affected by either pasture species or plant parts. Stem CP values were, on average 41%, 60% and 43% lower than their counterparts of leaf CP for BM, GP, and RR, respectively. Leaf and whole plant NDICP were significantly lower in BM compared to GP and RR. Leaf in vitro NDF digestibility was affected by pasture species, with GP recording the highest digestibility (66.6%), but stem and whole plant NDFD did not change between pasture species. The interspecies differences were not significant for IVTD for leaf, stem, and whole plant. Leaf and whole plant ME were significantly different between pasture species and the highest ME concentration (10.4 MJ kg<sup>-1</sup> DM and 10 MJ kg<sup>-1</sup> DM) was reported for BM, followed by GP (10.2 MJ kg<sup>-1</sup> DM and 9.2 MJ kg<sup>-1</sup> DM) and RR (9.5 MJ kg<sup>-1</sup> DM and 8.9 MJ kg<sup>-1</sup> DM). Metabolisable energy associated with leaf was significantly higher in all pasture species. Leaf, stem, and whole plant WSC, ESC, CF, lignin, and ash were not significantly different between pasture species or plant parts.

### 3.5. Mineral Composition

Table 6 shows the effect of pasture species and plant parts on herbage mineral concentrations. Leaf Ca and P did not change between pasture species, but Mg, K and Na were significantly different ( $p < 0.05$ ). The highest concentration of Mg (0.81% DM) was measured in BM and the lowest (0.25% DM) in RR. Leaf K concentration of BM was the highest (2.4%). Greater stem Ca was produced by RR (0.33%) and P concentration of the stem was shown to be not statistically significant. Magnesium was highest in BM (0.53%) followed by GP (0.38%) and RR (0.20%). Regardless of the pasture species, Ca, P and Mg concentrations in the stem were lower than in the leaves. Unlike the Ca, P and Mg concentrations, K and Na were higher in stems than leaves, with a greater amount of K (3.06%) and Na (1.56%) in the stems of BM and GP, respectively.

**Table 6.** Effect of pasture species on mean minerals concentrations measured in leaf and stem fractions of five harvest times at Gatton Research Dairy, Queensland, Australia from November 2020 to May 2021. Calcium (Ca), Phosphorus (P), Magnesium (Mg), Potassium (K), Sodium (Na), Sulphur (S), Chloride (Cl) expressed as percentage dry matter and Iron (Fe), Zinc (Zn), Copper (Cu), Manganese (Mn), Molybdenum (Mo) expressed as PPM and Dietary Cation–Anion Difference (DCAD) in mEq 100 g<sup>-1</sup>. *Brachiaria* Mulato II (BM), Gatton panic (GP), Rhodes grass Reclaimer (RR).

Pastures	Minerals												
	Ca	P	Mg	K	Na	Fe	Zn	Cu	Mn	Mo	S	Cl	DCAD
Leaf													
BM	0.51	0.46	0.81 <sup>a</sup>	2.47 <sup>a</sup>	0.08 <sup>b</sup>	223	45.2 <sup>a</sup>	7.4 <sup>b</sup>	77.6	0.36 <sup>b</sup>	0.25 <sup>b</sup>	0.94 <sup>b</sup>	24.4
GP	0.60	0.46	0.51 <sup>b</sup>	1.55 <sup>b</sup>	1.12 <sup>a</sup>	185	38.2 <sup>ab</sup>	10.4 <sup>a</sup>	70.2	0.60 <sup>b</sup>	0.22 <sup>b</sup>	1.30 <sup>ab</sup>	30.2
RR	0.52	0.45	0.25 <sup>c</sup>	1.33 <sup>b</sup>	1.01 <sup>a</sup>	216	27.4 <sup>b</sup>	10.2 <sup>a</sup>	86.2	1.04 <sup>a</sup>	0.41 <sup>a</sup>	1.88 <sup>a</sup>	13.1
SEM	0.05	0.05	0.04	0.08	0.09	30	3.7	0.7	10.1	0.15	0.02	0.19	6.6
Stem													
BM	0.20 <sup>a</sup>	0.39	0.53 <sup>a</sup>	3.06 <sup>a</sup>	0.24 <sup>b</sup>	129.8 <sup>b</sup>	46.8 <sup>a</sup>	5.5	83.2	0.10 <sup>a</sup>	0.19 <sup>a</sup>	1.82	25.8
GP	0.21 <sup>a</sup>	0.35	0.38 <sup>b</sup>	1.75 <sup>b</sup>	1.43 <sup>a</sup>	83.6 <sup>b</sup>	33.0 <sup>ab</sup>	5.6	60.4	0.50 <sup>a</sup>	0.14 <sup>a</sup>	2.26	34.0
RR	0.33 <sup>b</sup>	0.37	0.20 <sup>c</sup>	1.76 <sup>bc</sup>	1.56 <sup>a</sup>	162.4 <sup>a</sup>	25.6 <sup>b</sup>	5.4	100.0	1.44 <sup>b</sup>	0.40 <sup>b</sup>	1.98	21.0
SEM	0.03	0.02	0.03	0.26	0.14	19.8	5.0	0.4	15.3	0.27	0.02	0.51	8.9
Whole plant													
BM	0.45	0.44	0.76 <sup>a</sup>	2.58 <sup>a</sup>	0.11 <sup>b</sup>	202	44.7 <sup>a</sup>	7.1	78.2	0.29 <sup>b</sup>	0.24 <sup>b</sup>	1.13 <sup>b</sup>	24.1 <sup>a</sup>
GP	0.42	0.42	0.45 <sup>b</sup>	1.65 <sup>b</sup>	1.26 <sup>a</sup>	138	36.2 <sup>ab</sup>	8.2	65.9	0.49 <sup>b</sup>	0.18 <sup>b</sup>	1.71 <sup>a</sup>	37.0 <sup>a</sup>
RR	0.46	0.42	0.23 <sup>c</sup>	1.49 <sup>b</sup>	1.26 <sup>a</sup>	197	26.5 <sup>b</sup>	8.5	91.6	1.21 <sup>a</sup>	0.41 <sup>a</sup>	2.04 <sup>a</sup>	6.7 <sup>b</sup>
SEM	0.05	0.05	0.05	0.11	0.09	28.5	2.9	0.8	12	0.16	0.02	0.24	4.2

SEM: Standard error of the mean. Means in columns followed by different superscripts are significantly different ( $p < 0.05$ ).

Iron, Zn, Cu, Mn, and Mo were all measured as microminerals, and Fe, Mn were not significant among pastures ( $p < 0.05$ ). A greater concentration of Zn was measured in BM (45.2 ppm), whereas it was lowest in RR (27.4 ppm). Comparatively lower S, Cl, Mo, and Cu concentrations were measured in BM leaves (0.25 ppm, 0.94 ppm, 0.36 ppm, and 7.4 ppm), whereas values were higher in RR (0.41 ppm, 1.88 ppm, 1.04 ppm, and 10.2 ppm, respectively). Leaf and stem DCAD were not shown to be significant among pastures but RR whole plant reported significantly lowest DCAD (6.7 mEq 100 g<sup>-1</sup>;  $p < 0.05$ ).

## 4. Discussion

Contrasting morphology, nutritional/fertility requirements, and relative growth rates of different tropical pastures affects photosynthesis [15,16,40], which was also reflected in the present study. The photosynthetic efficiency ( $\varphi$ ) characterises the ability of the plants to assimilate CO<sub>2</sub> under low light conditions. The greater  $\varphi$  value for BM compared to GP and RR in the present study suggests the strong ability of BM to utilise the lower light and its adaptability to long-term shaded environments and shading within the pasture canopy. Similar  $\varphi$  was reported for *B. brizantha* cv. Marandu under full sunlight (0.044  $\mu\text{mol photon}^{-1}$ ) and shaded plants (0.052 CO<sub>2</sub>  $\mu\text{mol photon}^{-1}$ ) and for GP

( $0.049 \text{ CO}_2 \mu\text{mol photon}^{-1}$ ) [15]. However,  $\phi$  value of GP and RR were below the previously reported values [16,40] and also the generally accepted  $\phi$  for  $\text{C}_4$  species ( $0.054 \text{ CO}_2 \mu\text{mol photon}^{-1}$ ) [16]. The maximum photosynthetic rate reported in the present study agreed with other studies at equivalent temperature and  $\text{CO}_2$  concentrations [11,40,41]. Relatively higher  $A_{max}$  of BM is presumed to be related to higher plant N concentration. Higher maximum photosynthetic rate ( $A_{max}$ ) at saturating light combined with lower  $R_d$  is believed to be more favourable for higher carbon assimilation due to low utilisation for respiration. The respiration rate reported for BM in the present study agrees with similar results reported in previous studies [11,16,40], however higher  $R_d$  is not conducive for accumulation of higher forage mass as plants consume higher organic matter. This is reflected in the biomass accumulation results of the present study which showed reduced forage yield for BM. Plant photosynthetic capacity ( $P_a$ ) characterises the maximum potential of  $\text{CO}_2$  fixation under sufficient light and  $\text{CO}_2$  concentrations. Photosynthetic efficiency for  $\text{CO}_2$  explains the efficiency of a plant to fix C under conditions of low  $\text{CO}_2$  concentration. This combination of higher  $A_c$  and  $\beta$  increases the biomass accumulation which is also evident with higher biomass accumulation by GP in the present study. Balance between the  $V_{cmax}$  and  $J_{max}$  determines the  $\text{CO}_2$  dependence of photosynthesis. As  $V_{cmax}$  and  $J_{max}$  limit the photosynthetic rate at low and high  $\text{CO}_2$  concentrations, respectively [42], the greater biomass accumulation results of GP in present is consistent with the high  $\beta$  reported for GP and the observed lower  $\beta$  for BM and RR and their respective lower biomass accumulations compared to the GP. Therefore, present study partially supported the hypothesis. *Brachiaria* Mulato II had greatest photosynthetic efficiency of the three species evaluated although GP outperformed BM and RR in photosynthetic capacity.

Herbage production is regulated by environmental variables, plant morphogenesis and sward characteristics [18]. Tropical pasture growth in subtropical regions is limited at times due to occasional frost, shorter day lengths and low temperature [43], and the present study observed a similar pattern, with growth reducing after the fourth defoliation (late March). Despite the interspecies variation within harvest, the observed significant temporal dynamics of growth of the same pasture species is closely aligned to temperature stress [44]. Ivory and Whiteman [45] studied five tropical pastures including Rhodes grass cv. *Callide* and Green panic in subtropical Australia, reporting plant development was considerably restricted in all five species at  $10\text{--}15^\circ\text{C}$  while maximum growth occurred at  $29\text{--}35^\circ\text{C}$ . Furthermore, relatively shorter day length decreased the light interception (Table 4) and reduced the canopy net photosynthesis, minimising the pasture growth, and resulting in thinner leaves (high SLA) and lower canopy height. However, BM managed to produce relatively higher biomass in its last harvest and the reason may be its efficient photosynthesis under low light conditions.

Leaf appearance is mainly a function of temperature and water availability and the results of the present study reflected this, with grasses producing a low number of leaves towards the end of the warm season. *Brachiaria* Mulato II is efficient in carbon partitioning to leaves under ideal growing conditions [10,13,46–48], and the greater leaf-associated canopy structure parameters (leaf: stem, LAI, SLA, leaf bulk density) reported in the present study agreed with previous findings. Pasture canopy structure is partly determined by genetics and is expected to vary within genotypes. *Brachiaria* Mulato II is an improved *Brachiaria* hybrid developed to produce quality herbage for livestock [10,49], and observed canopy structure parameters of the present study confirmed its superior agronomic performances reported in other tropical and subtropical areas around the world [13,46–48,50–52]. In addition, the higher forage yield of GP explains the forage-yielding potential of the genus *megathyrsus* explained elsewhere [2]. The greater plant height and number of leaves per tiller contribute to its higher biomass accumulation. These morphological characteristics of GP show its relative advantage and vigour over other species, particularly in greater light interception. The ability to rapidly respond after rainfall/irrigation [2] and higher stem production (higher stem weight) associated with GP has also resulted in marked yield differences which was also evident in the present study (Figure 2b, Table 3). Given that

BM is a relatively new grass to the Australian subtropical environment, no studies have yet compared it with RR and GP [53–55]. However, Lawes et al. [56] studied Rhodes grass and GP under a subtropical climate in Australia, and reported that both had similar yield potential, which was not observed in the present study. Rhodes grass cv. *Katambora* and GP were studied by Ward et al. [55] and results demonstrated that Rhodes grass was faster to establish and produced more DM compared to GP. Greater biomass accumulations of GP and RR within the present study were not consistent with previously reported results for GP and RR [44,55,57], possibly due to irrigation in the present study reducing soil-water deficit during dry periods. *Brachiaria* Mulato II in present study showed slightly lower forage accumulation than an irrigated study reported elsewhere [46] under similar defoliation management (height and interval) and the contrasting soil and climate could be a possible reason for this yield gap. At the same defoliation interval, higher dead material was accumulated by GP; this potentially renders the use of GP as inefficient, resulting in decreased yield due to greater dead material losses and reduce grazing efficiency as cows show a selection preference for the green leaves. Of the three pasture species, the morphological compositional results supported the hypothesis and highlight the potential of BM to produce higher leaf DM production and lower stem production [10,13,46,48,58], which makes BM an attractive forage for livestock under tropical and subtropical conditions. Further evaluation to determine the greater agronomic performance of BM demonstrated in this study hold under multiple years seem warranted due to the limited data collection period of the present study.

Tropical pasture grasses are more heterogeneous in their composition from the top to bottom of the canopy compared to temperate pasture grasses [59]. In the present study, all pasture grasses exhibited a heterogeneous vertical structure typical of tropical pastures, with a top leafy and bottom stemmy stratum. However, the interspecies sward structure was greatly varied for sward height, depth of leaf and stem strata, and herbage density. For a given herbage accumulation, swards with a higher leaf to stem ratio generally result in a higher utilisation of herbage by grazing animals than swards with a higher pseudostem or stem to leaf ratio [21]. Therefore, the greater leafy stratum depth of BM (lower stem height) observed in the present study, compared to RR and GP, appeared to be more favourable for greater diet quality and herbage utilisation by dairy cows. Relatively higher stem height associated with GP and RR is likely to change the vertical orientation and horizontal dispersion of the canopy structure, reducing the proportion of easily ingested leafy stratum, and in turn imposing a greater restriction to the accessibility of herbage to defoliation (by grazing), and lowering the diet quality [25]. The decrease in tropical forage quality with advancing plant maturity is well elucidated when analysing the entire forage structure [2,46,48,60]. Therefore, the quality consequences associated with advancing maturity/longer defoliation interval would be more evident in GP and RR due to their characteristic greater stem production compared to BM. The present study was not intended to evaluate the herbage quality between different vertical strata; however, a comprehensive analysis was undertaken on the nutritive profile and mineral contents of leaf, stem, and whole plant of all three pasture species. These results together with pasture stem height and leaf height may potentially explain the vertical distribution of nutritive values in the overall sward. Generally, results of the present study supported the hypothesis that BM outperformed the other two species in quality parameters in relation to the leaf, stem, and whole plant, which was in agreement with a number of other studies [2,46,47,51,60]. The reason for BM producing relatively higher quality herbage is predominantly associated with its plant morphological composition (high leaf: stem) [10].

The concentration of CP was consistent in BM, GP, and RR, though the whole plant CP was high in BM. The stem CP concentration was approximately 50% less than that of the leaf of all three pasture species. Neutral detergent insoluble protein concentration varied due to pasture species. The lower NDICP of BM (2.5% DM) suggests that there is a higher percentage of N present in a usable form for ruminants. The fibre content (defined by NDF and ADF), an estimate of the amount of plant cell wall rather than cell contents, is

negatively linked to digestibility and intake of forages. The higher TDN and lower fibre (defined by ADF and aNDFom) concentration of BM in relation to GP and RR is presumed to be related to its higher leaf proportion which can increase the digestibility and rumen passage rate. In addition, higher fractions of starch, WSC, ESC, and NFC reported for BM are attributed to the greater proportion of nonstructural carbohydrates present in the plant. Nonstructural carbohydrates in grasses are characterised as the readily utilizable energy source for dairy cows, and their degree of accumulation is considered important to the overall herbage quality [61]. There are interspecies variations in fat content in tropical forages [62] and the present study shared similar results, with the greatest fat percentage present in BM. Most of the tropical grasses (either native or improved pastures) have ME values ranging from 7.0 to 11.0 MJ kg<sup>-1</sup> DM when cutting between 2–8 weeks [63] and the average ME of all three pastures of the present study were consistent with these results. The greater ME of BM observed in the present study agreed with previous findings, and it is presumed to be attributed by the high TDN, fat, NSC observed in BM [10].

Concentrations of all macro- and microminerals of all three pastures, except for Ca and Na, met the minimum concentrations required by lactating dairy cows suggested by the NRC (2001) [31]. Of all three pastures, BM contained the highest concentrations of minerals (Table 6), with its greater Mg, K, Fe, Zn concentration in leaf and stem. All pastures appeared to be inadequate in Ca and Na concentrations [10,63]. This suggests that the dairy cows grazing pastures dominated by BM, GP, or RR are likely to suffer Ca and Na deficiencies and may require supplementation when these pastures constitute a significant portion of their diet. Results of the present study are in agreement with results from Esehie (1992) [64], who studied the distribution of minerals in six plant parts of six tropical pastures including Rhodes grass and *Panicum maximum* and reported that leaf blades of all six species contained adequate levels of minerals (P, K, Ca, Mg, Na, Cu, B, An, Mn, and Fe) for the diet of lactating dairy cows. Dietary cation–anion difference is largely dependent on Na, K, Cl, and S concentrations of the plant, and DCAD has a greater seasonal variation [65]. The optimum DCAD value for lactating cows reported in NRC (2001) is in the range of +23 to +30 mEq 100 g<sup>-1</sup> of dietary DM [31]. West et al. [66] reported increases in milk production up to a DCAD of +32.4 mEq 100 g<sup>-1</sup> irrespective of the seasonal influences. In the current study, BM has an ideal DCAD value (+24.1 mEq 100 g<sup>-1</sup>) range around the value reported by NRC (2001) [31] highlighting the forage value of BM for feeding dairy cows. Gatton panic and RR showed a DCAD value well above (+37.0 mEq 100 g<sup>-1</sup>) and well below (+6.7 mEq 100 g<sup>-1</sup>) the recommended level, respectively. This higher DCAD of GP is explained by the higher plant Na concentration while the lower DCAD of RR is due to the high concentrations of plant S and Cl. This lower DCAD of RR will depress the feed intake, milk production, and milk fat concentration while higher DCAD of GP will make feed more alkaline and unpalatable, resulting in reduced feed intake [67,68].

## 5. Conclusions

*Brachiaria* Mulato II was more photosynthetically efficient and performed well under lower light conditions compared to GP and RR, suggesting its potential to grow in shaded environments. The efficiency of carbon assimilation and biomass accumulation was greater in GP. In terms of, canopy structure parameters, biomass accumulation in the more productive (high nutritive value) leafy stratum, and chemical and mineral compositions, BM showed pronounced results compared to GP and RR. Therefore, these favourable agronomic characteristics suggest selecting BM as a better forage option despite the potential yield penalties observed over high yielding GP. Overall, results from the present study suggested that if the aim is for a quantity of feed (e.g., feeding dry cows), growing a sward dominated by GP is useful, whereas growing a sward dominated by BM is recommended for lactating dairy cows under the tropical and subtropical pasture-based dairy production systems.

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