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Investigation of Tropical Pasture Species to Improve Dairying in the Tropics

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Abstract

Despite the ever-increasing demand for dairy products, dairy production in tropical regions is often lower than in temperate regions, due to a range of factors including the lower nutritive value of pastures. The availability of high-quality tropical pastures is a key requirement to increase the productivity of dairy cows as well as manage enteric methane emissions. Warm-season perennial grasses are the dominant forages in tropical and subtropical regions, and thus exploring their nutritive characteristics and evaluating their likely performance in existing dairy production systems, is imperative in the effort to improve dairy productivity. This thesis was undertaken to investigate tropical pasture species for improving dairying in the tropics via a modelling and simulation approach.

A dearth of data comparing the nutritive values of tropical pastures grown across different environments limits the selection of forages for livestock in the tropics. A database was constructed containing a total of 4750 records, with 1277 measurements of nutritive values representing 56 tropical pasture species and hybrid cultivars grown in 26 different locations in 16 countries, in order to compare the nutritive values and greenhouse gas production across different forage species, climatic zones, and defoliation management regimes. The average edaphoclimatic (with minimum and maximum values) conditions within this data set were characterized as 22.5°C temperature (range 17.5–29.30°C), 1253.9 mm rainfall (range 104.5–3390.0 mm), 582.6 m elevation (range 15–2393 m), and a soil pH of 5.6 (range 4.6–7.0). The data revealed spatial variability in nutritive metrics across bioclimatic zones and between and within species. The ranges of these nutrients were as follows: neutral detergent fibre (NDF) 50.9–79.8%, acid detergent fibre (ADF) 24.7–57.4%, crude protein (CP) 2.1–21.1%, dry matter (DM) digestibility 30.2–70.1%, metabolisable energy (ME) 3.4–9.7 MJ kg^{-1} DM, with methane (CH_4) production at

132.9–133.3 g animal^{-1} day^{-1}. The arid/dry zone recorded the highest DM yield, with decreased CP and high fibre components and minerals. Furthermore, the data revealed that climate, defoliation frequency and intensity, in addition to their interactions, have a significant effect on tropical pasture nutritive values and CH_4 production. Overall, hybrid and newer tropical cultivars performed well across different climates, with small variations in herbage nutritive value. Results revealed that greater pasture nutritive values and lower CH_4 production can be potentially achieved through the selection of improved pastures and subsequent management.

Subsequently, the suitability of three improved tropical perennial pastures: *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) for tropical dairy production was evaluated using their carbon assimilation, canopy structure, herbage plant-part accumulation and nutritive value parameters under irrigated conditions. A field 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. The efficiency of CO_2 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 leaves 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.

The BM also demonstrated greater nutritive value (Total digestible nutrients (TDN), ADF, NDF, neutral detergent insoluble protein (NDICP), starch, non-fibre carbohydrates (NFC), ME, mineral profile (Mg, P, K, Fe, Zn) and dietary cation-anion difference (DCAD)) for leaf, stem, and the whole plant. Overall, the observed greater quantum efficiency, leaf accumulation, and nutritive value of BM suggested that BM is an attractive forage option for dairying in pasture-based systems in tropical and subtropical climates.

The DairyMod-SGS, a mechanistic biophysical pasture model was parametrised and robustly validated for the prediction of the growth of the three tropical pastures (BM, GP, and RR), aiming to use the model as an effective tool to explore the likely performances of newer species under different edaphoclimatic and agronomic management practices. The model was calibrated using measurements of biomass components, canopy structure, and carbon assimilation collected from the field experiment at the Gatton Research Dairy Farm. Subsequently, the model was tested extensively using the published and unpublished data (16 data sets, 32 experiments, 14 different locations across South America, North America, Australia and Africa) to ensure that the parameterised model performed well and was reliable across a diverse set of environments and management practices. In the model parameterisation stage, the model predicted the above-ground biomass with good agreement for all tropical pastures with a high R^2 of 0.92, 0.98, 0.74 and low RMSE of 341, 583, 848 kg DM ha^{-1} for BM, GP, and RR, respectively. The model agreement was good for the validation data with R^2 of 0.86, 0.80, 0.87 and RMSE of 954.5, 790.5, and 633.2 kg DM ha^{-1} for BM, GP, and RR, respectively. The predicted leaf and stem partitioning was relatively poor, and the model also struggled to simulate realistic pasture growth in Mediterranean and desert environments ($R^2 < 0.50$). The present study has improved the robustness and accuracy of DairyMod-SGS in relation to tropical pastures and indicated that the model can be successfully used for investigating the likely performance of improved tropical pastures under a broad range of conditions.

The validated DairyMod-SGS pasture model was applied to simulate the long-term pasture production of three improved pastures (BM, GP, and RR) in major dairying regions of Sri Lanka under three management scenarios: 1) rainfed pasture production system under the industry average nitrogen (N) fertiliser rate (Y_t^{WN} = yield over time under water and N limitation); 2) rainfed pasture production system under non-limiting N fertilisation (Y_t^{W} = yield over time with no N limitation but water limitation); and 3) potential pasture production system under non-limiting N and irrigation (Y_t = yield over time with no N and water limitations). Simulations were carried out for 16 sites across Sri Lanka (8 sites in the dry zone (DZ), 5 sites in the intermediate zone (IZ), and 3 sites in the wet zone (WZ)) over a 30-years period (1980–2010). The model simulated that the long-term pasture production greatly varied between climate zones, pasture species and management scenarios. Overall, the Y_t^{WN} scenario showed a seasonal cycle following the rainfall pattern, with a reduction in growth rates in dry seasons (May to September). Growth rate and herbage accumulation were greater in GP at Y_t^{WN}, and BM at Y_t^{W} and Y_t, while RR always showed the lowest growth rate. The variability of pasture growth between climate zones was highest in DZ (May to September) whereas the variability between species was lowest in RR. Pasture accumulation of both BM and GP outperformed their standard cultivars currently grown in Sri Lanka. In general, the pasture accumulation under Y_t^{W} increased (doubled) the growth rate, while the Y_t scenario substantially increased (nearly tripled) the growth rate. Overall, the finding of this thesis suggested that all three pasture cultivars tested (BM, GP, and RR) are suitable for growing across major dairying regions in Sri Lanka, and that appropriate fertiliser and irrigation management can greatly intensify the herbage accumulation. In particular, BM appeared to be promising in terms of nutritive value, and agronomic and physiological traits. However, regional edaphic conditions, and the management ability of the farmers with respect to inputs and defoliation management, will ultimately determine the performance of improved cultivars such as those used in this thesis. There is a need for extension activities to support farmers in the management required to achieve best performance (yield, nutritive value and persistence) from these species.

Future research is recommended to: 1) validate the model under Sri Lankan conditions, using both unimproved and improved cultivars, to determine its suitability in estimating tropical pasture yield; and 2) use additional models to evaluate the performance of improved tropical pastures in the context of the whole farm system, to identify the likely impact on dairy production and economic return.

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Table of Contents

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

Appendix

List of Tables

List of Figures

Abbreviations

The abbreviations are defined at the first use and then without definitions throughout the thesis. Abbreviations are redefined in each chapter.

ADF	Acid Detergent Fibre
ADL	Acid Detergent Lignin
AOAC	Association of Official Agricultural Chemists
APSIM	Agricultural Production Systems Simulator
ASRIS	Australian Soil Resource Information System
BD	Bulk Density
BM	Brachiaria Mulato II
CF	Crude Fat
CHIRPS	Climate Hazards Group Infrared Precipitation with Stations
CIAT	Centro Internacional De Agricultura Tropical
CP	Crude Protein
CSIRO	Commonwealth Scientific and Industrial Research Organisation
CV	Coefficient of Variation
DCAD	Dietary Cation-Anion Difference
DE	Digestible Energy
DM	Dry Matter
DMD	Dry Matter Digestibility
DMI	Dry Matter Intake
DSSAT	Decision Support System for Agrotechnology Transfer
DZ	Dry Zone
EC	Electrical Conductivity
EE	Ether Extract
ESC	Ethanol-Soluble Carbohydrates
Etc	Crop Evapotranspiration
FAO	Food and Agriculture Organisation
FC	Field Capacity
GHG	Green House Gas
GIS	Geographic Information System

GLF	Growth Limiting Factor for Water
GLFN	Growth Limiting Factor for Nitrogen
GP	Gatton Panic
ILRI	International Livestock Research Institute
IPCC	Intergovernmental Panel on Climate Change
IVTD	Invitro True Digestibility
IZ	Intermediate Zone
KJ	Kilojoules
LAI	Leaf Area Index
LI	Light Interception
LME	Linear Mixed Effects Models
MAE	Mean Absolute Error
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
MB	Mean Bias
ME	Metabolisable Energy
MEF	Modelling Efficiency
MJ	Megajoules
MSL	Mean Sea Level
N	Nitrogen
NDF	Neutral Detergent Fibre
NDFD	Neutral Detergent Fibre Digestibility
NDICP	Neutral Detergent Insoluble Protein
NFC	Non-Fibre Carbohydrates
NHA	Net Herbage Accumulation
NIRS	Near-Infrared Spectroscopy
NRC	National Research Council
NSDI	National Spatial Data Infrastructure
NSE	Nash-Sutcliffe Efficiency
OM	Organic Matter
OMD	Organic Matter Digestibility
PAR	Photosynthetically Active Radiation

PB	Percentage Bias
PPF	Photosynthetic Photon Flux
PPM	Parts Per Million
RMSE	Root Mean Square Error
RR	Rhodes Grass Reclaimer
RUBP	Ribulose 1,5–Bisphosphate
SAT	Saturated Soil Limit
SD	Standard Deviation
SE	Standard Error
SEM	Standard Error of Mean
SILO	Scientific Information for Land Owners
SLA	Specific Leaf Area
TDM	Total Dry Weight
TDN	Total Digestible Nutrients
VFA	Volatile Fatty Acids
VRI	Veterinary Research Institute
WP	Wilting Point
WSC	Water-Soluble Carbohydrates
WZ	Wet Zone

Chapter 1

General Introduction

Demand for dairy products is ever increasing across the world, and approximately 47% of global milk comes from tropical and subtropical regions (Hemme & Otte, 2010). Due to increasing population, global dairy production needs to substantially increase in the future, as the demand is expected to nearly double by 2050 (Thornton & Herrero, 2010). Tropical dairy production is a biologically efficient system whereby large quantities of warm-season (C_4) grasses, the most abundant feed in the tropics (Moran, 2005), are converted into milk (Cooke et al., 2020). 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 (Sage & Kubien, 2003). In addition, increasing atmospheric temperatures due to climate change may favour the dominance of C_4 species in different ecosystems where they are not currently present (Sage & Kubien, 2003). Consequently, these pastures constitute a key resource to fulfil livestock nutritional requirements and increase dairy production in tropical and subtropical regions (Baptistella et al., 2020; Paul et al., 2020).

Dairy production per animal and per unit land area in tropical regions is lower than in temperate regions, due to a range of factors including the lower nutritive value of pastures, lack of access to inorganic nitrogen (N) fertiliser, generally infertile soils (lacking in major nutrients), and adverse climatic conditions (Paul et al., 2020). Most tropical cattle are fed a diet that is based essentially on pasture species of overall low nutritive value, with large seasonal variations in yield and nutritive characteristics (Boval et al., 2015). However, intensification of management through planting improved forage species and cultivars, in addition to adopting appropriate harvesting, fertilising, and grazing practices (Capstaff & Miller, 2018), have substantially improved the nutritive value of tropical pastures. These improved tropical forages include a wide variety of perennial pasture species that are well adapted to wider edaphoclimatic conditions, have improved nutritive value, and are used for either grazing or mechanical harvest (Paul et al., 2020; Sollenberger et al., 2020). A broader understanding of pasture species prior to their introduction into a system is important to see how well they may adapt, in order to achieve the right balance between yield, seasonality of yield and nutritive value (Lowe et al., 2016). However, a paucity of data comparing the nutritive values of tropical pastures grown across different environments limits the selection of these forages for livestock. Therefore, gauging the performances of different pasture species and cultivars across different environments aids in identifying different spatial and temporal niches that are suitable for growing tropical pastures, in order to improve dairy cattle nutrition.

The fundamental basis of pasture growth is carbon assimilation by photosynthesis (Silva et al., 2016). Tropical grasses have long been recognised for their high photosynthetic potential (Volenec et al., 2007; Habermann et al., 2019; Sollenberger et al., 2020), although detailed species-specific descriptions related to carbon assimilation are scarce, especially for recently developed pasture cultivars (Dias-Filho, 2002; Pedreira et al., 2015). Understanding the carbon assimilation process of tropical pastures allows for a better understanding of the species-specific physiological adaptation and yield potential (Pedreira et al., 2015). In addition, pasture canopy structure has an important effect on both herbage yield and herbage nutritive value (Baumont et al., 2000; Lemaire et al., 2009). The pasture yield and nutritive value can be described in a two-dimensional way (vertical and horizontal) through the pasture profile. Length, vertical orientation, and horizontal dispersion of produced pseudo-stems or stems of the grass determine the sward structure and partly the accessibility of herbage to defoliation by grazing (Gastal & Lemaire, 2015). In addition, the 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 (Hodgson, 1982). 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 metabolisable energy (ME), and a lower neutral detergent fibre (NDF), acid detergent fibre (ADF), and tensile fracture (Jacobs et al., 1999; Jacobs et al., 2011). 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, still remains to be understood. Consequently, such information has largely been overlooked in the decision-making of tropical pasture species selection and adaptation of subsequent agronomic management practices.

Simulation models are widely used in modern agriculture to simulate forage (crop and pasture) growth and to complement expensive field research by predicting and understanding the likely performances of forage species under a range of soil, climate, and management strategies. However, models must be calibrated and tested for new species and cultivars before their application can be extrapolated to predict forage responses accurately. There are several different simulation models including DairyMod-SGS (Johnson, 2008), Agricultural Production Systems Simulator (APSIM) (Holzworth et al., 2014), GrassGro (Clark et al., 2000), GRASP (Littleboy & Mckeon, 1997) and CROPGRO (Pedreira et al., 2011). Despite these models having been extensively parameterised for crops and temperate grasses, they have not been widely used in tropical areas (Andrade et al., 2016; Silva & Giller, 2021). According to Andrade et al. (2016), there are only a few empirical models that can successfully predict the growth and herbage accumulation of genera *Megathyrsus* (Pezzopane et al., 2012; Araujo et al., 2013; Moreno et al., 2014) and *Brachiaria* (Cruz et al., 2011; Pezzopane et al., 2018), however, they are location specific, which limits their extrapolation as they do not consider the underlying physiological and physical principles of pasture growth. Therefore, parameterising and more widely validating a pasture model for a wider range of tropical pasture species would expand the application of the model, and also provide more opportunities to explore the likely performances of newer forage options to improve livestock production in the tropics.

The dairy industry in Sri Lanka serves as the most important livestock subsector, due to the need to address the growing demand for dairy and dairy products, and its potential influence on the rural economy (Vyas et al., 2020). The present milk consumption in Sri Lanka is largely driven by the consumption of imported milk and milk products (53% of demand) rather than domestically produced fresh milk (Ministry of Finance, 2021). An inadequate supply of quality forage is the major factor limiting dairy production in Sri Lanka (Houwers, 2015). In general, the climate and soil in Sri Lanka do not create restrictions on forage production and the country has a significant tropical forage production capacity that could support a greater production of milk domestically (Premaratne & Premalal, 2006). The country needs to introduce improved grasses adapted to the local soil and climate which are more leafy and digestible, to exploit the maximum genetic potential of the dairy herds and subsequently intensify management through appropriate defoliation in combination with more intensive fertiliser application (Houwers, 2015; Opio et al., 2017; Prowurst, 2019; Premaratne & Samarasinghe, 2020). However, no studies have been undertaken to broadly evaluate the potential of improved forage species that could be introduced to Sri Lanka. While traditional agronomic experiments are often labour-intensive, time-consuming, and expensive, leading to season-specific and site-specific results, simulation and modelling can aid to mimic the long-term field experiments and promote data-driven decision-making processes (Ara et al., 2020; Silva & Giller, 2021; Ahmed et al., 2022). Nevertheless, despite this increase in simulation and modelling knowledge, application of models in the tropical pasture production system is still limited (Andrade et al., 2016).

This thesis aims to investigate tropical pasture species to improve dairying in the tropics via an agronomic evaluation, and a modelling and simulation approach. The specific objectives proposed to achieve this main aim were:

1. to undertake a meta-analysis to compare the nutritive value of tropical pastures grown in different bioclimatic environments;
2. to study the suitability of three improved tropical pastures; *Brachiaria* Mulato II (BM), *Megathyrsus maximus* ‘Gatton Panic’ (GP), and *Chloris gayana* ‘Rhodes grass cv. Reclaimer’ (RR) for use in a subtropical and tropical environment;
3. to parameterise the DairyMod-SGS pasture model for these three tropical pastures and to validate the model across multiple environments; and
4. to apply the DairyMod-SGS pasture model for simulating the growth of BM, GP, and RR across the key livestock production zones under three different pasture production scenarios, and characterise the long-term forage production, seasonality, spatial variability, and possible implications for dairying in Sri Lanka.

Chapter 2

Review of Literature

2.1 Dairy production in the tropical regions

Dairy production is a key element of agriculture in the tropics, and it is estimated that 47% of global ruminant milk comes from tropical and subtropical regions (Gerber et al., 2013). Tropical dairy production is a biologically efficient system whereby large quantities of warm-season (C_4) grasses, the most abundant feed in the tropics (Moran, 2005), are converted into milk (Cooke et al., 2020). A large diversity of dairy production systems in terms of feeding management, the scale of production, and dairy animal breeds has been observed in the tropics (de Leeuw et al., 1998). Tropical dairying ranges from varying degrees of grazing and/or feeding of cut forages, to pastoral and agro-pastoral systems, to feeding grain concentrates, and these vary regionally (Moran, 2005). In Latin America, cattle are raised largely on sown pastures, while in West Africa, cattle graze native pastures (rangelands) and crop residues. In tropical Asia, cut-and-carry systems and crop residues predominate as the major feed types (Hernández-Castellano et al., 2019).

The milk in tropical dairy regions is predominantly produced by small-scale (smallholder) farmers, and tropical pastures constitute a key component of these systems, providing essential feed resources for the livestock (Moran, 2005; Rao et al., 2015). The majority of tropical pasture-based systems face challenging production conditions (e.g., prolonged dry seasons, unreliable wet seasons, low soil fertility, pests, and diseases) which affect both the quantity and quality of forage produced, and thus limit livestock productivity (Rao et al., 2015). In addition, unlike most temperate regions, tropical regions have hot and/or humid climates that are unfavourable for livestock and this creates inherent challenges for tropical dairying (de Leeuw et al., 1998). Therefore, in many countries, dairy productivity is constrained by poor-quality feed resources, dairy animals' low genetic potential for milk production, diseases, limited access to markets, services and technologies (Teufel et al., 2010; Hernández-Castellano et al., 2019).

2.2 Present status of dairying in Sri Lanka

The dairy industry in Sri Lanka is an important livestock subsector, due to the need to address the growing demand for dairy products, and also its potential positive influence on the rural economy (Vyas et al., 2020). Milk production in Sri Lanka is predominantly managed by smallholder farmers, who account for about 70% of the domestic milk production (Opio et al., 2017; Gedara et al., 2023). Dairy cattle management systems in different parts of the country have largely been influenced by the climate, availability of grazing land, and genetic make-up of the animals (Premaratne & Premalal, 2006; Opio et al., 2017). The agroecological zoning and feed resources are the dominant factors that influence the distribution of the livestock sector in Sri Lanka.

Considering the livestock production, the country is divided into four production zones (Figure 2.1), namely upland and mid-country, coconut triangle, wet lowland, and dry lowland (Ibrahim et al., 1999; Premaratne & Premalal, 2006; Opio et al., 2017). The upland and mid-country region contributes 43% of total milk production and are characterised by smallholdings under either intensive or semi-intensive management, with pure-bred or cross-bred European breeds of cattle, zero-grazing with high inputs of feed. The coconut triangle only contributes 18% of total milk production, although it is an area with a high potential for dairy development due to its climate (Premaratne & Premalal, 2006). It is characterised by small herds managed under a semi-intensive system with either tethered or free grazing on natural pastures/legumes under coconut and other perennial crops (Ranaweera, 2009). The wet lowland is the most intensively exploited zone, with 67% of its area under permanent agriculture.

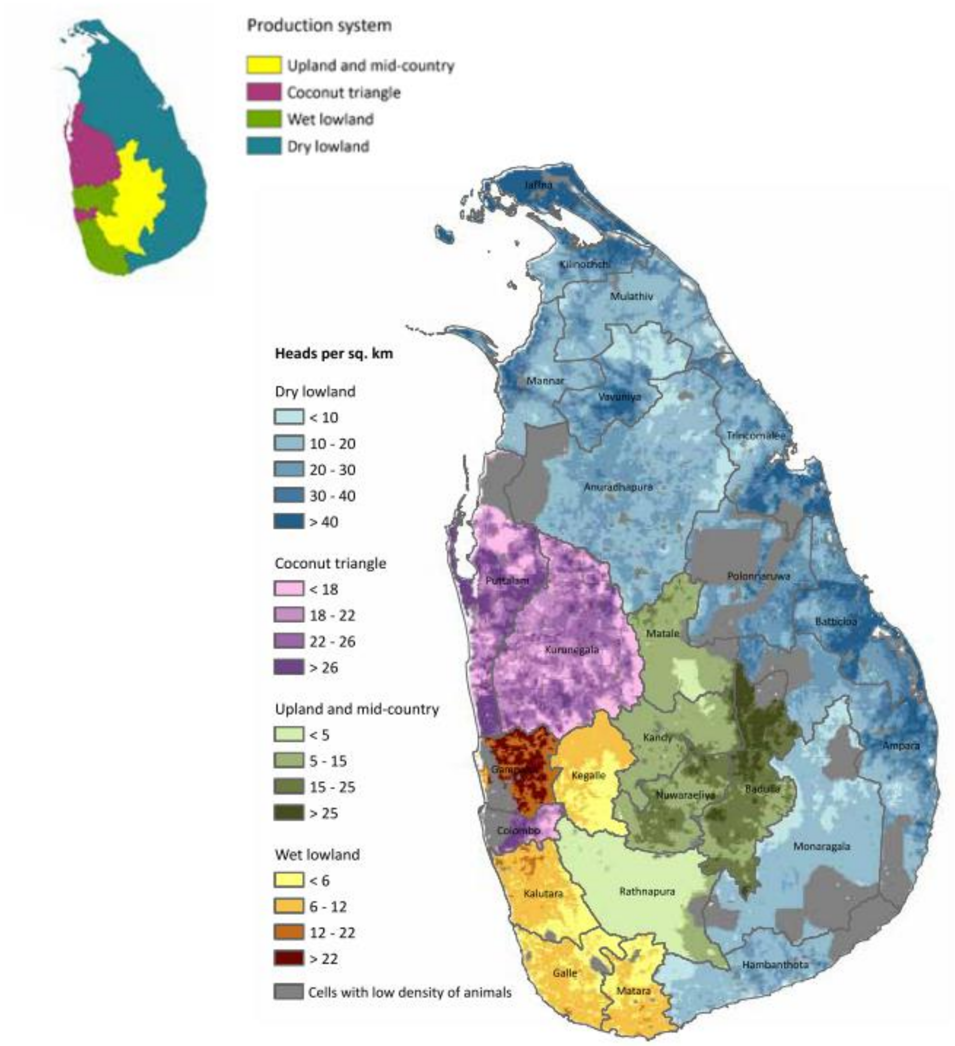

Figure 2.1. Geographical distribution of dairy cattle herd across the four major livestock production zones in Sri Lanka. Source: Opio et al. (2017)

The cattle comprise of crosses of exotic breeds, zebu types, indigenous animals and their crosses, with limited grazing and mostly cut-and-carry from roadsides, accounting for 8% of total milk production. The dry lowland covers two-thirds of the island and encompasses a considerable variety of settings, from sub-humid forest to dry scrub. The largest number of cattle is found in the dry lowland zone, where herd sizes are also the largest, however currently it only produces 31% total milk production of the country (Premaratne & Premalal, 2006; Opio et al., 2017). Available cattle herds are characterised by indigenous cattle, zebu cattle and their crosses and buffaloes, generally free grazing (Opio et al., 2017).

Currently, milk consumption in Sri Lanka is largely driven by imported milk (53% of demand) rather than domestically produced (Ministry of Finance, 2021) due to a number of reasons, mainly including inadequate supply of quality forage, low genetic merit of cows, and poor farm management (Opio et al., 2017). The dairy industry is treated as a priority area for investment and development to achieve Sri Lanka's aim of self-sufficiency in milk and reduce the imports of dairy products (Ministry of Finance, 2021). The Sri Lankan Government has identified the intensive management of livestock, improvement of fodder and pasture management, and promoting feed conversion (silage and hay) (Premaratne & Samarasinghe, 2020), along with data-driven, smart tech-based agricultural practices, to enable a rapid transition of the dairy industry (Prowurst, 2019).

2.3 Fodder and pasture production in Sri Lanka

At present the dairy industry in Sri Lanka primarily depends on natural pasture (nearly 12 000 km^2 of the total land area is under grass) (Premaratne & Premalal, 2006) and fodder available on roadsides, tank bunds, uncultivated lands and fallow paddy fields. Due to the non-availability of quality pasture cultivars and species in the marketplace, and lack of pasture and forage establishment and management experience, pasture improvement is not commonly practiced to any great extent in Sri Lanka (Premaratne & Premalal, 2006; Houwers, 2015; Gedara, 2019; Prowurst, 2019; Premaratne & Samarasinghe, 2020; Vyas et al., 2020) especially by smallholder dairy farmers who produce a major proportion (70%) of the national milk production (Gedara et al., 2023). Table 2.1 presents the currently available forages for different dairy production systems in Sri Lanka.

Good-quality forage is the most indispensable input for efficient and low-cost dairy production in Sri Lanka. Quality forages, in the sufficient quantity, will substantially reduce the feed shortages that limit productivity of dairy cattle, and help Sri Lanka achieve self-sufficiency in milk production. In general, the climate and soils in Sri Lanka are conducive to forage production and there is significant capacity to produce tropical forage for greater production of milk domestically (Premaratne & Premalal, 2006). Houwers (2015) estimated that the biophysical potential for milk production in Sri Lanka was eight times higher than the current milk production, under a scenario of intensified forage supply. The strategic changes for improving forage production in Sri Lanka have been broadly explored (Houwers, 2015; Opio et al., 2017; Gedara, 2019; Prowurst, 2019; Premaratne & Samarasinghe, 2020), and key approaches include the introduction of improved grasses adapted to the local soil and climate, which are more leafy and digestible, to exploit the maximum genetic potential of the dairy herds and subsequently intensify management through appropriate defoliation in combination with more intensive fertiliser application.

Table 2.1. Forage available for different systems in Sri Lanka Source: Premaratne & Samarasinghe (2020)

Common name Fodder/pasture grasses	Scientific name	Available system
Hybrid Napier- CO-3	*Pennisetum purpureum X, P. americanum*	Cut-and-carry system
Hybrid Napier- CO-4	*Pennisetum purpureum X, P. americanum*	Cut-and-carry system
Guinea-VRI 435	*Panicum maximum*	Cut-and-carry system
Guinea-TD 58	*Panicum maximum*	Cut-and-carry system
Guinea-Makueni	*Panicum maximum*	Cut-and-carry system
Setaria	*Setaria sphacelata*	Cut-and-carry system
Signal grass	*Brachiaria brizantha or B. decumbens*	Grazing system
Ruzi grass	*B. ruziziensis*	Grazing system
Ryegrass*	*Lolium perenne*	Grazing system
Kikuyu grass*	*Pennisetum clandestinum*	Grazing system
Gamba grass	*Andropogan gayanus*	Cut-and-carry system
Fodder sorghum (Sugar graze, Jumbo, BMR6)	*Sorghum bicolor*	Cut-and-carry system
Fodder maize (Pacific, local varieties)	*Zea mays*	Cut-and-carry system
Fodder legumes		
Gliricidia	*Gliricidia sepium*	Cut-and-carry system
Ipil-Ipil	*Leucaena leucocephala*	Cut-and-carry system
Desmanthus	*Desmanthus virgatus*	Cut-and-carry system
Sesbania	*Sesbania sesban*	Cut-and-carry system
Erythrina	*Erythrina orientalis*	Cut-and-carry system
Caliandra	*Caliandra calothrysus*	Cut-and-carry system
Pasture legumes		
White clover*	*Trifolium repens*	Grazing system
Red clover*	*Trifolium pratens*	Grazing system
Stylo-fine stem	*Stylosanthus guyanensis*	Grazing system
Stylo-Verano	*Stylosanthus hamata*	Grazing system
Greenleaf Desmodium	*Desmodium intortum*	Grazing system
Silverleaf Desmodium	*Desmodium uncinatum*	Grazing system

* Species only available in cooler climatic zones

2.4 Soil in Sri Lanka

Soils in Sri Lanka do not pose a major limitation to forage and other crop production (Premaratne, 2006). Reddish-brown earth and immature brown loams (Cutanic Luvisols and Haplic Cambisols) are the major soil types (2.68 million ha), followed by red-yellow podzolic (Colluvic Regosols) (1.52 million ha) (Mapa, 2020). Fertility in terms of organic matter is higher in dry zone soils due to higher decomposition of organic matter under high temperatures (Dassanayake et al., 2020a). Wet zone soils are generally low in fertility due to lower organic matter decompositions, along with extensive leaching of soluble nutrients due to high precipitation. Compared to the wet zone and intermediate zone, the dry zone environment has less complexity in terms of climate, elevation and geology (Dassanayake et al., 2020a). However, there is a variation of topography and parent material due to slight differences in microclimate in the dry zone, which has resulted in the formation of different soil types (Dassanayake et al., 2020a).

The soils of the dry zone, wet zone and intermediate zone have been extensively studied and published with respect to their location, morphology, taxonomy and land use description, along with their physical and chemical characterisation (Mapa et al., 1999; Mapa et al., 2005; Mapa et al., 2010). According to Mapa et al (2005), reddish-brown earth soil, the major group of soil present in Sri Lanka, has sandy loam to sandy clay loam throughout its profile. The percentage of clay increases with the depth of profile (12.4%–32.1%), and the bulk density ranges from 1.42–1.59 Mg m^{-3}. Saturated hydraulic conductivity is 33.1 cm h^{-1} in horizon A and reduces to 3.6 cm h^{-1} in the lower horizon (110–140 cm). Soil pH (H_2O) ranges between 6.4–6.8 and electrical conductivity ranges from 0.09–0.06 mS cm^{-1}. Base saturation is high in these soils at 99% in 0–25 cm (horizon A), gradually reducing to 78% and 72% in the B1 and B2 horizons, respectively. Organic carbon is reported as 1.05% on the top 25 cm soil layer (Mapa et al., 2005).

2.5 Climate in Sri Lanka

The climate is characterised as tropical, hot, and humid throughout the year (Punyawardena, 2020). The crop production in the country is largely determined by these climatic features, thus the understanding of the temporal and spatial variation of the climate is key in integrating new crop varieties including forages into the existing production systems (Premaratne & Premalal, 2006).

In the dry lowlands, the mean annual temperature is 27°C and the mean daily range is 6°C. Maximum temperature ranges from 32 to 35°C and the minimum ranges from 22 to 24°C. However, the daily maximum temperature can exceed 37°C during March and April and also in late August. Given the prevailing uniform temperature conditions, rainfall is the most important climatic parameter which governs agricultural production in Sri Lanka (Punyawardena, 1998). The rainfall distribution of Sri Lanka is seasonally influenced by conventional precipitation and two monsoons (Punyawardena, 2020). The Southeast monsoon occurs from May to September with rainfall varying from 100 to over 3000 mm, and the Northeast monsoon occurs from late November to late January with rainfall over 1200 mm, providing more island-wide distributed rainfall. The inter-monsoonal convectional rains are also effective from March to April (first Inter-monsoon 250–700 mm rainfall) and October to November (second Inter-monsoon > 400 mm rainfall), providing intermittent precipitation with varying intensities (Punyawardena, 2020).

Sri Lanka can be divided into three agroclimatic zones based on mean annual precipitation (MAP): wet zone (MAP > 2500 mm), dry zone (MAP < 1750 mm) and intermediate zone (MAP 1750–2500 mm). The dry zone (4.13 million ha) and the intermediate zone (0.85 million ha) account for 75% of the surface area of the island. Relative humidity depends on geographical location and generally ranges from 70–90% and from 55–80% during the morning and evening, respectively. Very low relative humidity (55–60%) is reported in the dry lowland region especially mid-year when the temperate is high (Punyawardena, 2020). Evaporation is reported to be higher (5–8 mm day^{-1}) during April to September and then reduces (2–5 mm day^{-1}) from October to February with high precipitation. These three agroclimatic zones are divided into 24 agroecological zones representing several heterogeneous agroecological regions which are based on agroclimatic (rainfall, temperature), soils, and terrain, and which support particular farming systems including livestock and forage production (Premaratne & Premalal, 2006).

2.6 Tropical pastures

Tropical pastures constitute a key component of the tropical livestock production systems, providing essential feed resources (Sollenberger et al., 2020). These tropical grasses are well adapted to warm and dry regions and are considered resilient under adverse environmental conditions (e.g., high temperature, water stress, and saline soils), which is attributed to a combination of morphological (leaf anatomy, root system) and physiological (C_4 carbon assimilation pathway, reduced photorespiration, high water, and nitrogen (N) use efficiency) mechanisms (Tubiello et al., 2007; Sollenberger et al., 2020). In addition, increasing atmospheric temperatures due to climate change may favour the dominance of C_4 species in different ecosystems where they are not currently present (Sage & Kubien, 2003).

2.6.1 Brachiaria Mulato II

‘*Brachiaria* grass’ is the common name for the species within the genus *Brachiaria* (syn. *Urochloa*) (Baptistella et al., 2020). *Brachiaria* Mulato II (BM) is a *Brachiaria* hybrid cultivar of Centro Internacional de Agricultura Tropical (CIAT) produced from three-generation hybridisation of tetraploidised 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 (Argel et al., 2007). According to Argel et al (2007), BM is a perennial, tetraploid hybrid, with a semi-erect growth habit which can grow up to 0.8–1 m height. Mulato II produces strong cylindrical stems with soft down and they are capable of rooting when coming to contact with the soil due to a semi-decumbent growth habit. Interestingly, the grass is well adapted to a wide range of growing conditions in the tropics and subtropics including a long (up to 6 months) dry period. According to Argel et al. (2007), BM has grown well in low fertile, acidic soils with high aluminium contents and has adapted to a wide range of soils, climate, disease tolerance (spittlebug diseases) and recovery after burnings and moderate shade, but is not tolerant to frost (11°C base temperature, (Pequeno et al., 2014)) or to prolonged waterlogged conditions (Baptistella et al., 2020).

Mulato II has shown a high responsiveness to fertiliser application, especially N, and its initial upright growth habit is compatible with stoloniferous legumes (Argel et al., 2007). Mulato II is a high-quality C_4 grass, and its nutritive value varies with age, plant-part, soil fertility, and season of the year (Argel et al. 2007). CIAT (2006) reported 9.1% CP and 66.6% dry matter digestibility (DMD) in the rainy season, and 8.4% CP and 61.0% DMD in the dry season, and these values were significantly higher than other *Brachiaria* cultivars (Mutimura & Ghimire, 2020).

2.6.2 Rhodes grass

Rhodes grass (*Chloris gayana*) is a strongly stoloniferous perennial grass (Lowe et al., 2016) native to Africa, that has been extensively introduced as a forage grass for dairy farms in tropical and subtropical regions of Australia, Japan and South America). The plant height can vary from about 0.6 m in the cool season (short days) to about 1.8 m in the summer (long days). The grass possesses moderate to high drought tolerance and is widely adapted to different soil and climatic conditions (Boschma et al., 2017). Rhodes grass prefers high fertility soils with low acidity (up to pH 4.5) for optimum yield. The grass produces smooth and shiny creeping stems of 4–5 mm diameter with 2–4 mm diameter upright stems bearing hairless leaves of an average 15–50 cm long and 10–20 mm wide. Rhodes grass is moderately frost tolerant, however, the base temperature for many cultivars is 12°C (Agnusdei et al., 2012), below which little or no growth occurs (Ivory & Whiteman, 1978). Rhodes grass well responds to applied fertiliser, and is very tolerant of cutting or grazing, producing high quality feed under appropriate management (Boschma et al., 2015, 2017). Unfertilised swards produced forage with 6.3% CP and 49 to 56% DMD, whereas with adequate fertiliser application, monthly defoliation resulted in higher CP (10.4–13.8%) and DMD 61–65% (Boschma et al., 2017). Currently, a large number of Rhodes grass cultivars are available, in both diploid and tetraploid types. 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, along with improved agronomic characteristics like fine stems and leafy growth habit (Bachie, 2018). Reclaimer Rhodes grass variety flowers over a wider period than other cultivars, and flowering is insensitive to daylength (Bachie, 2018).

2.6.3 Gatton Panic

Guineagrass [*Panicum maximum* (Jacq.) syn. *Megathyrsus maximus* (Jacq.)] is well known for its high forage yield potential, making it an attractive forage option in the tropics (Pontes et al., 2017). *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 (Descheemaeker et al., 2014). Gatton Panic is an upright perennial bunch grass with broad and long leaves. The plant height can greatly vary from 0.5 m during the cooler seasons to 1.5–2.0 m during warmer months. It has a deep root system that enables better utilisation of soil minerals and water, and prefers good quality soils to maximise its production potential (Moore et al., 2014). However, it is not the most grazing-tolerant species and needs to be managed accordingly in grazed situations. Generally, GP is of high quality compared to other tropical grasses, with DMD and CP values ranging from 55–65%, and 8–14%, respectively. Fibre content of GP can vary greatly with its prominent stem production characteristics, with NDF ranging from 60–70% under longer defoliation intervals. Overall, GP is a nutritious tropical pasture that can support the growth and production of livestock in tropical and subtropical regions (Lawes et al., 2014; Thomas et al., 2014).

2.7 Tropical pasture regrowth dynamics

2.7.1 Plant morphogenesis and regrowth

The fundamental basis of pasture growth is carbon assimilation by photosynthesis (Silva et al., 2016). Tropical forage grasses have long been recognised for their high photosynthetic potential, although detailed species-specific descriptions related to carbon assimilation are scarce, especially for recently developed pasture cultivars (Pedreira et al., 2015; Silva et al., 2016). Understanding the carbon assimilation process of tropical pastures allows for better understanding of the species-specific physiological adaptation and links the pasture morphological variables with their regrowth dynamics (Lemaire et al., 2009; Pedreira et al., 2015).

Herbage production is influenced by variables like environment, morphogenesis of plant species, and characteristics of the pasture (Lemaire et at., 2009) (Figure 2.2). Plant tissues accumulate through leaf appearance and elongation and subsequently, aging and senescence, which leads to accumulation of litter and later decomposition. The efficient use of pasture herbage is a trade-off between optimising light interception by leaves for carbon assimilation and harvesting leaf (defoliation through either cutting or grazing) before senescence (Parsons, 1988). During the vegetative growth stage, leaf appearance rate, leaf elongation, and leaf lifespan are the major morphogenetic characters that determine the plant sward structure (Da Silva et al., 2015) (Figure 2.2), but stem elongation is an important additional morphogenetic characteristic in tropical grasses (Hodgson, 1982; Da Silva et al., 2015). This accumulation of stem largely determines the herbage mass, composition and nutritive value of tropical pastures.

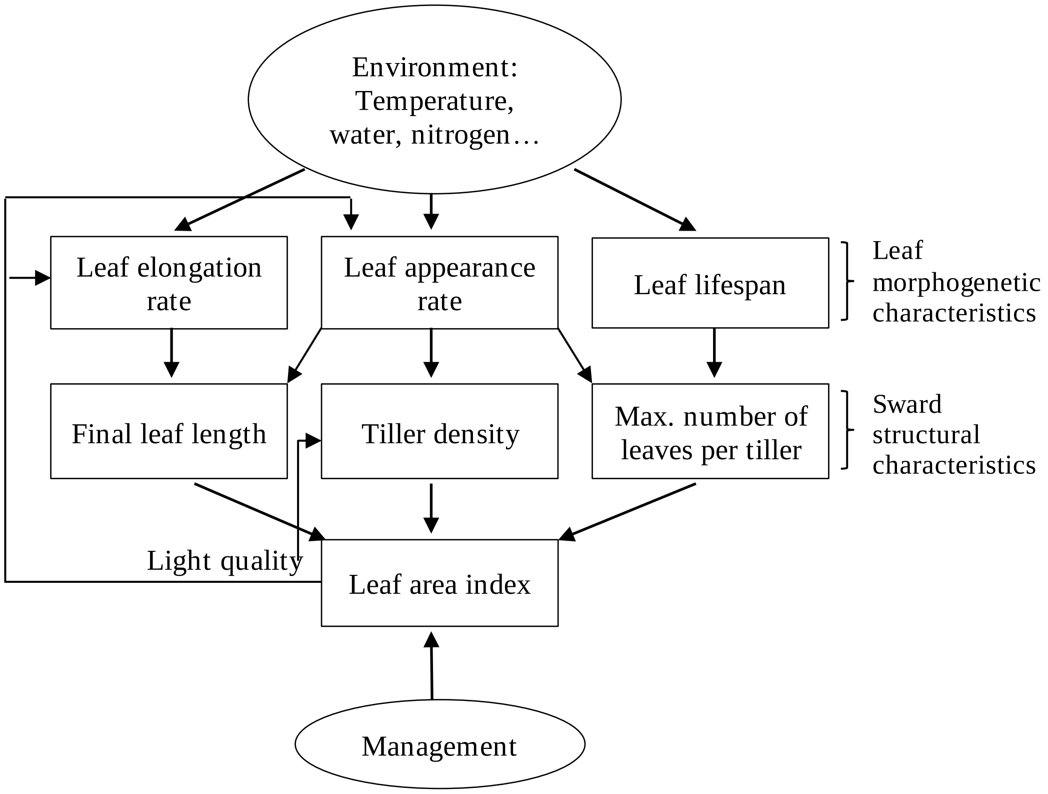

Figure 2.2. Relationship between morphogenetic variables and sward structural traits Lemaire et al. (2009)

These morphogenetic variables related to the growth dynamics have been described for temperate grasses, and are useful to study the coordination of plant development and to characterise pasture regrowth (Nelson & Moser, 1994; Lemaire et al., 2009; Silva et al., 2019). In addition, the differences in the plant morphology and tissue flow of different pasture species can be useful in designing efficient defoliation management strategies (Da Silva et al., 2015; Silva et al., 2019). This requires accurate information on the morphological characteristics of cultivated species, which is especially the case with tropical pasture species, which have not been researched to the same degree as temperate species.

2.7.2 Pasture sward structure

Pasture morphogenetic variables largely determine the sward structural traits (Figure 2.2). The pasture canopy structure has an important effect on both sward productivity (herbage mass), and herbage nutritive value (Baumont et al., 2000; Lemaire et al., 2009). The sward productivity and nutritive value in pastures can be described in a two-dimensional way (vertical and horizontal) in the pasture profile. The nutritive value of the sward components of tropical pastures (leaf and stem) are substantially different, with leaves being superior in terms of feed quality compared with stems (higher CP, lower NDF and ADF, higher digestibility and ME), and have lower tensile fracture than stems (Jacobs et al., 2011). 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 (Hodgson, 1982). Length, vertical orientation, and horizontal dispersion of produced pseudo-stems (sheath) or stems of the grass, which is triggered by competition for light, determine the sward structure and partly the accessibility of herbage to defoliation (either by grazing or cutting) (Matthew & Pereira, 2017). The quality of the sward reduces vertically from the top leafy stratum (high leaf:stem ratio) to the bottom stemmy stratum (low leaf:stem ratio) (Ungar & Ravid, 1999; Benvenutti et al., 2016; Benvenutti et al., 2017). Therefore, the management of tropical pasture swards is targeted at maximising leaf material while limiting the production of lower quality stem. In addition, sward structural variables can be a useful indicator to select suitable pasture species. Although it is recognised that sward structure plays a major role in tropical pasture production, composition, and nutritive value, there is a paucity of knowledge of how sward structure differs between species and with management, especially for improved tropical forages, which limits their use in Sri Lanka.

2.8 Defoliation management strategies for tropical pastures

Forage production and sward characteristics are very sensitive to environmental conditions such as rainfall, air temperature, and solar radiation (Buxton & Fales, 1994; Buxton, 1996). Further, as herbage growth becomes restricted due to variable growing conditions such as seasonality, plant nutrient constraints, and environmental limitations (which are expected to increase under climate change predictions), the efficiency of herbage use also decreases. Therefore, fixed defoliation periods do not match the underlying environmental conditions and this may result in forage losses through senescence or excessive accumulation of stem material in the sward. According to Da Silva et al. (2015), such fixed grazing parameters result in forages with lower nutritive value, reducing animal performance and negatively impacting on the whole farm productivity. According to Parsons & Chapman (2000), it is more sensible to base pasture defoliation on plant-related indicators associated with regrowth, and this approach will also maximise pasture production and persistence (Lemaire et al., 2009).

The study and understanding of morphological and physiological characteristics of forage plants are key for optimising management strategies for each grass under varying environmental conditions (Lemaire et al., 2009; Silva et al., 2019), soil and climate conditions, and considering specific objectives of the forage-livestock system (Da Silva et al., 2015). This also allows for the identification of management specificities in terms of ecophysiological limits of forage plants, and increases the efficiency of pasture utilisation (Da Silva et al., 2015).

2.9 Classification and use of models

Agricultural system models are tools that provide a synthesis and quantification to evaluate the effects of water, soil, crops, management practices, and climate on the sustainability of agricultural production. These models can range from very simple to extremely complex (Thornley & Johnson, 1990; Hunt & Boote, 1998). A model to accurately predict crop growth and subsequently its yield should be sufficently simple to be understood, yet include enough details to ensure robustness under a broad range of environmental conditions (Thornley & Johnson, 1990; Ahmed et al., 2022). Models are clasified in numerous ways: static or dynamic, dicreete or continuous, deterministic or stochastic, and mechanistic or empirical (Andrade et al., 2016). Dynamic models describe the change of variables over time, while static models do not account for any change. Both the discrete and continuous models are dynamic; in continuous models, time is an actual value (e.g., 5.15 h), whereas in discrete models, time is determined by integer values (e.g., 2 h). Stochastic models include a random factor or probability distributions, while the deterministic models do not. The models used in pasture simulations are generally dynamic and deterministic, representing the system responses over time without an associated probability distribution (Thornley & Johnson, 1990). These pasture models can also be mechanistic and emperical in nature. While mechanistic models consider the underlying knowledge of the physical, chemical and biological reactions (e.g., photosynthesis, light capture, water balance, nutrient absorption, carbon partitioning), emperical models consider little or no underlying processes (Johnson & Parsons, 1985; Thornley & Johnson, 1990). These emperical models are often designed to obtain the correlation between the pasture production with one or more variables (e.g. temperature, solar radiation, rainfall, plant available water in the soil), hence they are often location-specific, and prone to errors (Andrade et al., 2016). Mechanistic models can summarise greater amounts of complex processes to predict responses, however development of such models requires greater effort and a sound understanding of the underlying processes (Ahmed et al., 2022).

2.10 Pasture modelling

Pasture models have been an effective tool to understand agricultural systems and interactions among edaphic, climatic and agronomic components. These models can simulate pasture growth and complement expensive field research by predicting the likely performance of pasture species under a range of soil, climate, and management strategies. There are a number of different simulation models including DairyMod-SGS (Johnson, 2008), Agricultural Production Systems Simulator (APSIM) (Holzworth et al., 2014), GrassGro (Clark et al., 2000), GRASP (Littleboy & Mckeon, 1997) and CROPGRO (Pedreira et al., 2011). Despite these models having been extensively parameterised for crops and temperate grasses, they have not been widely used in most tropical areas (Andrade et al., 2016; Silva & Giller, 2021). According to Andrade et al. (2016), there are only a few empirical models that can successfully predict the growth and herbage accumulation of genera *Megathyrsus* (Pezzopane et al., 2012; Araujo et al., 2013; Moreno et al., 2014) and *Brachiaria* (Cruz et al., 2011; Pezzopane et al., 2018), however, they are location-specific, which limits their extrapolation as they do not consider the underlying physiological and physical principles of pasture growth. However, when the physiological processes are well understood, especially for newer, more widely used cultivars, process-based pasture models can be used to mathematically describe the physiological, physical and biochemical processes (Hunt & Boote, 1998; Boote et al., 2013). The parameterising of a biophysical model to accurately predict tropical pasture growth would be a significant achievement, and allow simulation of the long-term effects of environmental variations (e.g. weather patterns and soil characteristics) and management on plant responses, however, such a model must be well tested with measured data before its application can be extrapolated to accurately predict plant responses (White et al., 2008). Essentially, in tropical regions where it may not be feasible to run large-scale field trials to evaluate forage species and cultivars under different management regimes, due to financial limitations (Andrade et al., 2016), the option to parameterise models to accurately simulate the performance of tropical forages would be a significant advancement in exploring the tropical pastures for improving forage-based dairy production systems.

2.10.1 DairyMod-SGS model

DairyMod-SGS is a mechanistic biophysical grazing system simulation model which models pasture growth, utilisation by grazing animals, animal growth and production, soil water, and nutrient dynamics under different pasture management (irrigation, fertiliser application, harvesting for silage or hay and grazing) (Johnson et al., 2008). According to Johnson (2008), the biophysical nature of the DairyMod-SGS model allows the exploration of new management strategies, plant characteristics and likely performances of grasses under different soil and climates. The model allows the simulation of annual and perennial temperate (C_3) and tropical (C_4) pasture species (Johnson, 2008). The present study selected the DairyMod-SGS given its relative easiness to set up for new species, and lower number of parameters required compared to other pasture models. Furthermore, the model has limited tropical pasture species (e.g. Rhodes grass, Kikuyu).

The model has predicted the growth dynamics of temperate forage species across a range of climates, soil types, and management under conditions in Australia and New Zealand

and outside of Oceania (Chapman et al., 2008a; Cullen et al., 2008; Johnson et al., 2008; White et al., 2008; Jenna, 2015; Christie et al., 2018; Perera et al., 2019) (Table 2.2). Chapman et al. (2008) used the model to simulate perennial ryegrass pasture in non-irrigated dairy farms in Southern Australia, and Christie et al. (2018) simulated the seasonal responses of perennial ryegrass, annual ryegrass and kikuyu pastures in contrasting soil types across Australia under rainfed and irrigated conditions to evaluate N fertiliser responses. A more extensive study by Cullen et al. (2008) has modelled net herbage accumulation (NHA) rate in eight different sites ranging from cool temperate to subtropical environments in Australia and New Zealand. Modelled data have shown that DairyMod-SGS can realistically simulate NHA and seasonal yields of ryegrass-based pastures in temperate and subtropical environments, under both cutting and grazing across a wide range of soil types and pasture management (irrigated vs. dryland, varying applications of N fertiliser). However, results highlighted higher accuracy in temperate than in subtropical environments and in winter and summer than in autumn and spring. Johnson et al. (2008) described the biophysical nature of DairyMod-SGS and its current application in the dairy industry, and summarized the wide range of applications including simulating both irrigated and rainfed pastures and N fertiliser management across contrasting edaphoclimatic conditions, and highlighted the flexibility of the model to simulate tropical pastures, based on results from an irrigated Rhodes grass study at Mutdapilly Research Station, South-East Queensland. Apart from analysing variations in forage supply, long-term pasture growth rate variation, climate variability and change in forage production have also been highlighted. Chapman et al. (2008) have also discussed the application of the model in analysing variation in forage supply and business risk in non-irrigated dairy systems in Southern Australia. A recent study by Perera et al. (2020) has also studied the annual, seasonal and monthly pasture production, variability and climate effect on the persistence of temperate pastures species in a range of soil types and environments comprising temperate and native C_4 grasses in South-East Australia. Outside Australia and New Zealand, the DairyMod-SGS simulated Tall fescue pastures with reasonable accuracy under a wide range of climatic and management conditions (N fertiliser levels, irrigation) in Argentina (Berger et al., 2014). The ability to modify the default parameters to fit with the herbage growth of a variety of species, allows DairyMod-SGS to be used to model a range of different pastures under a wide variety of conditions (Johnson et al., 2008; White et al., 2008; Berger et al., 2014). White et al (2008) described EcoMod, which has a similar underlying structure to DairyMod-SGS for simulating the growth rate and plant compositions of dryland and irrigated pasture production in New Zealand with a long-term data set (1966–2003). Modelled and observed total annual and monthly pasture growth rates showed close agreement under dryland and irrigated environments and pasture module parameters were modified to better represent measured pasture growth data. Default parameters have been set as a starting point for simulating various pasture species in EcoMod, and parameters may be adjusted to give realistic results (White et al., 2008).

Plants differ in their optimum growing conditions, responses to water and nutrient requirements, and so parameters within the model may be modified to better represent different species and growing conditions (Johnson, 2008; White et al., 2008). This highlights the identification of parameter values more specific to the pasture species being evaluated and to the scenario(s) being tested, rather than relying on the default values available in the simulation model (Johnson, 2008; White et al., 2008). Therefore, a similar approach can be taken to model new species in DairyMod-SGS where the particular species are defined through species-specific basic model parameters (Johnson, 2008).

Table 2.2. Application of DairyMod-SGS model for simulation of different pasture production scenarios. (NHA= net herbage accumulation, N= nitrogen)

	Country	Climate	Species	Scenarios tested	Specific model application	Reference
1.	Australia and New Zealand	Subtropical and Temperate	Perennial ryegrass White clover Rhodes grass	Different soil, climate Irrigated N fertiliser applied Cut and grazing	NHA rate Long-term growth patterns Dairy farming production system modelling	Johnson et al., (2008)
2.	Australia and New Zealand	Subtropical and temperate	Perennial ryegrass Annual ryegrass White clover Kikuyu	Different soil, climate Irrigated N fertiliser applied Cut and grazing	NHA rate Evaluate seasonal pattern	Cullen et al., (2008)
3.	Australia	Temperate	Annual ryegrass Perennial ryegrass Summer crops	Different soil and climate Cut trial Different forage mixtures	The net pasture growth rate Use as a pasture growth simulator to dairy production and economic model	Chapman et al. (2008a)
4.	Australia	Temperate	Perennial ryegrass Annual ryegrass Summer crops	Different soil and climate Different forage mixtures Intercropping	The net pasture growth rate Intercropping and inter-annual climate variability Use as a pasture growth simulator to dairy production and economic model	Chapman et al. (2008b)

Table 2.2. Cont.

	Country	Climate	Species	Scenarios tested	Specific model application	Reference
5.	Australia	Subtropical and temperate	Rhodes grass Native C_3/C_4 perennial grasses Phalaris Subterranean clover Perennial ryegrass White clover	Different soil, climate Different CO_2 levels Reduced rainfall	NHA rate Net effect of future climate scenarios on pasture production systems (elevated CO_2 and reduced rainfall) Species composition under climate change Soil water balance	Cullen et al. (2009)
6.	Australia	Temperate	Perennial ryegrass	Different soil and climate Different irrigation levels Different N fertiliser rates Cut trial	Pasture production Effect of N fertiliser and irrigation schedules Model N leaching Model water drainage and runoff in irrigation schedules	Rawnsley et al. (2009)
7.	Australia	Temperate	Perennial ryegrass	Different soil and climate Grazing management Higher fertiliser inputs	The net pasture growth rate Use as a pasture growth simulator to dairy production and economic model	Chapman et al. (2011)
8.	Argentina	Temperate	Tall fescue	Different soil, climate N fertiliser rates Irrigated	Test flexibility to use the model to represent herbage accumulation in Argentina	Berger et al. (2014)

Table 2.2. Cont.

	Country	Climate	Species	Scenarios tested	Specific model application	Reference
9.	Australia	Temperate	Perennial ryegrass	Different soil Rainfed N fertiliser applied Grazing	Farm system simulation Simulate pasture intake, supplementary feed intake, milk production, N leaching and N_2O emissions	Christie et al. (2014)
10.	New Zealand	Temperate	Perennial ryegrass White clover	Different soil Different N fertiliser rates Different irrigation levels	Pasture growth rate Simulate soil water flow Test irrigation schedules	Jenna (2015)
11.	South Africa	Subtropical	Kikuyu Perennial ryegrass Lucerne Tall fescue White clover	Different soil and climate Different irrigation schedule	Growth analysis Crop model parameters estimation Study the irrigation requirements	Wayne. et al. (2016)
12.	Australia	Subtropical and temperate	Perennial ryegrass Kikuyu	Different soil, Climate Different N fertiliser rates Cut and grazing Rainfed and irrigated	Effect of N fertiliser rates on pasture production in contrasting sites, seasons	Christie et al. (2018)

Table 2.2. Cont.

	Country	Climate	Species	Scenarios tested	Specific model application	Reference
13.	Australia	Temperate	Perennial ryegrass Cocksfoot Tall fescue Chicory	Heat and drought stress In glasshouse conditions	Model effect of leaf/air temperature on photosynthesis Simulate drought and heat stress on pasture production	Perera et al. (2019)
14.	Australia	Subtropical	Annual ryegrass Kikuyu	Different N fertiliser rates Rain fed Different irrigation schedules	N use efficiency of pasture production Farm system simulation Plant N% Pasture utilisation Total pasture production	Smith et al. (2019)
15.	Australia	Subtropical and temperate	Perennial ryegrass Annual ryegrass White clover Subterranean clover Phalaris Native C_4 grasses	Different soil, climate Cut and grazing	Long-term (1960–2015) pasture growth rates Climate and seasonal pasture production variability	Perera et al. (2020)
16	Zimbabwe	Tropical	*Urochloa* *Mosambicensis* *Eragrostis curvula*	Different soil Grazing	Parameterised for tropical pastures Model testing under rangeland conditions	Svinurai et al. (2021)

2.10.2 Parameterising the DairyMod-SGS model for new species

Parameters are quantities which appear in modelling equations which are not supposed to vary with time (Thornley et al., 2007). However, parameters may be altered to obtain a better agreement between the output and measured data or to examine the sensitivity of a particular output of the model to the given parameter. Model parameterising, sometimes referred as to calibration, is a process of determining the best parameter value to match measured and simulated output of a particular pasture (Boote et al., 2013). Due to the generic variations among cultivars of any pasture species (Jones et al., 2015), cultivar-specific parameters are required if a pasture model is applied to simulate the performance under specified soil, climate and management conditions. Sometimes for a given pasture species, certain cultivar-specific parameters remain the same but there are many popular grass cultivars used in the tropics in which the pasture-specific parameters are unknown or scarce and this limits the ability of these grasses to be effectively modelled (Andrade et al., 2016). Therefore, estimation of pasture-specific parameters through well-coordinated field experiments, validating and integrating them to DairyMod-SGS, would expand the model's application to tropical regions.

With regards to the DairyMod-SGS, pasture-specific parameters relating to pasture growth can be divided into single-value parameters (directly measured) and parameters which associate with physiological relationships (indirectly estimated) (Table 2.3). Canopy structure and carbon partitioning, plant senescence, plant N composition, non-structural carbohydrate and fat composition, nutrient uptake and N fixation are categorised as single-value parameters whereas leaf area index (LAI) and plant canopy height, leaf appearance in response to temperature, relative root distribution, leaf photosynthesis in response to light interception, temperature and CO_2, determine the parameters linked to the physiological relationships of the model for a new species (Johnson, 2008; Johnson et al., 2008).

Table 2.3. Default parameters for generic C_4 species in the DairyMod-SGS pasture module (N = nitrogen, LAI = leaf area index, GLF = growth limiting factor, P_{max} = rate of single leaf gross photosynthesis at saturating photosynthetic photon flux, WP = wilting point, FC = field capacity, NDF = neutral detergent fibre, C = carbon).

Parameter group	Parameter name	Default value for generic C_4 species
Canopy structure		
Canopy structure and partitioning	Carbon partitioned to shoot with no water or N stress (%)	70
	Leaf fraction of new shoot growth (%)	60
	Specific leaf area at ambient CO_2, (m^2 kg^{-1})	20
	Live leaves per tiller	5
Plant senescence	The scale factor for non-leaf turnover rate relative to leaves (%)	80
	Root senescence rate (fraction day^{-1})	2
	Transfer of standing dead to litter (fraction day^{-1})	10
Plant nitrogen composition		
	Optimum N (%)	3
	Maximum N (%)	4
	Non-leaf shoot scale factor	0.5
	Root scale factor	0.5
	Non-structural carbohydrate plus fat: live (%)	25
	Non-structural carbohydrate plus fat: dead (%)	15
Height		
	Maximum height (cm)	50
	LAI for half maximum height (m^2m^{-2})	2
Mass flux		
Leaf appearance in response to temperature		
	Max leaf appearance interval (days)	10
	Min temperature (°C)	10
	Temperature for max rate (°C)	25
	Curvature coefficient	2
	Water stress response of leaf flux	

Table 2.3. Cont.

Parameter group	Parameter name	Default value for generic C_4 species
	Scale factor at GLF water = 0	1
	GLF water value when scale factor = 1	0.5
	Curvature coefficient	2
Roots		
	Root depth (cm)	100
	Depth for 50% root distribution (cm)	25
	Scale factor	3
Photosynthesis		
Plant response to defoliation	Effective minimum LAI (m^2 m^{-2})	0.5
Leaf photosynthesis	P_{mx} at ref conditions (µmol CO_2 $m^{-2}s^{-1}$)	20
	Minimum temp for P_{max} (°C)	12
	Optimum temp for P_{max} at ambient CO_2 (°C)	35
	Temperature curvature coefficient	1.5
CO_2 function	Value at saturating CO_2 (unitless)	1.1
	Value at double ambient CO_2 (unitless)	1.05
Canopy photosynthesis Light interception and attenuation	Light extinction coefficient	0.5
Respiration parameters	Cell wall growth efficiency (%)	85
	Protein growth efficiency (%)	55
	Maintenance coefficient (fraction day^{-1})	2.5
Nitrogen		
	N uptake coefficient: NO_3 (g N t $root^{-1}$) ppm^{-1}) day^{-1}	200
	N uptake coefficient: NH_4 (g N t $root^{-1}$) ppm^{-1}) day^{-1}	200
	Respiratory cost of NO_3 uptake (kg C kg N^{-1})	0.6
	Respiratory cost of N fixation (kg C kg N^{-1})	-
	Potential nitrogen remobilization (%)	0.5
	Minimum N fixation (%)	-

Table 2.3. Cont.

Parameter group	Parameter name	Default value for generic C_4 species
Transpiration		
	Scale factor between WP and FC for the onset of water stress	0.8
	Transpiration reduction at saturation	0.5
Grazing		
	Digestibility of live NDF under non-limiting water (%)	60
	Digestibility of dead NDF (%)	30
	Grazing selection parameter	1
	Leaf weighting parameter	1.2
	Live weighting parameter	1

Reference conditions: atmospheric CO_2 concentration, 380 ppm, air temperature, 25°C and leaf nitrogen concentration, 3%. Johnson (2008).

2.10.3 Photosynthesis submodule structure in DairyMod-SGS

Photosynthesis and respiration lie at the core of the DairyMod-SGS and act as the primary source of carbon for the whole plant system (Johnson, 2008). Generally, the submodule describes the leaf gross photosynthesis in response to photosynthetic photon flux (PPF) μmol photons, protein (leaf N) including photosynthetic enzymes, temperature and CO_2. The submodule defines the light interception and attenuation through the plant canopy with respect to the incident and diffused light and integrates the gross canopy photosynthesis. Therefore, canopy photosynthesis and canopy structure parameters interact in the model to give the gross leaf and subsequently canopy photosynthesis. Daily gross carbon assimilation is adjusted with the daily plant growth and maintenance (respiration) to calculate the net carbon assimilation of the plant canopy.

2.10.3.1 Leaf gross photosynthesis

The leaf is the single plant production unit and the photosynthesis equation in the DairyMod-SGS pasture module needs to be defined for new species with pasture-specific parameters. The rate of single leaf gross photosynthesis, P_ℓ, g µmol CO_2 (m^2 leaf)$^{-1}$s^{-1}, is described in response to the incident PPF on the leaves, I_ℓ µmol photons (m^2 leaf)$^{-1}$s^{-1}, by the non-rectangular hyperbola (Equation. 2.1) (Cannell & Thornley, 2000; Johnson et al., 2010).

$$\theta {P_\ell}^2 - (\alpha I_\ell + P_m)\, P_\ell + \alpha I_\ell P_m = 0 \qquad 2.1$$

Where

P_m = rate of single leaf gross photosynthesis at saturating PPF (µmol CO_2 (m^{-2} leaf)$^{-1}$s^{-1})

α = leaf photosynthetic efficiency (mol CO_2 (mol photons)$^{-1}$)

θ = curvature parameter (dimensionless and range $0 \le \theta \le 1$)

P_ℓ is given by the lower root of Equation 2.1, hence

$$P_\ell = \frac{1}{2\theta}\left[(\alpha I_\ell + P_m) - \{(\alpha I_\ell + P_m)^2 - 4\theta\alpha I_\ell P_m\}^{\frac{1}{2}}\right] \qquad 2.2$$

Overall, the effect of temperature, CO_2 and the leaf N level on leaf photosynthesis is denoted by the effect of rate of single leaf photosynthesis at saturating PPF (P_m) (Equation 2.2). Leaf photosynthetic efficiency (α), also depends on temperature and CO_2, although to a lesser extent than P_m (Johnson, 2008), but less evidence is available for the effect of temperature, CO_2 and N supply, or protein concentration on the θ (Johnson et al., 2010; Thornley et al., 2007). In the DairyMod-SGS pasture module, P_m associated pasture-specific parameters are important in simulating pasture growth. Therefore, temperature, light, leaf N and CO_2 responses to leaf photosynthesis need to be well understood when integrating new species into the model. In the model, plant growth responses to temperature are described by a generic empirical curve defining the minimum, optimum, and maximum temperatures for photosynthesis, based on a representative daytime temperature (Johnson, 2008). According to Johnson (2008), P_m increases from zero as the temperature gradually increases from some low value and when temperature reaches its optimum, no further increase in P_m occurs. Increasing optimum temperature reduces the P_m due to high photorespiration cost, however the rate of photosynthesis in the single leaf at saturating PPF remains stable or declines slightly in tropical pasture species. This may give an advantage to tropical pastures when competing in variable and changing climates. The rate of single leaf gross photosynthesis at saturating PPF increases as leaf N (photosynthetic enzyme concentration) increases in tropical pastures, however, tropical species show little photosynthetic response to increasing CO_2 above the ambient level (380 ppm). This combined response of temperature, CO_2 and leaf N is expressed by the following equation:

$$P_{m=}P_{m,ref}\, f_c(C)\, f_{Pm,TC}(TC)\, f_{Pm,\ N}\, (f_N) \qquad 2.3$$

Where

$f_c(C)$ = CO_2 response
$f_{Pm,TC}(TC)$ = combined response of CO_2 and temperature
$f_N\,(f_N)$ = leaf N response to the rate of photosynthesis in a single leaf at saturating PPF
$P_{m,ref}$ = estimated reference value for P_m at reference temperature (25°C), ambient CO_2 concentration (380 ppm) and reference N level (3%).

The value of P_m for generic tropical species is considered as 20 µmol mol^{-1} (Johnson, 2008).

Minimum and optimum temperatures for P_m are estimated as 12°C, and 35°C, respectively, for the generic tropical species (Johnson, 2008; Johnson et al., 2010), however, values are expected to vary between different species. Therefore, species-specific leaf photosynthesis-related parameters need to be accurately estimated for different tropical pasture species.

2.10.4 Canopy photosynthesis

The DairyMod-SGS pasture module links single-leaf photosynthesis to canopy structure parameters to determine the canopy photosynthesis, hence accurate species-specific parameters relating to canopy structure are important in expressing the net canopy carbon (C) assimilation. Canopy gross photosynthesis is simply expressed as a summation of all single-leaf photosynthesis rates in the canopy and is denoted by:

$$P_g = \int_0^L P_\ell(I_\ell)\, d\ell \qquad 2.4$$

Where

P_ℓ = rate of leaf gross photosynthesis (µmol CO_2 (m^{-2} leaf)$^{-1}$$s^{-1}$)

I_ℓ = PPF incident on the leaf (m^{-2} leaf)$^{-1}$$s^{-1}$)

L = total canopy leaf area index (m^2 leaf m^{-2} ground)

ℓ = dummy variable defines the cumulative leaf area index through the depth of the canopy.

Considering the pasture canopy structure, leaf N composition (photosynthetic enzymes) reduces with the canopy depth. The leaf N gradient is fairly linear at the top of the canopy and then curves at the bottom of the canopy. Photosynthetic photon flux incident on a leaf also varies with the canopy gradient. Considering the average PPF alone can result in overestimation of the gross canopy photosynthesis, whereas adjusting the PPF to direct and diffused components gives a more realistic value (Johnson, 2008). Therefore, the canopy gross photosynthesis equation is expressed as:

$$P_g = \int_0^L P_\ell(I_{\ell,s})e^{-k\ell}\, d\ell + \int_0^L P_\ell(I_{\ell,d})(1 - e^{-k\ell})\, d\ell \qquad 2.5$$

Where

ℓ, s = direct PPF (µmol photons (m^{-2} leaf)$^{-1}$$s^{-1}$)

$I_{\ell,d}$ = diffused PPF (µmol photons (m^{-2} leaf)$^{-1}$$s^{-1}$)

k = light extinction coefficient (unitless)

In DairyMod-SGS, the light extinction coefficient (k) is used to calculate the canopy light interception and attenuation for the canopy photosynthesis calculation. The coefficient value may vary depending on the species' growth behaviour, therefore the estimation of crop-specific k for the species is required for the parameterisation of DairyMod-SGS to predict the canopy gross photosynthesis.

Canopy gross photosynthesis (P_g) is used to estimate the daily canopy gross photosynthesis (mol CO_2 (m^{-2} ground) day^{-1}) and it is estimated as the integral of P_g throughout the day with any daily distribution of PPF and temperature determined by the location-specific climate file in the DairyMod-SGS. The equation is:

$$P_{g,day} = 0.012 \times 10^{-6} \int_0^{\tau} P_g \, dt \qquad 2.6$$

Where

t = time (s)
τ = daylight period of the day (s)

2.10.5 Daily canopy respiration

Daily canopy respiration comprises the use of synthesised C for the growth and maintenance of the plant and excludes photorespiration (Thornley & Johnson, 1990; Johnson et al., 2010). There are at least nine identified processes in which plants use energy associated with growth and maintenance (Cannell & Thornley, 2000). Among them, six quantifiable (growth, nitrate reduction, N_2 fixation, N uptake, other ion uptake and phloem loading) and three residual processes (protein turnover, maintaining cell ion concentrations/ gradients and all wastage respiration) have been identified. Many studies based on plant growth and maintenance showed that the growth and quantifiable maintenance respiration are directly or indirectly related to protein contents, suggesting that the respiration rate of leaves, stems and roots are more closely related to the Kjeldahl N contents than to their masses, volumes or areas (Johnson & Thornley, 1985). Further, maintenance respiration rates per unit N vary among plant species, tissue type and different growth rates and therefore maintenance coefficient of respiration is used in the respiration model (Cannell & Thornley, 2000).

Growth respiration is defined as the unit of C appearing in new biomass per unit of C utilized for growth (Thornley & Johnson, 1990). The DairyMod-SGS considers that growth respiration is associated with the daily assimilation of C, whereas maintenance respiration is more closely linked to plant nutrient uptake and proportional to the variation in plant protein content in response to the plant N status. According to Johnson (2008), maintenance respiration is related to plant dry weight and enzyme concentration, and is assumed to be an indicator of overall maintenance cost. Enzymic activities are influenced by the temperature in the reaction medium, hence daily maintenance respiration is given by:

$$R_{m,day} = m_{ref} \, f_m \, (T) \, \frac{f_N}{f_{N,ref}} \, W \qquad 2.7$$

Where

$f_m \, (T)$ = maintenance temperature response function at reference temperature

W = shoot mass (kg C m^{-2})

f_N = canopy N concentration kg N (kg C^{-1})

$f_{N,ref}$ = reference N concentration N (kg C^{-1})

m_{ref} = maintenance coefficient at reference N and temperature (day^{-1})

DairyMod-SGS uses a maintenance coefficient at reference N and temperature as a respiration parameter and the default value is 0.025d^{-1} / 2.5 % day^{-1}. Reference conditions for the estimation of the rate of single leaf gross photosynthesis at saturating PPF (P_m) are used for the estimation of the maintenance coefficient in the DairyMod-SGS and the value remains constant across the different pasture species.

There are different respiratory costs associated with synthesising plant cell wall and protein, and growth respiration is defined as an increase in plant structural components (Thornley & Johnson, 1990). According to the growth respiration theory, one unit of substrate utilised for growth results in Y units of plant structural material and (*1*-*Y*) units of respiration, where Y is the growth efficiency (for cell wall and protein). Hence, growth respiration R_g is given by:

$$R_g = \left(\frac{1-Y}{Y}\right)\mathrm{G} \qquad 2.8$$

Where

G = total plant growth rate

Plant composition usually comprises the cell wall, protein and sugars, if the molar concentrations are f_w, f_p, f_s respectively, and where

$$f_w + f_p + f_s = 1 \qquad 2.9$$

If the growth efficiencies for cell wall and protein are Y_w and Y_p, then overall growth efficiency is given by:

$$\frac{1-Y}{Y} = \left(\frac{1-Y_w}{Y_w}\right)f_w + \left(\frac{1-Y_p}{Y_p}\right)f_p \qquad 2.10$$

This explains the influence of growth respiration on the plant structure (cell wall and protein) and default parameter values for DairyMod-SGS Y_w and Y_p are given as 0.85 (85%) and 0.55 (55%), respectively (Johnson, 2008). According to the literature, Y_w and Y_p values are calculated using experimental data (Thornley 1970) or chemical analysis of plant material (Thornley & Johnson, 1990) and for most of vegetative plant tissues, growth efficiency ranges from 0.70–0.85. According to Cannell & Thornley (2000), equivalent values of Y_G, in units of g C in product per g C in glucose substrate are 0.85 to 1.0 for carbohydrates, 0.8 to 0.85 for lignin, 0.7 for lipids (palmitate), and 0.5 to 0.8 for proteins and nucleic acids, however, the overall C cost for vegetative plant biomass is constant (Cannell & Thornley, 2000).

2.10.6 Canopy structure submodule in DairyMod-SGS

Canopy structure parameters in the DairyMod-SGS describe the plant structure and carbon partitioning during regrowth, plant senescence, plant N composition, non-structural carbohydrate and fat, and the plant height and LAI relationship. Parameters in canopy structure provide inputs to the photosynthesis submodule and pasture growth submodule incorporating leaf area expansion and senescence. Further values for LAI as a function of plant mass, and the C partitioning between leaf and stem within the shoot, are necessary to evaluate the canopy respiration which is a function of the canopy net photosynthesis calculation (Johnson et al., 2010).

DairyMod-SGS explains plant growth with respect to the distribution of the net C assimilation through the C partitioning to shoot (leaf and stem) and root. The growth submodule considers a grass that carries three live leaves (i.e. ryegrass) and the total above-ground biomass is divided into four categories including growing leaf (W_1), first fully expanded leaf (W_2), second fully expanded leaf (W_3), and senescing leaf (W_4) (Figure 2.3). Total structural weight W_G is given by:

$$W_G = W_1 + W_2 + W_3 + W_4 \tag{2.11}$$

If the pasture storage weight is W_S, the total pasture weight is expressed as,

$$W = W_S + W_G \tag{2.12}$$

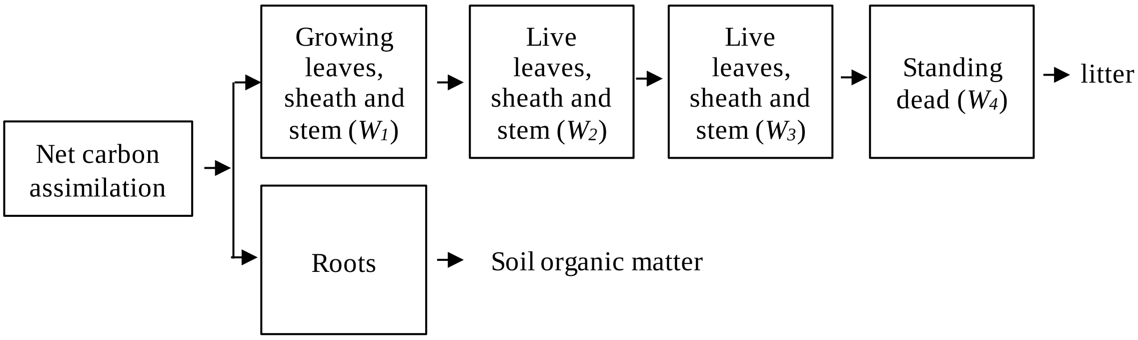

Figure 2.3. Assimilated carbon partitioning during the pasture growth in DairyMod-SGS.

2.10.7 Shoot to root partitioning

To allow plant root growth and maintenance, a fraction of the assimilated C is partitioned for shoot growth and a balance is allocated for root growth. Partitioning of C between shoot and root is affected by the water and N stress in the plant microenvironment.

Partitioning of new growth to the shoot, G_{shoot} kg C m^{-2} d^{-1} is defined as:

$$G_{shoot} = \rho_{shoot,ref}\ (\Omega_{water}\Omega_N)^{1/2}G \qquad 2.13$$

Where

Ω_{water} = water stress growth limiting factor
Ω_N = N stress growth limiting factor
G = total plant growth rate

According to Equation 2.13, both N stress and water stress decrease the shoot partitioning and increase the C allocated to root growth. The C allocation between shoot and root varies as the supply of CO_2 increases, and generally increases the root growth (Johnson, 2008). However, because changing the level of CO_2 available during a plant growth period is unrealistic, for a healthy plant growing in average atmospheric CO_2 conditions, the shoot mass is defined as a function of plant-specific leaf area (SLA), LAI, and the leaf fraction of the shoot.

Shoot mass (*W*) is defined as:

$$L = \sigma\rho\frac{W}{\varsigma} \qquad 2.14$$

Where

L = leaf area index (m^2 m^{-2})
σ = specific leaf area (m^2 kg^{-1})
ρ = leaf fraction of the shoot
ς = dry weight to mole conversion (37 mol C kg^{-1})

Therefore, root growth (G_{Root} kg C m^{-2} d^{-1}) is given by the remaining C between the total plant growth and the partitioning to shoot (Equation 2.15).

$$G_{Root} = G - G_{Shoot} \tag{2.15}$$

While CO_2 is not likely to change during plant regrowth, different plant responses have been observed due to difference in leaf age categories (number of boxes in Figure 2.3), and higher temperatures, lower light and variations in N fertiliser. DairyMod-SGS captures this plant variation through parameters of plant C partitioning to shoot and root, SLA and the leaf fraction of the shoot, all of which vary among species. Default parameters for a generic C_4 grass are 70%, 30% and 16 m^2 kg leaf dry weight^{-1}, respectively, for C partitioned to the shoot with no water or N stress, leaf fraction of new shoot growth, and SLA at reference CO_2. Therefore, when planning to use DairyMod-SGS to model new species, each of these parameters is required to be defined for the pasture species.

2.10.8 Growth dynamics

DairyMod-SGS defines the C movement through growing tissue, standing dead to litter (Figure 2.3) through a flux parameter ($\gamma\ d^{-1}$). The flux parameters for the leaves relate to the number of live leaves per tiller and the leaf appearance rate.

The flux parameter for leaves (γ_l) defined as:

$$\gamma_l = \phi \frac{Number\ of\ leaf\ age\ categories}{Number\ of\ live\ leaves\ per\ tiller} \tag{2.16}$$

Where

ϕ = leaf appearance rate (day^{-1})

The number of live leaves per tiller provides the input for the flux parameter functions, hence it needs to be parameterised for the species before integrating into the model. Generally, DairyMod-SGS values are set as 5 and 10 for the number of live leaves per tiller and minimum leaf appearance interval (days) for generic C_4 species, and this needs to be modified when introducing new species into DairyMod-SGS.

The rate of leaf appearance strongly depends on the environmental temperature, and flux parameters are expected to change with the daily temperature variation in the climate file that is uploaded into DairyMod-SGS.

Flux parameters of leaves are defined as a function of daily temperature as:

$$\gamma = f_\gamma(T)\gamma_{ref} \qquad 2.17$$

Where

$f_\gamma(T)$ follows the temperature function on DairyMod-SGS.

DairyMod-SGS uses two types of temperature models, one of which deals without optimum temperature (Q_{10} model) and another more complex model with optimum temperature included (Johnson & Thornley, 1985; Thornley et al., 2007). These models are linked with the mass flux of plant leaves through leaf appearance response to the parameters, minimum and maximum temperature and curvature coefficient.

According to the studies of Thornley (1998) and Thornley et al. (2007), the empirical temperature response function is given by:

$$f_T(T) = \left(\frac{T-T_{mn}}{T_r-T_{mn}}\right)^q \left(\frac{T_{mx}-T}{T_{mx}-T_r}\right) \qquad 2.18$$

Where

T_{mn} = minimum temperature (°C)
T_{mx} = maximum temperature (°C)
T_r = reference temperature (°C)
q = curvature coefficient (unitless)

The optimum temperature is given by:

$$T_{opt} = \frac{T_{mn}+qT_{mx}}{1+q} \qquad 2.19$$

Where T_{mx} is given by:

$$T_{mx} = \frac{(1+q)\,T_{opt} - T_{mn}}{q} \qquad 2.20$$

For the generic C$_4$ species, DairyMod-SGS describes the minimum and maximum temperature as 10°C and 25°C, respectively, whereas the curvature coefficient is 2. According to Johnson (2008), q is in the range of 2 to 3. According to Pequeno et al. (2014), base and optimum cardinal temperatures for perennial pasture grasses at the vegetative stage can be varied even within the same species. Therefore, new species introduced to DairyMod-SGS need to be defined through their specific minimum and maximum temperatures to fit with the temperature function, and growth dynamics need to be calculated using leaf flux parameters.

2.10.9 Canopy height and leaf area index function in DairyMod-SGS

Canopy height and LAI are linked with the theory of canopy light interception and attenuation (Johnson, 1989), in which DairyMod-SGS uses the canopy height and LAI relationship to calculate the light interception for species in a mixed stand where canopies are not uniform (Johnson, 2008). According to the photosynthetic function (Equation 2.2) in DairyMod-SGS, first, light interception and irradiance on a leaf within the canopy are calculated according to Beer’s law, and the leaf photosynthetic rate is obtained as a function of irradiance. Subsequently, LAI is integrated with the leaf photosynthetic rate to calculate the canopy photosynthesis. If the pasture is growing in a mixed stand, canopy height and LAI relationship explain the light interception on the canopy leaves (Johnson, 1989).

According to the non-rectangular hyperbola discussed by Johnson (1989), LAI and height are given as:

$$h = \frac{1}{2\xi}\left[\alpha L + h_m - \{(\alpha L + h_m)^2 - 4\alpha\xi h_m L\}^{1/2}\right] \qquad 2.21$$

where

L = leaf area index (m^2 leaf ground m^{-2})
h = height (cm)
α = initial slope of the response (unitless)
h_m = maximum canopy height (cm)
ξ = curvature parameter (0.9)

Further, L and h are given by:

$$\alpha = h_m \frac{(2-\xi)}{2L_{half}} \qquad 2.22$$

Where

L_{half} = half maximum height (cm)

Maximum height (L) and as a result the half-maximum height (L_{half}) are likely to vary significantly among species, especially tropical pastures, hence DairyMod-SGS need to be defined with pasture-specific parameters.

2.10.10 Root distribution function in DairyMod-SGS

DairyMod-SGS requires the root distribution parameters for species and gives inputs for the calculations of water, nutrient uptake and soil organic matter (Johnson, 2008). According to Gerwitz & Page (1974), root distribution is described using an exponential equation (Equation 2.23).

DairyMod-SGS describes the relative distribution of roots as:

$$f_r\,(Z) = \frac{1}{1+\left(\frac{Z}{d_{r,h}}\right)^{q_r}} \qquad 2.23$$

Where

$d_{r,h}$ = depth of 50% relative root mass (cm)
q_r = scaling parameter (unitless)

By default, DairyMod-SGS has added greater root depth (100 cm) for generic C_4 species, and the depth for 50% relative root mass, and the scaling factor, are presumed to be 25 cm and 3, respectively (Johnson, 2008). These parameters also have to be updated with respect to any new species introduced into the model.

2.10.11 Calibration of parameters in DairyMod-SGS pasture module

All parameters in pasture models are difficult to estimate. Some of the parameters are poorly known and rarely available in the literature, and this is also the case for DairyMod-SGS. Therefore, model calibration is an essential step in pasture modelling where these parameters are estimated through fitting the model data to observed data (Soetaert & Petzoldt, 2010). This process is also known as inverse modelling. In literature, many methods are available to use for pasture model calibration, such as trial and error (Wallach et al., 2001), genetic algorithms (West & Wilcox, 1997; Baldi et al., 1998), and simulated annealing (Vanier & Bower, 1996; Baldi et al., 1998). The trial and error method is commonly practiced and has been previously used for DairyMod-SGS by Cullen (2008), however, this process is difficult when the model contains multiple parameters and has a high degree of parameter interactions (Jones et al., 2015). Furthermore, the trial and error method is difficult to replicate (Wallach et al., 2001). The automatic calibration process is more practicable, however, DairyMod-SGS has no automatic calibration method (Johnson, 2008). Given the circumstances, the fitted generic parameters for tropical pastures in DairyMod-SGS can be used as the starting point to calibrate the parameters by optimising the goodness-of-fit criterion for field measured data.

2.10.12 Evaluation of DairyMod-SGS performance

A combination of both statistical indexes and graphical presentations have been extensively used in modelling studies to evaluate the performance of models with respect to measured data (Tedeschi, 2006). Graphical representation provides a general overview of the model performance and behaviour over time. Graphs of observed vs modelled scatter plots, time series plots, and Blend-Altman plot (Cullen, 2008) are commonly used to visualize the modelled and measured data. In addition, quantitative assessment of the model can be achieved through a combination of statistical indexes. One statistical index measures only one aspect of model error (Chai & Draxler, 2014), therefore modelled (E) and measured (O) data are commonly compared to a range of statistical indexes.

The different statistical indexes (Tedeschi, 2006) are:

a) Mean observed and modelled weights.

b) Linear regression and coefficient of determination (R^2).

Observed and modelled values of each variable are subjected to linear regression analysis followed by the determination of R^2. The model precision is classified as unsatisfactory ($R^2 \leq 0.6$), satisfactory ($R^2 > 0.6$ to ≤ 0.7) good ($R^2 > 0.7$ to ≤ 0.8) and very good ($R^2 > 0.8$).

c) Per cent Bias (PB)

Per cent bias (PB) measures the average tendency of the modelled values to be larger or smaller than their observed ones (Equation 2.24). The optimal value of PB is 0.0, with low-magnitude values indicating accurate model simulation. Positive values indicate overestimation bias, whereas negative values indicate model underestimation bias. The equation used is:

$$PB = 100\ \frac{\sum_{i=1}^{n}(Ei-Oi)}{\sum_{i=1}^{n}Oi} \qquad 2.24$$

d) Nash-Sutcliffe Efficiency (NSE)

The NSE is interpreted as the proportion of variation explained by the fitted line Y = X (Equation 2.25). The NSE equals one when the observed and modelled values are in perfect agreement. The lower bound is negative infinity and if the NSE is negative, the modelled values are worse than the observed mean.

The equation used is:

$$NSE = 1 - \frac{\sum_{i=1}^{n} (O_i - f\ (E_{1,\ldots} E_p)i)^2}{\sum_{i=1}^{n} (O_i - \bar{O})^2} \qquad 2.25$$

e) Mean Absolute Error (MAE)

Mean absolute error measures the accuracy of continuous data. The MAE varies from zero to infinity, with zero representing the perfect fitness of modelled and observed data. The MAE is given by:

$$MAE = \left(\frac{1}{n}\right) \sum_{i=1}^{n} |E_i - O_i| \qquad 2.26$$

f) Root Mean Square Error (RMSE)

Root mean squared error is the square root of the mean of the square of all of the error (Equation 2.27). It shows how far the modelled values fall from the measured data. The RMSE value with zero indicates that the model has a perfect fit. The lower the RMSE, the better the agreement between modelled and measured data.

$$RMSE = \sqrt{\left[\left(\frac{1}{n}\right) \sum_{i=1}^{n} (O_i - E_i)^2\right]} \qquad 2.27$$

2.11 Summary of the knowledge gap

Dairy production in the tropics is comparatively lower than in temperate regions due to a range of factors including low-quality pastures, inadequate pasture supply, and large seasonal variation in both yield and quality of forages. The introduction of improved pastures along with intensified tropical pasture management offer substantial potential to increase dairy production in the tropics through better quality pastures, improved total yield, and reduced pasture yield variability. However, there is little information available comparing the nutritive value parameters of improved tropical pastures, and no comprehensive evaluation of their physiological, agronomic, and nutritive characteristics. Furthermore, unlike temperate pasture-based dairy systems, there are a lack of tools to assess the performance of potential pasture species under varying edaphic conditions and management.

To address these knowledge gaps, this thesis focused on investigating improved tropical pasture species in terms of nutritive, physiological, and agronomic parameters. The findings were then utilised to parameterise DairyMod-SGS, a dedicated pasture model that was subsequently used to explore the potential performance of improved tropical pasture species under diverse soil, climate, and management scenarios via a simulation and modelling approach.

Chapter 3

Comparison of nutritive value of tropical pasture species grown in different environments, and implications for livestock methane production: A meta-analysis

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Abstract

The demand for dairy products is ever increasing across the world. The livestock sector is a significant source of greenhouse gas (GHG) emissions globally. The availability of high-quality pasture is a key requirement to increase the productivity of dairy cows as well as manage enteric methane emissions. Warm-season perennial grasses are the dominant forages in tropical and subtropical regions, and thus exploring their nutritive characteristics is imperative in the effort to improve dairy productivity. Therefore, we have collated a database containing a total of 4750 records, with 1277 measurements of nutritive values representing 56 tropical pasture species and hybrid cultivars grown in 26 different locations in 16 countries; this was done in order to compare the nutritive values and GHG production across different forage species, climatic zones, and defoliation management regimes. Average edaphoclimatic (with minimum and maximum values) conditions for tropical pasture species growing environments were characterized as 22.5 °C temperature (range 17.5–29.3°C), 1253.9 mm rainfall (range 104.5–3390.0 mm), 582.6 m elevation (range 15–2393 m), and a soil pH of 5.6 (range 4.6–7.0). The data revealed spatial variability in nutritive metrics across bioclimatic zones and between and within species. The ranges of these nutrients were as follows: neutral detergent fibre (NDF) 50.9–79.8%, acid detergent fibre (ADF) 24.7–57.4%, crude protein (CP) 2.1–21.1%, dry matter (DM) digestibility 30.2–70.1%, metabolisable energy (ME) 3.4–9.7 MJ kg^{-1} DM, with methane (CH_4) production at 132.9–133.3 g animal^{-1} day^{-1}. The arid/dry zone recorded the highest DM yield, with decreased CP and high fibre components and minerals. Furthermore, the data revealed that climate, defoliation frequency and intensity, in addition to their interactions, have a significant effect on tropical pasture nutritive values and CH_4 production. Overall, hybrid and newer tropical cultivars performed well across different climates, with small variations in herbage quality. The current study revealed important factors that affect pasture nutritive values and CH_4 emissions, with the potential for improving tropical forage through the selection and management of pasture species.

Keywords: dairying; grasses; methane; meta-analysis; tropical pasture; quality

3.1 Introduction

Demand for dairy products is ever-increasing across the world; however, the livestock sector is a significant source of global greenhouse gas (GHG) emissions (Opio et al., 2013). Forage plants provide feed for an estimated 1.5 billion cattle and 0.2 billion buffalo around the world, supplying humans with our daily protein requirements (FAOSTAT, 2018). Approximately 47% of global milk comes from tropical and subtropical regions (Gerber et al., 2013). Due to increasing populations in developing countries, global food production needs to substantially increase in the future; the demand is expected to nearly double by 2050 (Thornton, 2010). Parallel to the expansion of food production, GHG emissions have climbed; anthropogenic emissions account for a substantial proportion (58%) of these global emissions (EPA, 2011), with 18% (5.0–5.8 Gt CO_2eq yr^{-1}) of that generated by agriculture (Smith et al., 2014), contributing 25% of methane (CH_4) production from the enteric fermentation of ruminants (Thornton, 2010). Dairy production in tropical regions is often lower than in temperate regions, due to a range of factors including the lower nutritive value of forage grasses, lack of access to inorganic nitrogen (N) fertiliser, infertile soils, and adverse climatic conditions (Thornton et al., 2011). Mostly tropical cattle are fed a diet that is based essentially on pasture species that generally have low nutritive value, with large seasonal variations in quantity and quality (Boval et al., 2015), However, nutrient intensification through planting improved forage options (Capstaff & Miller, 2018), in addition to adopting appropriate harvesting, fertilizing, and grazing practices (Paul et al., 2020), have substantially improved the nutritive value of tropical pastures.

The largest differences in nutritive values of herbage have been observed among different groups of forages (grasses and legumes, tropical and temperate species), but there are still substantial differences between species and even between different cultivars within a species (Boga & Ayasan, 2022). Improving dairy cattle nutrition through adequate feeding of quality forage, and choice of appropriate herbage species and cultivars depends on the adaptability of selected species to the farm environment and the resulting balance between quantity and quality (Boga & Ayasan, 2022). However, a paucity of data that compares the nutritive values of tropical pastures grown across different environments limits the selection of forages for livestock. Therefore, gauging the performances of different pasture species and cultivars across different environments aids in identifying different spatial and temporal niches that are suitable for growing tropical pastures, in order to improve dairy cattle nutrition and lower GHG emissions in the tropics.

The age of the plants at their time of utilisation (by grazing or cutting) is an important aspect to consider in tropical pasture production, as this significantly affects their yield and chemical composition, which consequently affects milk production (Congio et al., 2018). While dry matter (DM) production significantly increases with maturity, the digestibility, and the crude protein (CP) content both rapidly decline with advancing plant maturity (Inyang et al., 2010; Da Silva et al., 2020). Although forage maturity reduces its nutritive value, environmental and agronomic management factors can alter the relationship between plant maturity and forage nutritive value (Da Silva et al., 2020; Moyo & Nsahlai, 2021). Herbage accumulation and the nutritive value of grasses are both strongly affected by management factors, such as defoliation (grazing and cutting) frequency and intensity, and the application of N fertiliser (amount and frequency) (Woodard & Sollenberger, 2011; Pontes et al., 2017). Sward characteristics are highly sensitive to environmental conditions such as rainfall, air temperature, and incident solar radiation (Gastal & Lemaire, 2015). Therefore, herbage nutritive value might vary considerably in plants harvested at the same stage of maturity, if they are grown in different environments. Variable environmental conditions (e.g., increased temperature, low precipitation) can induce physiological and phenological changes in plants to delay or hasten anthesis, which is associated with greater stem production (increased stem: leaf ratio) (Gardarin et al., 2014; Kering et al., 2011), leading to variations in nutritive value. Therefore, systematically assessing the nutritive values of various tropical pasture species in relation to the growing conditions and agronomic management approaches (defoliation frequency and intensity) across different climates allows some of these interactions to be identified; in turn, this information can provide a basis to explore options for the intensification of tropical livestock production systems.

In addition to increasing milk production, improving the nutritive value of tropical pasture species may also have environmental co-benefits in terms of reducing GHG emissions (Paul et al., 2020). Forages generally have enhanced nutritive value for livestock if they contain a greater proportion of readily fermentable components, such as sugars, organic acids, and proteins, as well as a lower proportion of fibre (Hoskin & Gee, 2004). The chemical composition and morphology of pasture species determine their preference and subsequently influence the feed intake, the efficiency of rumination, the rates of weight gain, the quality and volume of milk produced, and the reproductive performance of grazing ruminants (Herrero et al., 2015); moreover, the chemical composition and morphology of pasture species may also change the environmental footprint of livestock products in terms of CH_4 emissions. Increased pasture nutritive value can reduce CH_4 emissions by 5% with increasing total tract neutral detergent fibre digestibility (NDFD) (Knapp et al., 2014), and this also is expected to increase the production of volatile fatty acids (VFA), thereby increasing milk production (Knapp et al., 2014). Furthermore, better nutritive values of herbages increase the DM intake (DMI) and subsequently decrease CH_4 emissions by 2–6% for each kilogram of increased DMI (Knapp et al., 2014).

Despite the array of individual studies conducted that relate to tropical pasture production and nutritive value assessment, no study has accessed the multiple nutritive metrics of commonly cultivated tropical pasture species and newer cultivars in different agroclimatic conditions under varying defoliation management regimes (frequency and intensity). Further, subsequent effects of nutritive value on possible CH_4 emissions have not been well elucidated. Therefore, this meta-analysis aimed at the following: (i) to compare the nutritive value variation between tropical pasture species grown in different bioclimatic environments with implications for subsequent CH_4 production from dairy cows; and (ii) to evaluate the effect of defoliation interval, intensity, and bioclimate on nutritive values and CH_4 emissions using a georeferenced tropical pasture nutritive metrics database.

3.2 Materials and methods

3.2.1 Data collection

We constructed a georeferenced database from the tropical forage experimental data. Experiments that were included were identified by systematically searching the available literature on the Discover, Web of Science, Scopus, and Google Scholar databases from 15 March–20 April 2021. Initial search terms used were ‘defoliation’, ‘harvesting time’, ‘cutting interval’, ‘methane gas’, ‘CH_4 gas’, and ‘emission’, combined with ‘tropical pasture’, ‘pasture quality’, and ‘nutritive value’. The searched articles were included in the database (Supplementary Table 3.1) if the nutritive value or chemical composition had been analysed for a specific tropical grass species, or for those that were hybrid grown and tested under field conditions at a defined location and harvested more than once. This meta-analysis did not intend to explore tropical legumes, herbs, and cereal grasses;

therefore, such articles were excluded. All experiments that tested in climate-controlled environments (e.g., glasshouses) were also excluded from the database.

Collated articles were closely scrutinized based on important descriptive statistics, in order to be considered as data input for the analysis. Experimental, site-specific geospatial data (latitude, longitude, altitude, mean sea level (MSL)), as well as climate parameters (mean annual temperature (MAT) and mean annual rainfall (MAR)), were also recorded where available. Google Earth Pro Version 7.3.1 (Google Inc, California, USA) was used to supplement missing geospatial data for certain locations. Similarly, missing climate variables were obtained from the NASA POWER data access viewer (https://power.larc.nasa.gov (accessed on 22 April 2021) by generating agroclimatology files. Site-specific climate data were used with criteria in the Koppen–Geiger climate classification (Kottek et al., 2006), in order to identify the climatic types for each experimental location. Soil physical properties such as soil type and soil pH were also included, where possible, in order to describe the experimental site. All species and hybrids were designated with unique codes; in addition, for each grass species, defoliation frequency and nutritive value metrics were assigned to a new row as a treatment in the database. Defoliation frequency was recorded in days for each defoliation event. In total, 35 individual studies consisting of 294 treatments were included in the database (Supplementary Table 3.1).

The dry matter yield of the pasture species was recorded in units of t ha^{-1}year^{-1}. Organic matter (OM) and forage nutritive values (CP, acid detergent fibre (ADF), NDF, and acid detergent lignin (ADL)) were included if analysed by either the Association of Official Agricultural Chemists (AOAC, 1975) or by near-infrared spectroscopy (NIRS) methods and recorded as either percentages of DM or g kg^{-1}. Wherever forage CP was analysed using wet chemistry and expressed as N content, CP was estimated by multiplying the determined nitrogen (N) content by 6.25. Tropical forage digestibility metrics (DM digestibility (DMD) and OM digestibility (OMD)) were included in the database if they were estimated using *in vivo*, *in vitro* or NIRS techniques, and if forage energy values (MJ kg^{-1} DM) were expressed in terms of metabolisable energy (ME)(Moran, 2005) .

3.2 Data processing and analyses

The metabolisable energy (Moran, 2005) and OMD (Benaouda et al., 2020) of each tropical pasture were estimated using the following equations:

$$\mathrm{ME} = (0.16 \times \mathrm{OMD}) - 1.8 \tag{3.1}$$

$$\mathrm{OMD}\ (\%) = 3.802 + 0.97051 \times \mathrm{DMD}\ (\%) \tag{3.2}$$

Methane gas (g CH_4 animal^{-1} day^{-1}) was estimated using the NDF and DMI in the database for tropical pasture species using a published relationship (Equation 3.3). This selected equation that follows was a product of a meta-analysis (Benaouda et al., 2020) where the database consisted mainly of tropical pastures fed to cattle in tropical regions:

$$CH_4\ (\mathrm{g}\ CH_4\ \mathrm{animal}^{-1}\ \mathrm{day}^{-1}) = 17.0\ (\pm 0.99) \times \mathrm{DMI} + 0.03\ (\pm 0.01) \times \mathrm{NDF} \tag{3.3}$$

According to the meta-analysis of Lee et al. (2017), the average DMI of tropical cattle was assumed to be 7.7 kg day^{-1} (Patra, 2017).

Nutritive value parameters and CH_4 production were descriptively analysed and correlated with the frequency of defoliation.

Following data processing, weighted, restricted maximum likelihood linear mixed-effects (LME) models were fitted (Bates et al., 2015), as shown below, in order to determine the nutritive value and CH_4 production variation between bioclimatic zones as well as the effects of environmental and management determinants:

$$Y_{ij} = B_0 + b_0 + B_1 \times\ 1ij\ + b_1 \times_{1ij}\ +\ B_2\ \times_{2ij}\ + \ldots\ldots + B_p\, X_{pij} + e_{ij} \tag{3.4}$$

where Y_{ij} represents the nutritive value parameters and CH_4 in the i^{th} treatment of the j^{th} study; B_0, $B_1 \times_{1ij}$,$B_2 \times_{2ij}$…., $B_p X_{pij}$ are the fixed effects (intercept and effects of independent variables); b_0 (intercept) and b_1(slope) are the random study effects (i = 1…. n treatments and j = 1…. n studies); and e_{ij} is the sampling error.

Model fitting was carried out by including nutritive metrics and CH_4 as response variables with multiple potential explanatory variables and their interactions. Defoliation frequency and defoliation intensity, along with the climatic type, were added as fixed effects. Different cultivars from the same site were recorded in the database and were repeatedly measured for the same nutritive metrics; therefore, when defining random effect, observations (treatment) were nested within cultivars, and different cultivars in the same study were nested within the study (site) in the LME model. Furthermore, mean annual rainfall, mean annual temperature, and mean sea level were added as covariates. Soil pH and soil type were shown to have no significant relationships ($p > 0.05$) with nutritive metrics and CH_4; thus, these variables were not considered in the initial LME model. All the data were analysed using R (version 4.0.5) statistical computing software (RCoreTeam, 2021).

3.3 Results

3.3.1 Description of the analytical database

The database contained a total of 4750 records, with 1277 measurements of nutritive value parameters representing 56 tropical pasture species and hybrid cultivars grown in 26 different tropical environments in 16 countries (Figure 3.1). In some studies, not all of the chosen variables were reported; therefore, the number of observations was not uniform (Table 3.1). According to the collated data, tropical forage growing environments were characterized as 22.5°C MAT (range 17.5–29.3°C), 1253.9 mm MAR (range 104.5–3390.0 mm), 582.6 m MSL (range 15–2393 m), and 5.6 (range 4.6–7.0) mean soil pH.

Crude protein was the most commonly measured nutritive value (in 83% of the records), followed by NDF (70%), and ADF (67%). Acid detergent lignin was the least measured metric (15%), followed by OM (19%). According to the database of the present study, records were the most numerous from the tropical/equatorial bioclimatic zone, comprising 55% of the data set, compared with 36% from the warm temperate and 9% from the arid/dry bioclimatic zones. Multiple nutritive metrics contained in tropical/equatorial bioclimatic zone studies contributed to the largest total number of measurements in the database. Interestingly, the genus *Brachiaria* was the most commonly reported (34%) tropical pasture, followed by *Cynodon* (19%), and *Pennisetum* (16%). Within the genus, *Brachiaria* Mulato II was the most popular cultivar (20%). Descriptive statistics of key variables across all types of tropical pasture species are summarised in Table 3.1. There were large differences between minimum and maximum values (see Table 3.1) in the data set for climate (MAT, MAR, MSL), defoliation frequency (days), DM yield, and nutritive values (CP, ADF, DMD, OMD, and ME).

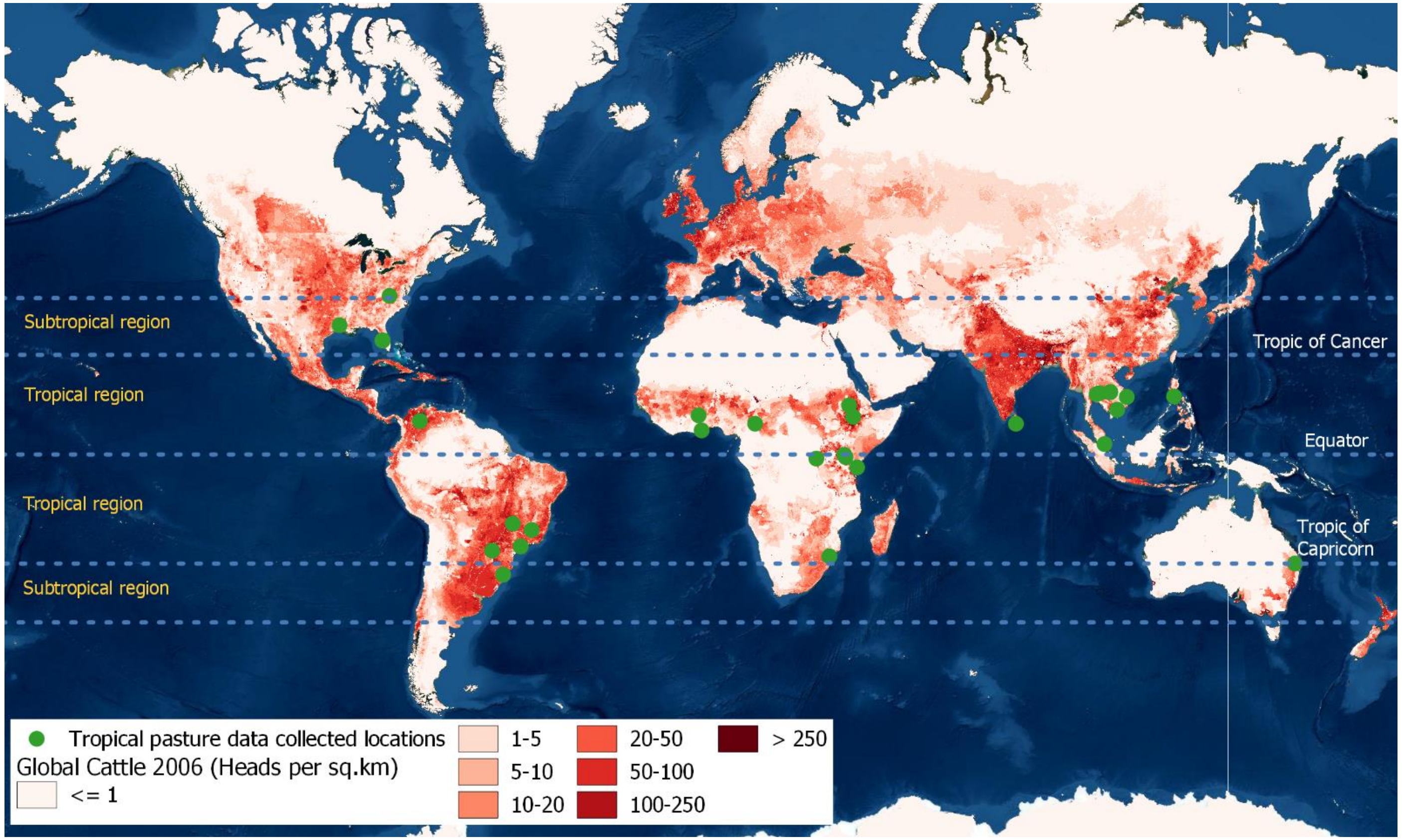

Figure 3.1. Spatial distribution of the tropical pasture data. Base map: global cattle distribution using the Gridded Livestock of the World 2 global distribution (Gilbert et al., 2018) derived from ArcGIS Pro 2.8.6 (ESRI, California, USA) (ESRI, 2021).

Table 3.1. Descriptive statistics of key variables.

Item	*n*	Mean	SD	Minimum	Maximum
Climate					
MAT (°C)	294	22.8	3.45	17.5	29.30
MAR (mm)	294	1229.5	603.57	104.5	3390.0
MSL (m)	294	516.2	627.61	15.0	2393.0
Defoliation frequency (days)	294	59.51	35.68	14.0	180.0
Defoliation intensity (mm)	285	100.1	50.36	40.0	200.0
Forage yield (DM t ha^{-1})	188	7.84	6.75	0.33	46.01
Nutritive metrics (DM)					
NDF (%)	186	67.32	5.73	50.91	79.80
ADF (%)	160	38.85	5.86	24.70	57.44
ADL (%)	30	5.69	1.42	2.83	8.20
Ash (%)	88	8.75	3.18	4.40	15.20
CP (%)	254	10.97	4.08	2.11	21.10
DMD (%)	49	56.01	7.13	30.20	70.10
OMD (%)	145	57.99	7.30	33.11	72.20
ME (MJkg^{-1} DM)	136	7.41	1.16	3.50	9.75
OM (gkg^{-1})	43	894.1	81.93	590.00	957.00
CH_4 production					
$^1CH_4$ (g CH_4 animal^{-1} day^{-1})	186	132.92	0.17	132.43	133.30

(*n* = number of records, MAT = mean annual temperature, MAR = mean annual rainfall, MSL = mean sea level, CP = crude protein, ADF = acid detergent fibre, NDF = neutral detergent fibre, minerals, OMD = organic matter digestibility, ME = metabolisable energy. ^{1}Methane gas production was estimated using CH_4 (g CH_4 animal^{-1} day^{-1}) = 17.0 (±0.99) × dry matter intake + 0.03 (±0.01) × neutral detergent fibre.

3.3.2 Comparisons of the nutritive values

Nutritive values across all tropical pasture species are summarised (Supplementary Table 3.2), and ascending median values of main nutritive value components (CP and ME) and CH_4 production are presented in Figure 3.2, Figure 3.3, and Figure 3.4, respectively. There were substantial variations in nutritive values both within and between species in different environments.

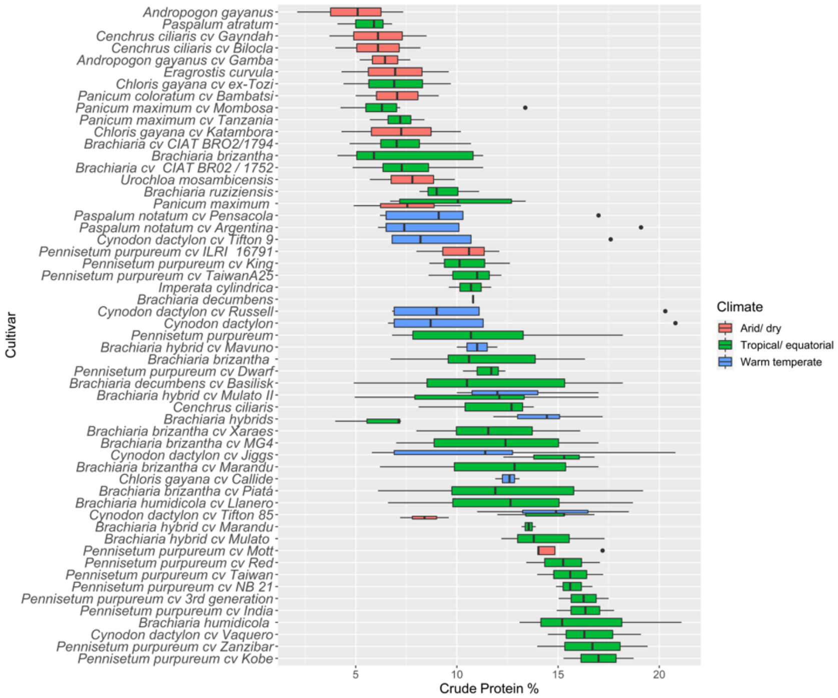

Figure 3.2. Ascending median values of crude protein (% DM) in tropical pasture species and cultivars grown in different environments.

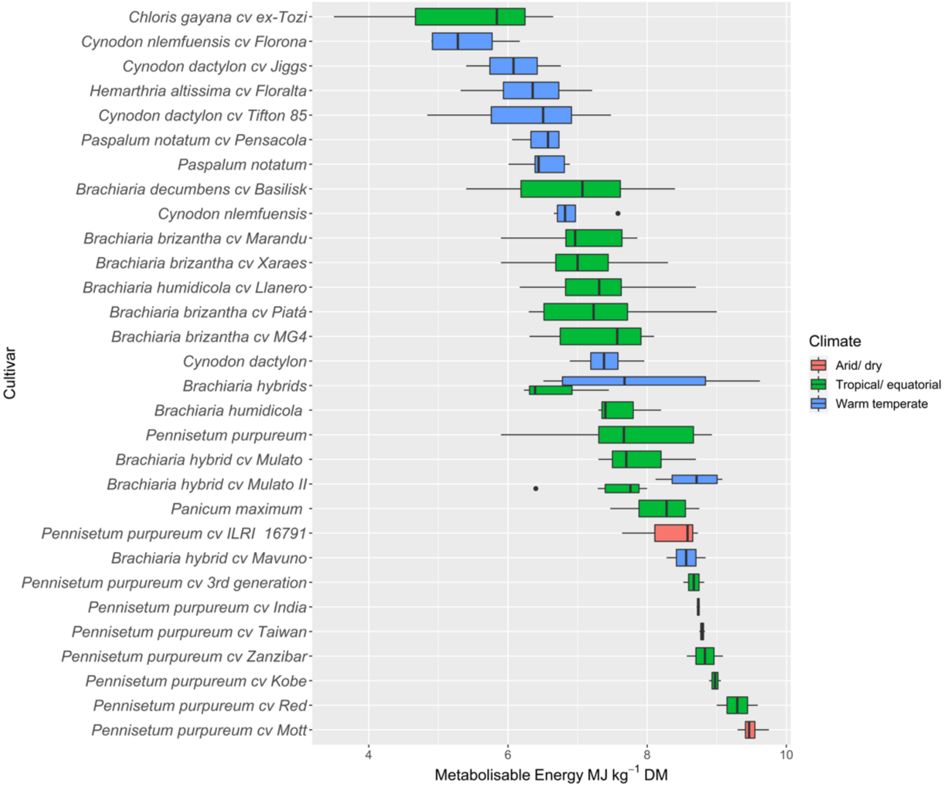

Figure 3.3. Ascending median values of metabolisable energy (MJ kg^{-1} DM) in tropical pasture species and cultivars grown in contrasting environments.

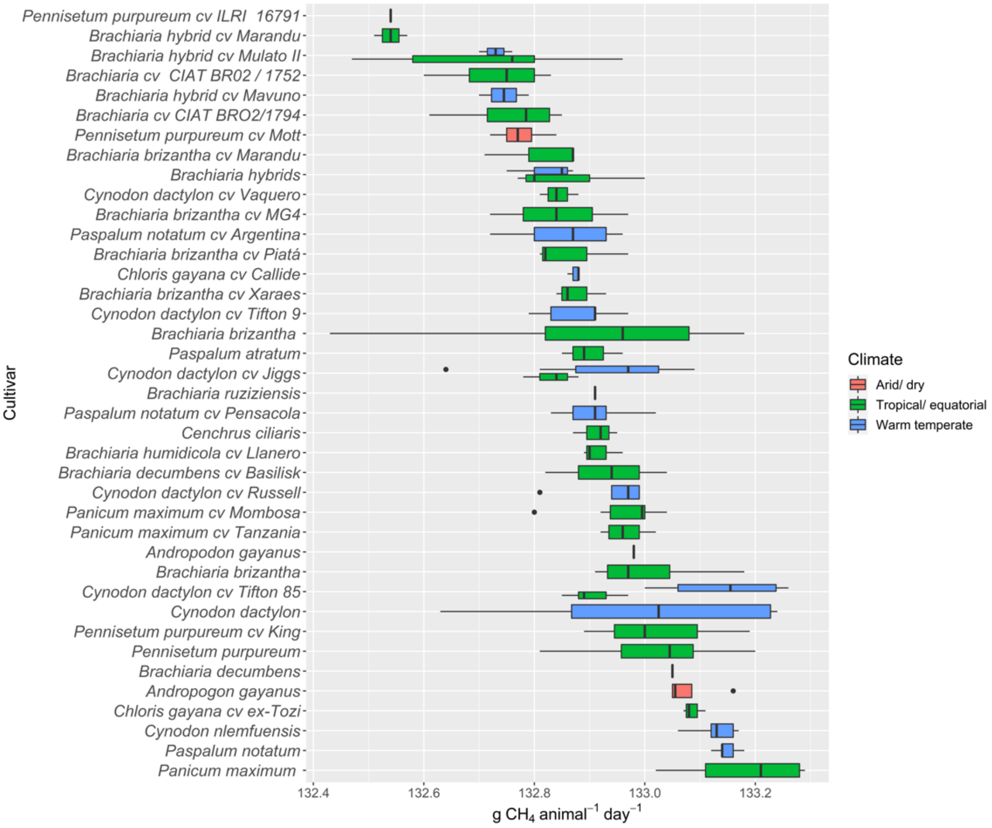

Figure 3.4. Ascending median values of estimated methane production (g CH$_4$ animal^{-1} day^{-1}) in tropical pasture species and cultivars grown in contrasting environments. Methane gas production was estimated using CH$_4$ (g CH$_4$ animal^{-1} day^{-1}) = 17.0 (±0.99) × dry matter intake + 0.03 (±0.01) × neutral detergent fibre.

3.3.2.1 Crude protein

The largest absolute CP values were recorded from the grasses *Pennisetum purpureum* cv. Kobe at 17%, *Pennisetum purpureum* cv. Zanzibar at 16.7%, and *Brachiaria humidicola* at 16.4%. Minimum average CP values were measured for *Andropogon gayanus* at 4.6%, *Chloris gayana* cv. ex-Tozi at 7%, and *Panicum maximum* cv. Mombosa at 7.1%, across all growing environments. Among all tropical pasture species, *Pennisetum* species reported greater mean CP percentages, followed by *Brachiaria*; in contrast, *Paspalum* and *Panicum* species had lower CP values. Between species, *Brachiaria* (7.36–16.4%) and *Pennisetum* (10.2–17%) recorded the largest ranges of CP values; within species, *Brachiaria* had higher variations.

3.3.2.2 Fibre

Fibre components of the tropical pasture species were recorded in terms of NDF and ADF percentages. There were substantial variations in NDF values between and within species (see Supplementary Table 3.2). The highest NDF values were recorded from *Panicum* with a maximum of 76.2%, *Paspalum notatum* at 74.9%, and *Cynodon dactylon* cv. Tifton 85 at 74.7%. The minimum values for NDF were recorded for the *Pennisetum* and *Brachiaria* species, where *Pennisetum purpureum cv ILRI* 16791 and *Brachiaria* cv. CIAT BR02/1752 had mean NDF values of 54.7% and 61.3%, respectively; both *Brachiaria hybrid* cv. Mavuno and *Brachiaria* Mulato II consisted of 61.5% NDF. For ADF, maximum values were measured for *Chloris gayana* cv. ex-Tozi at 48.1%, *Brachiaria brizantha* at 47%, and *Panicum maximum* at 45.9%. *Cynodon dactylon*, *Cynodon nlemfuensis*, and *Brachiaria* cv. CIAT BRO2/1794 accounted for the lowest ADF values at 31%, 32.8%, and 33.1%, respectively. Within and between species, all ADF values were below 50%, and the majority ranged between 30 and 45%, whereas the majority of NDF values ranged between 60 and 70%. Within species, *Brachiaria* had a substantial variation of ADF and NDF at 33.1–47% and 61.5–71.7%, respectively.

3.3.2.3 Digestibility

The mean digestibility of the tropical grasses was reportedly 57.9%. Comparatively higher OMDs were recorded for *Pennisetum purpureum*, with the cultivar *Pennisetum purpureum* cv. Red having the greatest absolute OMD at 69.3% across all reported tropical pasture species. The organic matter digestibility of *Brachiaria brizantha* followed that of *Pennisetum purpureum*. *Brachiaria* recorded an average of 58.1% OMD for all *Brachiaria* species and ranged between 61.9 and 54.6%. Across the genus *Brachiaria*, *Brachiaria hybrid* cv. Mavuno and *Brachiaria Mulato II* had greater digestibilities at 64.75% and 61.2%, respectively. The minimum average OMDs were measured for the *Chloris gayana* cv. ex-Tozi, *Cynodon nlemfuensis* cv. Florona, and *Cynodon dactylon* cv. Jiggs varieties at 44.1%, 45%, and 49.2%, respectively. Interestingly, 73.3% of tropical pasture species from the database had OMDs that were greater than 55%, and all species were improved hybrid varieties of standard tropical pastures.

3.3.2.4 Metabolisable energy

The metabolisable energy of tropical pasture species in the database ranged between 5.4–9.3 MJkg^{-1} DM at a mean ME of 7.4 MJ kg^{-1} DM. Between species, the maximum absolute ME values were measured for the *Pennisetum purpureum* cultivars, consisting of a mean ME of 8.6 MJkg^{-1} DM that ranged between 7.7 and 9.3 MJ kg^{-1} DM, followed by *Brachiaria brizantha* at a mean ME of 7.5 MJ kg^{-1} DM. The metabolisable energy level for *Brachiaria brizantha* ranged between 6.9–8.1 MJ kg^{-1} DM for *Brachiaria decumbens* cv. Basilisk and Mulato II, respectively. Between and within species, *Chloris gayana* cv. ex-Tozi and *Cynodon nlemfuensis* cv. Florona had the lowest MEs at 5.3 MJ kg^{-1} DM and 5.4 MJ kg^{-1} DM, respectively.

3.3.2.5 Methane gas

Estimated enteric CH_4 emissions (g CH_4 animal^{-1} day^{-1}) of tropical pasture species are presented in Figure 3.4. Results did not show a substantial variation in CH_4 emissions between and within species. Between different tropical pasture species, *Panicum maximum* at 133.19, *Paspalum notatum* at 133.15, and *Cynodon dactylon* cv. Tifton *85* at 133.14 g CH_4 animal^{-1} day^{-1} had the maximum estimated enteric CH_4 emissions. The minimum values for the estimated CH_4 were recorded for the *Pennisetum* and *Brachiaria* species, where *Pennisetum purpureum* cv. ILRI 16791 and *Brachiaria* cv. CIAT BR02 1752 recorded mean values of 132.5 and 132.7 g CH_4 animal^{-1} day^{-1}, respectively.

3.3.3 Bioclimatic variations in nutritive metrics

The nutritive values across a range of tropical pasture species are presented in Table 3.2, for three different bioclimatic zones (arid/dry, tropical/equatorial, and warm temperate). Greater mean DM yields were reported for the arid/dry zone, followed by the tropical/equatorial zone at 17.5 t ha^{-1} and 10.3 t ha^{-1}, respectively, while DM yield in the warm temperate zone averaged only 4.0 t ha^{-1}. All nutritive metrics except NDF, digestibility, ADL, and CH_4 showed significant differences between bioclimatic zones. Higher CP values were found in tropical pasture species grown in the warm temperate zone, and values were lower in warmer regions (arid and tropical). The highest mean ADF was reported for the tropical/equatorial zone followed by the arid/dry zone, whereas NDF did not significantly vary ($p > 0.05$) between zones.

Digestibility parameters (OMD and DMD) did not vary significantly between warm temperate and tropical zones. High ash content was reported in the arid zone while ADL and OM contents were high in forage samples collected across the tropical zone, and ME was higher in pasture species grown in the arid zone. Methane production did not vary between zones. Tropical pastures grown in warm temperate climates had higher nutritive values than those from tropical/equatorial and arid/dry bioclimatic zones, although nutritive values significantly varied between the three bioclimatic zones. Overall, results showed that tropical pasture species grown in warmer regions tend to have lower nutritive values despite their higher yields compared to those in temperate regions.

Table 3.2. Least squares mean (±SE) of nutritive values within bioclimatic zones described by the Koppen–Geiger climate classification system.

Nutritive metrics	*n*	Climate			*p*-value
		Arid/Dry	Tropical/ Equatorial	Warm Temperate	
CP (%)	245	7.15 ^{b} ± 0.97	11.25 ^{a} ± 0.42	12.02 ^{a} ± 0.76	<0.0001
NDF (%)	175	63.64 ± 2.40	67.47 ± 0.87	68.50 ± 1.21	0.1989
ADF (%)	164	37.82 ± 2.27 ^{ab}	40.97 ^{a} ± 0.82	35.21 ± 1.36 ^{b}	<0.0001
OMD (%)	142	-	58.76 ± 1.14	56.17 ± 1.57	0.1845
DMD (%)	53	-	54.37 ± 1.44	52.33 ± 3.60	0.6039
ME (MJ kg^{-1} DM)	142	8.67 ^{a} ± 0.55	7.60 ^{b} ± 0.18	7.19 ^{b} ± 0.25	0.0477
ADL (%)	34	4.58 ± 0.78	6.07 ± 0.42	4.50 ± 1.37	0.1913
Ash (%)	88	13.17 ^{a} ± 2.33	10.15 ^{a} ± 0.58	5.93 ^{b} ± 0.93	<0.0001
OM (g kg^{-1} DM)	47	726.17 ^{b} ± 35.30	899.35 ^{a} ± 13.57	-	<0.0001
^{1}CH$_4$ (g CH$_4$ animal^{-1} day^{-1})	169	132.81 ± 0.07	132.93 ± 0.03	132.96 ± 0.04	0.1858

$^{a–b}$ Different superscript letters in the same raw data are significantly different as identified by the linear mixed models ($p < 0.05$). All nutritive metrics are given as a percentage of the dry matter unless specified. *n* = number of records. Nutrient metrics are as follows: CP = crude protein, NDF = neutral detergent fibre, ADF = acid detergent fibre, OMD = organic matter digestibility, DMD = dry matter digestibility, ME = metabolisable energy, ADL = acid detergent lignin, minerals, OM = organic matter. ^{1}Methane gas production was estimated using CH$_4$ (g CH$_4$ animal^{-1} day^{-1}) = 17.0 (±0.99) × dry matter intake + 0.03 (±0.01) × neutral detergent fibre.

3.3.4 Management and environmental determinants

Tropical pasture species harvested at different fixed defoliation frequencies in contrasting environments were correlated against their nutritive metrics and estimated methane production (Table 3.3). Results revealed that the NDF, ADF, minerals, ME, OM, and estimated CH$_4$ were positively correlated with the defoliation frequency of tropical pastures. There were significant relationships for all positively correlated nutritive metrics except for OM. Crude protein, ADL, DMD, and OMD were negatively correlated with defoliation frequency. Acid detergent lignin showed no significant relationship in the data set.

Table 3.3. Pearson correlation coefficients (r) between tropical forage nutritive values and estimated methane production vs. defoliation frequency in the database.

Nutritive metrics (% DM)	Defoliation frequency	
	r	*p*-value
NDF	0.29	< 0.001
ADF	0.35	< 0.001
ADL	−0.26	0.112
Minerals	0.19	0.060
CP	−0.31	< 0.001
DMD	−0.36	0.005
OMD	−0.38	< 0.001
ME (MJ kg^{-1} DM)	0.38	< 0.001
OM (g kg^{-1})	0.14	0.334
[1]CH_4 (g CH_4 $animal^{-1}$ day^{-1})	0.29	< 0.001

(Nutritive metrics are as follows: CP = crude protein, NDF = neutral detergent fibre, ADF = acid detergent fibre, OMD = organic matter digestibility, DMD = dry matter digestibility, ME = metabolisable energy, ADL = acid detergent lignin, minerals, OM = organic matter. [1]Methane gas production was estimated using CH_4 (g CH_4 $animal^{-1}$ day^{-1}) = 17.0 (±0.99) × DMI + 0.03 (±0.01) × NDF.

According to the fitted LME model, mean annual rainfall, mean annual temperature, or mean sea level were shown to be significant only for the DM yield in the data set. Defoliation frequency and its interaction with climate were significant for all nutritive metrics (CP, NDF, ADF, ME, DMD, OMD, CH_4, ADL, Ash) of tropical pasture species ($p < 0.0001$). There was a significant effect of defoliation intensity for NDF, ME, OMD, DMD, CH_4, and Ash ($p < 0.0001$), whereas intensity had an interaction with climate for ADF and CP. The fitted model shows a positive effect for NDF, ADF, CH_4, and ADL, with increasing defoliation frequencies and values of the same nutritive metrics decreasing with increasing defoliation intensity of tropical pastures (Table 3.4). Crude protein decreased in longer defoliation frequencies, and CP values increased with increasing defoliation intensity. Metabolisable energy and ADL values decreased due to both higher defoliation frequencies and intensities. Digestibility parameters (OMD, DMD) were negatively affected by longer defoliations, and values increased with higher intensities (Table 3.4).

Table 3.4. Effect of defoliation frequency and defoliation intensity on nutritive values of tropical pasture species estimated from the linear mixed-effects models.

Nutritive metrics	Effect	Estimate	Se	DF	t Value	*p*-value
CP	Intercept	12.41	0.85	37	14.47	< 0.0001
	Defoliation frequency	−0.082	0.007	78	−10.45	< 0.0001
	Defoliation intensity	0.083	0.087	78	0.96	0.3411
NDF	Intercept	59.59	2.54	30	23.4	< 0.0001
	Defoliation frequency	0.092	0.035	73	2.59	0.0117
	Defoliation intensity	0.031	0.308	73	0.1	0.9192
ADF	Intercept	39.13	3.93	39	9.95	< 0.0001
	Defoliation frequency	0.038	0.011	107	3.24	0.0016
	Defoliation intensity	−0.524	0.316	107	−1.66	0.1005
ME	Intercept	6.29	0.43	40	14.55	< 0.0001
	Defoliation frequency	−0.013	0.004	87	2.72	0.0078
	Defoliation intensity	0.126	0.037	87	3.37	0.0011
OMD	Intercept	50.59	2.7	40	18.71	< 0.0001
	Defoliation frequency	−0.083	0.03	87	−2.72	0.0078
	Defoliation intensity	0.793	0.235	87	3.37	0.0011

Table 3.4. Cont.

Nutritive metrics	Effect	Estimate	Se	DF	t Value	*p*-value
DMD	Intercept	47.51	4.86	12	9.78	< 0.0001
	Defoliation frequency	0.028	0.082	31	0.34	0.7336
	Defoliation intensity	0.7	0.19	31	3.59	0.0011
$^1CH_4$	Intercept	133.18	0.12	42	1027.65	< 0.0001
	Defoliation frequency	0.00031	0.00082	108	0.39	0.701
	Defoliation intensity	−0.0254	0.0099	108	−2.56	0.012
ADL	Intercept	7.77	2.56	9	3.03	0.0142
	Defoliation frequency	0.22	0.061	12	3.7	0.003
	Defoliation intensity	−0.094	0.073	12	−1.29	0.221
Minerals	Intercept	14.78	3.19	19	4.63	0.0002
	Defoliation frequency	−0.051	0.0085	59	−6.05	< 0.0001
	Defoliation intensity	−0.44	0.2	59	−2.2	0.0315

(Nutritive metrics are as follows: CP = crude protein, NDF = neutral detergent fibre, ADF = acid detergent fibre, OMD= organic matter digestibility, DMD = dry matter digestibility, ME = metabolisable energy, ADL = acid detergent lignin, minerals, OM = organic matter. [1]Methane gas production was estimated using CH_4 (g CH_4 animal^{-1} day^{-1}) = 17.0 (±0.99) × DMI + 0.03 (±0.01) × NDF).

3.4 Discussion

3.4.1 Nutritive value of tropical pastures

There was a significant variation in the nutritive values of tropical pastures between and within species. According to Lean et al. (2014), a minimum CP of 10–12% DM is required in dairy cattle diets in order to maintain adequate rumen function and DMI. Lactating cows require more CP (16–19%) according to their body weight, pregnancy status, level of milk production, and milk composition (NRC, 2001; Lean et al., 2014). Although the present data set showed an average CP of 10.9% DM across all tropical pasture species at any given harvest interval, the CP content of hybrid cultivars (i.e., *Brachiaria, Pennisetum*) ranged between 16.4% and 17% DM, suggesting that hybrids only would be adequate to meet the CP requirements of lactating cows, apart from peak lactation. While the average NDF in the present data set (67.5% DM) is similar to the average value (66.2% DM) reported for tropical pastures by Van Soest (1994), it is well above the minimum required NDF (25–33% DM) for lactating cows (NRC, 2001) and may therefore affect DMI negatively. This is especially true of NDF under longer harvesting intervals. The ADF in this data set had a greater range (previously mentioned) as well as a higher average (38.8% DM) than that reported for tropical pastures by Katoch (2022) (range 31.9–35.4% DM, average 33.6% DM); furthermore, all ADF values were again above the minimum required ADF (17–21% DM) recommended for lactating cows (NRC, 2001). Metabolisable energy was reported for tropical grasses as 5 to 11 MJ kg^{-1} DM (Adesogan et al., 2000), and the average ME of this data set was recorded as 7.5 MJ kg^{-1} DM. The present data set reported that ME was below the NRC-recommended (NRC, 2001) energy content required for lactating cows (8.4–10.3 MJ kg^{-1} DM, average 9.3 MJ kg^{-1} DM). Overall, the findings of this meta-analysis provide preliminary evidence about the existing limitations of tropical pastures for a productive dairy system in terms of their inherently poor average nutritive value compared with some other feed types (e.g., concentrates and temperate grasses).

An increase in the average nutritive value of tropical pastures will have a greater impact on pasture-based dairy systems. According to Hall et al. (2007) and Ayele et al. (2012), one of the main approaches used to increase the nutritive value and deliver quality forages on a consistent basis is to develop improved forage options and evaluate for their yield, nutritive value, and impact on animal productivity parameters. Lowe et al. (2016) observed substantial nutritive value differences between species and between cultivars within the same species. Van Soest (1994) reported that even under identical conditions, not all forages have the same quality. Results from this data set agree with Lowe et al. (2016) and Van Soest (1994) in that the majority of nutritive values for tropical pastures vary largely among species and within cultivars. This variation is also attributed to cultivar breeding (genotypic variation) for improved quality (Capstaff & Miller, 2018) and different physiological responses (adaptations) of individual plants to environmental factors (Van Soest, 1994). This appeared to be more evident in this data set, as protein and digestibility values were generally higher for hybrids and cultivars within the same species (e.g., *Brachiaria, Pennisetum purpureum* cultivars). Apart from using hybrids and cultivars, an appropriate defoliation management regime has a greater impact on the average nutritive values of tropical pasture species. In addition to improving nutritive value, efforts are needed to increase and satisfy the long-term feed requirement in tropical regions. Rao et al. (2015) explained the “LivestockPlus” concept for sustainable intensification of forage-based systems in the tropics under three intensification processes (genetic, ecological, and socio-economic). These enable the use of better pasture management approaches along with improved pasture species to produce better yields and nutritive values that ultimately provide livelihood (better milk production) and ecosystem (reduced GHG) benefits. Therefore, this data set that compares the nutritive values of tropical pasture species grown across different environments provides a basis for the selection of quality forage options (e.g., *Brachiaria*, *Pennisetum purpureum* cultivars) that perform better across a wider geographical background and can consequently improve tropical pasture-based dairy production systems.

3.4.2 Bioclimatic variation

The data collected for this study covered a wide range of geographical locations (with different mean annual temperatures, mean annual rainfall values, mean sea levels, and soils), and results showed interaction between the defoliation management approach (defoliation frequency and intensity) and climate, through nutritive metrics. Van Soest (1994) reported that climate has an effect on forage nutritive values, accounting for regional variations in composition. According to Jégo et al. (2013), warmer regions have been associated with taller, slow-growing, and less nutritious forages. This data set showed that the biomasses of tropical pastures harvested from arid/dry and tropical/equatorial areas were generally lower in CP, and higher in ADF, ADL, and minerals. Conversely, tropical pastures harvested from warm temperate areas were higher in CP. Both Lee et al. (2017) and Lee (2018) studied a range of forages in different bioclimatic zones and revealed similar results for warm and cooler areas. However, average values for NDF, ME, and digestibility metrics are different. This is explained by our data set comprising fixed defoliation frequencies for tropical pastures. These defoliation frequencies generally varied from 14 to 140 days for some tropical pastures (*Brachiaria brizantha*, *Paspalum notatum, Cynodon dactylon* cv. Tifton 85) sampled in warm temperate areas where the frequencies ranged between 14 to 90 days in arid/dry and tropical/equatorial areas. The high NDF, low ME, and digestibility may be driven by increased structural substances (greater stem: leaf ratios) due to less intense management as well as adaptations to heat stress and water loss. Herbage production in the data set was high in warm areas, and results are in agreement with Lowe et al. (2016) that DM yield is more than double in tropical areas when both the fertility and moisture are non-limiting. This greater DM yield may also explain the lower CP in warm areas that is attributed to N dilution effects caused by greater herbage accumulation (Inyang et al., 2010).

The interactions of nutritive values with climate in the present data set revealed that DM yield and sward characteristics are sensitive to variables such as the environment (Chapman et al., 2014b; Moyo & Nsahlai, 2021) and the morphogenesis of plant species (Lemaire et al., 2009). This may also explain the lower correlations between nutritive values across multiple pasture species and defoliation frequencies in the present data set. Therefore, the generic defoliation management options for tropical pastures are unlikely to produce better agronomic results, as they do not consider the species-specific growth, nor the physiological stages induced by climate. Ruolo et al. (2019) highlighted that plant-related indicators that are associated with regrowth are more sensible to use in determining pasture defoliation. This may require good information on the morphological characteristics of cultivated species. In particular, for improved tropical pastures which have not been explored to a similar degree as temperate species in order to determine the suitability for specific conditions of pasture production and management.

3.4.3 Management determinants

The present study assessed all edible plant-parts rather than focusing on their botanical compositions (leaf, stem, and dead materials). The greater range of values may be explained by the combination of different proportions of plant materials. Herbage maturity influences the forage nutritive value due to phenological and physiological changes in the plant (Inyang et al., 2010). Even though the nutritive value changes due to these phenological and physiological changes were not disentangled in our meta-analysis, the relationships reported in Table 3.3 explain the typical changes in the nutritive value of tropical pasture species during maturity. It is widely known that CP and DMD decrease as harvesting intervals increase (Tessema et al., 2002; Arthington & Brown, 2005; Pembleton et al., 2009; Tessema et al., 2010; Vendramini et al., 2014; Hughes et al., 2022) and that NDF, ADF, and ADL increase with increasing harvesting intervals (Tessema et al., 2002; Inyang et al., 2010; Tessema et al., 2010; Vendramini et al., 2014). This data set is also consistent with the previous literature. In addition, the fitted LME model for the nutritive metrics explained the same relationships based on the frequency of defoliation. Defoliation intensity greatly affects the pasture nutritive value. It further explains the significant relationship between the intensity of defoliation for ME, OMD, DMD, CH_4, and ash. Metabolisable energy, OMD, and DMD all increased as a result of increasing defoliation intensity, while CH_4 and ash decreased. Defoliation intensities for all tropical pastures ranged between 50 and 200 mm (100 mm average) in the data set, and this may change the vertical sward canopy structure (Barbosa et al., 2007) and nutritive composition (Chapman et al., 2014b; Moyo & Nsahlai, 2021) that is largely determined by the leaves and stem accumulation in each stratum (Ungar & Ravid, 1999; Benvenutti et al., 2016; Benvenutti et al., 2017; Benvenutti et al., 2020).

3.4.4 Implications for livestock methane production

Direct measurement of enteric CH_4 has begun relatively recently due to high equipment costs and the sophisticated methodologies that are required to measure CH_4 emissions from live animals (Benaouda et al., 2020). Therefore, mathematical models are commonly used to estimate CH_4 emissions from cattle. Current livestock models that are available to estimate CH_4 production require many inputs that are not readily available across all experiments, and these models do not account for variations between animal breeds, regions, and climate-driven pasture nutritive values (Lee et al., 2017). Therefore, the present meta-analysis only attempted to estimate the CH_4 production of tropical pasture species grown in different climates as a function of NDF, based on an average DMI that is consumed by tropical dairy cattle. However, actual values may differ due to variations in DMI and diet selection, especially in grazing scenarios. The chemical composition of the forage determines enteric CH_4 production (Ruggieri et al., 2020). Forages rich in structural carbohydrates tend to result in greater CH_4 amounts than diets higher in non-structural carbohydrates (Sauvant & Giger-Reverdin, 2009; Berça et al., 2019; Neto et al., 2017). This is explained by the nutritive value results of this study that show the minimum estimated enteric CH_4 emissions values for the *Pennisetum* and *Brachiaria* species. According to Hegarty (2009) as well as Liu et al. (2017), the amount of feed intake, moderated by feed digestibility and animal characteristics, affects enteric fermentation and CH_4 production. The CH_4 production for *Brachiaria* pasturelands was studied by Ruggieri et al. (2020), who revealed that CH_4 emissions varied from 106 to 177 g CH_4 animal^{-1} day^{-1}, at an average of 141.5 g CH_4 animal^{-1} day^{-1}. Our data set also produced similar results for a constant dry matter intake of 7.7 kg d^{-1} (Patra, 2017). The Intergovernmental Panel on Climate Change (IPCC) default CH_4 emissions factor for tropical pastures is considered to be 149 g CH_4 animal^{-1} day^{-1} (Eggleston et al., 2006);

the data set presented here showed lower average values across all tropical pasture species. According to the fitted model, the effect of both intensity and frequency of defoliation, and their interaction with climate, have been shown to be significant for CH_4 production. This relationship verified the finding of Chaves et al. (2006) who found that diet quality affected CH_4 production. Moreover, Boadi et al. (2002) demonstrated that steers that grazed on young developing growth pastures produced up to 45% less CH_4 than if they grazed on mid and late-season pastures. Beauchemin et al. (2008) also highlighted that harvesting forage at an earlier maturity stage is a strategy that can be used to decrease enteric CH_4 production. Meister et al. (2021) also found that CH_4 production for *Panicum maximum* cv. Tanzania increases linearly with the number of grazing days, possibly reflecting a reduction in quality. De Souza Filho et al. (2019) revealed that the intensity of defoliation affected CH_4 production in the tropics, and a target height of 230–300 mm has the potential of reducing CH_4 emissions by 13–14%. Overall, these results provide important insights into the potential of utilising lower CH_4-producing pasture species and the potential for low-emissions dairy farming through nutritive value improvements in tropical pastures through better management.

3.5 Conclusions

This meta-analysis showed that nutritive value, digestibility, and ME of tropical pastures greatly vary between and within species. Tropical pasture species *Pennisetum purpureum* followed by *Brachiaria* species showed high CP, OMD, and ME, and low NDF. Furthermore, the analysis demonstrated the variations in nutritive values of tropical pasture species across bioclimatic environments, and that nutritive values are lower in warmer and drier regions. The newer and hybrid cultivars performed better than the standard cultivars across wider bioclimatic areas, with the least quality variations suggesting their ability to deliver improved livestock forage options for tropical areas. The frequency of defoliation, defoliation intensity, climate, and their interactions had a significant effect on multiple agronomic nutritive metrics and CH_4 production of tropical pastures. The climate was found to be a key variable that determines tropical pasture nutritive values. This information explains the importance of setting climate-sensible defoliation strategies in order to improve tropical pasture nutritive value for sustainable dairy farming in the tropics. These results could also form the basis for further studies that research pasture agronomy from a livestock study prospective, as pastures are grown to rear livestock that ultimately produce food products for humans.

Supplementary materials

Supplementary Table 3.1: Details of the studies included in the meta-analysis.

Reference	Country	Climate
Hare, 2013a	Thailand	Tropical/ equatorial
Hare, 2013b	Thailand	Tropical/ equatorial
Tessema et al., 2010	Ethiopia	Arid/ dry
Ansah, 2010	Ghana	Tropical/ equatorial
Lounglawan et al., 2014	Thailand	Tropical/ equatorial
Bacorro, 2018	Philippines	Tropical/ equatorial
Wassie et al., 2018	Ethiopia	Warm temperate
Johnson et al., 2001	USA	Warm temperate
Bayble, 2007	Ethiopia	Tropical/ equatorial
Ribeiro et al., 2014	Brazil	Arid/ dry
Arthington & Brown, 2005	USA	Warm temperate
Haryani H., 2018	Malaysia	Tropical/ equatorial
Van Man & Wiktorsson, 2003	Vietnam	Tropical/ equatorial
Kozloski et al., 2003	Brazil	Arid/ dry
Kozloski et al., 2005	Brazil	Arid/ dry
Meale et al., 2012	Ghana	Tropical/ equatorial
Lima, 2018	Brazil	Tropical/ equatorial
Taffarel et al., 2016	Brazil	Warm temperate
Mutimura, 2017	Rwanda	Tropical/ equatorial
Ronquillo et al., 1998	Venezuela	Tropical/ equatorial
Vendramini et al., 2014	USA	Warm temperate
Inyang et al., 2010	USA	Warm temperate
Enoh, 2005	Cameroon	Tropical/ equatorial
McRoberts et al., 2018	Vietnam	Tropical/ equatorial
Dore, 2006	USA	Warm temperate
Da Silva et al., 2020	USA	Warm temperate
Ehrlich et al., 2003	Australia	Warm temperate
Tudsri et al., 2002	Thailand	Tropical/ equatorial
Hare et al., 2001	Thailand	Tropical/ equatorial
Muir and Abrao, 1999	Mozambique	Arid/ dry
Premarathne, 1993	Sri Lanka	Tropical/ equatorial
Pequeno et al., 2015	Brazil	Tropical/ equatorial
Ondiko et al., 2016	Kenya	Tropical/ equatorial
Nyambati et al., 2016	Kenya	Warm temperate
Njarui et al., 2016	Kenya	Tropical/ equatorial

Supplementary Table 3.2: Nutritive value (mean ± standard deviation) of different tropical pasture species and cultivars.

Cultivar name	CP	ADF	NDF	OMD	Minerals	ME	$^{1}CH_4$
Andropogon gayanus	4.91±2.24	39.40±1.41	72.67±1.71	-	-	-	133.08±0.05
Andropogon gayanus cv. Gamba	6.45±1.76	-	-	-	-	-	-
Brachiaria brizantha	11.17±3.20	47.02±6.34	66.48±7.81	-	11.49±1.33	-	132.89±0.23
Brachiaria brizantha cv. Marandu	12.33±4.11	37.30±1.76	63.80±3.03	55.35±4.59	13.50±1.35	7.06±0.73	132.81±0.09
Brachiaria brizantha cv. MG4	12.07±4.02	39.27±3.42	64.80±4.25	57.14±4.76	11.80±1.95	7.34±0.76	132.84±0.13
Brachiaria brizantha cv. Piata	12.53±4.82	42.27±5.84	65.57±2.98	57.00±6.35	11.77±1.46	7.32±1.02	132.87±0.09
Brachiaria brizantha cv. Xaraes	11.85±2.98	38.17±2.42	65.77±1.53	55.38±5.11	11.93±1.15	7.06±0.82	132.87±0.05
Brachiaria cv. CIAT BR02 / 1752	7.68±2.70	33.53±2.71	61.03±3.33	-	-	-	132.73±0.10
Brachiaria cv. CIAT BRO2/1794	7.36±2.49	33.14±3.23	61.90±3.53	-	-	-	132.76±0.11
Brachiaria decumbens	10.80	41.70	71.70	-	-	-	133.05
Brachiaria decumbens cv. Basilisk	11.48±5.10	41.07±2.14	67.77±3.71	54.61±6.96	11.30±2.50	6.94±1.11	132.93±0.11
Brachiaria humidicola	16.47±4.15	-	-	58.96±3.08	-	7.63±0.49	-
Brachiaria humidicola cv. Llanero	12.55±4.41	40.60±0.20	67.23±1.27	56.97±5.43	11.60±0.62	7.31±0.87	132.92±0.04
Brachiaria hybrid cv. Mavuno	11.00±1.41	-	61.50±2.12	64.75±2.47	-	8.56±0.40	132.75±0.06
Brachiaria hybrid cv. Mulato	14.43±2.61	-	-	60.63±4.51	-	7.90±0.72	-
Brachiaria hybrid cv. Mulato II	11.45±3.49	34.76±2.94	61.54±3.92	61.91±4.90	13.80±2.08	8.11±0.78	132.75±0.12
Brachiaria hybrids	11.56±4.45	45.33±4.62	64.61±3.01	57.96±7.79	8.61±2.23	7.47±1.25	132.84±0.09
Brachiaria ruziziensis	9.41±1.51	38.70	67.10	-	8.4	-	132.91
Brachiaria ruziziensis cv. Kennedy	-	-	-	-	-	-	-
Cenchrus ciliaris	11.54±3.02	35.97±0.67	67.07±1.46	-	-	-	132.91±0.04

Supplementary Table 3.2. Cont.

Cultivar name	CP	ADF	NDF	OMD	Minerals	ME	$^1CH_4$
Cenchrus ciliaris cv. Bilocla	6.10±2.96	-	-	-	-	-	-
Cenchrus ciliaris cv. Gayndah	6.1±3.39	-	-	-	-	-	-
Chloris gayana cv. ex-Tozi	7.00±2.65	48.10±2.33	72.87±0.81	44.56±10.23	8.80±0.62	5.33±1.64	133.09±0.02
Chloris gayana cv. Callide	12.53±0.60	-	65.73±0.47	-	-	-	-
Chloris gayana cv. Katambora	7.25±4.17	-	-	-	-	-	-
Cynodon dactylon	10.86±5.86	31.00±3.17	70.34±7.54	57.50±2.52	5.92±1.50	7.40±0.40	133.01±0.23
Cynodon dactylon cv. Jiggs	11.04±5.30	33.84±3.69	67.61±5.10	49.25±6.01	6.24±1.91	6.08±0.96	132.93±0.15
Cynodon dactylon cv. Russell	10.82±5.59	33.38±2.94	67.90±2.56	-	5.88±1.10	-	132.94±0.08
Cynodon dactylon cv. Tifton 85	14.83±3.15	44.50±2.55	74.73±4.16	50.72±6.05	-	6.31±0.97	133.14±0.12
Cynodon dactylon cv. Tifton 9	10.02±4.53	35.46±2.01	66.10±2.43	-	5.72±0.84	-	132.88±0.07
Cynodon nlemfuensis	-	32.84±1.14	74.20±1.46	54.68±2.31	-	6.95±0.37	133.13±0.04
Cynodon nlemfuensis cv. Florona	-	-	-	45.05±3.82	-	5.41±0.61	-
Eragrostis curvula	6.95±3.74	-	-	-	-	-	-
Hemarthria altissima cv. Floralta	-	-	-	50.68±4.95	-	6.31±0.79	-
Imperata cylindrica	10.67±1.05	-	-	-	-	-	-
Panicum coloratum cv. Bambatsi	7.05±2.86	-	-	-	-	-	-
Panicum maximum	9.28±2.48	45.93±3.41	76.26±3.30	62.47±3.06	7.05±1.56	8.20±0.49	133.19±0.10
Panicum maximum cv. Mombosa	7.12±3.23	42.30±2.80	68.63±2.92	-	-	-	132.96±0.09
Panicum maximum cv. Tanzania	7.13±1.13	40.80±1.88	68.73±1.46	-	-	-	132.96±0.04
Paspalum atratum	5.60±1.37	38.73±1.61	66.56±1.87	-	-	-	-
Paspalum notatum	-	35.48±1.32	74.92±0.68	51.92±2.22	-	6.51±0.35	133.15±0.02
Paspalum notatum cv. Argentina	9.84±5.41	34.16±2.27	65.24±3.27	-	6.12±1.08	-	132.86±0.10
Paspalum notatum cv. Pensacola	9.82±4.37	35.66±1.76	67.02±2.35	51.80±2.02	5.68±0.94	6.49±0.32	132.91±0.07

Supplementary Table 3.2. Cont.

Cultivar name	CP	ADF	NDF	OMD	Minerals	ME	$^1CH_4$
Pennisetum purpureum cv. 3rd generation	16.27±1.75	-	-	65.44±1.33	-	8.67±0.21	-
Pennisetum purpureum cv. Dwarf	11.46±1.06	-	-	-	-	-	-
Pennisetum purpureum cv. ILRI 16791	10.23±2.07	38.93±2.61	54.70±0.10	63.23±3.67	13.17±0.78	8.32±0.59	132.54±0.00
Pennisetum purpureum cv. India	16.35±2.01	-	-	65.84±0.22	-	8.74±0.04	-
Pennisetum purpureum cv. King	10.46±2.01	42.42±4.05	70.93±5.20	-	-	-	133.03±0.16
Pennisetum purpureum cv. Kobe	17.00±2.45	-	-	67.34±0.75	-	8.98±0.12	-
Pennisetum purpureum cv. Mott	13.83±1.64	36.08±2.37	63.36±1.97	67.18±4.22	-	8.95±0.68	132.80±0.06
Pennisetum purpureum cv. NB 21	15.75±0.52	-	-	-	-	-	-
Pennisetum purpureum cv. Red	15.25±2.57	-	-	69.34±2.61	-	9.30±0.42	-
Pennisetum purpureum cv. Taiwan	15.60±2.31	-	-	66.19±0.35	-	8.79±0.06	-
Pennisetum purpureum cv. TaiwanA25	10.60±1.83	-	-	-	-	-	-
Pennisetum purpureum cv. Zanzibar	16.70±3.86	-	-	66.44±2.30	-	8.83±0.37	-
Urochloa mosambicensis	7.80±2.96	-	-	-	-	-	-

Nutritive value (mean ± standard deviation) metrics are as follows: CP = crude protein, NDF = neutral detergent fibre, ADF = acid detergent fibre, OMD= organic matter digestibility, DMD = dry matter digestibility, ME = metabolisable energy, ADL = acid detergent lignin, minerals, OM = organic matter. [1]Methane gas production was estimated using CH_4 (g CH_4 animal^{-1} day^{-1}) = 17.0 (±0.99) × DMI + 0.03 (±0.01) × NDF).

Chapter 4

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_2 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, non-fibre 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

4.1 Introduction

Globally, warm-season (C_4) grasses predominate in the tropical and subtropical climates and are the primary source of feed for grazing livestock including dairy cattle (Cooke et al., 2020; Sollenberger et al., 2020). 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 (Nelson & Moser, 1994; Volenec et al., 2007; Sollenberger et al., 2020). In addition, increasing atmospheric temperatures may favour the dominance of C_4 species in different ecosystems where they are not currently present (Sage & Kubien, 2003). Consequently, these pastures constitute a key resource to fulfil livestock nutritional requirements and increase dairy production in tropical and subtropical regions (Baptistella et al., 2020; Paul et al., 2020). 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 (Thornton, 2010; Lowe et al., 2016). In addition, scarcity of quality feed on a consistent basis is often reported as a major constraint to dairy production (Paul et al., 2020). 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 wider edaphoclimatic conditions, have improved nutritive value, and are used for either grazing or mechanical harvest (Paul et al., 2020; Sollenberger et al., 2020).

Grasses of the genus *Brachiaria* (syn. *Urochloa*) are widely used across the tropics and subtropics (Baptistella et al., 2020; Sollenberger et al., 2020). *Brachiaria* Mulato II (BM) is a recently introduced *Brachiaria* hybrid cultivar of Centro Internacional de Agricultura Tropical produced from three-generation hybridisation of tetraploidised 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 (Argel et al., 2007). It grows well in low fertile, acidic 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 (Fisher & Kerridge, 1996; Argel et al., 2007). Guineagrass [*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 (Pontes et al., 2017). *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 (Lowe et al., 2016; Sollenberger et al., 2020). Rhodes grass (*Chloris gayana*) is a long-leaved grass broadly used in grazing systems in warm areas (Sollenberger et al., 2020). *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 (Lowe et al., 2016; Sollenberger et al., 2020).

The fundamental basis of pasture growth is carbon assimilation by photosynthesis (Silva et al., 2016). Tropical forage grasses have long been recognised for their high photosynthetic potential (Volenec et al., 2007; Habermann et al., 2019; Sollenberger et al., 2020), although detailed species-specific descriptions related to carbon assimilation are scarce, especially for recently developed pasture cultivars (Dias-Filho, 2002; Pedreira et al., 2015). Understanding the carbon assimilation process of tropical pastures allows for better understanding of the species-specific physiological adaptation and yield potential (Pedreira et al., 2015).

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 (Baumont et al., 2000; Lemaire et al., 2009). 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 pseudo-stem (sheath) or stem: leaf ratio (Peyraud et al., 1996). Length, vertical orientation, and horizontal dispersion of produced pseudo-stems or stems of the grass determine the sward structure and partly the accessibility of herbage to defoliation by grazing (Gastal & Lemaire, 2015). 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 (Hodgson, 1982). 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 (Jacobs et al., 2011). 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) (Ungar & Ravid, 1999; Benvenutti et al., 2016; Benvenutti et al., 2017; Benvenutti et al., 2020). 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.

4.2 Methodology

4.2.1 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 4.1). 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%) (Isbell, 2016). Soil characteristics for the experimental area (depth 0–30 cm) in September 2019 were pH ($CaCl_2$) 7.6; organic matter (Walkley black) 1.33%; nitrate (NO_3^{-1}) 28 mg kg^{-1}; ammonium (NH_4^{+3}) 3.5 mg kg^{-1}; phosphorus (P) (Colwell) 58.5 mg kg^{-1}, bulk density 1.35 t m^{-3}; 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^{-1} 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 06 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_4 grasses.

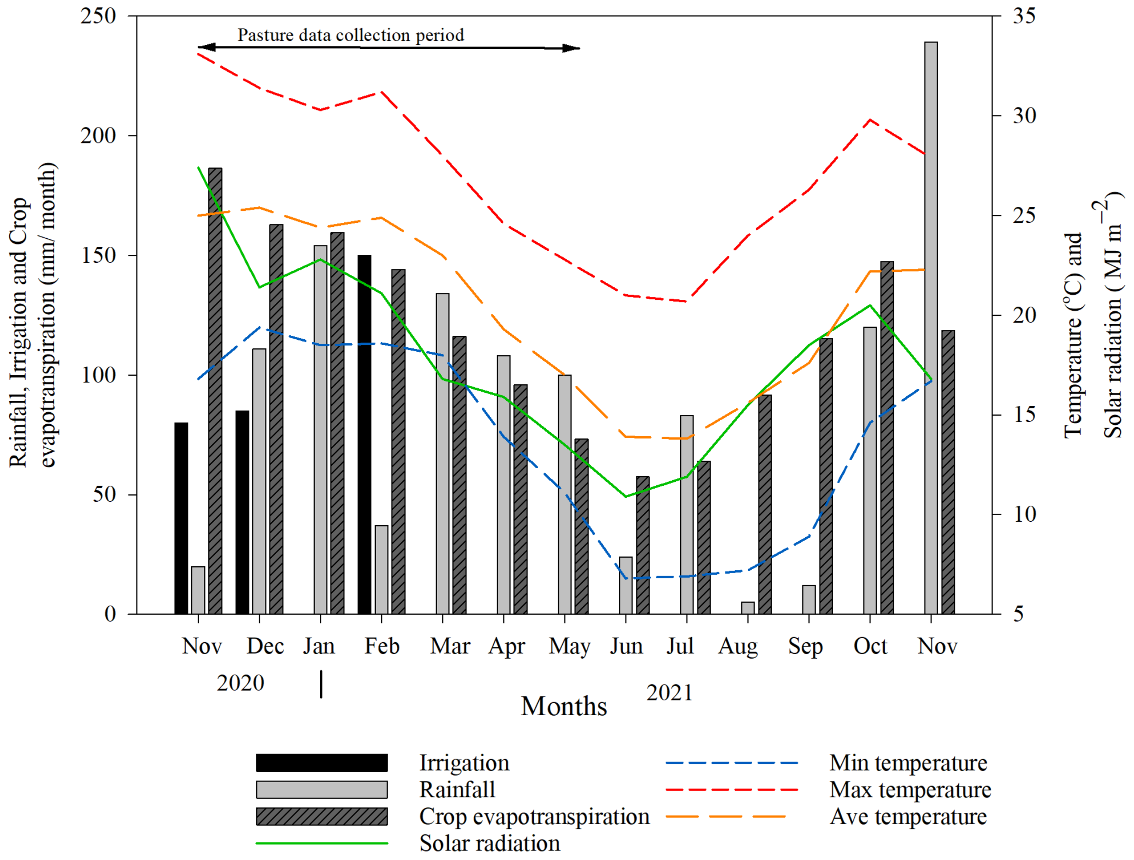

Figure 4.1. Monthly average weather data at the Gatton Research Dairy, Queensland, Australia from November 2020 to November 2021. Rainfall, irrigation, and temperature data were collated from an automatic weather station at the experimental site and evapotranspiration and solar radiation data were collated 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 (Allen et al., 1998). 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^{-1}, 6.6 kg P ha^{-1}, 40.5 kg K ha^{-1} and 58.8 kg S ha^{-1}. Urea (46% N) and CK77 were applied on 18 January 2021 and 19 February 2021 at a rate of 69 N kg ha^{-1} and 26 N, 4.4 P, 27 K and 39.2 S kg ha^{-1} respectively. Plots were spot sprayed with Titan Glyphosate 450 (450 gL^{-1} Glyphosate present as Isopropylamine salt) for weeds (*Sorghum halepense*) at a rate of 2 kg ha^{-1} on 11 December 2020 and 7 January 2021.

4.2.2 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 ($n = 4$) (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 (Silva et al., 2016; Sollenberger et al., 2020). 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 pseudo-stem (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^{-1}). 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.

4.2.3 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 centre 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 ($n = 8$) were categorised 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 leavers per tiller was used to calculate the leaf appearance rate. Sward canopy bulk density was determined as total above-ground pre-harvesting 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.

4.2.4 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, Utah, USA). In each plot, 2 readings of incoming PAR (PAR_i) above the canopy level and 8 readings of transmitted PAR (PAR_t) 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 pre-harvest 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 pre-set 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 PPF$\mu mol^{-1} mol^{-1} m^{-2}$) with a reference CO_2 concentration of 400 ppm. Similarly, carbon and water exchange of leaves in two plots ($n = 2$) were measured under a range of 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 PPF$\mu mol^{-1} mol^{-1} m^{-2}$. All carbon exchange measurements were taken at 30°C leaf temperature inside the chamber (reflective of the ambient temperature at the trial site).

4.2.5 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 (Easlon & Bloom, 2014). 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).

4.2.6 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 (DairyOne, 2020) for dry matter (DM), CP, NDICP, ADF, NDF, lignin, non-fibre 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 (DairyOne, 2020) using NRC equations 4.1 and 4.2 (NRC, 2001). Subsequently, whole plant nutritive values were calculated based on DM proportion.

$$\text{ME (KJkg}^{-1}\text{ DM)} = [(1.01\times (\text{DE}) - 0.45) + 0.0046 \times (\text{EE}-3)] \times 4.184 \qquad 4.1$$

Where

DE = digestible energy (KJ kg^{-1} DM)

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

4.2.7 Calculations and statistical analyses

4.2.7.1 Fitting light response curve

All model fittings and statistical analyses were performed using the R (version 4.0.5) statistical computing software (RCoreTeam, 2021). Significant effects and differences were accepted when $p \leq 0.05$.

Photosynthetic light response curves were fitted using a non-rectangular hyperbolic model framework (Equation (4.3)) (Leverenz & Jarvis, 1979; Marshall & Biscoe, 1980). A fit was made for each pasture species separately and parameters were determined.

$$A(I) = \frac{\varphi I + A_{max} - \sqrt{(\varphi I + A_{max})^2 - 4\theta\varphi I A_{max}} - R_d}{2\theta} \qquad 4.3$$

Where

A = photosynthesis rate (µmol CO_2 m^{-2} s^{-1})
I = light intensity (PPFµ$mol^{-1}mol^{-1}m^{-2}$)
A_{max} = maximum leaf photosynthetic rate (µmol CO_2 m^{-2} s^{-1})
φ = quantum yield (µmol CO_2 $photon^{-1}$)
R_d = dark respiration (µmol CO_2 m^{-2} s^{-1})
θ = convexity constant (unitless)

According to the equation 4.3, 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 $A(I)$.

4.2.7.2 Fitting the CO_2 response curve (A/C_i curve)

Non-rectangular hypobaric function (Equation (4.4)) was fitted to the internal leaf CO_2 concentration and photosynthetic data to derive the A/C_i curve (Medlyn et al., 2002). Maximum carboxylation rate (V_{cmax}) (represented by Ac in Equation (4.5)) and maximum electron transfer rate (J_{max}) (represented by Aj in Equation (4.5)) were calculated using Equation (4.5) (Farquhar et al., 1980; Duursma, 2015).

$$A(\mathrm{C}) = \frac{\beta C + P_a - \sqrt{(\beta C + P_a)^2 - 4\theta\beta C P_a} - R_c}{2\theta} \qquad 4.4$$

$$Am = \frac{Ac + Aj\ - \sqrt{(Ac + Aj)^2\ -\ 4\theta Ac\, Aj}\quad -\ R_c}{2\theta} \qquad 4.5$$

Where

Am = hyperbolic minimum of Ac and Aj (µmol CO_2 m^{-2} s^{-1})

Ac = gross photosynthetic rate when the Rubisco activity is limiting (µmol CO_2 m^{-2} s^{-1})

Aj = gross photosynthetic rate when RUBP regeneration is limiting (µmol CO_2 m^{-2} s^{-1})

R_c = respiratory rate (µmol CO_2 m^{-2} s^{-1})

θ = convexity constant (unitless)

The Linear mixed-effect model (LME) approach was used to analyse the forage yield, canopy structure data using the '*lme4'* package in R (Bates et al., 2015). 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 in R (Lenth, 2016). 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.

4.3 Results

4.3.1 Carbon exchange characteristics and photosynthesis biochemistry

Leaf photosynthetic light response parameters were affected by the pasture species (Table 4.1). *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 4.1). 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 4.1. 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}) (µmol CO_2 m^{-2} s^{-1})	15.79 ± 0.4 ^{c}	28.95 ± 0.98 ^{a}	25.04 ± 1.34 ^{b}
Photosynthetic efficiency (φ) (µmol CO_2 $photon^{-1}$)	0.026 ± 0.001 ^{c}	0.056 ± 0.004 ^{a}	0.031 ± 0.002 ^{b}
Dark respiration (R_d) (µmol CO_2 m^{-2} s^{-1})	0.79 ± 0.1 ^{c}	2.41 ± 0.3 ^{a}	0.91 ± 0.3 ^{b}
Curvature parameter (Θ)	0.86 ± 0.04 ^{a}	0.84 ± 0.06 ^{a}	0.87 ± 0.07 ^{a}
Light compensation point (I_c) (µmol CO_2 m^{-2} s^{-1})	30.70 ^{b}	43.70 ^{a}	29.01 ^{c}
Light saturation point (I_s) (µmol CO_2 m^{-2} s^{-1})	1242.46 ^{b}	1208.22 ^{b}	1538.66 ^{a}

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

The effect of pasture species on photosynthetic CO_2 response parameters is summarised in Table 4.2. Maximum photosynthetic capacity (P_a) was reported to be the higher in GP and BM followed by RR. There was no significant difference between the A_c of GP and BM. Gatton panic had greater efficiency for CO_2 (0.24 µmol CO_2 photon^{-1}), indicating that GP is photosynthetically efficient under low CO_2 concentrations. Gatton panic (4.23 µmol CO_2 m^{-2} s^{-1}) and BM (4.42µmol CO_2 m^{-2} s^{-1}) showed higher R_c than RR. These high P_a and R_c 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_{cmax}) was higher in GP followed by RR and BM, whereas maximum electron transfer rate (J_{max}) was highest in BM followed by RR and GP.

Table 4.2. Pasture species effects of photosynthetic CO_2 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_a) (µmol CO_2 m^{-2} s^{-1})	15.79 ± 0.4 ^{b}	33.54 ± 1.7 ^{a}	34.27 ± 4.4 ^{a}
Photosynthetic efficiency (β) (µmol CO_2 photon^{-1})	0.02 ± 0.001 ^{c}	0.13 ± 0.02 ^{b}	0.24 ± 0.11 ^{a}
Respiration rate (R_c) (µmol CO_2 m^{-2} s^{-1})	2.04 ± 3.5 ^{b}	4.42 ± 0.93 ^{a}	4.23 ± 4.05 ^{a}
Curvature parameter (Θ)	0.86 ± 0.04 ^{a}	0.83 ± 0.06 ^{a}	0.65 ± 0.18 ^{b}
Maximum carboxylation rate (V_{cmax}) (µmol CO_2 m^{-2} s^{-1})	83.51± 41.23 ^{b}	71.00 ± 4.33 ^{c}	92.60 ± 17.90 ^{a}
Maximum electron transfer rate (J_{max}) (µmol CO_2 m^{-2} s^{-1})	118.24± 16.48 ^{b}	122.56 ± 4.60 ^{a}	106.35± 10.93 ^{c}

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

4.3.2 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 4.2 a, 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 4.2d). Dead material accumulation was significantly affected by the harvest time.

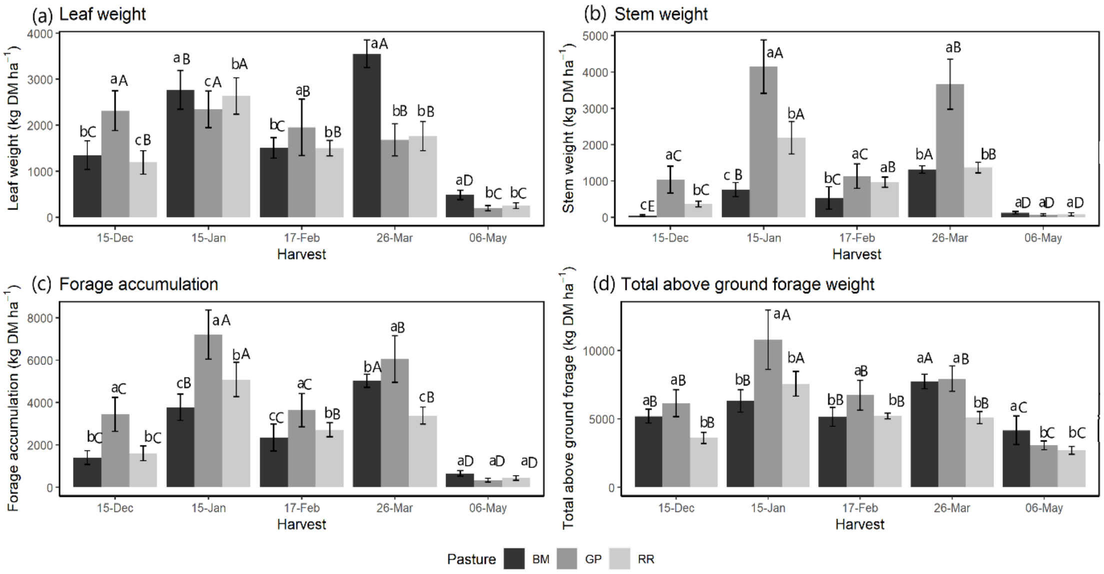

Figure 4.2. Leaf weight (a), stem weight (b), forage accumulation (c) and total above-ground forage yield (d) of *Brachiaria* Mulato II (BM), Gatton panic (GP), Rhodes grass Reclaimer (RR) measured in five harvests at Gatton Research Dairy, Queensland, Australia from 2020 November to 2021 May. Error bars represent the standard error of means (kg DM ha^{-1}). 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^{-1}), followed by BM (28,590 kg DM ha$^{-1)}$ and RR (24,210 kg DM ha^{-1}). Total forage accumulation over the experimental period was 36% greater in GP (20655 kg DM ha^{-1}) and there was no significant difference between BM and RR (p = 0.0289). (Table 4.3). Total leaf weight was highest (9660 kg DM ha^{-1}) in BM, and lowest (7335 kg DM ha^{-1}) in RR. Stem production was significantly different between the three pasture species (Table 4.3), with GP having 72% greater stem production (10,040 kg DM ha^{-1}) than BM which produced the lowest value (2775 kg DM ha^{-1}). Dead material accumulation was not affected by pasture species; however, the total dead matter was greatest (1200 kg DM ha^{-1}) in GP.

Table 4.3. Effect of pasture species on total forage mass, forage accumulation and plant-part composition (kg ha^{-1}) 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	Total leaf mass	Total stem mass	Total dead mass
	(kg ha^{-1}) DM				
BM	28,590 ^{b}	13,200 ^{b}	9660 ^{a}	2775 ^{c}	732
GP	34,725 ^{a}	20,655 ^{a}	8495 ^{b}	10,040 ^{a}	1200
RR	24,210 ^{b}	13,220 ^{b}	7335 ^{b}	4955 ^{b}	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).

4.3.3 Sward structural parameters

Leaf appearance rate was affected by pasture species (p < 0.001), harvest time (p < 0.001) and pasture species × harvest interactions (p < 0.001), where the highest leaf appearance rate was reported for GP (0.17 leaf day^{-1}) and varied from 0.09–0.17 leaf day^{-1}. The leaf appearance rate varied for BM and RR from 0.08–0.10 leaf day^{-1} and 0.09–0.16 leaf day^{-1}, respectively. There was a pasture species × 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 4.4), 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 × 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^2 m^{-2}), 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^{-1} cm^{-1}) followed by GP and RR. Leaf bulk density was highest in BM (139.2 kg ha^{-1} cm^{-1}) followed by RR; however, it was lowest in GP (70.1 kg ha^{-1} cm^{-1}) due to the higher stem accumulation (Figure 4.2, Table 4.3). 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 ($p < 0.001$).

4.3.4 Nutritive composition

Nutritive composition values changed between pasture species (Table 4.5). 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 4.4. 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^{-1})	Canopy height (cm)	Stem height (cm)	Stem: canopy height	Leaf: stem ratio	LAI (m^2 m^{-2})	SLA (m^2 kg^{-1})	Canopy light interception (%)	Canopy bulk density (kg ha^{-1} cm^{-1})	Stem bulk density (kg ha^{-1} cm^{-1})	Leaf bulk density (kg ha^{-1} cm^{-1})
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}

Table 4.4. Cont.

Sward structural parameters	Leaf appearance rate (Leaf day^{-1})	Canopy height (cm)	Stem height (cm)	Stem: canopy height	Leaf: stem ratio	LAI (m^2 m^{-2})	SLA (m^2 kg^{-1})	Canopy light interception (%)	Canopy bulk density (kg ha^{-1} cm^{-1})	Stem bulk density (kg ha^{-1} cm^{-1})	Leaf bulk density (kg ha^{-1} cm^{-1})
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 Dec 2020, 2; 15 Jan 2021, 3; 17 Feb 2021, 4; 26 Mar 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.

Table 4.5. 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), non-fibre carbohydrates (NFC), crude fat (CF), ethanol-soluble carbohydrates (ESC) total digestible nutrients (TDN), in vitro true digestibility 24 hr (IVTD), in vitro NDF digestibility 24 h as % of NDF (NDFD) are presented as g kg^{-1}. Metabolisable energy (ME) is given in MJ kg^{-1} 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 ^{a}	163	282 ^{b}	504 ^{b}	26 ^{b}	15 ^{a}	72	63	167 ^{a}	35	51	115	776	560 ^{b}	10.4 ^{a}
GP	678 ^{ab}	172	327 ^{a}	553 ^{a}	67 ^{a}	11 ^{b}	64	48	105 ^{b}	40	52	118	814	666 ^{a}	10.2 ^{a}
RR	646 ^{bc}	145	334 ^{a}	607 ^{a}	58 ^{a}	07 ^{b}	63	50	80 ^{b}	37	43	124	764	618 ^{a}	9.5 ^{b}
SEM	10	16	13	25	05	01	05	05	07	04	02	08	21	27	0.2
							Stem								
BM	605	96	380	641 ^{b}	18	10 ^{a}	53	51	121 ^{a}	49	29 ^{a}	113	722	562	8.4
GP	598	68	432	677 ^{ab}	19	07 ^{ab}	51	37	127 ^{a}	48	19 ^{b}	109	546	434	7.9
RR	554	83	407	709 ^{a}	25	05 ^{bc}	47	31	72 ^{b}	48	20 ^{bc}	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 ^{a}	151 ^{a}	300 ^{b}	527 ^{b}	25 ^{b}	14 ^{a}	69	61	158 ^{a}	37	47	115	766	560	10.0 ^{a}
GP	629 ^{ab}	127 ^{b}	375 ^{a}	608 ^{ab}	45 ^{a}	09 ^{ab}	58	45	113 ^{b}	44	37	113	710	570	9.2 ^{ab}
RR	616 ^{b}	124 ^{b}	360 ^{a}	641 ^{a}	46 ^{a}	07 ^{b}	59	45	77 ^{c}	42	35	121	729	589	8.9 ^{b}
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 4.5). 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^{-1} DM and 10 MJ kg^{-1} DM) was reported for BM, followed by GP (10.2 MJ kg^{-1} DM and 9.2 MJ kg^{-1} DM) and RR (9.5 MJ kg^{-1} DM and 8.9 MJ kg^{-1} 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.

4.3.5 Mineral composition

Table 4.6 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.

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^{-1}; $p < 0.05$).

Table 4.6. 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^{-1}. *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 ^{a}	2.47 ^{a}	0.08 ^{b}	223	45.2 ^{a}	7.4 ^{b}	77.6	0.36 ^{b}	0.25 ^{b}	0.94 ^{b}	24.4
GP	0.60	0.46	0.51 ^{b}	1.55 ^{b}	1.12 ^{a}	185	38.2 ^{ab}	10.4 ^{a}	70.2	0.60 ^{b}	0.22 ^{b}	1.30 ^{ab}	30.2
RR	0.52	0.45	0.25 ^{c}	1.33 ^{b}	1.01 ^{a}	216	27.4 ^{b}	10.2 ^{a}	86.2	1.04 ^{a}	0.41 ^{a}	1.88 ^{a}	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 ^{a}	0.39	0.53 ^{a}	3.06 ^{a}	0.24 ^{b}	129.8 ^{b}	46.8 ^{a}	5.5	83.2	0.10 ^{a}	0.19 ^{a}	1.82	25.8
GP	0.21 ^{a}	0.35	0.38 ^{b}	1.75 ^{b}	1.43 ^{a}	83.6 ^{b}	33.0 ^{ab}	5.6	60.4	0.50 ^{a}	0.14 ^{a}	2.26	34.0
RR	0.33 ^{b}	0.37	0.20 ^{c}	1.76 ^{bc}	1.56 ^{a}	162.4 ^{a}	25.6 ^{b}	5.4	100.0	1.44 ^{b}	0.40 ^{b}	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 ^{a}	2.58 ^{a}	0.11 ^{b}	202	44.7 ^{a}	7.1	78.2	0.29 ^{b}	0.24 ^{b}	1.13 ^{b}	24.1 ^{a}
GP	0.42	0.42	0.45 ^{b}	1.65 ^{b}	1.26 ^{a}	138	36.2 ^{ab}	8.2	65.9	0.49 ^{b}	0.18 ^{b}	1.71 ^{a}	37.0 ^{a}
RR	0.46	0.42	0.23 ^{c}	1.49 ^{b}	1.26 ^{a}	197	26.5 ^{b}	8.5	91.6	1.21 ^{a}	0.41 ^{a}	2.04 ^{a}	6.7 ^{b}
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 ($p < 0.05$).

4.4 Discussion

Contrasting morphology, nutritional/fertility requirements, and relative growth rates of different tropical pastures affects photosynthesis (Ludlow & Wilson, 1971; Dias-Filho, 2002; Pedreira et al., 2015), which was also reflected in the present study. The photosynthetic efficiency (φ) characterises the ability of the plants to assimilate CO_2 under low light conditions. The greater φ 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 φ was reported for *B. brizantha cv.* Marandu under full sunlight (0.044 µmol photon^{-1}) and shaded plants (0.052 CO_2 µmol photon^{-1}) and for GP (0.049 CO_2 µmol photon^{-1}) (Pedreira et al., 2015). However, φ value of GP and RR were below the previously reported values (Ludlow & Wilson, 1971; Dias-Filho, 2002) and also the generally accepted φ for C_4 species (0.054 CO_2 µmol photon^{-1}) (Dias-Filho, 2002). The maximum photosynthetic rate reported in the present study agreed with other studies at equivalent temperature and CO_2 concentrations (Ludlow & Wilson, 1971; Fisher & Kerridge, 1996; Sonawane et al., 2017). 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 (Ludlow & Wilson, 1971; Fisher & Kerridge, 1996; Dias-Filho, 2002), 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 CO_2 fixation under sufficient light and CO_2 concentrations. Photosynthetic efficiency for CO_2 explains the efficiency of a plant to fix C under conditions of low CO_2 concentration. This combination of higher A_c and β 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 CO_2 dependence of photosynthesis. As V_{cmax} and J_{max} limit the photosynthetic rate at low and high CO_2 concentrations, respectively (Onoda et al., 2004), the greater biomass accumulation results of GP in present study is consistent with the high β reported for GP and the observed lower β 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 (Lemaire et al., 2009). Tropical pasture growth in subtropical regions is limited at times due to occasional frost, shorter day lengths and low temperature (Boschma et al., 2015), 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 (Lawes & Robertson, 2008). Ivory & Whiteman (1978) 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 10–15 °C while maximum growth occurred at 29–35 °C. Furthermore, relatively shorter day length decreased the light interception (Table 4.4) 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 (Argel et al., 2007; Vendramini et al., 2012; Hare, 2013a; Pequeno et al., 2015; Silva et al., 2016), 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 (Argel et al., 2007; Simeao et al., 2021), and observed canopy structure parameters of the present study confirmed its superior agronomic performances reported in other tropical and subtropical areas around the world (Inyang et al., 2010; Vendramini et al., 2012; Hare, 2013a; Moreno et al., 2021; Nouhoun et al., 2021; Pequeno et al., 2015; Silva et al., 2016). In addition, the higher forage yield of GP explains the forage-yielding potential of the genus *megathyrsus* explained elsewhere (Sollenberger et al., 2020). 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 (Sollenberger et al., 2020) 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 4.2b, Table 4.3). Given that BM is a relatively new grass to the Australian subtropical environment, no studies have yet compared it with RR and GP (Ward et al., 2012; Descheemaeker et al., 2014; Thomas et al., 2014). However, Lawes et al. (2014) 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. (2012) 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 (Lawes & Robertson, 2008; Pembleton et al., 2009; Ward et al., 2012), 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 (Pequeno et al., 2015) 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 (Argel et al., 2007; Hare, 2013a; Pequeno et al., 2015; Silva et al., 2016; Pedreira et al., 2017), 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 (Sollenberger & Burns, 2001). 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 pseudo-stem or stem to leaf ratio (Hodgson, 1982). 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 (Benvenutti et al., 2016). The decrease in tropical forage quality with advancing plant maturity is well elucidated when analysing the entire forage structure (Hare, 2013a; Vendramini et al., 2014; Pequeno et al., 2015; Sollenberger et al., 2020). 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 (Vendramini et al., 2012; Vendramini et al., 2014; Pequeno et al., 2015; Sollenberger et al., 2020; Moreno et al.,

2021) . The reason for BM producing relatively higher quality herbage is predominantly associated with its plant morphological composition (high leaf: stem) (Argel et al., 2007). 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 non-structural carbohydrates present in the plant. Non-structural 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 (Wilson, 1975). There are interspecies variations in fat content in tropical forages (Khan et al., 2015) 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^{-1} DM when cutting between 2–8 weeks (López et al., 2000) 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 (Argel et al., 2007).

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 (NRC, 2001). Of all three pastures, BM contained the highest concentrations of minerals (Table 4.6), with its greater Mg, K, Fe, Zn concentration in leaf and stem. All pastures appeared to be inadequate in Ca and Na concentrations (López et al., 2000; Argel et al., 2007). 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 Esechie (1992), 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 (McNeill et al., 2002). The optimum DCAD value for lactating cows reported in NRC is in the range of +23 to +30 mEq 100 g^{-1} of dietary DM (NRC, 2001). West et al. (1991) reported increases in milk production up to a DCAD of +32.4 mEq 100 g^{-1} irrespective of the seasonal influences. In the current study, BM has an ideal DCAD value (+24.1 mEq 100 g^{-1}) range around the value reported by NRC (NRC, 2001) 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^{-1}) and well below (+6.7 mEq 100 g^{-1}) 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 (Chan et al., 2005; Apper-Bossard et al., 2006).

4.5 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.

Chapter 5

Modelling of tropical pasture growth using DairyMod-SGS: Model parameterisation and validation across multiple environments

This chapter has been submitted and currently under review in

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Abstract

Tropical forages are the primary feed source for livestock production in tropical and subtropical regions. Biophysical modelling has been an effective tool to explore the likely performances of forage species under different edaphoclimatic and agronomic management practices. The existing models are lacking in parameterised and validated tropical pastures, thus hindering their use for tropical and subtropical regions. The aims of this study were to parameterise the DairyMod-SGS, a mechanistic biophysical pasture model and robustly validate the species-specific parameters for the prediction of the growth of the three tropical pastures, *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). The model was calibrated using measurements of biomass components, canopy structure, and carbon assimilation collected from a field experiment at the Gatton Research Dairy Farm (27° 54' S, 152°33' E, 89 m asl) Queensland, Australia. The model was tested extensively using the published data from a diverse set of environments and management practices (16 data sets, 32 experiments, 14 different locations across South America, North America, Australia, and Africa). In the model parameterisation stage, DairyMod-SGS pasture model predicted the above-ground biomass with good agreement for all tropical pastures with a high R^2 of 0.92, 0.98, 0.74 and low RMSE of 341, 583, 848 kg DM ha^{-1} for BM, GP and RR, respectively. The model agreement was good for the validation data with R^2 of 0.86, 0.80, 0.87 and RMSE of 954.5, 790.5, 633.2 kg DM ha^{-1} for the BM, GP and RR, respectively. The model prediction of leaf and stem partitioning was relatively poor, and the model also struggled to simulate realistic pasture growth in Mediterranean and desert environments ($R^2 < 0.50$). The present study has improved the robustness and accuracy of DairyMod-SGS in relation to tropical pastures. Our robust and widely tested model can be successfully used for broader explorations of tropical pastures for improving livestock production systems in the tropics and subtropics.

Keywords: Tropical pasture modelling, *Brachiaria* Mulato II, Gatton panic, Rhodes grass Reclaimer, DairyMod-SGS pasture model

5.1 Introduction

Globally, warm-season (C_4) perennial grasses predominate in the tropical and subtropical climates being the primary source of feed for ruminants (Cooke et al., 2020) responsible for 50% of beef and 40% of milk production worldwide (Simeao et al., 2021). Furthermore, the distribution of C_4 grasses is likely to expand into more areas where they are not currently present, due to the effect of atmospheric warming associated with changing climate (Sage & Kubien, 2003). Therefore, these tropical and subtropical grasses have a high potential to feed ruminants and supply the ever-growing global demand for animal protein. Despite this potential, scarcity of both consistent quantity and nutritive value of livestock feed are often revealed as a major constraint. According to Ayele et al. (2012), one of the main approaches to address the feed scarcity and deliver quality feed on a consistent basis has been to develop improved forage options and evaluate them for their yield, nutritive value and impact on animal productivity. Further, integration of these improved forage varieties into the existing feeding practices can improve the productivity (Paul et al., 2020), and potentially decrease the environmental footprint, of tropical forage-based livestock production systems (Rao et al., 2015).

Pasture models have been an effective tool to understand agricultural systems and interactions among edaphic, climatic and agronomic components. These models can simulate pasture growth and complement expensive field research by predicting the likely performance of forage species under a range of soil, climate, and management strategies. There are a number of different simulation models including DairyMod-SGS (Johnson, 2008), Agricultural Production Systems Simulator (APSIM) (Holzworth et al., 2014), GrassGro (Clark et al., 2000), GRASP (Littleboy & Mckeon, 1997) and CROPGRO (Pedreira et al., 2011). Despite these models having been extensively parameterised for crops and temperate grasses, they have not been widely used in most tropical areas

(Andrade et al., 2016; Silva & Giller, 2021). According to Andrade et al. (2016), there are only a few empirical models that can successfully predict the growth and herbage accumulation of genera *Megathyrsus* (Pezzopane et al., 2012; Araujo et al., 2013; Moreno et al., 2014) and *Brachiaria* (Cruz et al., 2011; Pezzopane et al., 2018) , however, they are location specific, which limits their extrapolation as they do not consider the underlying physiological and physical principles of pasture growth. However, when the physiological processes are well understood, especially for newer, more widely used cultivars, process-based pasture models can be used to mathematically describe the physiological, physical and biochemical processes (Hunt & Boote, 1998; Boote et al., 2013).

Different pasture species have their optimum growing conditions, responses to water and nutrient requirements due to differences in genotypic-dependent physiological behaviours. Consequently, pasture-specific parameters are required, if a model is applied to simulate the pasture performance under specified soil, climate, and management conditions (Jones et al., 2015). Many modelling platforms are being used to understand the processes involved in pasture growth. Among them, DairyMod-SGS is a mechanistic biophysical grazing system simulation model which models pasture growth, utilisation by grazing animals, animal growth and production, soil water, and nutrient dynamics under different pasture management (irrigation, fertiliser application, harvesting for silage or hay and grazing) (Johnson et al., 2008). The pasture growth module is the core to DairyMod-SGS (Johnson et al., 2008) and evolved from the initial models described by Johnson & Parsons (1985), Johnson & Thornley (1985), Parsons et al. (1988), Thornley & Johnson (1990), Cannell & Thornley (2000), Thornley et al. (2007) and Johnson et al. (2010). The model has predicted the growth dynamics of temperate forage species across a range of climates, soil types, and management in Australia (Cullen et al., 2008; Cullen et al., 2009; Rawnsley et al., 2009; Chapman et al., 2011; Christie et al., 2014; Christie et al., 2018; Perera et al., 2020), New Zealand (Cullen et al., 2008; White et al., 2008; Jenna, 2015), Argentina (Berger et al., 2014), and South Africa (Wayne. et al., 2016). Limited studies on the DairyMod-SGS modelling of tropical regions are reported except the recent study in southern Africa (Svinurai et al., 2021). The latest version of DairyMod-SGS (version 5.8.2) has the flexibility to simulate tropical pasture species (generic C_4, native C_4, native C_4 low quality and Rhodes grass). Johnson et al. (2003), Perera et al. (2020) and Svinurai et al. (2021) have shown that DairyMod-SGS can realistically simulate the growth and herbage accumulation of C_4 pasture grasses including *Chloris gayana*, *Urochloa mosambicensis* and *Eragrostis curvula* under contrasting edaphoclimatic and management conditions in subtropical Australia and southern Africa.

Currently, there are no species-specific parameters set up for the tropical forages *Brachiaria* Mulato II or Gatton Panic in the DairyMod-SGS pasture model. Furthermore, the available Rhodes grass model needs to be more widely validated. Parameterising and more widely validating the DairyMod-SGS pasture model for a wider range of tropical pasture species would expand the application of the model, and also provide more opportunities to explore the likely performances of newer forage options for improving livestock production in the tropics. The objectives of the present study were: (i) to develop and implement species-specific parameters for the tropical pasture species *Brachiaria* Mulatto II and Gatton Panic in DairyMod-SGS, and (ii) to robustly validate species-specific parameters for the prediction of the growth of the three tropical pastures *Brachiaria* Mulatto II, Gatton Panic and Rhodes grass using previously published and unpublished data from different sites, climates and management conditions.

5.2 Materials and methods

5.2.1 Pasture-specific parameter development

The data used to develop the pasture-specific parameters and calibrate the DairyMod-SGS pasture model for tropical pasture; *Megathyrsus maximus* 'Gatton Panic' (GP) and *Brachiaria ruziziensis x B. decumbens x B. brizantha* '*Brachiaria* Mulato II' (BM) were collected in a field experiment conducted in Gatton Research Dairy (27° 54' S, 152°33' E, 89 m asl) Queensland, Australia. The climate at this location is sub-humid and subtropical with long hot summers (28–33°C) and short mild winters (6–20°C) with an annual average rainfall of 763 mm. 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%) (Isbell, 2016). Full experimental details including experimental design, pasture species, their agronomic management practices and quantification of herbage mass, canopy structure parameters measurements and compositional analysis were described in Jayasinghe et al. (2022b) (Chapter 4), so only details related to pasture-specific parameter development are provided here.

Tropical pasture root systems in each plot were sampled on 15 April 2021 using a 95 mm core root corer. Soil cores (n=2) were taken in fully established swards avoiding areas of low plant population and 1 m from the edge of the plots. Soil cores to a depth of 1000 mm were taken and cut into lengths of 0–100, 100–200, 200–300, 300–500, 500–700 and 700–1000 mm. Root subsamples were washed through a 2 mm mesh and dried at 70°C for 48 hrs to estimate root dry weight. Subsequently, relative root distribution (Equation. (5.1)) was estimated to derive the root parameters (depth for 50% relative root mass ($d_{r,h}$) using a scaling parameter (q_r)) (Supplementary Figure 5.3).

$$f_r(z) = \frac{1}{1 + \left(\frac{z}{d_{r,h}}\right)^{qr}} \qquad 5.1$$

Where

$d_{r,h}$= depth for 50% relative root mass (cm)

q_r = scaling parameter (unitless)

Root samples were then ground to pass through a 1 mm screen and a subsample (~50g) of each of the three tropical pastures were separately analysed for nitrogen (N) at Dairy One Laboratory (Ithaca, NY)(DairyOne, 2020).

The spatial average of photosynthetically active radiation (PAR) transmitted through the canopy was measured immediately before each harvest (n = 5) using a MQ-301 light meter (Apogee Instruments, Inc, Logan, Utah, USA). In each plot, 2 readings of incoming PAR (PAR_i) above the canopy level and 8 readings of transmitted PAR (PAR_t) at ground level (placing the quantum sensor bar close to the soil between the pasture clumps) were taken. Measured canopy PARs were used to calculate the fraction of PAR intercepted (I) by the canopy and subsequently the light extinction coefficient (k) as shown in Equation. (5.2). Leaf area index data were used from Jayasinghe et al. (2022b).

$$k = -\left[\frac{ln\left(1 - \frac{I}{100}\right)}{LAI}\right] \qquad 5.2$$

Where

k = light extinction coefficient (unitless)

I = photosynthetically active radiation interception (%)

LAI= leaf area index ($m^2\ m^{-2}$)

Net leaf carbon exchange measurements were completed on 11 February 2021 and 12 February 2021 at the pre-harvest stage with a portable photosynthesis meter, model LI-6400XT with broad leaf chamber and LED light source (LI-COR Biosciences, USA) according to the method described in Jayasinghe et al. (2022b). Photosynthetic light response curves were fitted using a non-rectangular hyperbolic model framework (Johnson et al., 2010) (Equation. 4.3). A fit was made for each pasture species separately and parameters, maximum light-saturated photosynthesis rate (P_m), and dark respiration rate (R_d) were determined (Supplementary Figure 5.1).

Measured photosynthetic response to CO_2 was fitted for a non-rectangular hyperbolic function (Johnson et al., 2010) (Equation.5.3) and $f_C(C)$ at saturating CO_2 and $f_C(C)$ at double ambient CO_2 concentration were derived (Supplementary Figure 5.2).

$$f_C(C) = \frac{\beta C + f_{C,m} - \sqrt{\left(\beta C + f_{C,m}\right)^2 - 4\theta_c \beta C f_{C,m}}}{2\theta_c} \qquad 5.3$$

where

C = atmospheric CO_2 concentration (ppm)
$F_{C,m}$ = maximum CO_2 response functions (unitless)
β = CO_2 function efficiency/ initial slope (unitless)
θ_c = curve convexity.(unitless)

All curve fitting was performed using the R (version 4.0.5) statistical computing software (RCoreTeam, 2021).

5.3 Parameterisation of DairyMod-SGS pasture module for tropical pastures

Generic C_4 and Rhodes grass parameters of the model were adopted as a reasonable starting point in this study to parameterise the model for BM, GP and Rhodes grass Reclaimer (RR). To develop the species-specific parameters, we used the data collected from the field experiment (Chapter 4) and values reported in the literature and adjusted to obtain appropriate model behaviour following the directions of Hunt & Boote (1998) and Johnson (2008). In agreement with White et al. (2008), Berger et al. (2014) and

Svinurai et al. (2021), some of the parameters in the C_4 generic and Rhodes grass were left as default (later described), assuming these physiological parameters do not significantly differ within C_4 species.

The climate data (rainfall, maximum and minimum temperature) were collected from an automatic weather station at the experimental site, and entered on a daily basis in the weather file for the model. Solar radiation for the experimental period was acquired through the University of Queensland, Gatton weather station which was 0.9 km from the experimental site (Table 5.1). The soil profile was characterised using the measured data and supplementing the data collected by Powell (1982) and APSoil database (https://www.apsim.info/apsim-model/apsoil/) (APSoil number 037) (APSoil ver. 3.37) (Table 5.2).

Table 5.1. Long-term (1913–2021) and monthly observed averaged weather data from November 2020 to November 2021 at the Gatton Research Dairy, Queensland, Australia. (T max = maximum temperature, T min = minimum temperature, SR = solar radiation)

Weather variable	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct
					2020–2021[1]							
T Max (°C)	33.1	31.4	30.3	31.2	28.0	24.6	22.8	21.0	20.7	24.0	26.3	29.8
T Min (°C)	16.8	19.4	18.5	18.6	18.0	13.9	11.1	6.8	6.9	7.2	8.9	14.6
Rainfall (mm)	19.6	111.0	154.0	37.2	134.4	107.8	100.1	24.0	83.0	5.0	12.0	120.0
SR (MJm^{-2})	27.4	21.4	22.8	21.1	16.8	15.9	13.5	10.9	11.9	15.5	18.5	20.5
					1913–2021 (98 years)[2]							
T Max (°C)	30.3	31.4	31.7	30.8	29.6	27.2	23.8	27.2	23.8	21.1	20.8	22.5
T Min (°C)	16.0	18.1	19.1	19.0	17.3	13.7	10.2	13.7	10.2	7.6	6.3	6.7
Rainfall (mm)	77.3	98.2	109.5	99.1	79.2	47.9	44.9	44.9	41.3	36	26.5	34.6
SR (MJm^{-2})	24.0	24.2	23.7	20.9	19.0	16.7	13.5	19.0	16.7	13.5	11.8	13.1

[1] Automatic weather station setup in the experimental site

[2] SILO (Scientific Information for Land Owners) database Jeffrey et al. (2001)

Table 5.2. Soil profile of the tropical pasture experimental site at the Gatton Research Dairy, Queensland, Australia (FC = field capacity, SAT = saturated soil limit, WP = permanent wilting point, AD = air dry soil, OM = organic matter, BD = bulk density, K_{sat} = saturated hydraulic conductivity)

Soil horizon depth (mm)	FC	SAT	WP	AD	²OM	BD	Clay	$^1K_{sat}$	$^2NO_3^{-1}$	$^2NH_4^{+3}$
	(%)	(%)	(%)	(%)	(%)	(g cm^{-3})	(%)	(cm day^{-1})	(mg kg^{-1})	(mg kg^{-1})
A (0–300)	43	47	26	13	1.33	1.32	48	9.9	22	1.7
B1 (300–1000)	49	51	28	23	1.15	1.30	42	3.2	34	4.7
B2 (1000–1400)	54	38	31	26	0.96	1.23	52	2.8		

$^1K_{sat}$ was extracted from the point data of Australian Soil Resource Information System (ASRIS) (http://www.asris.csiro.au/mapping) ²Data from the analysed soil samples on 07 September 2020.

The first step for the DairyMod-SGS pasture model parameterisation was to parameterise the photosynthesis submodule which lies as the core of the pasture submodule and acts as the main primary source of carbon. The rate of single leaf gross photosynthesis at saturating PAR (P_m), respiration at reference conditions (1000 PPF µmol^{-1} mol^{-1}m^{-2}, 400 ppm CO$_2$, 30°C), CO$_2$ function ($f_C(C)$) at saturating CO$_2$ and $f_C(C)$ at double ambient CO$_2$ concentration were directly estimated for three pastures using the measured carbon exchange data (Equation. 4.3 and Equation. 5.3, respectively). The parameters that describe the response of leaf photosynthesis to temperature (minimum temperature for P_m , optimum temperature for P_m and temperature curvature coefficient (θ_T)) were not estimated in the present study. Therefore, generic C$_4$ parameters were modified to represent the species-specific responses of BM (Pequeno, 2014; Moreno, 2017) and GP (Lara et al., 2012; Araujo et al., 2013; Descheemaeker et al., 2014) (Table 5.4). Default Rhodes grass parameters were set up for RR (Johnson et al., 2008). Canopy gross photosynthesis in the model is expressed as the sum of leaf photosynthesis through the canopy and is therefore influenced by the light attenuation through the canopy. Light extinction coefficient (*k*) explains the canopy light interception and attenuation and the value for *k* was estimated separately (Equation. 5.2) for BM, GP and RR using the measured canopy light interception data. In agreement with other DairyMod-SGS default C_4 parameter sets, respiration parameters (cell wall and protein growth efficiency and maintenance coefficient) were set to the C_4 generic defaults for BM, GP and RR (Table 5.4). Low temperature stress was implemented for all tropical pastures with default starting values (initial stress at 7°C, full stress at 3°C) and manually optimized using the measured biomass data over the summer to early winter (Moreno et al., 2014) (Table 5.4).

The second step was to add the parameters to the canopy structure submodule to describe the species-specific canopy responses during regrowth. The parameters describing plant structure during regrowth (carbon partitioning to shoot with no water or N stress, leaf fraction of new shoot growth, specific leaf area (SLA) and number of leaves per tiller) were added from the measured pasture regrowth data of BM and GP (Table 5.4). Plant senescence parameters were based on the values reported by Pequeno (2014) and Moreno (2017) for *Brachiaria* and Descheemaeker et al. (2014) and Lara et al. (2012) for *Megathyrsus*, assuming values do not significantly vary between cultivars within the same species. Senescence parameters for RR were set to defaults of Rhodes grass in the model. Plant N composition (leaf optimum and maximum N%) values were adapted from previous studies of BM (Pequeno, 2014; Moreno, 2017) and GP (Descheemaeker et al., 2014). Non-leaf shoot scale factor and root scale factor for N content were estimated using the N values of the leaf, stem and root samples analysed at Dairy One Laboratory. Similarly, plant non-structural carbohydrate and fat percentage parameters were estimated from the analysed leaf and stem samples (Jayasinghe et al., 2022a). Leaf appearance and temperature response are explained in the model using four parameters (minimum leaf appearance interval, minimum temperature for leaf appearance, and temperature for maximum leaf appearance rate and curvature coefficient). These values were not measured in the field study, but were adapted from previous studies with BM (Pequeno, 2014; Moreno, 2017; Bosi, 2018) and GP (Lara et al., 2012; Araujo et al., 2013; Descheemaeker et al., 2014). Defaults values in DairyMod-SGS were used for RR. Root distribution parameters were directly estimated from the measured root data (Equation. 5.1).

The third step was to add management operations to the management submodule. All simulations of model parameterisation were undertaken as “cut trials” in a 1 ha field using an average residual weight across 5 harvests. All the experimental conditions (mulching, N fertilisation, irrigation) during the data collection period were included in the management submodule. Simulations were carried out with soil carbon and N dynamics implemented, and initial nitrate, ammonium and organic matter were adjusted based on the measured soil data (Table 5.2). Initial soil water content was set to reflect the local conditions over the winter, with the water content in the upper layer (0–300 mm) at the crop lower limit and the lower layer (1000–1400 mm) at field capacity (Descheemaeker et al., 2014).

Finally, DairyMod-SGS was calibrated by adjusting the parameters for three tropical pastures through an iterative process until the estimated values of forage mass, leaf mass, stem mass and LAI achieved the best possible fit with the observed values from the field experiment. In general, canopy structure, root distribution, photosynthesis, temperature function, and temperature stress parameters were changed in the range of 10–20%, 40–60%, 35–45%, 5–20%, and 55–130%, respectively (Supplementary Table 5.1).

5.4 Model validation

The parameterised DairyMod-SGS model was tested using independent data sets collected from multiple locations (Figure 5.1). Data sets comprised previously published and unpublished experiments of tropical pastures grown in different edaphoclimatic and management conditions, allowing the model parameters to be robustly validated for different aspects of pasture growth (Table 5.3). Daily meteorological data (maximum and minimum temperatures, rainfall, solar radiation) for each location were sourced from the closest meteorological station to the experimental site and where no database was available for a given experimental location, climate data were retrieved from NASA Prediction of Worldwide Energy Resource (POWER)-Climatology Resource for Agroclimatology (https://power.larc.nasa.gov) using the R package *nasapower* (Sparks, 2018) and Climate Hazards group Infrared Precipitation with Stations (CHIRPS) data set (Funk et al., 2015) using the R package *chirps* (Sousa et al., 2020).

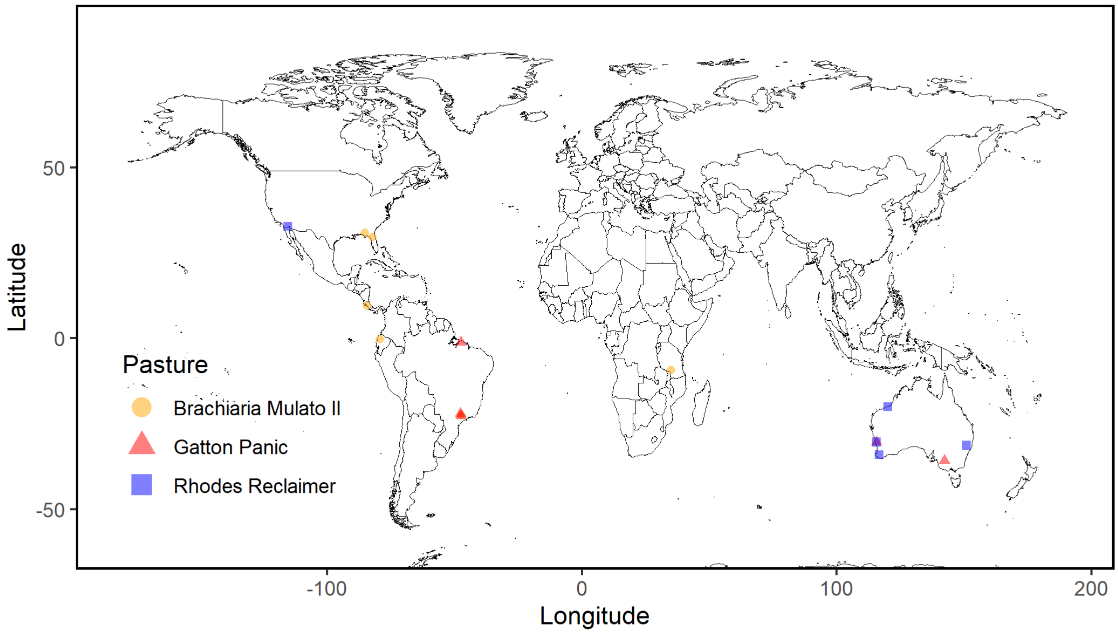


Figure 5.1. Map of the independent tropical pasture data sets used for DairyMod-SGS validation in the present study (some points in Australia and Brazil represent more than one data set).

Table 5.3. Description of data sets, locations and pasture management used for validation of BM, GP and RR parameterisations using the DairyMod-SGS (BM = *Brachiaria* Mulato II, GP = Gatton Panic, RR = Rhodes grass Reclaimer).

Site characteristics			Pasture management			No. of observations	Reference
Location (lat., long.)	Climate	Soil type	Irrigated/ Rainfed	N fertiliser (kg ha^{-1})	Defoliation (days)	Biomass	
			Brachiaria Mulato II				
Sao Paulo, Brazil (–22.56, –47.40)	Tropical	[5]Kandiudalfic Eutrudox	Irrigated	31–42	28	22	Pequeno (2014)
					42	14	
			Rainfed		28	23	
					42	15	
Gainesville, USA (29.65, –82.32)	Subtropical	[5]Entisol Thermic	Rainfed	120	28 Full sun	10	Moreno (2017)
			Rainfed		28 Shade 55%	10	
					28 Full sun	10	
				30	28 Shade 55%	10	
Gainesville, USA (29.65, –82.32)	Subtropical	[5]Entisol Thermic	Rainfed		35–42	7	Vendramini et al. (2012)
			Rainfed	40			
Atenas, Costa Rica[1] (9.57, –84.24)	Tropical	[4]Inceptisol	Rainfed	No fertiliser	35	14	CIAT (2004)
					56		
Santo Domingo, Ecuador[1] (–0.22, –79.26)	Tropical	[4]Andosol	Rainfed	120	14	2	Garay et al. (2017)
					28	2	
					42	2	
					56	2	
					70	2	

Site characteristics			Pasture management			No. of observations	Reference
Location (lat., long.)	Climate	Soil type	Irrigated/ Rainfed	N fertiliser (kg ha^{-1})	Defoliation (days)	Biomass	
Ikuna, Tanzania[2] (–9.20, 34.91)	Tropical	[5]Lixisols	Rainfed	390	30–90	8	Korir et al. (2021)
Gatton Panic							
Sao Paulo, Brazil[1] (–22.70, –47.50)	Tropical	[5]Kandiudalfic Eutrudox	Irrigated	36	28	4	Lara et al. (2012)
Sao Carlos, Brazil[1] (–21.96, –47.84)	Subtropical	[5]Oxisol	Irrigated	70	28–58	32	Araujo et al. (2013)
Hopetoun, Australia (–35.71, 142.27)	Mediterranean	Calcarosols	Rainfed	25	30–60	19	Descheemaeker et al. (2014)
Igarape-Acu, Brazil[1] (–1.12, -47.60)	Subtropical	[5]Ferrosol	Rainfed	17	14	35	Macedo et al. (2021)
				25	21	23	
				34	28	17	
				35	35	14	
				42	42	11	
				49	49	10	
Badgingarra, Australia (–30.34, 115.53)	Mediterranean	[5]Bleached-Orthic Tenosol	Rainfed	130	28–42	16	Moore et al. (2014)

Table 5.3. Cont.

Site characteristics			Pasture management			No. of observations	Reference
Location (lat., long.)	Climate	Soil type	Irrigated/ Rainfed	N fertiliser (kg ha^{-1})	Defoliation (days)	Biomass	
			Rhodes grass				
Duri, Australia (–31.26, 150.86)	Mediterranean	[5]Red Chromosol	Rainfed	0 50 100	14	30 30 30	Boschma et al. (2017)
Badgingarra, Australia (–30.34, 115.53)	Mediterranean	[5]Bleached-Orthic Tenosol	Rainfed	130	28–42	16	Moore et al. (2014)
Kojonup, Australia –34.00, 116.63)	Mediterranean	[5]Brown Chromosol	Rainfed	160	28–42	6	Moore et al. (2014)
Meloland, USA (32.80, –115.44)	Desert	Imperial soils	Irrigated	50	30–40	5	Bachie (2018)
Pilbara, Australia[3]	Tropical	Red deep sandy soil	Irrigated	23.75	8–47	31	(Paynter S. and Candy R., unpub. Data)

[1] Climate data were retrieved from NASA Prediction of Worldwide Energy Resource (POWER)-Climatology Resource for Agroclimatology (https://power.larc.nasa.gov)

[2] Rainfall data were retrieved from CHIRPS data (https://www.chc.ucsb.edu/data/chirps).

[3] A high input pasture production system irrigated with a centre pivot and receives a 23.75 kg ha^{-1} of N per every 1000 kg ha^{-1} of pasture grown. The exact coordinates are not provided at the request of the data provider.

[4] Soil profile data were extracted from the World Soil Information Service (WoSIS) soil profile database (https://www.isric.org/explore/wosis).

[5] Soil initial inorganic N and organic matter status were modified to reflect the values observed in the field.

For the 55% shaded experiment (Moreno, 2017) (see Table 5.3), solar radiation was reduced in the meteorological inputs by multiplying the incident radiation by a factor of 0.45. Latitude and elevation of the experimental sites were also included along with the climate data to accurately simulate the day length and atmospheric pressure of the experimental locations. Soil data for each location were extracted from the details described in the experiment or respective database outlined. Where such soil profile data were not readily available in the experiment, the World Soil Information Service (WoSIS) soil profile database (https://www.isric.org/explore/wosis) was used to retrieve the point based soil profile data using the R package *soilDB* (Beaudette et al., 2022). Soil data for the locations in Australia were sourced from ASRIS and APSoil (APSoil ver. 3.37) databases. Where data were available, initial soil inorganic N and organic matter status were modified to reflect the values observed in the field. Management operations (mowing, N fertiliser management and irrigation) in the simulations were set to mimic those applied in the field. Model outputs of total above-ground pasture dry matter (DM) yield or accumulated pasture DM yield (total DM–residual DM) from each simulation were compared with observed data to assess the DairyMod-SGS model performance against the validation data sets.

5.5 Model performance assessment

Observed and simulated data were visually compared using scatter plots, time series and Bland-Altman plots. Subsequently, observed, and simulated data were statistically analysed to evaluate the DairyMod-SGS model performance in terms of simulated total biomass, leaf and stem weight and LAI. In the validation stage, analyses were carried out for model simulations of the total biomass or biomass accumulation of each pasture. Later, analyses were partitioned to test the model performance in each location to be able to identify the sources of variability within the broader model testing data set. All statistical analyses were performed using the R (version 4.0.5) statistical computing software (RCoreTeam, 2021). The different statistical indexes (Tedeschi, 2006) were:

a) Mean observed and simulated weights

b) Linear regression and coefficient of determination (R^2)

Observed and modelled values of each variable are subjected to the linear regression analysis followed by the determination of R^2. The model precision was classified as unsatisfactory ($R^2 \leq 0.6$), satisfactory ($R^2 > 0.6$ to ≤ 0.7) good ($R^2 > 0.7$ to ≤ 0.8) and very good ($R^2 > 0.8$).

c) Percent Bias (PB)

Percent bias (PB) measures the average tendency of the simulated values to be larger or smaller than their observed ones. The optimal value of PB is 0.0, with low-magnitude values indicating accurate model simulation. Positive values indicate overestimation bias, whereas negative values indicate model underestimation bias.

The PB is given by:

$$PB = 100 \, \frac{\Sigma_{i=1}^{n} (Ei - Oi)}{\Sigma_{i=1}^{n} Oi} \qquad 5.4$$

d) Nash-Sutcliffe Efficiency (NSE)

The NSE is interpreted as the proportion of variation explained by the fitted line Y = X (Equation 5.6). The NSE equals one when the observed and modelled values are in perfect agreement. The lower bound is negative infinity and if the NSE is negative, the modelled values are worse than the observed mean.

$$NSE = 1 - \frac{\Sigma_{i=1}^{n} (O_i - f\ (E_{1,\ldots}E_p)_i)^2}{\Sigma_{i=1}^{n} (O_i - \bar{O})^2} \qquad 5.5$$

e) Mean Absolute Error (MAE)

Mean absolute error measures the accuracy of continuous data (Equation 5.7). The MAE varies from zero to infinity and zero represents the perfect fitness of modelled and observed data.

$$MAE = \left(\frac{1}{n}\right) \sum_{i=1}^{n} |E_i - O_i| \qquad 5.6$$

f) Root Mean Square Error (RMSE)

Root mean squared error is the square root of the mean of the square of all of the errors (Equation 5.8). It shows how far the modelled values fall from the measured data. The RMSE value with zero indicates the perfect fit

$$RMSE = \sqrt{\left[\left(\frac{1}{n}\right) \sum_{i=1}^{n} (O_i - E_i)^2\right]} \qquad 5.7$$

In addition, simulated N stress (GLFN) and water stress (GLFwater) data obtained from the DairyMod-SGS for each simulation were analysed along with the biomass difference (observed–modelled) to evaluate the performance of the parameterised model to accurately reproduce the reduction in observed biomass due to the soil water and N stress

5.6. Results

5.6.1 The parameterisation for tropical pastures

Parameters that make up the DairyMod-SGS pasture model are presented in Table 5.4, separated by the different submodules, canopy structure and carbon partitioning, plant senescence, plant N composition, leaf appearance, root distribution, leaf and canopy photosynthesis, and temperature stress for each species.

Table 5.4. Pasture-specific parameters of the DairyMod-SGS pasture module parameterised and calibrated for Gatton panic (GP), *Brachiaria* Mulato II (BM) and Rhodes grass Reclaimer (RR) evaluated between 2020 and 2021 at Gatton Research Dairy, Queensland, Australia. The default C_4 grass parameters described in the DairyMod-SGS pasture model by Johnson (2008) are provided for comparison.

Parameters	Unit	Pastures			
		GP	BM	RR	Default C_4
Canopy structure and partitioning					
Carbon partitioned to shoot with no water or N stress	-	82.00	75.00	70.00	70.00
Leaf fraction of new shoot growth (%)	-	70.00	52.00	48.00	60.00
Specific leaf area at ambient CO_2	m^2 leaf kg^{-1}	19.00	22.00	19.00	20.0
Live leaves per tiller	-	4.00	4.00	5.00	5.0
Scale factor for non-leaf turnover rate relative to leaves	-	80.00	80.00	80.00	80.00
Root senescence rate	Fraction day^{-1}	0.80	0.80	2.00	2.0
Transfer of standing dead to litter	Fraction day^{-1}	1.50	2.00	2.00	10.0
Plant nitrogen composition					
Optimum N	-	3.00	3.00	2.80	3.00
Maximum N (%)	-	3.50	4.00	3.50	4.00
Non-leaf shoot scale factor	-	0.50	0.50	0.50	0.50
Root scale factor	-	0.50	0.50	0.50	0.50
Non-structural carbohydrate plus fat: live (%)	-	25.00	25.00	25.00	25.00
Non-structural carbohydrate plus fat: dead (%)	-	15.00	15.00	15.00	15.00
Height					
Maximum height	cm	100.00	50.00	80.00	50.00
LAI for half maximum height	m^2 m^{-2}	2.00	2.00	2.00	2.00
Leaf appearance in response to temperature					
Maximum leaf appearance interval	days	16.00	15.00	15.00	10.00
Minimum temperature	°C	12.00	11.00	10.00	10.00
Temperature for maximum rate	°C	30.00	25.00	25.00	25.00

Table 5.4. Cont.

Parameters	Unit	Pastures			Default
		GP	BM	RR	C_4
Curvature coefficient	-	2.00	1.50	2.00	2.00
Roots					
Root depth	cm	100.00	100.00	150.00	100.00
Depth for 50% root distribution	cm	15.00	15.00	40.00	25.00
Scale factor		3.00	3.00	3.00	3.00
Photosynthesis					
Effective minimum LAI	$m^2\ m^{-2}$	0.50	0.50	0.50	0.50
P_{max} at reference conditions	$\mu mol\ CO_2 m^{-2} s^{-1}$	26.00	29.00	20.00	20.00
Minimum temperature for P_{max}	°C	13.60	15.00	12.00	12.00
Optimum temperature for P_{max} at ambient CO_2	°C	35.00	33.00	35.00	35.0
Temperature curvature coefficient		1.50	1.50	1.50	1.50
CO_2 function					
Value at saturating CO_2	-	1.20	1.18	1.10	1.10
Value at double ambientCO_2	-	1.10	1.08	1.05	1.05
Canopy photosynthesis					
Light extinction coefficient	-	0.55	0.48	0.50	0.50
Respiration parameters					
Cell wall growth efficiency	-	85.00	85.00	85.00	85.00
Protein growth efficiency	-	55.00	55.00	55.00	55.00
Maintenance coefficient	Fraction day^{-1}	2.50	2.50	2.50	2.50
Nitrogen					
N uptake coefficient: NO_3	(g N t $root^{-1}$) ppm^{-1} day^{-1}	200.00	200.00	200.00	200.00
N uptake coefficient: NH_4	(g N t $root^{-1}$) ppm^{-1} day^{-1}	200.00	200.00	200.00	200.00
Respiratory cost of NO_3 uptake	kg C kg N^{-1}	0.60	0.60	0.60	0.60
Potential nitrogen remobilization	0–1 fraction	0.50	0.50	0.50	0.50
Low temperature stress					
Implement		True	True	True	True
Full stress	°C	7.00	5.00	3.00	3.00
Initial stress	°C	11.00	11.00	7.00	7.00

Table 5.4. Cont.

Parameters	Unit	Pastures			Default
		GP	BM	RR	C_4
T-sum for recovery	°C	100.00	100.00	100.00	100.00
Transpiration					
Scale factor between WP and FC for onset of water stress	0–1 fraction	0.80	0.80	0.80	0.80
Transpiration reduction at saturation	0–1 fraction	0.50	0.50	0.50	0.50

The calculated k obtained for BM, GP and RR was 0.48, 0.55 and 0.50, respectively. The leaf P_{max} parameters changed between pasture species. The initial model (Equation. 5.3) estimated P_{max} values as 28.90, 25.04, and 15.79 µmol $CO_2m^{-2}s^{-1}$ for BM, GP and RR, respectively, and these were increased during calibration to match with observed data resulting in P_{max} values of 29, 26 and 20 µmol $CO_2m^{-2}s^{-1}$. Respiration at reference conditions varied between pasture species, and values were estimated to be 2.41, 0.90 and 1.50 µmol $CO_2m^{-2}s^{-1}$ for BM, GP, and RR, respectively. The CO_2 function ($f_C(C)$) at saturating CO_2 and the $f_C(C)$ at double ambient CO_2 concentration were changed for BM (1.18, 1.08) and GP (1.20, 1.10) based on the results (Equation. 5.4), but RR was unchanged as the CO_2 function values did not significantly change from defaults (1.10, 1.05). Low temperature stress parameters were optimised based on the observed biomass accumulation data. Initial stress temperature was increased from 7 to 11 for both GP and BM, and full stress temperature was increased from 3 to 7 for GP and from 3 to 5 for BM. These modified temperature parameters showed more realistic tropical pasture growth patterns compared to default temperature parameters towards late autumn and early winter under a subtropical climate (Figure 5.1a-c).

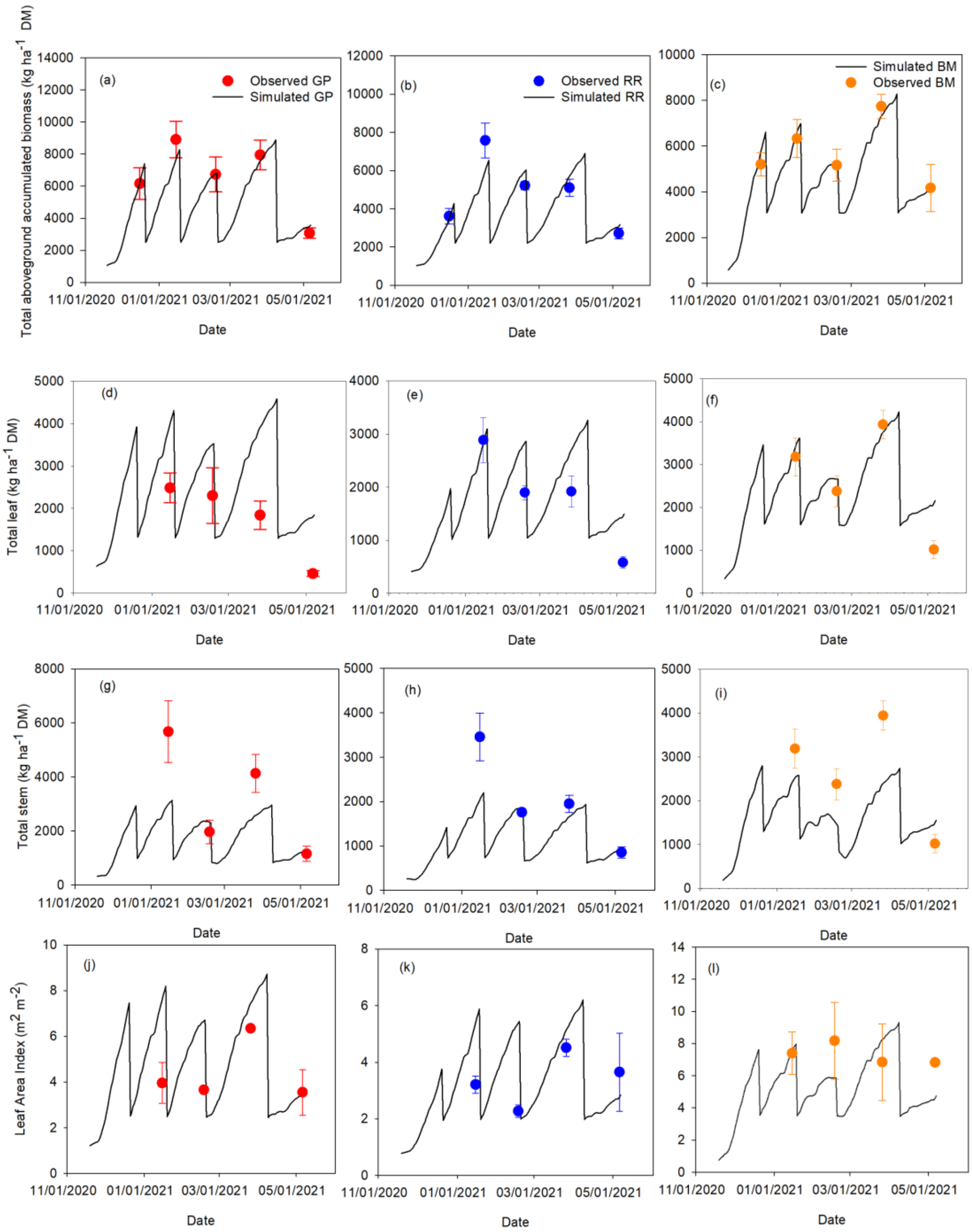


Figure 5.2. DairyMod-SGS pasture model simulations (lines) compared with observations (dots) from calibration experiment at Gatton Research Dairy, Queensland, Australia for *Brachiaria* Mulato II, Gatton panic and Rhodes grass Reclaimer. Error bars represent the standard error of means.

Dry matter partitioning to root growth was assumed to be 30% for the early growth of the sward as the root system was still growing. Therefore, carbon partitioning to above-ground biomass (leaf and stem) and leaf fraction of the new shoot parameters were optimised based on the initial value of 70% using the observed leaf and stem biomass results (Table 5.4). Forage above-ground biomass was simulated with high precision (R^2 between 0.74 and 0.98) and accuracy (NSE between 0.73 and 0.92) for all three tropical pastures (Figure 5.2a-c and Table 5.5). The leaf fraction of the new shoot growth was increased in RR from its default value of 40%, as the new RR cultivar was selected for its higher leaf to stem ratio. Following the modifications to carbon partitioning to leaves, the model simulated the leaf accumulation of tropical pastures with high accuracy (R^2 between 0.74 and 0.97) for BM and RR, however, leaf accumulation of GP was continuously overestimated (Figure 5.2d-e). Conversely, the model simulated the stem accumulation of RR and BM with reasonable accuracy, but failed to realistically capture the GP stem production (Table 5.5). Overall, the model underestimated the stem accumulation of the three tropical pastures, and a large discrepancy between observed and predicted stem accumulation was observed in GP (RMSE 1296.9 kg ha^{-1}), particularly in the second harvest (Figure 5.2g).

Table 5.5. Statistical indexes of total above-ground dry matter (TDM) (kg ha^{-1}), leaf (kg ha^{-1}), stem (kg ha^{-1}), Leaf Area Index (LAI) (m^{2} m^{-2}) for estimates of DairyMod-SGS simulation from the calibration experiment at Gatton Research Dairy, Queensland, Australia for *Brachiaria* Mulato II (BM), Gatton panic (GP) and Rhodes grass Reclaimer (RR).

R^2 = coefficient of determination, MB = mean bias (kg ha^{-1}), RMSE = root mean square error (kg ha^{-1}), NSE = Nash-Sutcliffe efficiency, MAE = mean absolute error (kg ha^{-1}), n = number of records.

Variable	Measured mean	Simulated mean	R^2	MB	RMSE	NSE	MAE	n
BM								
TDM	5718.3	5791.6	0.92	-73.34	341.1	0.92	268.4	5
Leaf	2629.9	2984.7	0.97	-354.8	577.1	0.71	448.5	4
Stem	1665.4	1970.5	0.08	-305.1	608.0	-1.56	413.1	4
LAI	6.2	6.5	0.93	-0.36	1.1	0.77	1.0	4
GP								
TDM	6550.4	6348.0	0.98	202.3	582.9	0.83	418.0	5
Leaf	1634.8	3308.4	0.81	1670.4	1716.8	-2.73	1670.4	4
Stem	3071.9	2333.5	0.81	777.7	1296.9	-3.19	1019.7	4
LAI	6.2	4.9	0.30	-1.3	2.8	-1.82	2.7	4
RR								
TDM	4841.8	4841.4	0.74	0.4	848.6	0.73	693.9	5
Leaf	1822.4	2281.4	0.79	-633.3	749.0	0.16	659.9	4
Stem	2004.2	1519.1	0.72	382.3	725.3	0.39	471.2	4
LAI	3.8	4.3	0.08	-0.8	1.8	-3.06	1.6	4

During the same harvest, observed pasture biomass varied widely between plots. These large discrepancies between the stem (RMSE 1716.8 kg ha^{-1}) and leaf (RMSE 1296.9 kg ha^{-1}) accumulation in GP meant that further calibration to better simulate the biomass partitioning is required, however, this was not possible due to the limited stem and leaf biomass data available. The model simulated the LAI of BM with high accuracy (R^2 =

0.93), however, model estimates of LAI were unsatisfactory for RR and GP (Figure 5.2h-i and Table 5.4), due to the higher variability of observed LAI data (Figure 5.2h-j), although this did not affect the estimated forage mass. This higher variability of LAI may be an effect of sampling errors very often related to leaf folding and leaf position differences.

5.6.2 Model validation

Model performance was statistically validated against independent multi-environment data sets (Table 5.3) for these tropical pastures. The biomass of all three tropical pastures was reasonably well predicted as indicated by the high R^2 (0.80–0.86) (Figure 5.3), NSE score (0.75–0.86) and RMSE values ranging from 633–954 kg DM ha^{-1}. The bias values for all three tropical pastures were below ±12%, but BM yields were often overestimated (11.6 % PB) while the yields for both GP (-4.6% PB) and RR (-6.1% PB) were underestimated (Table 5.6). The modelled and simulated forage mass comparisons for each data set of BM, GP and RR are presented in Supplementary Figures 5.4–5.6. Simulation outcomes showed a generally good visual agreement between these trends and modelled biomass data. This shows that the model was able to capture several trends of tropical pasture growth in the cut-and-carry system, however the model tended to underpredict the biomass accumulation at shorter defoliation intervals (14 days, 21 and 28 days) for BM (Supplementary Figure 5.4c-d) and GP (Supplementary Figure 5.5a-b). The model performance across data sets collected in multiple environments is given in Table 5.6. Although there were differences in model performances between the different data sets comprising different soil, climate and management in contrasting locations, all sites had relatively low RMSE ranging from 263–1124 kg DM ha^{-1}, except in sites Ikuna, Tanzania and Meloland, USA where RMSE was 1444 kg DM ha^{-1} and 2389 kg DM ha^{-1}, respectively. Overall, the model predicted the biomass yield of all three tropical pastures with high accuracy and precision ($R^2 > 0.75$; Table 5.6) at 9 out of 16 sites. In an additional 4 sites, the R^2 ranged from 0.50–0.65, and the biomass was poorly predicted at only 3 sites where the R^2 was below 0.50. The agreement of the model was particularly good in subtropical and tropical environments, which made up 67% of total validation data, as evidenced by a higher R^2 (0.77–0.98). According to Figures 5.4a and 5.4b, the differences between measured and simulated data were well within the ± 2 standard deviations in almost all the tropical and subtropical locations. Generally, the agreement of the model in Mediterranean and desert environments, which made up 33% of total validation data, was observed to be just below the satisfactory rating for model performance, with low R^2 (0.13–0.64), NSE (-6.50–0.26) and RMSE ranging from 138 kg DM ha^{-1} to a very high 5680 kg DM ha^{-1} value, except for the GP data set at Hopetoun, Australia and the high input RR data set at Pilbara, Australia which was shown to be in good agreement with the respective measured biomass data (Table 5.6). This was also evident in the Bland-Altman plot (Figures 5.4b and c), which showed the data points where the difference between measured and simulated data was greater than ± 2 standard deviations for the Mediterranean (Badgingarra, Duri, Kojonup sites in Australia) and desert environments (Meloland, USA).

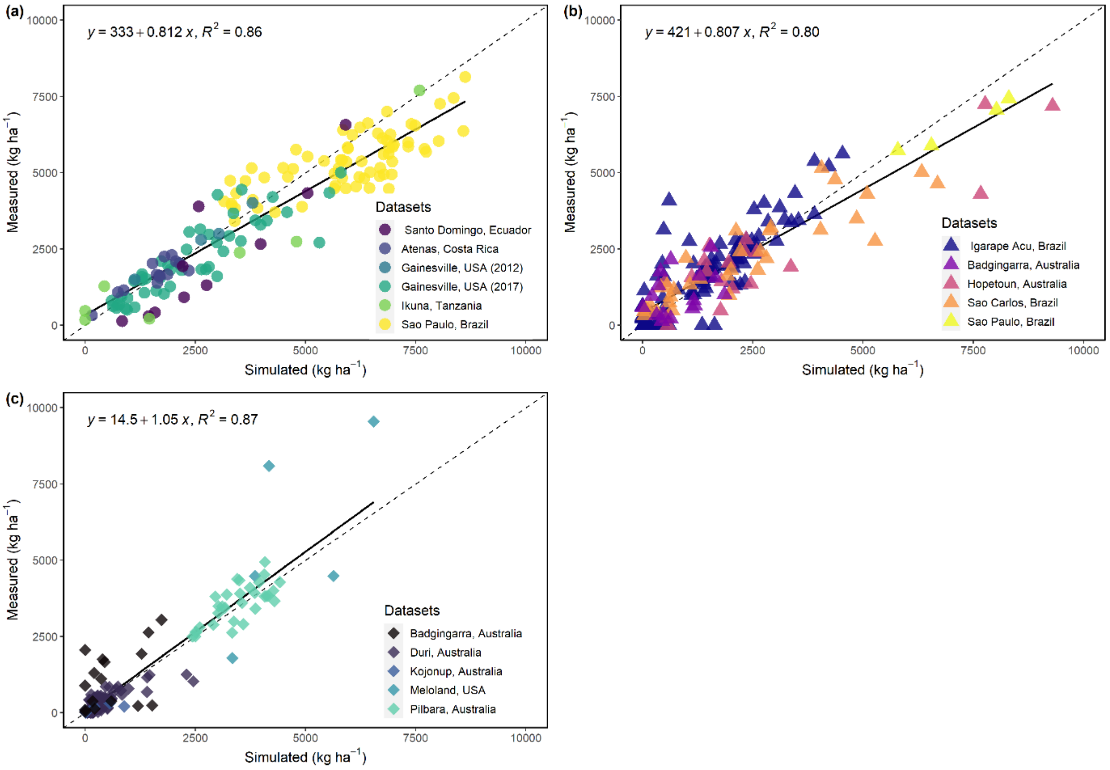


Figure 5.3. DairyMod-SGS simulated vs. observed forage biomass of (a) *Brachiaria* Mulato II, (b) Gatton Panic and (c) Rhodes grass Reclaimer. The solid line represents linear regression and the dotted line represents the 1:1 line. Statistical values for goodness of fit are shown in Table 5.2.

The model agreement statistics were poor across multiple Mediterranean and desert environments. However, time series plots (Supplementary Figure 5.5j and Supplementary Figures 5.6a-i) show that the model was able to capture the growth pattern of tropical pastures (GP and RR) and simulated values are generally closer to the range of observed average biomass ± standard errors. The model failed to realistically simulate the pasture production under long-term Mediterranean climates (Supplementary Figure 5.5j and 5.6h) and generally overestimated the biomass yield.

Table 5.6. Statistical indexes of total biomass production (kg DM ha^{-1}) for estimates of DairyMod-SGS simulation for validation data of *Brachiaria* Mulato II (BM), Gatton panic (GP) and Rhodes grass Reclaimer (RR).

R^2 = coefficient of determination, PB = Percent bias (%), RMSE = root mean square error (kg DM ha^{-1}), NSE = Nash-Sutcliffe efficiency, MAE = mean absolute error (kg DM ha $^{-1}$), n = number of records.

Statistical Indexes	n	Measured mean	Simulated mean	R^2	PB	RMSE	NSE	MAE
BM	153	3569.6	3984.8	0.86	11.6	954.5	0.77	742.5
Santo Domingo, Ecuador	10	2243.5	2861.4	0.82	27.6	1077.4	0.71	1012.2
Atenas, Costa Rica	14	1639.4	1581.2	0.75	-3.6	292.4	0.67	240.1
Gainesville, USA (2012)	4	2825.4	2648.3	0.98	-6.3	229.5	0.93	194.2
Gainesville, USA (2017)	48	2131.5	2385.6	0.77	11.9	685.4	0.67	508.4
Sao Paulo, Brazil	69	5339.4	5931.1	0.56	11.1	1124.2	-0.40	955.4
Ikuna, Tanzania	8	2351.4	3077.2	0.81	30.9	1444.5	0.63	1120.2
GP	181	1829.6	1745.9	0.80	-4.7	791.4	0.75	534.3
Igarape-Acu, Brazil	110	1592.2	1357.4	0.76	-14.7	692.5	0.73	426.5
Badgingarra, Australia	16	1031.2	829.3	0.13	-19.6	741.2	-0.12	608.5
Hopetoun, Australia	19	2338.5	2760.1	0.83	18.5	1157.5	0.63	857.4
Sao Carlos, Brazil	32	2158.5	2261.4	0.81	4.8	867.4	0.64	666.5
Sao Paulo, Brazil	4	6527.5	7168.4	0.95	9.8	734.2	-0.01	641.2
RR	145	1260.8	1183.8	0.87	-6.1	633.2	0.86	349.1
Badgingarra, Australia	16	1115.5	598.5	0.19	-46.4	1010.2	-0.15	837.4
Duri, Australia	87	288.2	341.5	0.64	18.2	263.5	0.29	162.4

Table 5.6. Cont.

Statistical Indexes	n	Measured mean	Simulated mean	R^2	PB	RMSE	NSE	MAE
Kojonup, Australia	6	138.5	280.4	0.56	103	298.4	-6.56	176.4
Meloland, USA	5	5680.5	4709.4	0.44	-17.1	2389.4	0.26	2052.4
Pilbara, Australia	31	3569.2	3457.7	0.54	-3.1	465.7	0.48	381.7
All data	479	2213.2	2290.9	0.87	3.5	805.3	0.84	544.4

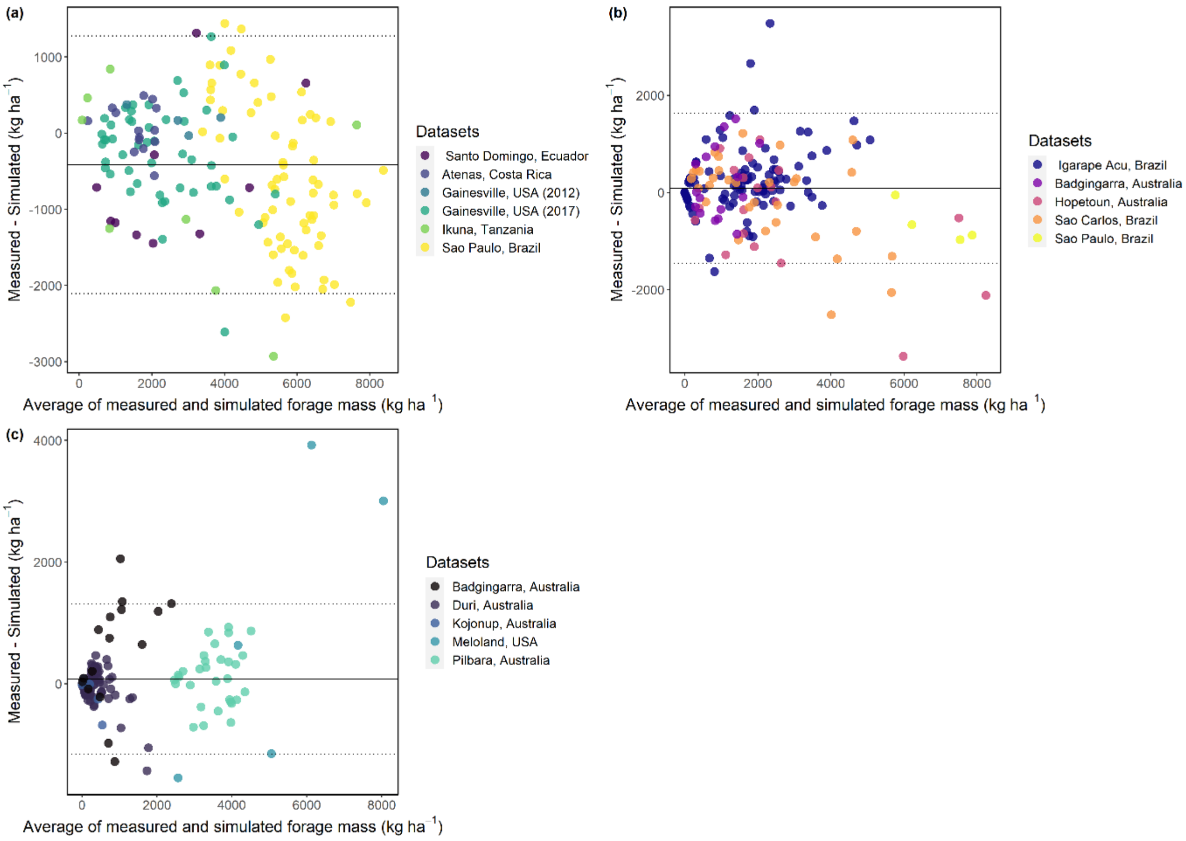


Figure 5.4. Bland-Altman plots for the forage biomass validation data of (a) *Brachiaria* Mulato II, (b) Gatton panic, and (c) Rhodes grass Reclaimer. The black solid line represents the mean difference between measured and simulated forage biomass, and the black dotted lines represent the mean ± 2 standard deviations.

Figure 5.5 shows the distribution of measured and simulated biomass yield difference (kg DM ha^{-}1) with respect to the simulated N stress (GLFN) and water stress (GLFwater) conditions across all validation data sets for three tropical pastures. According to Figures

5.5a-c, the model appeared relatively accurate at simulating the occurrence of water and N stress and the respective biomass production in the majority of locations across all three tropical pastures.

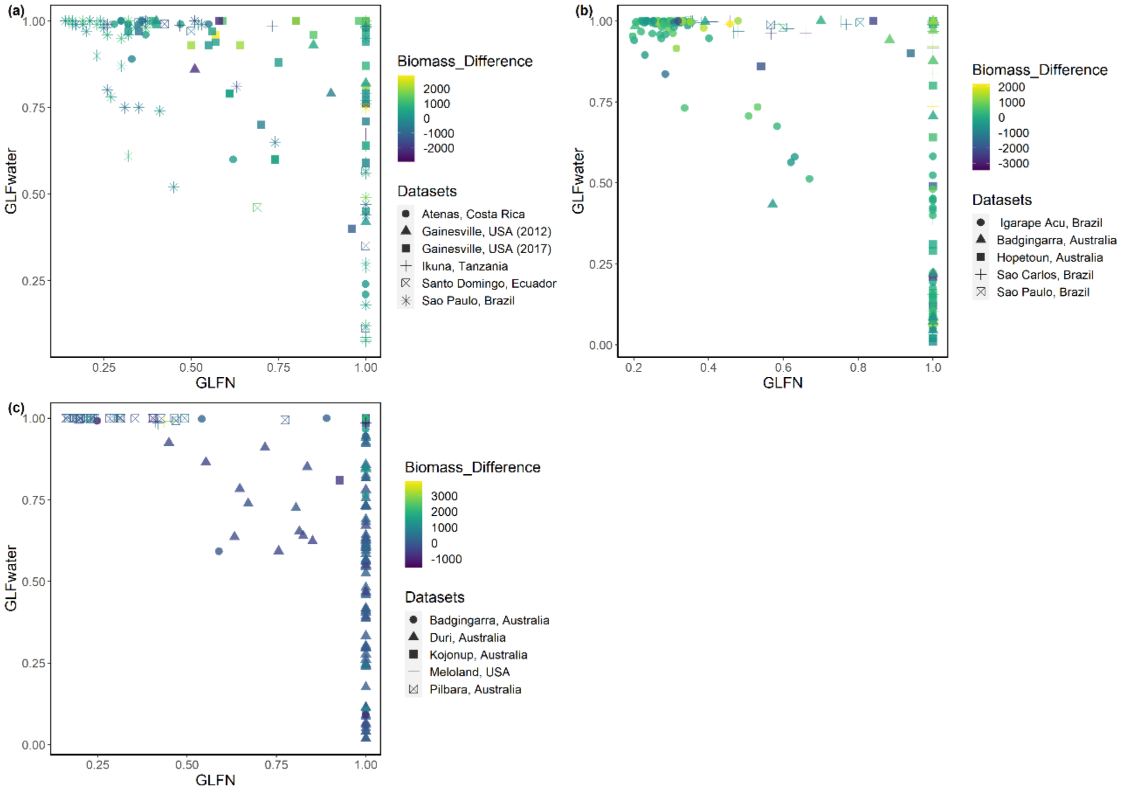


Figure 5.5. Colour-scaled scatter plots of water stress, nitrogen stress and the difference between observed and modelled forage biomass (kg DM ha^{-1}) of (a) *Brachiaria* Mulato II, (b) Gatton panic, and (c) Rhodes grass Reclaimer. GLFwater = Growth limiting factor for water and GLFN = Growth limiting factor for N which range from 1 to 0, where 1= no limitation to growth, and 0 = total limitation to growth.

The model underestimated the biomass production of BM (Figure 5.5a), GP (Figure 5.5b) and RR (Figure 5.5c) in Gainesville, Igarape Açu, Brazil and Meloland USA data sets, respectively, at the lower N level (> 0.5 GLFN). The model appeared to better represent the corresponding biomass production under the different GLFwater conditions than the GLFN in the field.

5.7 Discussion

The DairyMod-SGS pasture model was able to simulate established monocultures of BM, GP and RR pasture swards for their growth and biomass production under cut-and-carry management across a broad range of edaphoclimatic conditions (e.g., subtropical, tropical, Mediterranean, and desert environments), and agronomic management practices (e.g., irrigated, rainfed, N fertiliser, shaded). A more detailed and broader parameterisation and validation of DairyMod-SGS for BM, GP and RR in the present study allow broader exploration of tropical pasture species, and providing more opportunities to improve livestock production in the tropics. This also provides an opportunity to better understand and improve tropical pasture interactions with soil, water, and management, and also explore likely pasture production in the face of future climate variability.

The present study used the generic C_4 and Rhodes grass parameters in DairyMod-SGS, along with field experimental data from a range of studies, to develop species-specific parameters for BM, GP and RR. Key physiological and morphological processes, including photosynthesis, leaf appearance, respiration, canopy structure and carbon partitioning, were modified using the experimental data, in order for the model to simulate the species-specific performances in the field (Table 5.1). Parameters developed for RR using data from previous studies did not vary from the available Rhodes grass parameters in DairyMod-SGS.

The biomass accumulation in the DairyMod-SGS pasture model is primarily driven by leaf photosynthesis and the model links single leaf photosynthesis to canopy structure parameters to determine the canopy photosynthesis (Johnson, 2008). The relationship between measured and simulated total above-ground biomass of BM, GP and RR showed that the parameterised DairyMod-SGS pasture model captured the species-specific growth patterns and represented the total above-ground biomass reasonably well (Figure 5.2a-c). A reasonably high level of agreement between modelled and experimental data was observed in the present study for BM (0.92 R^2), GP (0.98 R^2) and RR (0.74 R^2), and these correlations are similar to the best parameterisation studies for tropical pastures reported elsewhere (Pequeno et al., 2018; Bosi et al., 2020a; Brunetti et al., 2021), confirming the efficacy of the DairyMod-SGS pasture model and its calibrated parameters. The model performance in simulating GP was better than that observed by Descheemaeker et al. (2014) (0.93 R^2, 753 RMSE kg DM ha^{-1}) between the observed and simulated shoot biomass data of four Panic cultivars grown at Hopetoun, Australia using the parameterised GRAZPLAN model. In addition, the ability of DairyMod-SGS to estimate pasture growth of BM was similar to that obtained by Pedreira et al. (2011) (538 RMSE kg DM ha^{-1}, 1.07 ratio between observed and simulated) for *Xaraés* palisade grass, by Pequeno (2014) (526 and 571 RMSE kg DM ha^{-1}) for Marandu palisade grass and Convert HD 364 *Brachiaria* grass, respectively, and by Bosi (2018) (0.89 R^2 and NSE = 0.85) for Piata palisade grass using the CROPGRO Perennial Forage model. Furthermore, the ability of DairyMod-SGS to simulate the growth of GP was similar to that reported by Lara et al. (2012) (494.2 RMSE kg DM ha^{-1}, 1.01 ratio between observed and simulated) for *Megathyrsus maximus* cv. Tanzania, and by Brunetti et al. (2021) (1768 RMSE kg DM ha^{-1}) for *Megathyrsus maximus* cv. Tanzania and Mombaca, also using the CROPGRO Perennial Forage model. Further, high agreement observed in the present study for BM was similar to results obtained by Bosi et al. (2020a) (0.92 R^2, 0.91 NSE, 638 RMSE kg DM ha^{-1}) for Piata palisade grass under cut-and-carry management in Brazil using the APSIM Next Generation model. However, Cullen et al. (2008) used the SGS-DairyMod model for fertilised perennial grasses in subtropical south eastern Queensland and observed an 0.58 R^2, and Doran-Browne et al. (2014) also obtained an

R^2 of 0.60 in native perennial and annual grasses in tropical northern Australia. Further, Svinurai et al. (2021) parameterised the SGS model for tropical pastures (*Urochloa mosambicensis* and *Eragrostis curvula*) in the southern region of Zimbabwe and showed that the model only explained 0.58 of herbage biomass accumulation (0.58 R^2). The direct measurement of the majority of model parameters in the present study could be the key reason for a significantly higher model agreement compared to DairyMod-SGS model performance reported elsewhere (Cullen et al., 2008; Doran-Browne et al., 2014; Svinurai et al., 2021) which also suggested the efficacy of the parameterised DairyMod-SGS model and its calibrated parameters for tropical pastures in the present study.

Photosynthesis lies at the core of the pasture submodule in DairyMod-SGS and is the primary source of carbon. The model adjusts the daily gross carbon assimilation with the daily plant growth (photosynthesis) and maintenance (nutrient uptake) respiration to calculate the net carbon assimilation of the plant canopy which is available for partitioning (growth) to shoot (leaf and stem) and root. The model defines the shoot mass as a function of plant SLA, LAI and the leaf fraction of the shoot (Johnson, 2008). Following the adjustments to carbon partitioning to leaves, live leaves per tiller and SLA, the model simulated the leaf accumulation of tropical pastures with high accuracy (R^2 between 0.74 and 0.97) for BM and RR, however leaf accumulation of GP was continuously overestimated (Figure 5.2d-e). Conversely, the model simulated the stem accumulation of RR and BM with reasonable accuracy, but failed to realistically capture the GP stem production (Figure 5.2g). Overall, the model underestimated the stem accumulation of all three tropical pastures, but showed a larger discrepancy for GP (RMSE 1296 kg ha^{-1}), particularly after the second defoliation (Figure 5.2g). During the same harvests, flowering was observed across all pasture plots and GP had a significant proportion of reproductive tillers. This poor stem simulation suggests that the model did not capture the onset of the plant reproductive phase and failed to explicitly simulate the phenological changes (i.e. changes in partitioning during flowering and stem elongation, which decrease the leaf: stem ratio). Similar responses by tropical pastures during their reproductive stage have been previously observed by Cullen et al. (2008) using DairyMod-SGS, by Bosi et al. (2020b); (Pedreira et al., 2011; Lara et al., 2012) using CROPGRO and by Bosi et al. (2020a) using APSIM. The stem and leaf accumulation of BM were better simulated as BM showed a delayed anthesis and a shift of carbon partitioning to the stem compared to RR and GP, resulting in a higher leaf to stem ratio being maintained. Introducing new parameters to the model to better describe the leaf and stem partitioning, especially during the reproductive phase, would be important for future modelling, as the plant morphological composition greatly determines the nutritive value of the harvested herbage.

Plant growth responses to temperature are described in DairyMod-SGS by a generic empirical curve defining the minimum, optimum, and maximum temperatures for photosynthesis based on a representative daytime temperature (Johnson et al., 2010). The present study did not estimate the temperature parameters for the three pastures and used previously published values (Table 5.4) for BM (Pequeno, 2014; Moreno, 2017; Bosi, 2018), GP (Lara et al., 2012; Araujo et al., 2013; Descheemaeker et al., 2014) and RR (Johnson, 2008). The model simulated the biomass accumulation reasonably well during the summer into the late autumn and early winter period under a subtropical climate (Figure 5.3a-c), suggesting that the optimised low temperature stress parameters better represented the tropical pasture growth patterns. Senescence parameters (non-leaf and root) in the model are assumed to not be different among the three pasture grasses, likely due to insufficient species-specific data available and also the similar senescence rates (%/day) used in previous studies (Pedreira et al., 2011; Lara et al., 2012; Pequeno, 2014;

Bosi et al., 2020a).

The parameterised DairyMod-SGS model was tested using independent data sets (Figure 5.1, Table 5.3) comprised of multiple environments under different management conditions. The majority of the published data (67%) belonged to tropical and subtropical environments whereas only 33% were associated with Mediterranean and desert climates. Overall, model testing results confirmed that the parametrised DairyMod-SGS model for BM, GP and RR can realistically simulate the above-ground biomass in tropical and subtropical climates, but underestimated the pasture biomass under Mediterranean and desert climate conditions. The validated model was able to accurately simulate the pasture production in a tropical climate under a high input system where the plants growth inputs are adequately supplied (Supplementary Figure 5.6j). The overall higher model performance for BM and GP is likely due to the model validation data sets mostly comprising the tropical and subtropical regions, whereas data from Mediterranean and desert regions primarily contributed to the RR validation (Table 5.3). The lower agreement between modelled and observed data for RR is likely due to the large variation in biomass production in the studies with RR. The present study used a five year data set of GP and RR collected at Badgingarra, Australia which has a hot-summer Mediterranean climate (Moore et al., 2014). The model overestimated both GP and RR biomass production towards the end of the experimental period and potentially failed to appropriately handle the deviation of plant persistency (plant density) over time and to capture the associated reductions in pasture growth rate under the suboptimal growing conditions. This was further confirmed by the plant persistency results of the study reported by Moore et al. (2014), where plant densities markedly declined between years 2 and 5, from 36 to 14 plants m^{-2} (GP) and from 29 to 7 plants m^{-2} (RR).

In addition, DairyMod-SGS was less accurate in simulating realistic tropical pasture recovery after the low temperature stress period and delayed the biomass accumulation of the subsequent harvest, due to simulating a longer lag phase between low temperature stress and full recovery. The present study used the Tsum = 100 (recovery from heat stress), the generic Tsum parameters for C_4 pastures as no data were available to support more pasture-specific parameterisation of the Tsum for low temperature stress recovery for BM, GP and RR. Perera et al. (2019) showed that parameterising the high temperature stress recovery function with Tsum = 20 improved modelled results of temperate perennial pastures (perennial ryegrass, cocksfoot, tall fescue and chicory) compared to using the default Tsum = 50 in the DairyMod-SGS. Similarly, DairyMod-SGS is likely to more accurately simulate tropical pastures if the model is parameterised with a species-specific low temperature recovery function.

The model underestimated the above-ground biomass for tropical pastures during the shorter defoliation intervals (e.g., 14, 21 and 28 days). This was more evident in GP simulations compared to experimental data in Igarape-Acu, Brazil (Supplementary Figure 5.5a-b) during the rainy season. In addition, pasture regrowth after more severe defoliation (shorter intervals and/or lower cutting heights) depends on plant carbohydrate reserves, but DairyMod-SGS does not explicitly account for plant reserves (Cullen et al., 2008). Also, the management submodule in the model only accommodates an average residual weight across all defoliations. However, the pasture residual weights and their composition in the field may be significantly different due to seasonal changes in above-ground herbage mass even the pasture cutting height was standardised. Therefore, the initial conditions of each pasture regrowth period may be poorly represented in the model. Johnson (2008) described the DairyMod-SGS pasture model behaviour (regrowth characteristics) under the reference climate conditions (20 MJ m^{-2} daily solar radiation, 14 hrs day lengths, 25°C Tmax, 10°C Tmin, 380 CO_2), and showed that the generic C_4

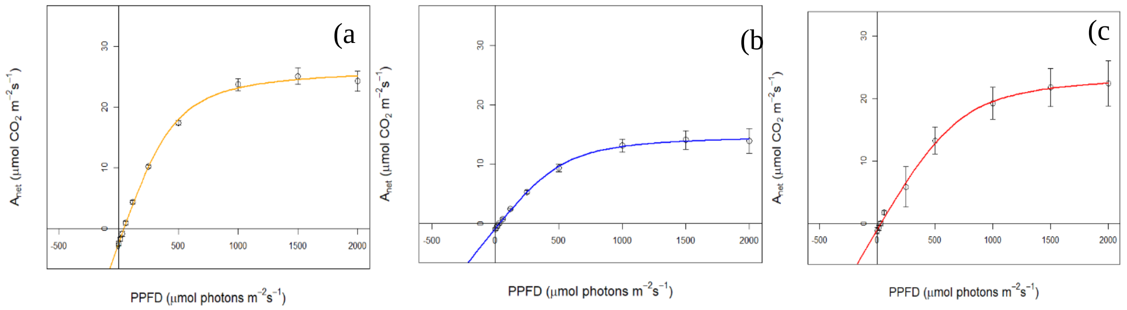
species tend to have a significantly lower mean growth rate and biomass accumulation below the 2 t ha^{-1} residual weight up to 40 days. Therefore, under a longer regrowth period, the model is less likely to carry over the effect of the initial pasture residual weight for the subsequent biomass accumulation. This is further confirmed by the reported DairyMod-SGS validation results being well within the observed data range for long-term defoliation than more severe defoliation experiments in the present study.

Both N and water stress limit pasture growth. The parameterised model accurately reproduced the reduction in observed biomass that was attributed to the GLFN and GLFwater factors. In addition, the model uses a GLFN that is defined as the ratio between the actual N uptake and the corresponding pasture demand to satisfy the optimum pasture growth (Johnson, 2008). The GLFwater is the ratio of actual to potential respiration and it can determine the rate of mass flow through age categories depending on the leaf appearance rate (Johnson, 2008). While an acceptable modelled representation of tropical pasture growth to water (irrigation and rainfall (Supplementary Figure 5.4a-b, 4e-j, 4l, Supplementary Figure 5.5g-i, Supplementary Figure 5.6j) and N (N fertiliser) (Supplementary Figure 5.5g-j, Supplementary Figure 5.6j) was observed in the parameterised DairyMod-SGS pasture model, some biomass data were underestimated. This may be explained by the low accuracy of the model to capture the slower recovery of pastures after the water stress (dry/reduced rainfall) period due to decreased root mass with a lower level of reserved carbohydrates and N (Korir et al., 2021). In addition, relatively high senescence of roots, particularly after the water and N stresses, negatively affects the water and nutrient uptake, causing the reduced simulation of pasture biomass by the model (Pedreira et al., 2011).

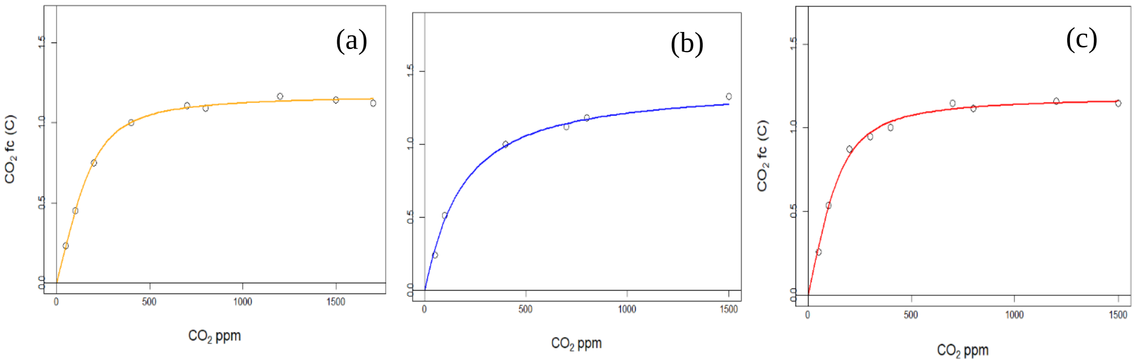
5.8 Conclusions

The present study has demonstrated that the parameterised and validated DairyMod-SGS pasture model of BM, GP and RR can successfully simulate the growth of these tropical pastures under a cut-and-carry system subject to various management (high input system, irrigated and rainfed, different N fertiliser, and defoliation intervals) and environmental conditions (tropical, subtropical). However, the model did not realistically simulate the tropical pasture biomass under Mediterranean or desert climate conditions, due to inadequate representation of reduced plant persistency over time. The present study has improved the robustness and accuracy of DairyMod-SGS in relation to tropical pastures, which makes the model a tool that could potentially explore the intensification of livestock production systems in the tropics and subtropics, and also explore likely pasture performance under a range of climate change scenarios. However, further model improvement would be useful in the area of biomass partitioning, and improvement for the low temperature recovery function and plant senescence using more pasture species-specific parameters. In addition, further model validation for grazing scenarios of these tropical pastures is also recommended.

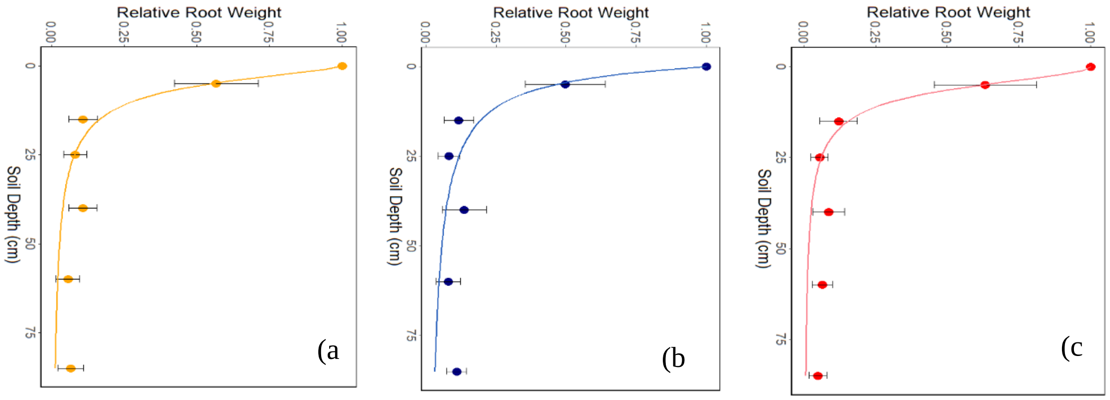
Supplementary materials



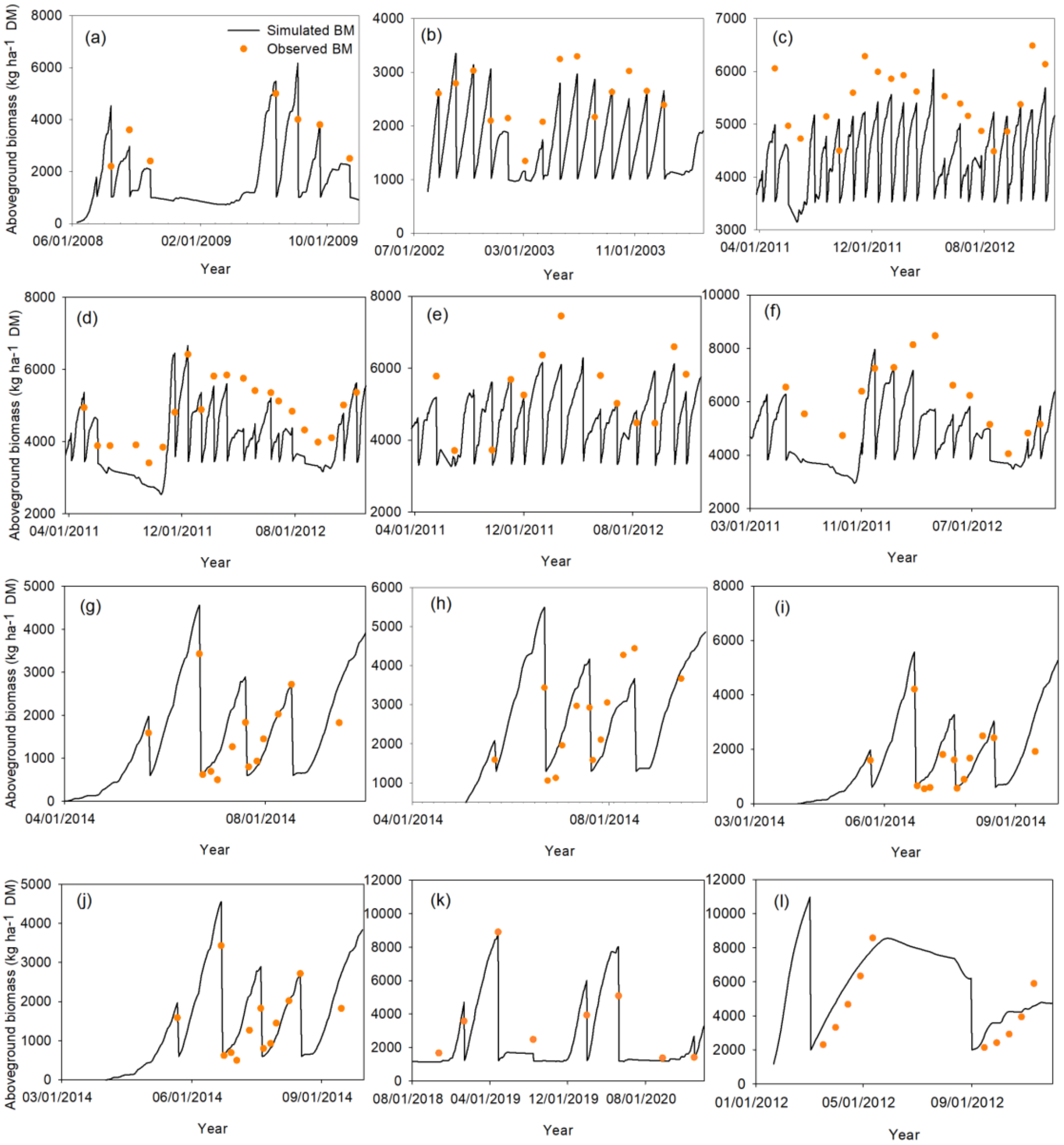
Supplementary Figure 5.1. Species-specific photosynthetic light response curves of (a) *Brachiaria* Mulato II (b) Rhodes grass Reclaimer (c) Gatton panic fitted by non-rectangular hyperbola function (Equation 3) for the net leaf carbon exchange measurements at Gatton Research Dairy, Queensland, Australia. Error bars represent the standard error of means.



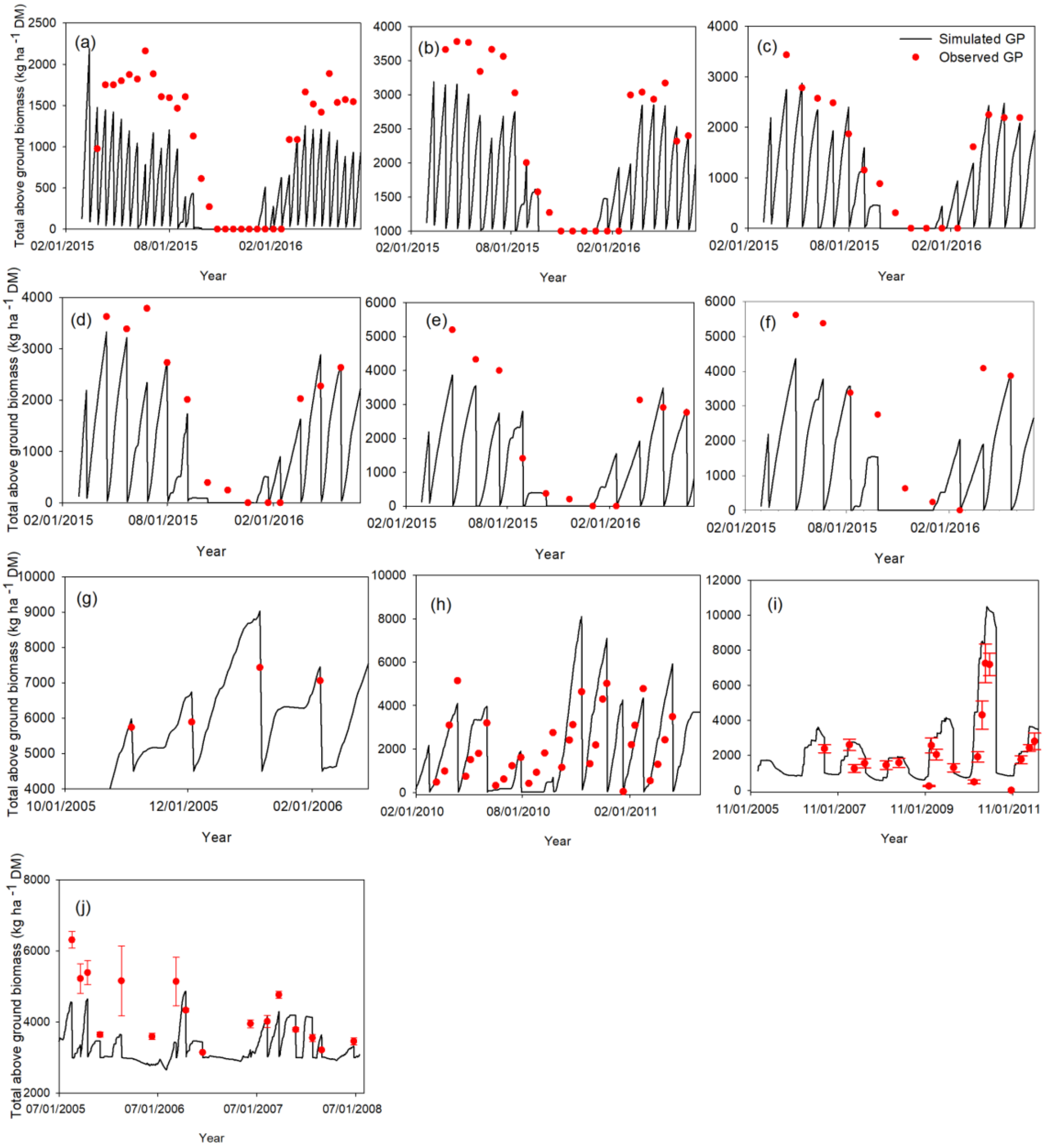
Supplementary Figure 5.2. Species-specific CO_2 response function $(f_C(C)$ curves of (a) Rhodes grass Reclaimer (b) *Brachiaria* Mulato II (c) Gatton panic fitted by non-rectangular hyperbola function (Equation 4) for the net leaf carbon exchange measurements at Gatton Research Dairy, Queensland, Australia.



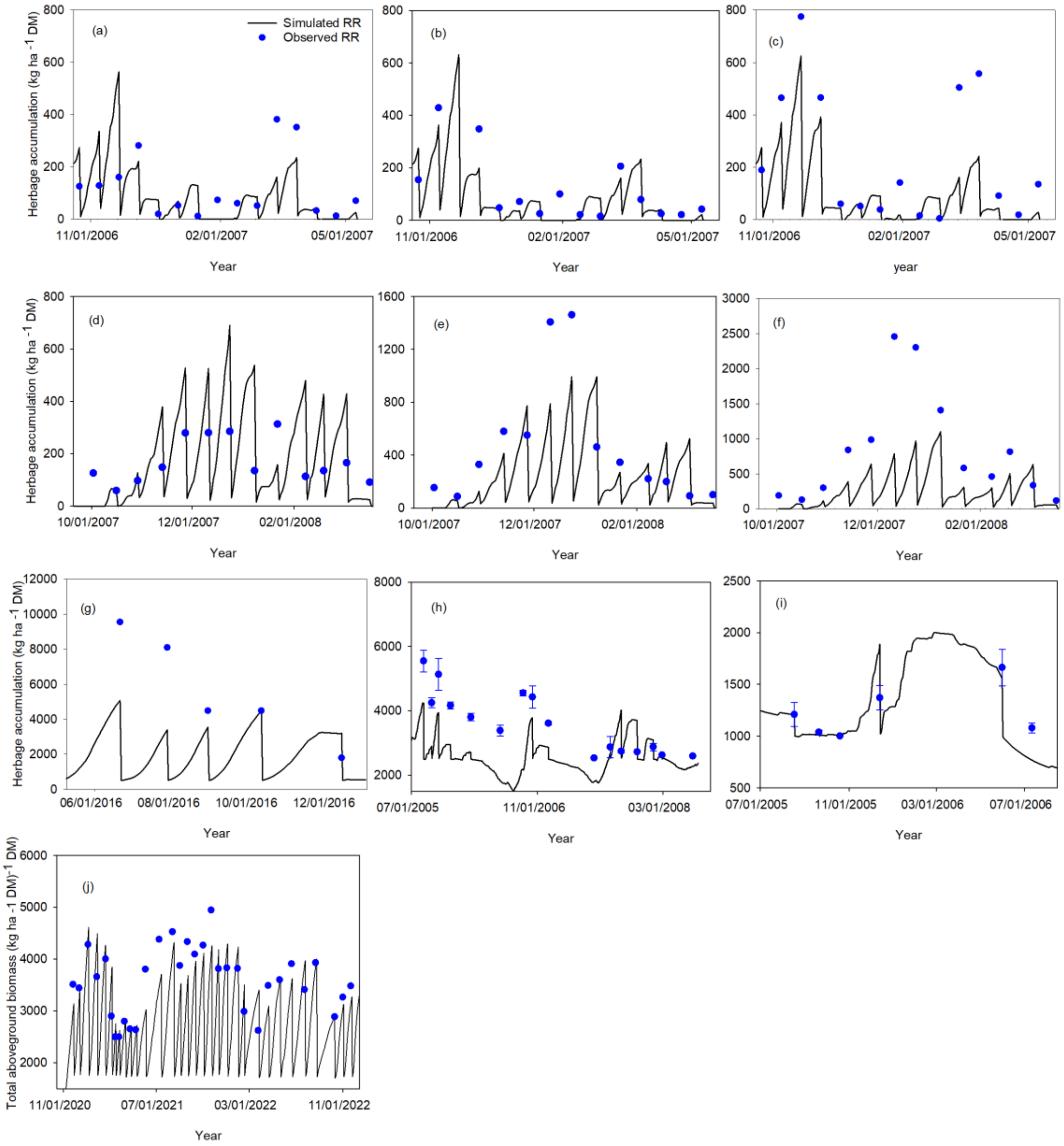
Supplementary Figure 5.3. Species-specific root distribution function (Equation 1) of (a) *Brachiaria* Mulato II (b) Rhodes grass Reclaimer (c) Gatton panic fitted for the root measurements at Gatton Research Dairy, Queensland, Australia. Error bars represent the standard error of means.



Supplementary Figure 5.4. DairyMod-SGS simulations (lines) compared with measured total above-ground biomass (kg ha^{-1} DM) (dots) of *Brachiaria* Mulato II validation for (a) Florida, USA (b) Atenas, Costa Rica (c) 28 days irrigated (d) 28 days rainfed (e) 42 days irrigated (f) 42 days rainfed in São Paulo, Brazil, (g) 30N full sun (h) 30 N 55% shade, (i) 120 N full sun, (j) 120 N 55% shade in Florida, USA, (k) Ikuna, Tanzania and (l) Campus Santo Domingo, Ecuador.



Supplementary Figure 5.5. DairyMod-SGS simulations (lines) compared with measured total above-ground biomass (kg ha^{-1} DM) (dots) of Gatton Panic validation for (a) 14 days (b) 21 days, (c) 28 days (d) 35 days , (e) 42 days, (f) 49 days rainfed in Igarape-Acu, Brazil (g) 28 days irrigated in Sao Paulo, Brazil (h) Sao Carlos, Brazil (i) Hopetoun, Australia, (j) Badgingarra, Australia. Error bars represent the standard error of means.



Supplementary Figure 6.6. DairyMod-SGS simulations (lines) compared with measured total above-ground biomass (kg ha^{-1} DM) (dots) of Rhodes grass Reclaimer validation for (a) 14 days without N (b) 14 days 50 N (c) 14 days 100N in 2006 year and (d) 14 days without N (e) 14 days 50 N, (f) 14 days 100N in 2007 year in Duri, Australia, (g) Meloland, USA, (h) Badgingarra, Australia (i) Kojonup, Australia and (j) Extremely high input pasture production system, Pardoo, Australia. Error bars represent the standard error of means.

Supplementary Table 4.1: Relative changes (%) of the pasture-specific parameters in DairyMod-SGS for Gatton panic (GP), *Brachiaria* Mulato II (BM), and Rhodes grass Reclaimer (RR) evaluated between 2020 and 2021 at Gatton Research Dairy, Queensland, Australia.

Parameters	Unit	Pastures				Relative changed from default C_4 (%)		
		GP	BM	RR	Default C_4	GP	BM	RR
Canopy structure and partitioning								
Carbon partitioned to shoot with no water or N stress	-	82	75	70	70	-17	-7	0
Leaf fraction of new shoot growth (%)	-	70	52	48	60	-17	13	20
Specific leaf area at ambient CO_2	m^2 leaf kg^{-1}	19	22	19	20	5	-10	5
Live leaves per tiller	-	4	4	5	5	20	20	0
Scale factor for non-leaf turnover rate relative to leaves	-	80	80	80	80	0	0	0
Root senescence rate	Fraction day^{-1}	0.8	0.8	2	2	60	60	0
Transfer of standing dead to litter	Fraction day^{-1}	1.5	2	2	10	85	80	80
Plant nitrogen composition								
Optimum N	-	3	3	2.8	3	0	0	7
Maximum N (%)	-	3.5	4	3.5	4	13	0	13
Non-leaf shoot scale factor	-	0.5	0.5	0.5	0.5	0	0	0
Root scale factor	-	0.5	0.5	0.5	0.5	0	0	0
Non-structural carbohydrate plus fat: live (%)	-	25	25	25	25	0	0	0
Non-structural carbohydrate plus fat: dead (%)	-	15	15	15	15	0	0	0
Height								
Maximum height	cm	100	50	80	50	-100	0	-60
LAI for half maximum height	m^2 m^{-2}	2	2	2	2	0	0	0
Leaf appearance in response to temperature								
Maximum leaf appearance interval	days	16	15	15	10	-60	-50	-50
Minimum temperature	°C	12	11	10	10	-20	-10	0
Temperature for maximum rate	°C	30	25	25	25	-20	0	0
Curvature coefficient	-	2	1.5	2	2	0	25	0
Roots								
Root depth	cm	100	100	150	100	0	0	-50
Depth for 50% root distribution	cm	15	15	40	25	40	40	-60
Scale factor		3	3	3	3	0	0	0
Photosynthesis								
Effective minimum LAI	m^2 m^{-2}	0.5	0.5	0.5	0.5	0	0	0

Supplementary Table 4.1. Cont.

P_{max} at reference conditions	µmol $CO_2 m^{-2} s^{-1}$	26	29	20	20	-30	-45	0
Minimum temperature for P_{max}	°C	13.6	15	12	12	-13	-25	0
Optimum temperature for P_{max} at ambient CO_2	°C	35	33	35	35	0	6	0
Temperature curvature coefficient		1.5	1.5	1.5	1.5	0	0	0
CO_2 function								
Value at saturating CO_2	-	1.2	1.18	1.1	1.1	-9	-7	0
Value at double ambient CO_2	-	1.1	1.08	1.05	1.05	-5	-3	0
Canopy photosynthesis								
Light extinction coefficient	-	0.55	0.48	0.5	0.5	-10	4	0
Respiration parameters								
Cell wall growth efficiency	-	85	85	85	85	0	0	0
Protein growth efficiency	-	55	55	55	55	0	0	0
Maintenance coefficient	Fraction day^{-1}	2.5	2.5	2.5	2.5	0	0	0
Nitrogen								
N uptake coefficient: NO_3	(g N t $root^{-1}$) ppm^{-1} day^{-1}	200	200	200	200	0	0	0
N uptake coefficient: NH_4	(g N t $root^{-1}$) ppm^{-1} day^{-1}	200	200	200	200	0	0	0
Respiratory cost of NO_3 uptake	kg C kg N^{-1}	0.6	0.6	0.6	0.6	0	0	0
Potential nitrogen remobilization	01 fraction	0.5	0.5	0.5	0.5	0	0	0
Low temperature stress								
Implement								
Full stress	°C	7	5	3	3	-133	-67	0
Initial stress	°C	11	11	7	7	-57	-57	0

Chapter 6

Long-term evaluation of pasture production, seasonality, and variability: An application of the DairyMod-SGS model for three tropical species

Prepared for submission to The Journal of Agricultural Sciences

Abstract

Long-term simulations are imperative for studying the performance of newer pasture species under varying soil and climate conditions. In this study, we applied the DairyMod-SGS, a biophysical model to simulate the long-term pasture production of three species (*Brachiaria* Mulato II (BM), *Megathyrsus maximus* 'Gatton Panic' (GP), and *Chloris gayana* 'Rhodes grass cv. Reclaimer' (RR)) across major dairying regions of Sri Lanka under different management scenarios. Simulations were carried out for 16 locations (8 locations in the dry zone (DZ), 5 locations in the intermediate zone (IZ), and 3 locations in the wet zone (WZ)) over a 30 years period (1980–2010). Three pasture management scenarios simulated were; 1) rainfed pasture production system under current industry average nitrogen (N) fertiliser rate (Y_t^{WN}), 2) rainfed pasture production system under non-limiting N fertilisation (Y_t^{W}), and 3) potential pasture production system under non-limiting N and irrigation (Y_t). The model simulated long-term pasture production varied greatly among climate zones, pasture species and management scenarios. Overall, the Y_t^{WN} scenario showed a seasonal cycle following the rainfall pattern, with a reduction in growth rates in dry seasons (May to September). Growth rate and herbage accumulation were greater in GP at Y_t^{WN}, and BM at Y_t^{W} and Y_t while RR showed the lowest growth rate at all times. Variability of pasture growth was high in DZ (May to September) and RR had the lowest growth variability. The pasture accumulation under Y_t^{W} increased (doubled) the growth rate while the Y_t scenario substantially increased (nearly tripled) the growth rate and growth pattern. The present simulation study suggested that the BM, GP and RR pastures are suitable for growing across major dairying regions in Sri Lanka while the appropriate fertiliser and irrigation management can greatly increase the herbage accumulation. However, the species-specific growth pattern, growth variability, yield potential under different managements and the possible implications for herbage quality need to be sensibly considered when selecting the appropriate species.

Keywords: DairyMod-SGS, Mulato II, Gatton panic, Rhodes grass, tropical pasture variability, modelling

6.1 Introduction

Sustainable livestock production systems are critical for ensuring food security in many tropical parts of the world. Tropical pastures constitute a key component of these systems, providing essential feed resources for livestock (Jayasinghe et al., 2022a; Jayasinghe et al., 2022b). The majority of tropical pasture-based systems face challenging production conditions (e.g., prolonged dry seasons, low soil fertility, pests, and diseases) which affect both the quantity and quality of feed produced, and thus limit livestock productivity (Rao et al., 2015). Adoption of improved pastures resilient to these challenging biophysical conditions (Tubiello et al., 2007) coupled with intensified pasture management (Rao et al., 2015) is essential to improve the seasonal distribution of forage growth and its year-round production, thereby increasing livestock productivity.

Increasing livestock utilisation of pastures often underpins higher profitability, because vegetative biomass is one of the cheapest sources of feed (Chapman et al., 2008a, b; Chapman et al., 2009). However, the efficient dairy cow feeding on pasture-based systems is hampered by the temporal (interannual variability) and spatial variability (between regions) of pasture growth rates associated with local climate, soil, and pasture species. Pasture growth rate data are usually reflected in the stocking rates, pasture management strategies and supplementary feeding decisions (Chapman et al., 2009). Variation in pasture supply is a significant source of business risk. Thus, the availability of accurate and timely quantitative estimates on possible pasture growth positively affects the biological efficiency and financial outcome of dairy production systems.

Crop simulation modelling is increasingly used in forage-based livestock production systems for exploring new species for environmental suitability, likely performance, growth rate variation, and trend analysis (Andrade et al., 2016; Jayasinghe et al., 2021;

Silva & Giller, 2021; Ahmed et al., 2022). These models can provide a great deal of information substituting the need for labour-intensive, time-consuming, and expensive traditional agronomic experiments that often lead to season-specific and site-specific results. Further, crop modelling research on long-term time series can provide data to guide policies and the decision-making process (Chapman et al., 2009; Quigley et al., 2019; Ara et al., 2020). Consequently, the model-aided policy can promote sustainable livestock farming to cater to the growing demand for livestock products (Silva & Giller, 2021).

The dairy industry in Sri Lanka is an important livestock subsector, due to a growing demand for dairy products, and its potential influence on the rural economy for livelihood (Vyas et al., 2020). Currently, milk consumption in Sri Lanka is largely reliant on imported milk (53% of demand) (Ministry of Finance, 2021). An inadequate supply of quality forage is the major factor limiting dairy production in Sri Lanka. Feed resources are either not available in sufficient quantities due to fluctuating weather conditions or even when available are of poor nutritional value. This can be attributed to the non-availability of quality pastures, lack of establishment and management experiences, and low awareness of improved forages (Premaratne & Premalal, 2006; Houwers, 2015; Gedara, 2019; Kumari et al., 2019; Vyas et al., 2020). This issue is compounded by seasonal variation in pasture conditions, with poor productivity and quality during dry seasons. Therefore, dairy cows are fed mostly local tropical forages, often harvested from along roadsides, uncultivated lands, and fallow paddy fields which have poor nutritive value (Premaratne & Premalal, 2006; Houwers, 2015; Premaratne & Samarasinghe, 2020). Consequently, the digestibility of these forages is low (58–62%) in all systems, resulting in poor outcomes in terms of low milk yields and short lactation, longer calving interval, and low animal body weights (Kumara et al., 2022), high enteric methane emissions per unit of metabolisable energy (Rao et al., 2015) and low profitability for farmers (Opio et al., 2017).

In general, the climate and soils in Sri Lanka are conducive to forage production and the country has a significant capacity to produce tropical forage for greater production of milk domestically (Premaratne & Premalal, 2006). Houwers (2015) estimated the biophysical potential for milk production in Sri Lanka as eight times higher than the current milk production under the increased supply of improved forages. The strategic changes for improving forage production in Sri Lanka have been broadly explored (Premaratne & Premalal, 2006; Houwers, 2015; Gedara, 2019; Kumari et al., 2019; Vyas et al., 2020). The key approaches are the introduction of improved grasses adapted to the local soil, and climate which are more leafy, and digestible to exploit the maximum genetic potential of the dairy herds and subsequently intensify management through appropriate defoliation in combination with improved plant nutrition through the increased use of fertilisers. While the impact of the non-availability of improved forages for dairying and the potential solutions to overcome have been widely studied (Houwers, 2015; Prowurst, 2019; Premaratne & Samarasinghe, 2020), no previous studies have been undertaken to broadly evaluate the potential of improved forage species under different soil and climatic and management conditions, which are vital to expanding the productivity of dairy farming.

The use of improved tropical forage species receives significant acknowledgment in many tropical and subtropical dairying regions due to their strong adaptability to wider edapho-climatic conditions, improved nutritive value, and disease and drought susceptibility (Rao et al., 2015; Paul et al., 2020). The genera, *Brachiaria*, *Megathyrsus*, and *Chloris* are native to most of the tropical regions including Sri Lanka (CABI, 2022), however, their promising newer cultivars are yet to be introduced and tested in Sri Lanka. Given that, no studies have been undertaken to investigate the *Brachiaria* Mulato II (BM), *Megathyrsus maximus* 'Gatton Panic' (GP), and *Chloris gayana* 'Rhodes grass cv. Reclaimer' (RR) for their suitability and likely agronomic performances in a broader range of soil and climatic conditions.

Pasture modelling tools, while being a simplified representation of actual systems, can provide a platform and additional insights to identify the process involved in forage growth and explore the potential species for new areas before establishing expensive and time-consuming field experiments. The DairyMod-SGS, a mechanistic biophysical pasture model has shown the flexibility to simulate tropical pasture species (Johnson et al., 2008) and it has been successfully used to simulate tropical pasture growth and herbage accumulation under contrasting edaphoclimatic and management conditions (Johnson et al., 2008; Berger et al., 2014; Wayne. et al., 2016; Perera et al., 2020; Jayasinghe et al., 2021; Svinurai et al., 2021). Therefore, the present study aimed to apply the DairyMod-SGS pasture model for simulating the growth of three tropical pastures (BM, GP, and RR) across the key livestock production zones under three different pasture production scenarios and characterise the long-term pasture growth, seasonality and spatial variability, and possible implication for dairying in Sri Lanka.

6.2 Materials and methods

6.2.1 Study area

The scope of the study encompasses the entirety of Sri Lanka, geographically located between 5°55′ to 9°51′ North latitude and between 79°42′ to 81°53′ East longitude. The climate is characterised as tropical, hot, and humid throughout the year (Punyawardena, 2020). The mean annual temperature varies from 27 °C in the coastal plains to 16 °C in the central highlands due to the altitudinal changes. The mean annual precipitation (MAP) ranges from under 900 mm in the driest parts of the southeast and northwest of the country to more than 5000 mm in the wet zone (Punyawardena, 2020). The country is divided into three major climatic zones; the dry zone (DZ) (MAP < 1750 mm) covers the east, northern, and south-east parts of the country which has a distinct dry season from May to September, the wet zone (WZ) (MAP > 2500 mm) in the central and south-west regions which has no distinct dry periods and the intermediate zone (IZ) (1750–2500 mm MAP) separating the two with a short and less prominent dry season (Figure 6.1).

Sri Lanka has a heterogeneous agroecological environment. A particular agroecological region represents fairly even agroclimatic, soils, and terrain conditions and would support a particular farming system with a certain range of crops and farming practices, including forage cultivation and livestock farming. The agroecological zones map was used from National Spatial Data Infrastructure (NSDI) (https://catalog.nsdi.gov.lk/) to identify the homogeneous climate zones and combined it with the map of the geographical distribution of dairy herds across climate zones (Opio et al., 2017) to identify the number of locations of simulations (Figure 6.1).

Sixteen locations were selected within three climatic zones; 8 locations in DZ (Anuradhapura, Puttalam, Ridiyagama, Ampara, Kantale, Mannar, Polonnaruwa, Jaffna), 5 locations in IZ (Kurunegala, Maho, Matara, Badulla, Monaragala) and 3 locations in WZ (Peradeniya, Kotadeniyawa, Galle). A large area of the wet zone (indicated by the black dashed line inside the dark green area in Figure 6.1) was ignored given the high elevation (up to 2400 m) and low mean daily temperature (10°C) during most of the days in the year (Punyawardena, 2020) which makes those areas unsuitable for growing tropical pastures.

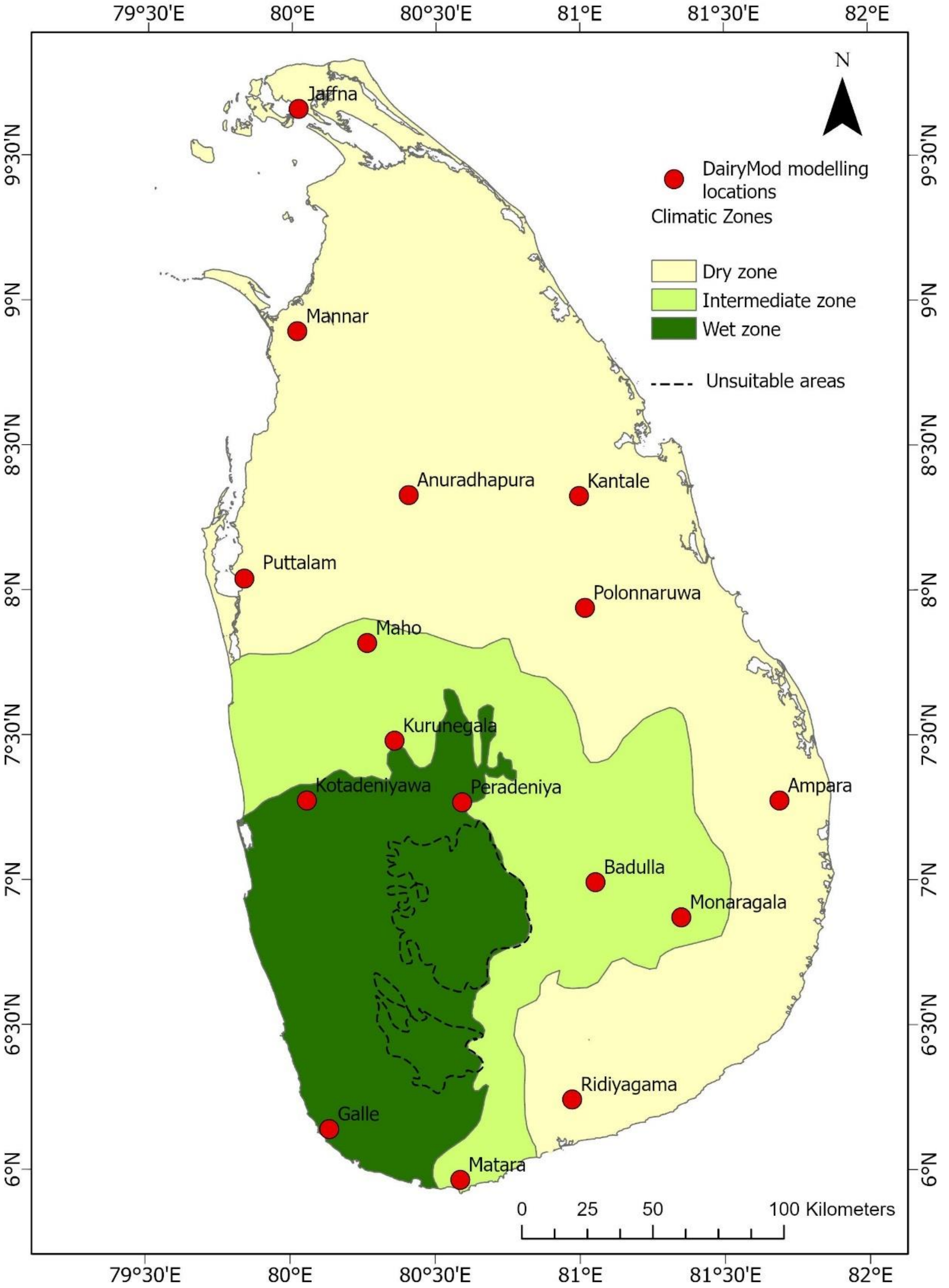


Figure 6.1. Map of the DairyMod-SGS model simulation locations (red dots) in three major climatic zones of Sri Lanka.

Table 6.1. Site-specific climate, and soil types at 16 locations used for the simulation of *Brachiaria* Mulato II, Gatton panic, and Rhodes grass Reclaimer growth representing major dairying regions in Sri Lanka. (DZ = Dry zone, IZ = Intermediate zone, WZ = Wet zone)

Location	Long (E)	Lat (N)	Climate Zone	Annual Rainfall (mm)[1]	Altitude (m)	Great Soil groups[2]	WRB (FAO) group[3]	Soil Series[4]
Ampara	81.69	7.27	DZ	1606	30	Reddish Brown Earth	Luvisols	Damana series
Polonnaruwa	81.02	7.94	DZ	1542	46	Reddish Brown Earth	Luvisols	Kaduruwela series
Puttalam	79.84	8.04	DZ	1151	10	Red Yellow Latasols	Regosols	Gambura series
Jaffna	80.03	9.66	DZ	1326	11	Red Yellow Latasols	Luvisols	Chankanai Series
Kantale	81.00	8.33	DZ	1555	46	Reddish Brown Earth	Luvisols	Seruwila series
Anuradhapura	80.44	8.1	DZ	1344	115	Reddish Brown Earth	Luvisols	Mahailupplama Series
Mannar	80.02	8.89	DZ	987	10	Grumusols	Vertisols	Murunkan series
Ridiyagama	80.97	6.24	DZ	1016	39	Reddish Brown Earth	Luvisols	Ranna series
Kurunegala	80.36	7.48	IZ	1984	120	Red Yellow Podzolic	Alisols	Kurunegala series
Badulla	81.05	6.99	IZ	1737	660	Red Yellow Podzolic	Luvisols	Badulla series
Maho	80.27	7.82	IZ	1619	90	Reddish Brown Earth	Luvisols	Maho series
Matara	80.56	6.08	IZ	2090	25	Red Yellow Podzolic	Alisols	Beliatta series
Monaragala	81.35	6.87	IZ	1732	154	Reddish Brown Earth	Luvisols	Bibela series
Peradeniya	80.59	7.27	WZ	1696	480	Reddish Brown Latosolic	Nitisols	Kandy series
Galle	80.14	6.14	WZ	2307	5	Red Yellow Podzolic	Alisols	Dodangoda series
Kotadeniyawa	80.06	7.28	WZ	2253	55	Red Yellow Podzolic	Alisols	Minuwangoda series

[1] Nisansala et al. (2020) and Department of Meteorology, Sri Lanka (http://www.meteo.gov.lk/)

[2] Moormann & Panabokke (1961)

[3] World Reference Base for Soil Resources (WRB) Dassanayake et al. (2020b)

[4] Mapa et al. (1999); Mapa et al. (2005); Mapa et al. (2010)

6.2.2 Soil and climate data

The agroecological zones map was overlaid on the soil map of Sri Lanka obtained from the NSDI and created a buffer with a radius of 15 km around each point in ArcGIS Pro 2.8.6 (ESRI, 2021) to determine the most representative soil series for each location. Subsequently, soil profile data for the respective soil series were extracted from the SRICANSOL Project database (Mapa et al., 1999; Mapa et al., 2005; Mapa et al., 2010). Observed minimum climate data required to run the long-term simulations were not available in Sri Lanka across multiple locations, therefore, the daily gridded weather data of maximum and minimum temperature, solar radiation and rainfall provided by AgMERRA (https://data.giss.nasa.gov/impacts/agmipcf/agmerra/) (Ruane et al., 2015) were used in the present study. The AgMERRA gridded data have been previously used for a similar purpose in several modelling studies in Sri Lanka (Gunarathna et al., 2019; Gunarathna et al., 2020; Wimalasiri et al., 2020). Long-term weather data (30 years) were extracted for the period from 1 January 1980–31 December 2010 using the multidimensional tool in ArcGIS Pro 2.8.6. Supplementary Figure 6.1 shows the long-term monthly climate variables for the 16 sites selected. The site-specific details including the climate and soil types are described in Table 6.1.

6.2.3 DairyMod-SGS model

The DairyMod-SGS model version 5.8.2 (Johnson, 2008) was used to run the long-term tropical pasture simulations. A comprehensive model description is given in Johnson et al. (2008), along with Chapter 2 and Chapter 5. Briefly, DairyMod-SGS is a mechanistic biophysical grazing system simulation model which models pasture growth, utilisation by grazing animals, animal growth and production, soil water, and nutrient dynamics with different pasture management (irrigation, fertiliser application, harvesting for silage or hay and grazing). The model has been previously parameterised and robustly validated for the pasture species, BM, GP and RR across multiple environments (Chapter 5). The validated model has shown good accuracy for pasture growth and biomass accumulation under the cut-and-carry management across a broad range of edaphoclimatic conditions (e.g., subtropical, tropical, Mediterranean, and desert environments), and agronomic management practices (e.g., irrigated, rainfed, nitrogen (N) fertiliser, shaded, high inputs). The present study used these pasture-specific parameters to simulate the likely pasture growth under the current edaphoclimatic conditions in Sri Lanka.

6.2.4 Pasture management scenarios

Three pasture management scenarios; a representation of the current pasture production system in Sri Lanka and two hypothetical pasture production systems were built in the DairyMod-SGS (Table 6.2). The resulting scenarios were: 1) rainfed pasture production system under the industry average nitrogen N fertiliser rate (water and N limited yield; Y_t^{WN}), 2) rainfed pasture production system under non-limiting N fertilisation (water-limited potential yield; Y_t^{W}), 3) potential pasture production system under non-limiting N and water (water and N unlimited yield; Y_t).

Y_t^{WN} - yield over time under water and N limitation (current practice under rainfed))

Y_t^{W} - yield over time with no N limitation but water limitation

Y_t- yield over time with no N and water limitations

Table 6.2. Pasture production scenarios and effect of water and nitrogen fertiliser

Pasture production scenarios	Definition	Water effect	N effect	Inorganic fertiliser
$\boldsymbol{Y_t^{WN}}$	Rainfed pasture production system under current N fertiliser rate (water and N limited yield)	Yes	Yes	240 kg N ha^{-1} year^{-1}
$\boldsymbol{Y_t^{W}}$	Rainfed pasture production system under non-limiting N fertilisation (water-limited potential yield)	Yes	No	-
$\boldsymbol{Y_t}$	Potential pasture production system under non-limiting N and water (water and N unlimited yield)	No (irrigated)[1]	No	-

[1] Irrigation (25 mm application^{-1}) when the cumulative rainfall deficit (rainfall–potential evapotranspiration) was 25 mm or greater.

6.2.5 Model initialisation and simulation setup

Each simulation was initialised before running the model for exporting the long-term data. By initialising, it was ensured that the soil carbon (C) and N pools reached a steady state and achieved a system equilibrium for each scenario. To set up the initialising conditions, the model was run for 30 years (1980–2010) with multiple loops ($n = 5$) to create more than 100 years of a long simulation to stabilise the soil N and C pools. The stabilised soil N and C pools were determined when the slope of the annualised average daily soil N mineralisation rate (g N ha^{-1} day^{-1}) over 30 years was < ±0.01, along with steady soil organic C pool and C: N ratio of the fast (labile) and fast + slow turnover pools (Supplementary Figure 6.2) (Christie et al., 2018; dos Santos et al., 2022). During the initialisation stage, pasture swards were defoliated on the last day of each month and received 20 kg N ha^{-1} month^{-1} in the form of urea to maintain a level of reasonable pasture production during the initialisation phase and reflect the lowest N fertiliser rate applied during the data extraction phase. Subsequently, the endpoint of the simulation was saved for the data exporting phase.

Simulations in DairyMod-SGS were conducted as a "cut-trial" where the pasture was mechanically defoliated on the last day of each month to a residual weight of 3 t DM ha^{-1} (Jayasinghe et al. (2022b). At each defoliation, herbage was removed from the field to reflect the conditions typical in cutting trials. Three tropical pastures were separately simulated as monoculture swards at all locations and the simulations were conducted for 30 years (1980–2010). The respective N fertiliser rate (for Y_t^{WN}) and irrigation (for Y_t) were defined in the management submodule in the DairyMod-SGS under the N fertiliser and irrigation options. Nitrogen fertiliser was applied in the form of urea at a rate of 240 N kg ha^{-1} year^{-1} and the frequency of application was aligned with the rainfall pattern of each climate zone resulting in 30 N kg ha^{-1}, 24 N kg ha^{-1}and 20 N kg ha^{-1} rate of N fertiliser in 8, 10 and 12 times (months) per year for the DZ, IZ and WZ, respectively. Consequently, the fertiliser application window was set as 15 September to 15 April, 15 August to 15 May, and after each defoliation for the DZ, IZ and WZ, respectively. All locations were irrigated for the Y_t scenario during the dry months to maintain the soil moisture at or near field capacity reflecting the non-limiting soil water conditions. Irrigation was applied (25 mm application^{-1}) when the cumulative rainfall deficit (rainfall–potential evapotranspiration) was 25 mm or greater in each location.

Average annual herbage accumulation and long-term monthly average herbage accumulation rates over 30 years were compiled for each site across the major three climate zones. Similarly, long-term pasture production data for the three simulated pasture management systems were summarised. The variability in herbage accumulation and growth rates were characterised using the coefficient of variation (CV%). Data analyses and visualizations were undertaken using the R (version 4.0.5) statistical computing software (RCoreTeam, 2021).

6.3 Results

6.3.1 Characteristics of long-term pasture growth and herbage accumulation

Overall, the mean pasture growth rates were comparatively lower in DZ and comparatively higher in WZ. All three pastures recorded relatively lower mean growth rates under the Y_t^{WN} pasture management scenario across all the simulated locations (Figure 6.2a-c) (Supplementary Figure 6.3). By comparison, DZ locations, namely; Jaffna, Mannar and Kantale displayed low mean pasture growth rates under Y_t^{WN}, Y_t^{W}, and Y_t pasture management scenarios. Across all locations, GP had the highest growth rate (53.4 kg DM ha^{-1} day^{-1}) for the Y_t^{WN} scenario compared to BM and RR which demonstrated a similar growth rate (45.0 and 46.6 kg DM ha^{-1} day^{-1}) (Figure 6.2a). The BM had a greater mean pasture growth rate (93.7 kg DM ha^{-1} day^{-1}) under water-limited potential yield (Y_t^{W}) than GP and RR. Similarly, BM showed the highest mean growth rate (138.4 kg DM ha^{-1} day^{-1}) under non-limiting nutrient and irrigated conditions (Y_t) (Figure 6.2b,c). Overall, BM had higher mean growth rates than GP and RR in all pasture management scenarios tested, except the Y_t^{WN}.

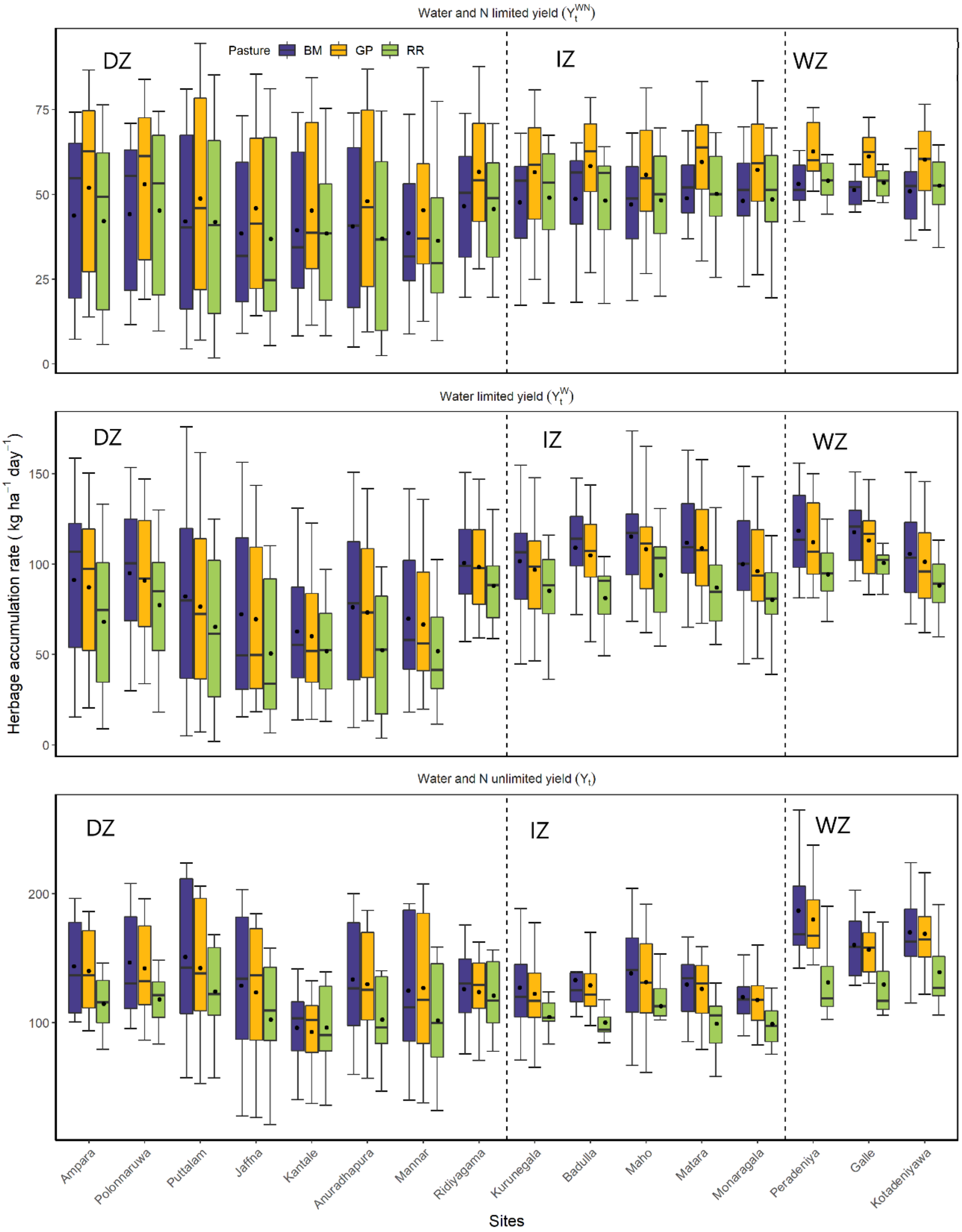


Figure 6.2. Long-term monthly pasture growth rates (kg ha^{-1} day^{-1}) distributions of *Brachiaria* Mulato II (BM), Gatton panic (GP), and Rhodes grass Reclaimer (RR) for the sites in three major climatic zones (separated by vertical dashed lines) (DZ = dry zone, IZ = intermediate zone, WZ = wet zone) under different pasture management scenarios in Sri Lanka. The black dots represent the mean value.

Long-term monthly pasture growth rates across the main three climatic zones and pasture management scenarios are summarised in Figure 6.3. Overall, interannual pasture growth rates showed the same tendency of monthly rainfall distribution (see supplementary Figures 6.1a-c) in the respective climate zones, resulting in the highest pasture growth rates in WZ across all management scenarios.

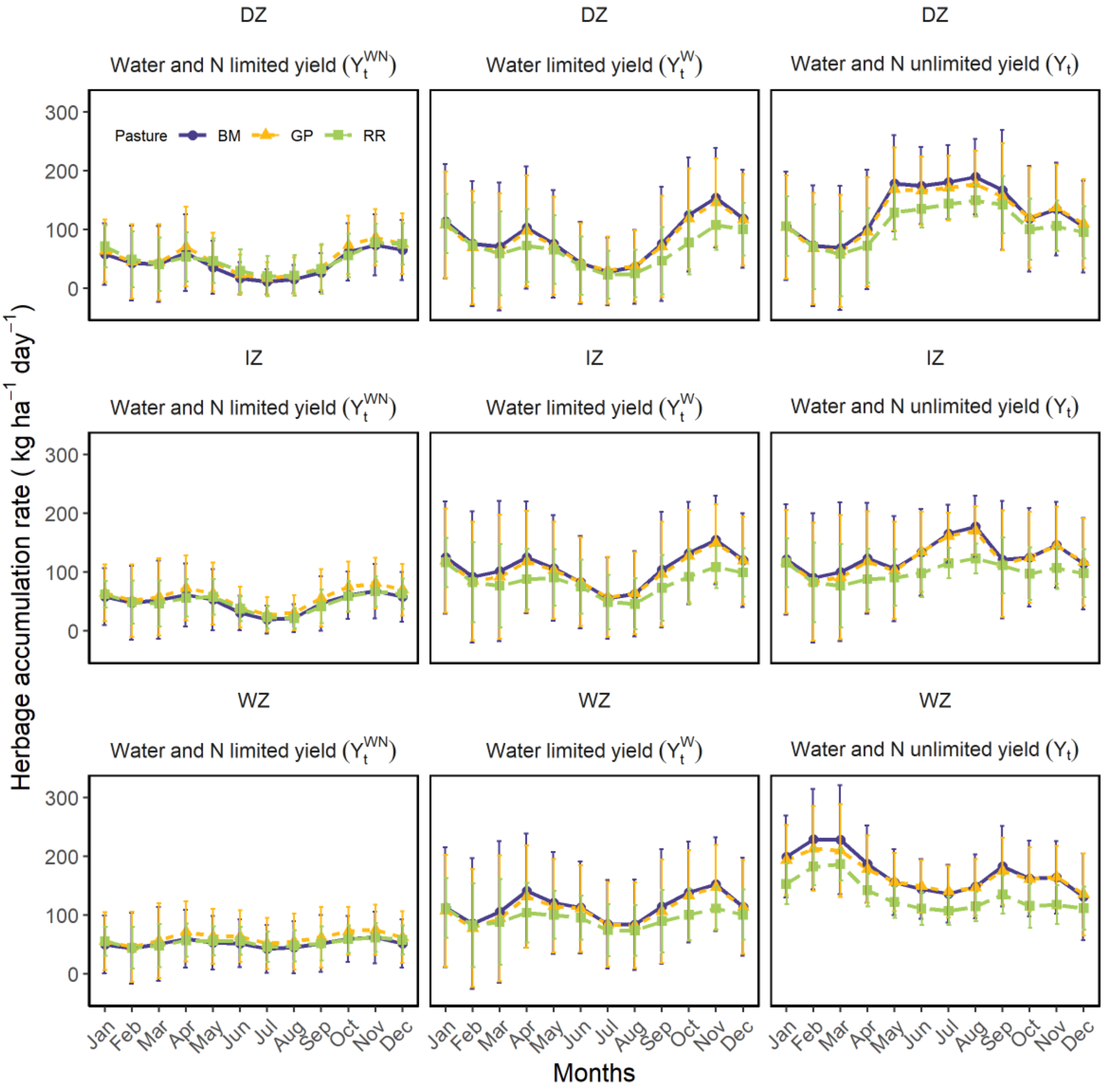


Figure 6.3. Long-term monthly pasture growth rates (kg ha^{-}1 day^{-}1) distributions of *Brachiaria* Mulato II (BM), Gatton panic (GP), and Rhodes grass Reclaimer (RR) for the sites in three major climatic zones (DZ = dry zone, IZ = intermediate zone, WZ = wet

zone) under different pasture management scenarios in Sri Lanka. Error bars represent the mean ± standard deviations.

Under the existing pasture management (Y_t^{WN}), monthly mean pasture growth rates showed a high seasonality, especially under dry and intermediate climates. Pasture growth rates under the Y_t^{WN} the scenario was markedly low from June to September in DZ and IZ and RR showed comparatively little growth (15.7 kg DM ha^{-1} day^{-1}) than BM (24.1 kg DM ha^{-1} day^{-1}) and GP (27.8 kg DM ha^{-1} day^{-1}). According to Figure 6.3, the Y_t^{W} scenario greatly improved the pasture growth rates of all three pastures across the climatic zones, however, the application of unlimited nutrients did not change the growth patterns. In general, both simulated rainfed scenarios (Y_t^{WN} and Y_t^{W}) showed lower growth rates in drier months regardless of the level of fertilisation in the pasture system. Increased pasture growth rates in the Y_t^{W} scenario was more noticeable in IZ and WZ than in the DZ. The mean monthly pasture growth rates in DZ increased from 41.7 to 81.1 kg DM ha^{-1} day^{-1}, 49.3 to 77.8 kg DM ha^{-1} day^{-1} and 44.2 to 63.1 kg DM ha^{-1} day^{-1} for BM, GP and RR, respectively. Switching the pasture production system to the unlimited nutrient application (from Y_t^{WN} to Y_t^{W}), the long-term average monthly pasture growth rates in IZ and WZ increased by 59.4, 45.4 and 36.6 kg DM ha^{-1} day^{-1} and 62.1, 47.4, 41.0 kg DM ha^{-1} day^{-1} for BM, GP and RR, respectively. Overall, the BM greatly responded to the increased soil nutrient level showing a higher growth rate than the GP and RR showed the lowest growth rates across all climates and pasture management scenarios (Figure 6.3). The differences between the Y_t^{W} and Y_t scenarios in Figure 6.3 illustrate the water-limited gap over the annual cycles of weather for different climate zones. The simulated average monthly growth rates increased greatly under the non-limiting nutrients and irrigated conditions (Y_t) across the climate zones and the amount of increased pasture growth rate was considerably high in DZ than the growth rates displayed in IZ and WZ. By comparison, the increase in growth rate was relatively higher for BM than the GP and RR under the same conditions (Figure 6.3). The average monthly pasture growth rates increased by 51.0 kg DM ha^{-1} day^{-1}, 49.9 kg DM ha^{-1} day^{-1} and 31.7 kg DM ha^{-1} day^{-1}, respectively for BM, GP and RR due to the changes in pasture management with irrigation. Simulated monthly pasture growth rates further revealed that the growth pattern greatly changed under the Y_t, resulting in higher growth rates during the drier months of the year. This change in the growth pattern was more evident in DZ than in IZ and WZ, producing a more constant pasture production throughout the year.

6.3.2 Pasture growth and herbage accumulation variability

The long-term interannual variability (CV%) of monthly pasture growth across three major climatic zones under different pasture management scenarios is presented in Figure 6.4. In many instances, the variability of pasture growth rates differed from each other within the locations. Higher variable pasture growth rates were observed from the locations in DZ and the observed average variability was 99%. The variable pasture growth pattern was more evident during the drier months (May to late September). Between climate zones, the locations in the WZ had the characteristically lowest pasture growth variability (59.9%) and the variable pasture growth pattern was less evident. The relationship between the long-term monthly pasture growth rates and the CV% of the BM, GP, and RR for the locations in three major climatic zones under different pasture management scenarios is presented in Figure 6.5. In general, when two or more plots overlap, the respective pastures display similar annual patterns in the relationship between the mean growth and variability in the annual growth cycle. While a variable pasture growth was noticeable between species, the characteristic variable pasture growth pattern was similar across the three pasture species. The variation in the pasture growth variability between species was more pronounced during the drier months of the year (May to September). According to Figure 6.5, the BM and GP plots are mostly overlapped while the RR plot is separately placed showing the similar annual pattern of GP and BM, and different patterns of RR in the relationship between the mean growth and variability. The RR has shown the lowest variability and recorded fairly resilient pasture growth during the drier months across all climatic zones and pasture management (Figure 6.4 and Figure 6.5). While a considerable variable pasture growth was observed between locations, climate zones and pasture species, the convergence of pasture growth between different pasture management scenarios was noted in all locations, climates and pasture species (Figure 6.4 and Figure 6.5). By contrast, the level of convergence was marked in DZ and IZ and had greatly improved under both the Y_t^W and Y_t pasture management scenarios. The more divergence pasture growth observed between pasture species under the Y_t^{WN} pasture management scenario within the typical N fertiliser (Y_t^{WN}) has greatly improved due to the change in pasture management. In general, RR showed the lowest pasture growth variability under all scenarios, however, the divergence pasture growth of BM has largely reduced under Y_t^W and Y_t scenarios compared to Y_t^{WN} which has also resulted in a lower variability between the three pasture species. Overall, the Y_t scenario has greatly reduced the variable drier months pasture production and produced a more consistent, and year-round pasture growth in all most all the locations.

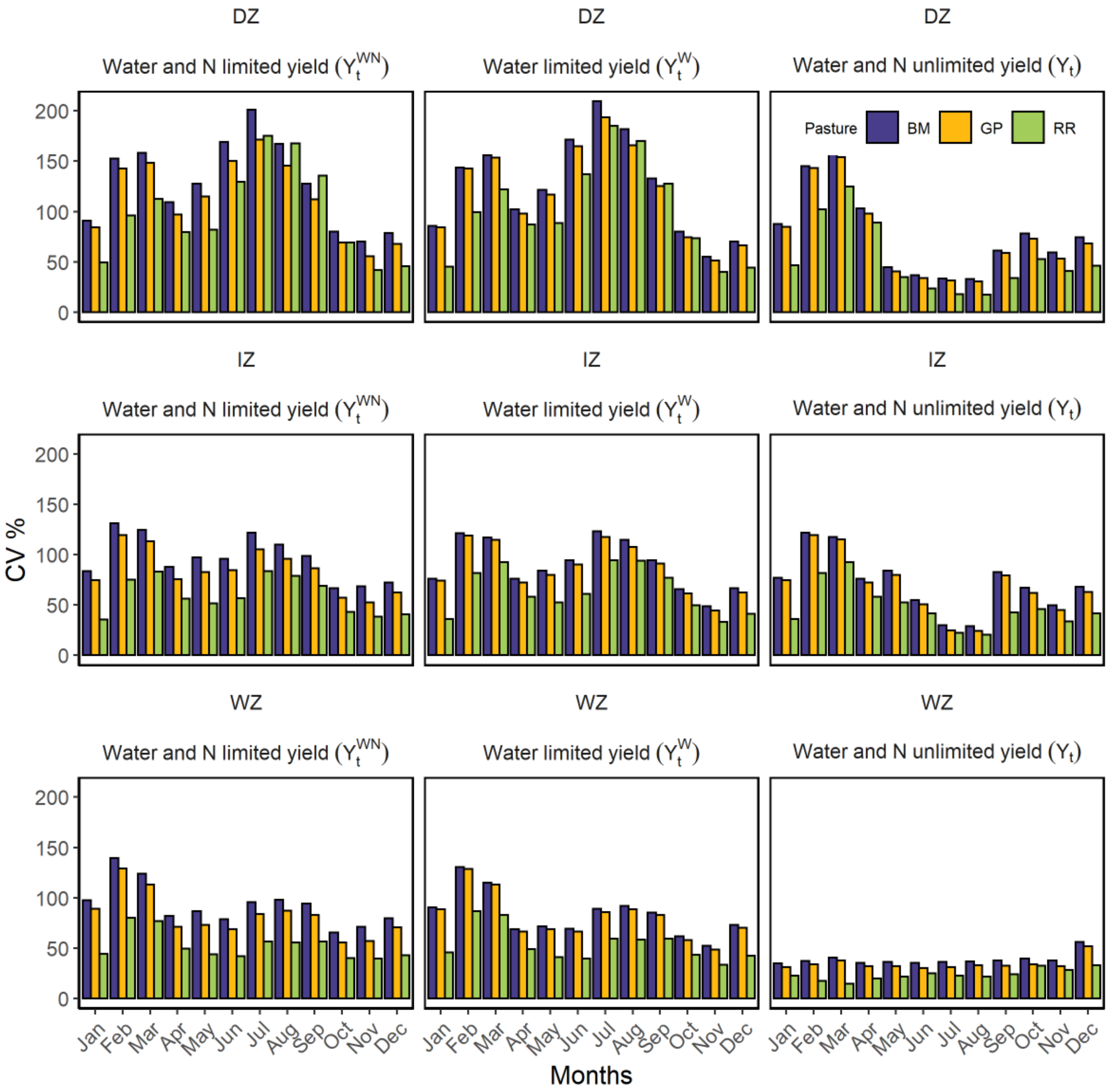


Figure 6.4. Long-term interannual variability (CV %) of monthly pasture growth of *Brachiaria* Mulato II (BM), Gatton panic (GP), and Rhodes grass Reclaimer (RR) for the sites in three major climatic zones (DZ = dry zone, IZ = intermediate zone, WZ = wet zone) under different pasture management scenarios in Sri Lanka.

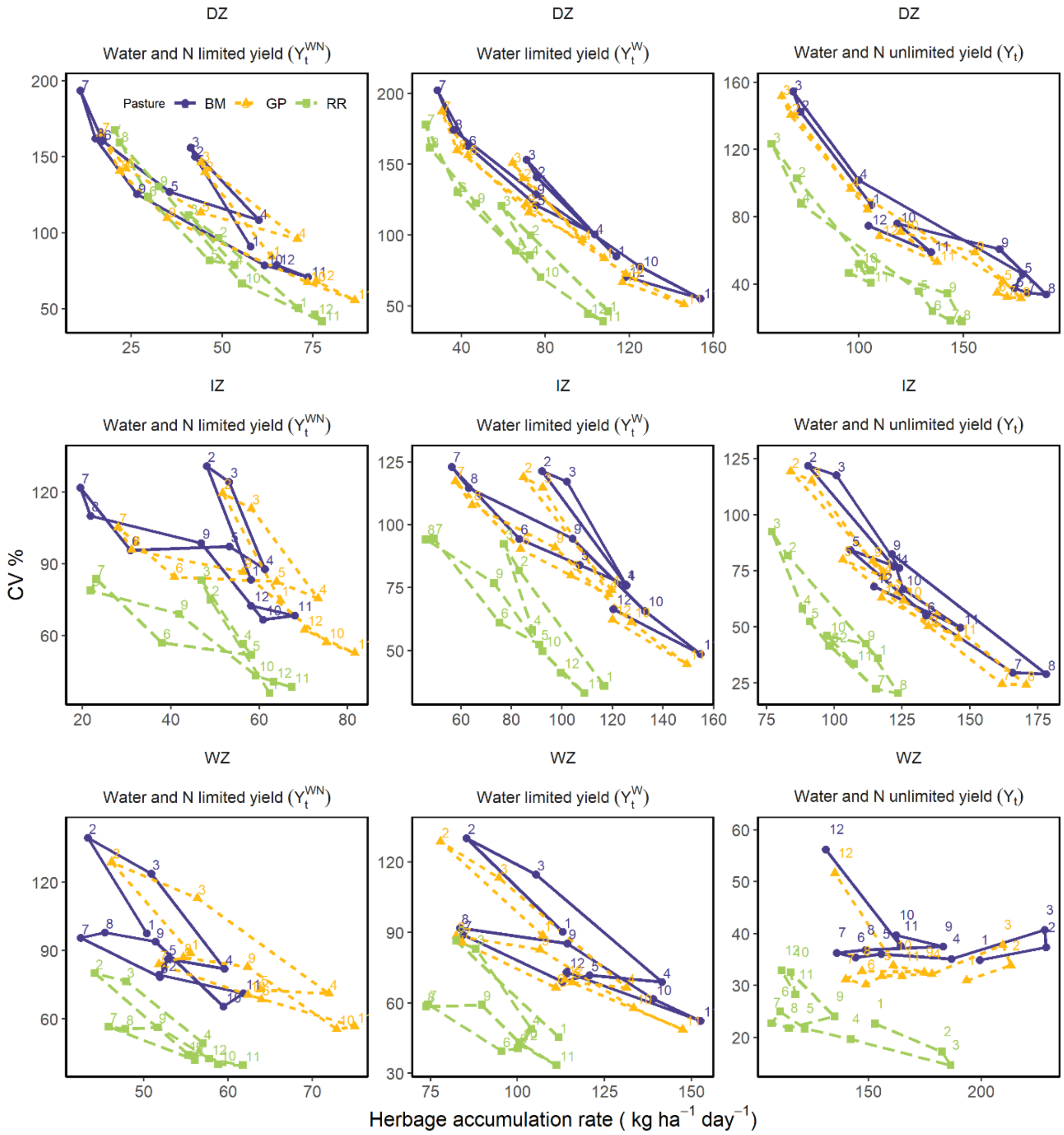


Figure 6.5. Long-term monthly pasture growth rates (kg ha^{-1} day^{-1}) and interannual variability (CV %) of *Brachiaria* Mulato II (BM), Gatton panic (GP), and Rhodes grass Reclaimer (RR) for the sites in three major climatic zones (DZ = dry zone, IZ = intermediate zone, WZ = wet zone) under different pasture management scenarios in Sri Lanka. The 1 to 12 numbers represent the months from January to December. Both the X and Y axes are adjusted to differentiate the plots.

6.4 Discussion

6.4.1 Long-term pasture growth and herbage accumulation

Growth rate and herbage accumulation were greater in GP at Y_t^{WN}, and BM at Y_t^{W} and Y_t while RR showed the lowest growth rate at all times. The actual (Y_t^{WN}) scenario showed a seasonal cycle following the rainfall pattern, with a reduction in growth rates in dry seasons (May to September). Overall, the pasture performance of the present study in terms of long-term herbage accumulation (Supplementary Table 6.2) outperformed the historical average annual herbage production (discussed later). In particular, Liyanage et al (1989) indicated that the *Megathyrus maximus* and *Brachiaria* pastures can yield up to 17 t DM ha^{-1} year^{-1} in well-fertilised WZ soils while the *Brachiaria mutica* can yield 12.4 t DM ha^{-1} year^{-1} in IZ soils in Sri Lanka. In the present simulation study, an estimate of 19 t DM ha^{-1} year^{-1} and 23 t DM ha^{-1} year^{-1} of average annual herbage mass was produced by the BM and GP, respectively in the WZ while the BM produced 17.7 t DM ha^{-1} year^{-1} in IZ. In another study, Senanayake et al (1991) extensively studied the *Brachiaria brizantha* in a cut-trial harvested in five weeks intervals across the 12 different regions of Sri Lanka and reported a mean DM yield of 10 t DM ha^{-1} year^{-1} (range from 2.7 to 33.7 t DM ha^{-1} year^{-1}). In contrast, the present study reported a 16.4 t DM ha^{-1} year^{-1} of average annual herbage across all locations. According to Premaratne & Premalal (2006) who presented the common forages and their yield potential under different management conditions, *Megathyrus maximus* produced up to 12–15 t DM ha^{-1} year^{-1} and 12–20 t DM ha^{-1} year^{-1} at the 45 days of cutting interval under the good management at 0.60 × 0.75 m and 0.50 × 1 m spacing, respectively. In addition, the *Brachiaria brizantha* produced an average yield of 10–12 t DM ha^{-1} year^{-1} at 35 days cutting interval in the IZ, Sri Lanka. By comparison, the long-term mean annual simulated pasture production of BM and GP are greater than the average values reported in the literature (Premaratne & Premalal, 2006) for the standard cultivars of *Brachiaria* and *Megathyrus* under the current pasture management (Y_t^{WN}) ranging from 4–7 t DM ha^{-1} year^{-1} and 5–8 t DM ha^{-1} year^{-1}, respectively. This greater variation in pasture production could be attributed to the improved traits of the pasture species including higher yield potential, adaptability to wider edaphoclimatic conditions, and improved disease and drought susceptibility. In contrast to the previously reported biomass data, the long-term average simulated herbage accumulation of BM and GP has doubled and nearly tripled under the Y_t^W and Y_t scenarios, respectively suggesting the likely yield performance of these tropical pastures under the edaphoclimatic conditions in Sri Lanka.

While classical validation of the models was not performed in the present study due to the lack of data as a result of BM, GP and RR not being previously tested in Sri Lanka, the mean herbage accumulation of standard cultivars reported in the previous studies in Sri Lanka were compared (previously discussed) with the long-term simulated growth data of the present study to observe the confidence of the model predictions. Even though the results of the previously reported studies about pasture yields are not entirely comparable with the simulated yields of the present study due to possible unaccounted factors (e.g., species, cutting intervals, cutting heights, planting spaces) between studies, those studies provide a better insight into the confidence of the model predicted pasture yield. Further, both the simulated and previously observed pasture data followed similarities in terms of the trends of pasture production within the species, and under different climatic zones. Comparison of the pasture production of RR was not possible as no studies have previously been undertaken to study the RR or its standard cultivars in Sri Lanka.

6.4.2 Pasture growth characteristics

In general, the greater pasture growth of GP under the existing management in the present simulation study is comparable with the results observed by Jayasinghe et al. (2022a). The higher pasture growth rate and associated forage yield of GP are attributed to the forage-yielding potential of the genus *Megathyrus* explained elsewhere (Sollenberger et al., 2020), and also the characteristically higher plant height, stem proportion and number of leaves (Jayasinghe et al., 2022a). Conversely, BM showed higher pasture growth rates under the Y_t^W and Y_t pasture management scenarios compared to GP and RR, highlighting the potential of BM for responding to fertiliser, particularly to the application of N at the optimum plant available water in the soil. According to Argel et al. (2007), the applications of N has increased DM yields of BM from 2.2 t harvest^{-1} with one application of N to 3.1 t harvest^{-1} with three application of N. Generally, the distribution of the rainall largely determines the growth rates and pasture yield between different climatic zones. This reflects the similar pasture growth rate and herbage accumulation across the locations within the same climatic zone showing the higher growth rates and yeilds in WZ than IZ and DZ.

6.4.3 Seasonality and spatial variability of the pasture growth

Pasture growth in tropical areas can experience significant variability due to a range of abiotic (e.g., climate, soil, altitude), biotic (e.g., pasture genotypic, soil microbiota) and pasture management (fertiliser, irrigation, harvesting) factors (Ara et al., 2020). The spatial and temporal variability of the monthly pasture growth observed in the present study (Figure 6.4 and Figure 6.5) is mainly driven by the main abiotic drivers of pasture growth like the interannual variability of the rainfall, plant available water in the soil, and possibly the solar radiation influenced by both the day length and cloud patterns. The temperature is less likely to have an impact on the temporal variability of the pasture production (Premaratne & Premalal, 2006), given the less deviation of the daily minimum and maximum temperature of a given site due to the lack of distinct seasonal changes in Sri Lanka (Punyawardena, 2020). However, the long-term pasture production between climate zones can be considerably affected by the temperature due to the clear regional differences in altitude, the seasonal movement of the sun and some modifications influenced by rainfall (Punyawardena, 2020). Overall, the higher pasture growth rate and herbage accumulation observed in the WZ, followed by IZ and DZ in the present study reflect the characteristic combination of optimum temperature (30–35°C) (Ivory & Whiteman, 1978) and rainfall (plant available water in the soil) for C_4 pasture growth in each climate zone. In addition, the pasture production peaks in DZ and IZ during January–April and late September–December due to increasing rainfall and soil moisture conditions, and troughs in May–early September (Figure 6.3 and Figure 6.4) as a result of low rainfall and soil moisture due to the inherent monsoon rainfall patterns in the area. Apart from the environmental factors, pasture species differ in their suitability to grow in different envioronments and it is largely determined by the morphological and physiological traits they possess (Simeao et al., 2021). These traits determine the fitness of the pasture species to grow, reproduce and survive under different environmental conditions. Overall, the RR had the least variable pasture growth rate across all scenarios and climates having increased plant productivity under drought conditions (Lowe et al., 2016), which may be attributed to its deep root system (~140 cm), higher carbon partitioning to roots providing more plant available water (White & Snow, 2012) and the reduced leaf area (small leaves) which potentially reduces the transpiration. In contrast, the higher variable pasture growth observed in BM is attributed to the quick growth response of the species determined by the higher photosynthetic rate, and high leaf area index to capture the solar radiation (Jayasinghe et al., 2022a). While the pasture management factors can grealty influence pasture growth and variability, the defoliation interval, N fertiliser, and irrigation can be discounted in the present study as such variables were kept constant across years and locations. However, between different scenarios, N fertiliser and irrigation largely affected the average monthly growth rate, herbage accumulation and pasture variability. This well-reflected effect of N fertiliser and irrigation in the long-term herbage results in the present study is mainly explained by the combined effect of soil, climate and species-specific responses to the N fertiliser and irrigation in the field.

6.4.4 Possible implications for dairying in Sri Lanka

The present study distinguishes the pasture growth and variability among species, climate zones, and different pasture management scenarios. However, to comprehend the potential consequences thoroughly, it is crucial to extend these results to the entire farm system. The productivity of pasture-based dairy systems can be influenced by the implications of pasture growth and variability, which generally depend on the balance between feed supply and demand. In addition to inadequate pasture supply, the variability of pasture growth can significantly impact its nutritive value due to the deterioration in sward structure and composition (Chapman et al., 2013). The annual forage supply is driven by the average pasture growth rate. Given the higher variability in growth rate during the drier months of the year, pastures do not produce enough biomass to meet the feed requirement of lactating cows resulting in poor milk production and reproduction. The year-round calving pattern currently observed in Sri Lanka, in particular among the low-input dairy farms, is likely to be more affected by the higher variability in pasture growth (Ibrahim et al., 1999). Therefore, supplying nutritionally balanced pastures during the peak of lactation is a considerable challenge under the current pasture management practice due to the limited supply of year-round pastures. While the superior pasture growth rate of BM and GP produced more herbage than their standard cultivars currently growing, the forage supply remains low during drier months due to a poor growth rate. However, the current average accumulated annual pasture yield (Y_t^{WN}) was more than double and nearly triple under the simulated Y_t^W and Y_t management scenarios for all pastures, and BM has relatively outperformed in yields. While the pasture growth patterns remained unchanged at Y_t^{WN} and Y_t^W, and Y_t^W produced greater biomass during rainy seasons producing a surplus of feed to be used in the drier months after properly conserved (e.g., hay, silage). In addition, pasture management Y_t further helped to substantially increase the pasture yield by changing the growth rate and also the growth pattern making a more consistent pasture supply during the drier months. Given the long-term average cut yield of BM, GP and RR in multiple locations tested, these pastures would be suitable to grow across the country which has similar edaphoclimatic conditions. Further, the observed potential of GP producing relatively more biomass under the Y_t^{WN} and BM under the Y_t^W and Y_t suggests that growing GP in low-input farming areas and the BM in high-input areas would be more suitable.

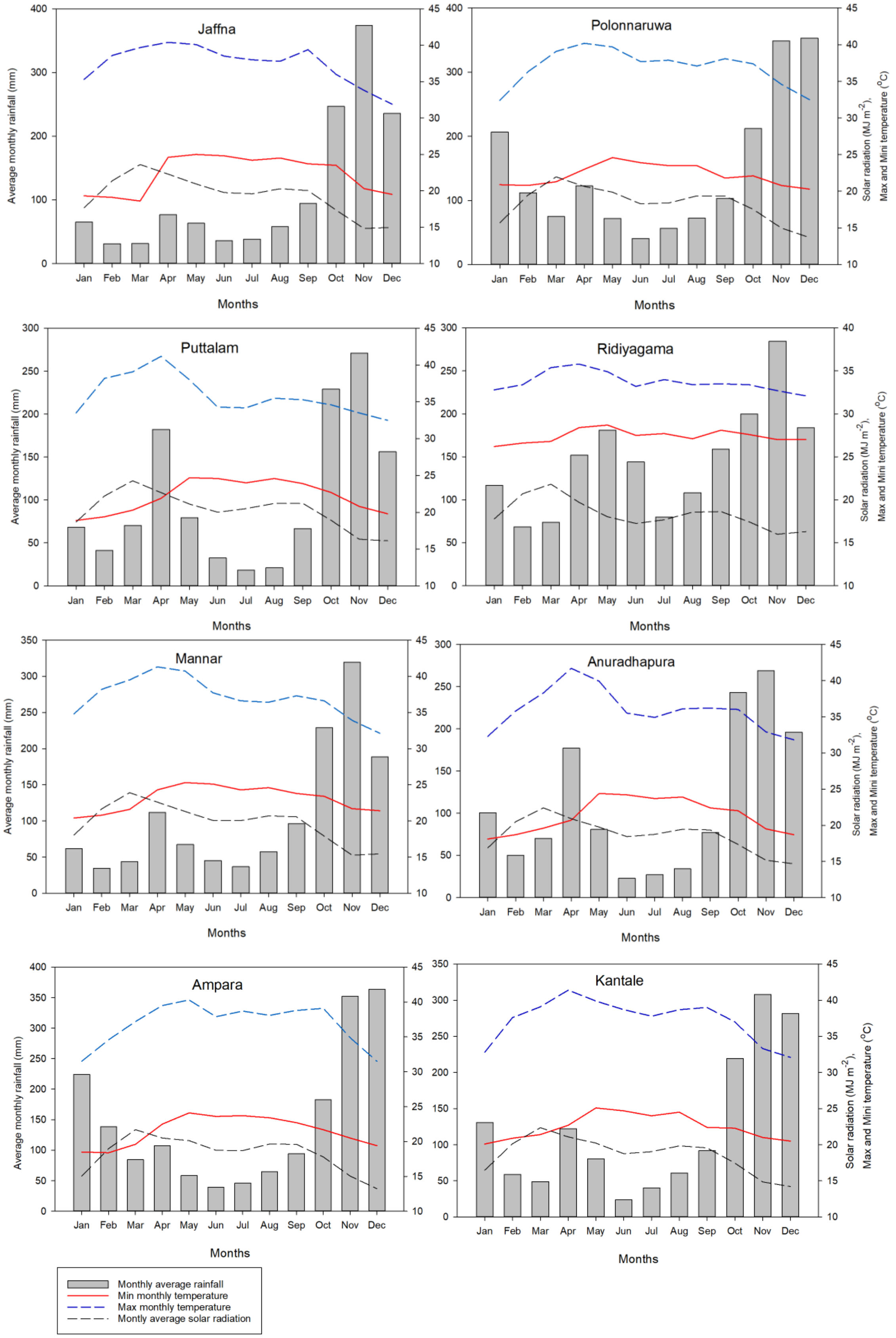
Tropical pastures can grow fast during favourable weather conditions (warm and high rainfall). The unconstrained growth during the peaked rainfall can produce taller pasture swards structured with more stems (low leaf: stem) and accumulated dead materials (due to light competition) resulting in poor-quality herbage. This could be further deteriorated by the sward structure determined by the pasture morphology. In particular, GP at a higher growth rate produces more stem (higher ratio of carbon partitioning to stem) than BM and RR resulting in a higher trade-off between quantity and quality. The present simulation used the monthly defoliation frequency (pasture harvested on the last date of each month), however, the accumulated high pasture yield indicates that the frequent defoliation of pastures (subjected to the potential herd size) during rainy months (January–April and September–December) would be more appropriate in practice to avoid excessive forage accumulation and maintain the herbage quality, particularly in the IZ and WZ under the Y_t^W and Y_t scenarios. Further, the reduced pasture growth during the drier and hotter months can limit the uptake of soil-available nutrients and also induce physiological (e.g., stem lignification, reduced leaf area) and phenological changes in plants (e.g., delay or hasten anthesis) leading to accumulation of poor quality herbage (Jégo et al., 2013). These quality changes are likely to be more evident in the pastures growing in either DZ or IZ under existing pasture management (Y_t^{WN}).

The simulated growth rate and herbage accumulation in the modelling studies are often higher than the typically measured pasture biomass under field conditions (White & Snow, 2012). This is primarily due to the model not being able to incorporate the possible effects of the pest, weed and disease pressure. In addition, all resources required to achieve high pasture growth are rarely simultaneously available at the same time, however exploring the resources that can be controlled (e.g., N fertiliser, irrigation) provides important insights around the possible intensification of pastures for improving dairy farming in Sri Lanka. It is a fact that high-input pasture production systems can generally incur a significant cost of production apart from the possible harm to the environment, therefore the economic and environmental viability of the Y_t^W and Y_t pasture production scenarios need to be investigated further. The present study highlights the potential use of DairyMod-SGS for the long-term simulation of tropical pastures, enabling the characterisation of pasture growth and variability under different management scenarios. The practical outcomes of this analysis provide confidence in the prospective use of this information for supporting pasture species selection, identifying responses to different pasture management practices, and making informed feed budgeting and feeding decisions.

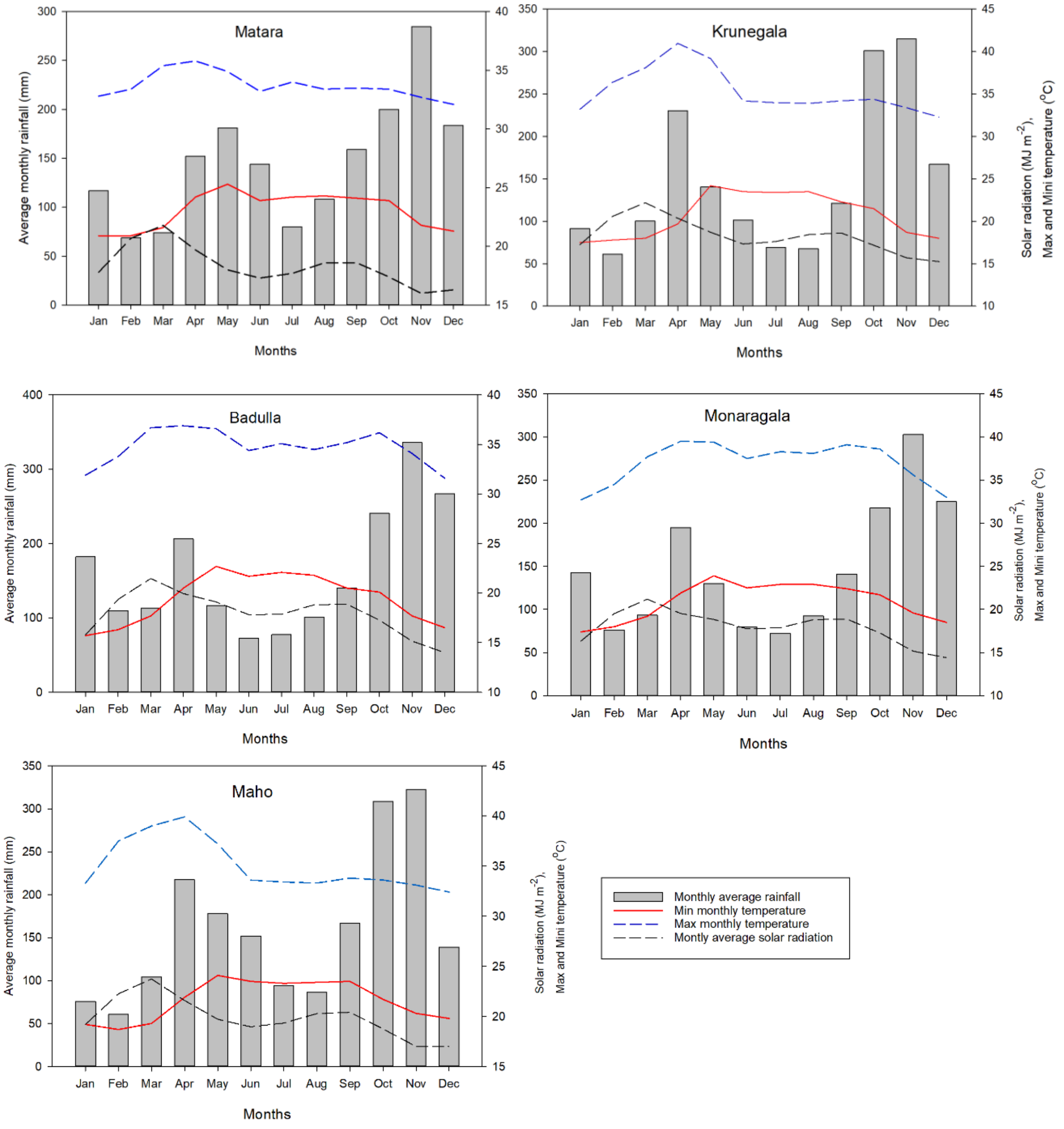
6.5 Conclusions

The present simulation study demonstrated that the DairyMod-SGS can successfully simulate long-term tropical pasture production. In addition, the model successfully captured the species-specific physiological adaptation and yield potential during the pasture growth simulation. The rainfall, climate zone, pasture species and management were the key drivers for the annual average herbage accumulation and variability of the pasture growth over the locations evaluated. The growth rates were high in GP under Y_t^{WN}, while the growth rate of BM was superior under both Y_t^W and Y_t and RR recorded the lowest growth rate throughout. The improved pastures tested in the present study produced considerably higher biomass than the standard cultivars available under the existing pasture management. Pasture accumulation under non-limiting nutrients (Y_t^W) increased the growth rate while the non-limiting nutrients and water (Y_t) scenario substantially increased both the growth rate and the growth pattern, in particular nearly doubled and tripled under Y_t^W and Y_t, respectively. Overall, the results of the present simulation study suggested that the improved pastures tested are edaphoclimatologically fit for growing across major dairying regions in Sri Lanka, however when selecting the appropriate species, the species-specific growth pattern, growth variability, yield potential under different managements and the possible implications for herbage quality need to be carefully considered.

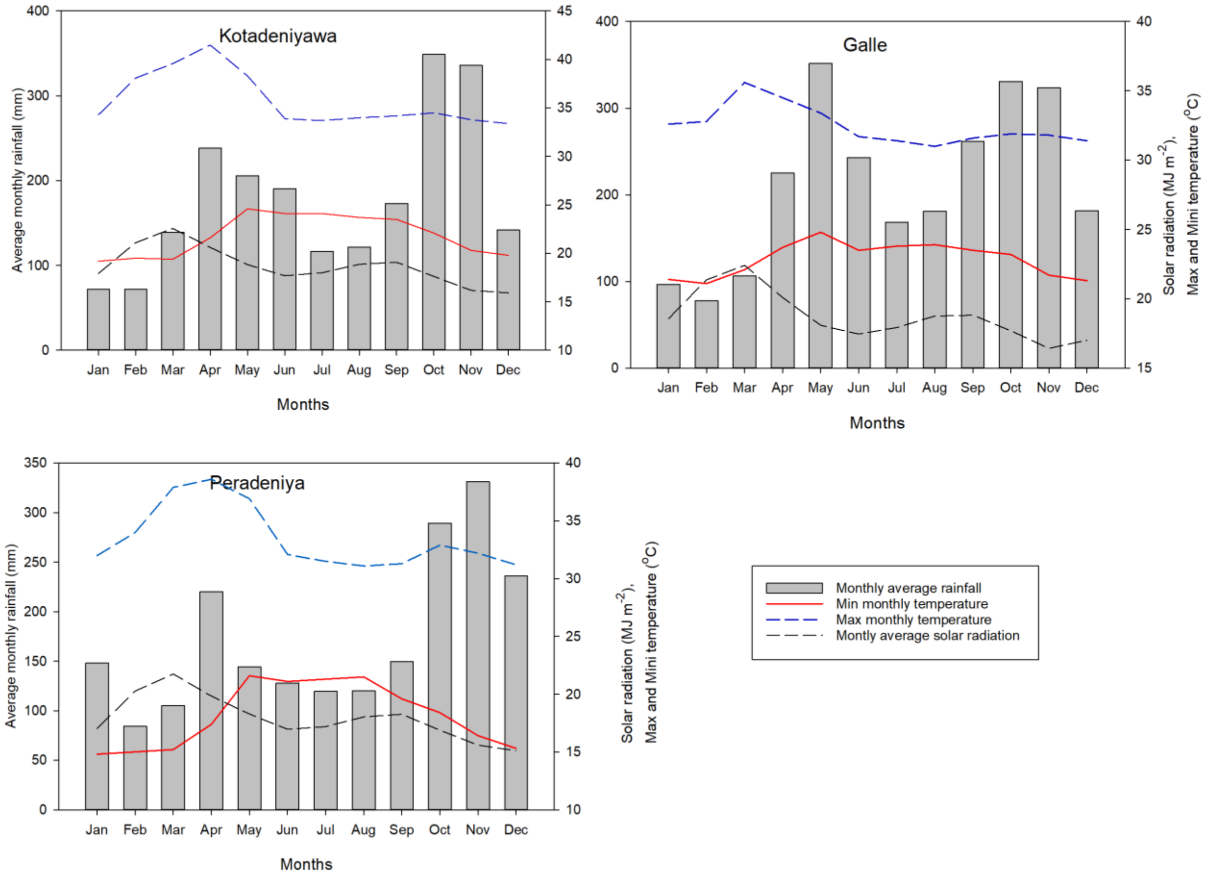
Supplementary materials



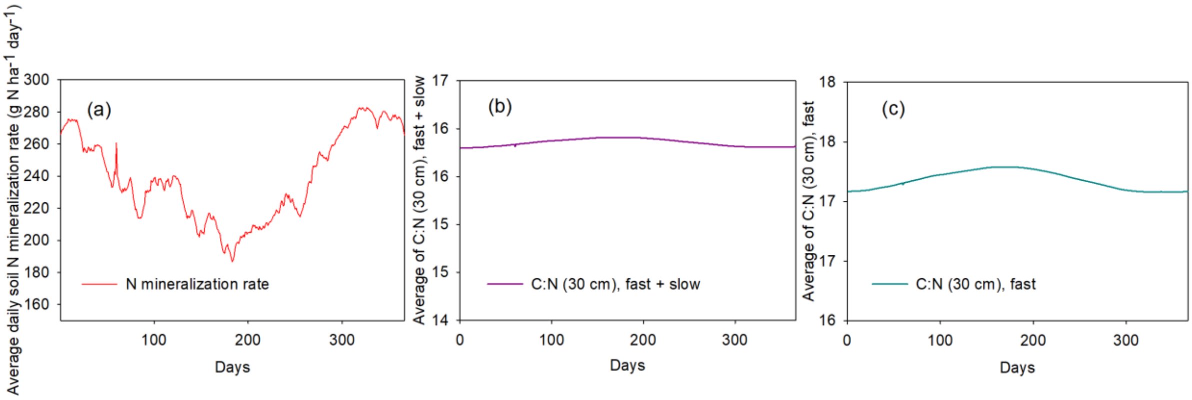
Supplementary Figure 6.1a. Long-term monthly average of rainfall (mm), minimum temperature (°C), maximum temperature (°C), and solar radiation (MJ m^{2} day^{-1}) distribution in dry zone sites.



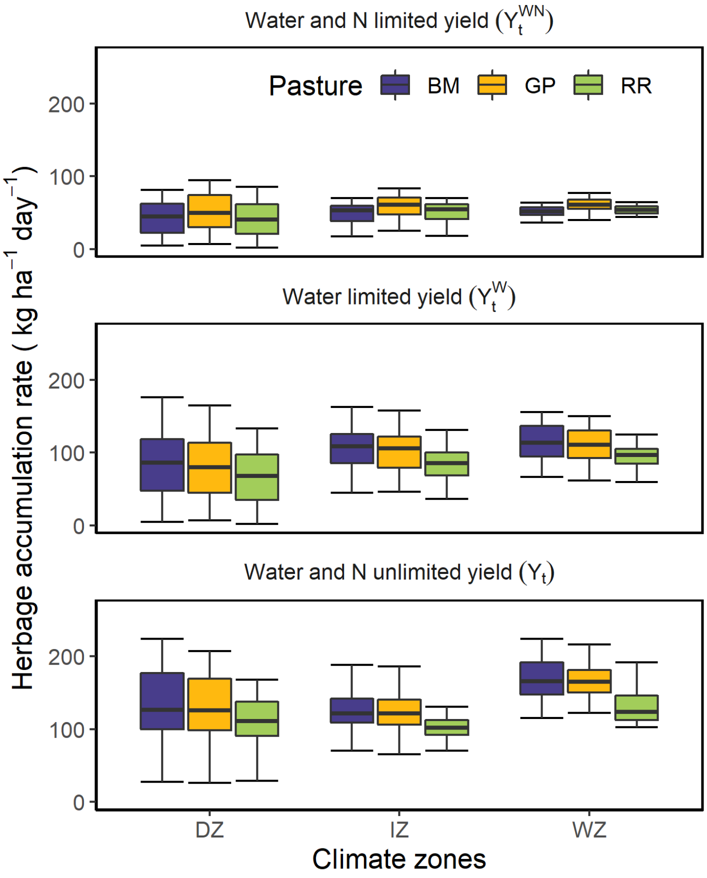
Supplementary Figure 6.1b. Long-term monthly average of rainfall (mm), minimum temperature (°C), maximum temperature (°C), and solar radiation (MJ m^2 day^{-1}) distribution in intermediate zone sites.



Supplementary Figure 6.1c. Long-term monthly average of rainfall (mm), minimum temperature (°C), maximum temperature (°C), and solar radiation (MJ m^2 day^{-1}) distribution in wet zone sites.



Supplementary Figure 6.2. DairyMod-SGS model initialisation results for (a) annualized average daily soil N mineralization rate (g N ha^{-1} day^{-1}) over 30 years, (b) steady soil organic C pool and C: N ratio of the fast (labile) and (c) fast + slow turnover pools.



Supplementary Figure 6.3. Long-term monthly pasture growth rates (kg ha^{-1} day^{-1}) distributions of *Brachiaria* Mulato II (BM), Gatton panic (GP), and Rhodes grass Reclaimer (RR) in three major climatic zones (DZ = dry zone, IZ = intermediate zone, WZ = wet zone) under different pasture management scenarios in Sri Lanka.

Supplementary Table 6.2. Average (1980–2010) annual accumulated herbage production (t DM ha^{-1}) of *Brachiaria* Mulato II, Gatton panic, and Rhodes grass Reclaimer for the 16 sites in three major climatic zones under three pasture management scenarios (Y_t^{WN} **=** water and nitrogen-limited yield, $\boldsymbol{Y_t^{W}}$ = water-limited potential yield, $\boldsymbol{Y_t}$ = water and nitrogen unlimited potential yield) in Sri Lanka. Sd = Standard deviation.

Climate	Location	*Brachiaria* Mulato II						Gatton Panic						Rhodes grass Reclaimer					
		Y_t^{WN}	Sd	Y_t^{W}	Sd	Y_t	Sd	Y_t^{WN}	Sd	Y_t^{W}	Sd	Y_t	Sd	Y_t^{WN}	Sd	Y_t^{W}	Sd	Y_t	Sd
Dry Zone	Ampara	15.8	0.3	33.7	0.6	54.1	0.8	19.3	0.3	32.6	0.6	52.8	0.8	15.4	0.3	25.2	0.4	43.1	0.6
	Jaffna	13.8	0.3	26.7	0.5	48.4	0.8	17.1	0.3	26.1	0.5	46.7	0.8	13.4	0.3	18.7	0.4	38.6	0.6
	Kantale	14.0	0.3	22.9	0.4	35.8	0.6	16.8	0.3	22.4	0.4	35.0	0.5	14.1	0.3	19.2	0.4	36.3	0.6
	Anuradhapura	14.5	0.3	28.0	0.5	50.3	0.8	17.8	0.3	27.4	0.5	49.0	0.8	13.4	0.3	19.3	0.4	38.6	0.6
	Mannar	13.9	0.3	25.7	0.5	49.7	0.8	16.9	0.3	25.0	0.5	47.9	0.8	13.2	0.3	19.1	0.4	38.3	0.6
	Polonnaruwa	16.0	0.3	35.2	0.6	55.1	0.8	19.8	0.3	34.0	0.6	53.7	0.8	16.7	0.3	28.8	0.5	44.4	0.7
	Puttaum	15.1	0.3	30.3	0.6	56.9	0.9	18.2	0.3	28.6	0.5	53.8	0.9	15.3	0.3	24.2	0.5	46.9	0.7
	Ridiyagama	17.0	0.3	37.4	0.6	47.3	0.7	21.2	0.3	36.9	0.6	46.6	0.7	17.3	0.5	33.1	0.5	44.5	0.8

Supplementary Table 6.2. Cont.

Wet Zone	Galle	19.0	0.3	44.0	0.7	60.2	0.9	23.0	0.3	42.5	0.7	59.0	0.9	20.1	0.3	37.9	0.6	48.8	0.7
	Kotadeniyawa	18.8	0.3	39.5	0.6	63.9	0.9	22.6	0.3	38.1	0.6	63.6	0.9	19.7	0.3	33.1	0.5	52.4	0.8
	Peradiniya	19.7	0.3	44.4	0.7	70.4	1.0	23.5	0.4	42.2	0.7	67.8	1.0	20.3	0.3	35.5	0.5	49.4	0.7
Intermediate Zone	Maho	17.3	0.3	43.1	0.7	52.0	0.8	20.9	0.3	40.7	0.7	49.6	0.8	18.0	0.3	35.2	0.6	42.5	0.7
	Badulla	17.9	0.3	40.7	0.6	50.0	0.8	21.9	0.3	39.4	0.6	48.6	0.7	18.0	0.3	30.5	0.5	37.7	0.6
	Kurunegala	17.5	0.3	37.8	0.6	47.8	0.7	21.2	0.3	36.4	0.6	46.1	0.7	18.3	0.3	32.0	0.5	39.4	0.6
	Monaragala	17.6	0.3	37.2	0.6	45.0	0.7	21.4	0.3	36.1	0.6	44.3	0.7	18.1	0.3	30.1	0.5	37.3	0.6
	Matara	18.0	0.3	41.8	0.7	48.7	0.7	22.3	0.3	40.9	0.6	47.6	0.7	18.8	0.3	32.7	0.5	37.4	0.6

Chapter 7

General Discussion

7.1. Introduction

Tropical perennial pastures constitute a key resource to fulfil the nutritional requirements of ruminants in tropical and subtropical regions (Cooke et al., 2020; Sollenberger et al., 2020). Despite the importance of tropical pastures in dairying, the volume of milk production associated with tropical pastures is consistently lower compared to temperate pastures (Lowe et al., 2016). This is mostly due to tropical pasture species generally having lower nutritive value, with large seasonal variations in quantity and quality, compared with temperate pasture species. However, nutrient intensification through planting improved forage options (Paul et al., 2020), in addition to adopting appropriate harvesting (Jayasinghe et al., 2022b), fertilising (Delevatti et al., 2019), and grazing practices (Da Silva et al., 2015), have substantially improved the nutritive value of tropical pastures. Further, the integration of these improved forage varieties into existing feeding practices can improve productivity (Paul et al., 2020), and potentially decrease the environmental footprint, of tropical forage-based livestock production systems (Rao et al., 2015).

An inadequate supply of quality forage is the major factor limiting dairy production in Sri Lanka. Feed resources are either not available in sufficient quantities due to fluctuating weather conditions, or even when available, are of poor nutritive value. The digestibility of tropical forages is often low (58–62%), resulting in poor outcomes in terms of low milk yields and short lactation, longer calving intervals, and low animal body weights (Kumara et al., 2022), high enteric CH_4 emissions per unit of ME, and low profitability for farmers (Opio et al., 2017). The strategies to improve forage production in Sri Lanka have been broadly explored (Premaratne & Premalal, 2006; Houwers, 2015; Opio et al. 2017; Prowurst, 2019; Premaratne & Samarasinghe, 2020; Vyas et al., 2020).

The key approaches often highlighted comprise the introduction of improved grasses adapted to the local soil and climate, which are more leafy and digestible, in order to exploit the maximum genetic potential of dairy cows, and then subsequently intensify management through appropriate defoliation in combination with more intensive fertiliser applications. While the impact of the non-availability of improved forages for dairying and the potential solutions to overcome this have been widely studied (Premaratne & Premalal, 2006; Houwers, 2015; Opio et al. 2017; Prowurst, 2019; Premaratne & Samarasinghe, 2020; Vyas et al., 2020), no studies have been undertaken to broadly evaluate the potential of improved forage species that could be introduced in different regions of Sri Lanka. In the absence of basic data regarding suitable improved forage species and their likely performances, efforts to expand the productivity of dairy farming remain inadequate and inefficient.

The general aim of the present thesis was to investigate tropical pasture species for improving dairying in Sri Lanka. The study comprised field experiments along with simulation modelling. Initially, the field experiments were planned to take place in a selected tropical environment in Sri Lanka. However, due to the Covid pandemic and subsequent travel restrictions between New Zealand and Sri Lanka, this plan was no longer feasible. Subsequently, a glasshouse experiment was planned at the Plant Growth Unit, Massey University, however, this was ultimately abandoned due to the biosecurity regulations at the New Zealand border concerning the purity of the tropical pasture seeds and the associated risk of possible weeds entering the country. The thesis was redesigned to include a field experiment collaboratively conducted with the Department of Agriculture and Fisheries Queensland, at the trial site of the University of Queensland, Gatton, Australia. The duration of the experiment was confined to seven months due to the Covid travel restrictions and not being able to travel to Australia to continue data collection. Thus, the final thesis was more focused on using the field data to model tropical pastures and on the model application within the context of the main thesis objective.

The specific objectives were to:

1. undertake a meta-analysis to compare the nutritive value of tropical pastures grown in different bioclimatic environments (Chapter 3);
2. study the suitability of three improved tropical pastures: *Brachiaria* Mulato II (BM), *Megathyrsus maximus* 'Gatton Panic' (GP), and *Chloris gayana* 'Rhodes grass cv. Reclaimer' (RR), for cultivation in subtropical and tropical environments by evaluating their carbon assimilation, canopy structure, herbage accumulation, and nutritive value parameters (Chapter 4);
3. develop parameters and calibrate the DairyMod-SGS model for these three tropical pastures and validate the parameterised model across multiple environments using published and unpublished data (Chapter 5); and
4. apply the DairyMod-SGS model to simulate the growth of the three tropical pastures and characterise their long-term forage production, seasonality, and spatial variability across the key livestock production zones under three different pasture production scenarios in Sri Lanka (Chapter 6).

The current chapter provides a general discussion of the results and findings from the thesis, highlighting the key contributions to science as well as the limitations of the thesis. It also identifies areas for future research and offers recommendations for policy and practice.

7.2. The key findings from this thesis and applications

Intensification, through planting new cultivars and adopting appropriate harvesting, fertilising, and grazing practices, has substantially improved the nutritional value of tropical pastures. The first research objective was to collate agronomic literature to study the management strategies and nutritive value of tropical pastures growing in contrasting environments, and to undertake a meta-analysis of the data (Chapter 3). Further, the implication for livestock CH_4 production was also investigated; this was the first study to provide a detailed overview and summary of tropical pastures (56 tropical pasture species and hybrid cultivars grown in 26 different locations in 16 countries), including their nutritive values (CP, NDF, ADF, ADL, minerals, DMD, OMD, OM, and ME) and imposed management (Chapter 3). Overall, the findings of Chapter 3 provided preliminary evidence about the existing limitations of standard tropical pasture cultivars for a productive dairy system in terms of their inherently poor average nutritive value compared with some other feed types (e.g., concentrates and temperate grasses) and also the potential of improved pastures for delivering quality livestock feed options in the tropics. A significant variation in the nutritive values and CH_4 production of tropical pastures between and within species was observed (Chapter 3), with more recently-released and hybrid cultivars performing better than the older, standard cultivars across wider bioclimatic areas, suggesting their ability to deliver improvements in livestock production in tropical areas. In particular, pasture species *Pennisetum purpureum* followed by *Brachiaria,* showed high CP, OMD and ME contents, and low NDF content and CH_4 production. The observed variations of nutritive value driven by cultivar breeding (genotypic variation) for improved quality (Capstaff & Miller, 2018) and different physiological responses (adaptations) of individual species to environmental factors (Van Soest, 1994), can be useful indicators for farmers to identify suitable pasture species. Chapter 3 further demonstrated that the average CP was 10.9% DM across all tropical pasture species at any given harvest interval, and the CP content of hybrid cultivars (i.e., *Brachiaria, Pennisetum*) ranged between 16.4% and 17% DM, indicating that hybrids are more able to meet the CP requirements of lactating cows, apart from during peak lactation. The average ME (7.5 MJ kg^{-1} DM) of the tropical pastures was below the NRC-recommended energy content required for lactating cows (8.4–10.3 MJ kg^{-1} DM, average 9.3 MJ kg^{-1} DM) (NRC, 2001). The climate, and its interaction with pasture management (frequency of defoliation, defoliation intensity), was found to be a key variable determining the nutritive value of tropical pastures (Chapter 3). Correlation between multiple nutritive values and CH_4 with pasture management variables and climate, further indicated that the nutritive value parameters and CH_4 production could be substantially improved by practising improved defoliation management (frequency and intensity), however, generic defoliation management options for tropical pastures are unlikely to produce better agronomic results, as they do not consider the species-specific growth nor the physiological stages induced by climate (Lemaire et al., 2009). Importantly, these results imply that investigation of tropical pastures, especially for improved cultivars in terms of tropical pasture regrowth, herbage production, composition, and nutritive value, is useful in broadening the comparative knowledge of plasticity between species and selecting suitable species for a wide range of environments. In this regard, the subsequent chapters of this thesis concentrated on BM, GP, and RR, three improved tropical pastures widely used in the tropics and subtropics, which have not been compared against each other in Sri Lanka (Jayasinghe et al., 2022a). To my knowledge, Chapter 4 was the first comprehensive study of these three tropical pastures concerning their physiology (carbon assimilation), morphology (canopy structure), herbage accumulation (leaf, stem, dead materials), and nutritive value parameters. Overall, Chapter 4 identified that plant-specific physiological and morphological parameters play a significant role in pasture production and nutritive value. In particular, the gas exchange results indicated that BM was more photosynthetically efficient and can perform well even under lower light conditions compared to GP and RR, suggesting its potential to produce greater biomass under shaded environments, such as those in silvopastoral systems (e.g. under coconut plantations in Sri Lanka) (Moreno et al., 2021). The higher respiration of BM was not conducive to the accumulation of greater forage mass, whereas the higher plant photosynthetic capacity of GP compared with both BM and RR, reflected the maximum potential for CO_2 fixation under sufficient light and CO_2 concentrations, and was reflected in greater biomass. In addition, the morphological characteristics of GP (taller plant height and more live leaves per tiller) showed its relative advantage and vigour over other species, particularly under conditions of full light interception. Through exploring the fundamental basis of pasture growth, species-specific physiological adaptation and yield potential, results from Chapter 4 should benefit farmers in selecting suitable species. In terms of pasture canopy structure, all pastures exhibited a heterogeneous vertical structure typical of tropical pastures, with a top leafy and bottom stemmy stratum (Sollenberger & Burns, 2001). While the interspecies sward structure greatly varied for leaf: stem, leaf area index, specific leaf area, sward height, depth of leaf and stem strata, and canopy bulk density, BM showed better sward structure parameters compared to GP and RR. The greater leafy stratum depth of BM due to lower stem height observed in the present study, compared to RR and GP, appeared to be more favourable for greater nutritive value 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 on the accessibility of herbage to defoliation through grazing, and lowering the diet quality (Benvenutti et al., 2016). In addition, the consequences to the nutritive value 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. A comprehensive analysis was undertaken on the nutritive profile and mineral contents of the leaf, stem, and whole plant of all three pasture species. The pasture nutritive values varied significantly between species and plant parts, and BM exhibited greater CP, NDICP, starch, WSC, ESC, NFC, ME, and mineral composition (Mg, K, Fe, Zn), along with a more balanced DCAD for lactating dairy cows (Chapter 4). While the nutritive value results of Chapter 4 supported results from the meta-analysis in Chapter 3, they were more relevant to understanding how the plant physiological and morphological component information might be used to influence pasture selection and subsequently manage the pasture (Lemaire et al., 2009). Collectively, the results of Chapter 4 indicated that BM was the best forage option for feeding lactating dairy cows, while GP would better suit feeding dry cows given its ability to produce a large quantity (but lower quality) of forage.

The last two experimental chapters of this thesis consisted of modelling, to enable an extrapolation of these field results to Sri Lankan conditions. The pasture model, DairyMod-SGS was selected given the relative ease of parameterising new pastures, and the comparatively lower number of parameters required (White et al., 2008; Berger et al., 2014; Svinurai et al., 2021). Results from Chapter 4 (i.e., photosynthesis, leaf appearance, respiration, canopy structure, carbon partitioning, and root distribution) together with data (i.e., plant growth responses to temperature, senescence parameters) reported in the literature (Pedreira et al., 2011; Lara et al., 2012; Descheemaeker et al., 2014; Pequeno et al., 2018; Bosi et al., 2020a;), were collectively used to parameterise and subsequently validate (using published and unpublished data sets) the DairyMod-SGS pasture model for BM, GP, and RR. This was the first study to parameterise the model for multiple tropical pasture species and to validate across a broad range of locations (16 data sets, 32 experiments, 14 different locations across South America, North America, Australia and Africa). Overall, the model performance statistics indicated that the DairyMod-SGS pasture model was able to successfully simulate established monocultures of BM, GP and RR pasture swards for their growth and biomass production under cut-and-carry management across a broad range of edaphoclimatic conditions (e.g., subtropical, tropical, Mediterranean, and desert environments), and agronomic management practices (e.g., irrigated, rainfed, N fertiliser, shaded, high input). The close agreement between the measured and simulated biomass data indicated that the model performance was similar to the best parameterisation studies for tropical pastures, indicating the efficacy of the parameterised DairyMod-SGS model and its calibrated parameters for tropical pastures in the present study (Pedreira et al., 2011; Lara et al., 2012; Descheemaeker et al., 2014; Pequeno et al., 2018; Bosi et al., 2020a; Brunetti et al., 2021). However, biomass partitioning results indicated that the model requires further calibration using additional leaf and stem data. In addition, results revealed that the low-temperature recovery function and plant senescence need to be improved using more pasture species-specific parameters. However, the present study has improved the robustness and accuracy of DairyMod-SGS in relation to tropical pastures, which makes the model a tool that could potentially explore likely pasture performance under a range of soil and climate conditions for livestock production systems in the tropics and subtropics.

Following the comprehensive model parameterisation and validation (Chapter 5), DairyMod-SGS was applied to characterise the three pasture species in terms of long-term forage production, seasonality, and spatial variability across the key livestock production zones under three different pasture production scenarios in Sri Lanka (Chapter 6). This was the first study to use the DairyMod-SGS pasture model for long-term simulation of tropical pastures, and also the first study to use a simulation and modelling approach to evaluate pasture performance in Sri Lanka. Chapter 6 analysed the pasture production at 16 sites (8 sites in the dry zone (DZ), 5 sites in the intermediate zone (IZ), and 3 sites in the wet zone (WZ)) over a 30-year period (1980–2010) under three pasture management scenarios [(1) rainfed pasture production system under current industry average N fertilisation (Y_t^{WN}), (2) rainfed pasture production system under non-limiting N fertilisation (Y_t^{W}), and (3) potential pasture production under non-limiting N and irrigation (Y_t)] across major dairying regions of Sri Lanka. Results indicated that the pasture production of BM, GP and RR under Y_t^{WN} was well synchronised with the annual rainfall distribution of each site and showed distinct growth patterns across three climate zones, producing more pasture biomass in WZ followed by IZ and then DZ. Long-term simulated pasture growth rates indicated that herbage accumulation was greater in GP at Y_t^{WN}, and BM at Y_t^{W} and Y_t, while RR had the lowest growth rates and biomass accumulation in all instances. These results suggest that GP would be better adapted to low-input farming areas and BM to high-input areas. While the superior pasture growth rate of BM and GP produced more herbage than the standard cultivars currently in use in Sri Lanka (Liyanage, 1989; Premaratne & Premalal, 2006; Premaratne & Samarasinghe, 2020), the forage supply remains low during drier months due to a poor growth rate. However, compared to the scenario under water and N limitation (Y_t^{WN}), simulated pasture yield was more than double and nearly triple under the Y_t^{W} and Y_t management scenarios for all pastures, and BM relatively outperformed in terms of growth rate and pasture yield (Chapter 6). While the pasture growth patterns remained unchanged during most of the months of the year at Y_t^{WN} and Y_t^{W}, Y_t^{W} resulted in a surplus of biomass during rainy seasons, which could be transferred to drier months as long as a suitable pasture conservation method (i.e.: hay, silage) was used. In addition, switching the pasture management from Y_t^{W} to Y_t substantially increased the pasture yield by changing the growth rate and also the growth pattern, resulting in a more consistent pasture supply during the drier months. These results suggest that intensification of pasture management through the application of fertiliser and irrigation can substantially improve pasture production in tropical regions. Further, these results highlighted that the response of different pastures to the intensification will vary between species due to their morphological and physiological traits, which determines the fitness of the pasture species to grow, reproduce, and survive under different environmental conditions. These results, together with the findings of Chapter 3 and Chapter 4, further reflect the importance of the diversity of the pasture species (e.g., deep root, drought tolerance, less variable growth rate, rapid growth after rainfall, rapid response to N fertiliser, high nutritive value, high biomass, plant-part composition) for sustainable pasture production, and provides information that will give greater flexibility to farmers in tropical regions, including Sri Lanka, to select the appropriate species fit for their purpose, location, and agronomic management practices. In addition, these large variations in pasture species can increase pasture resilience and resistance to challenging conditions under different soils and climates. Overall, Chapter 6 raised the potential of using DairyMod-SGS for the long-term simulation of tropical pastures. These results, together with the results of Chapter 3 and Chapter 4, revealed that when selecting the appropriate species, the species-specific growth pattern, growth variability, yield potential under different managements and the possible implications for herbage nutritive value need to be carefully considered.

7.3. Limitation of the current study

7.3.1. Meta-analysis

Expressing the nutritive value and mineral composition partitioned to plant parts (leaf, stem, whole plant) is useful for farmers to make decisions on the quality of their pastures, given the more heterogeneous sward structure of tropical pastures (Benvenutti et al., 2016; Benvenutti et al., 2017). However, a detailed analysis was not possible in the present meta-analysis due to a lack of studies that summarised the nutritive value and minerals of different plant parts. Alternatively, a comprehensive description of the nutritive value and mineral composition of three tropical pastures (*Brachiaria* Mulato II, Gatton panic and Rhodes grass Reclaimer) was presented in Chapter 4, which could be used to understand the partitioning of nutritive value into different plant parts.

7.3.2. Data collection and parameter development

The data collection period in the present study was limited to only seven months, and we were able to develop the majority of the pasture species-specific parameters using the direct field measured data during that period. However, longer, and more frequent, data collection would improve the parameterisation of carbon partitioning to leaf and stem, giving more realistic modelled leaf and stem accumulation. In addition, the present study used several generic C_4 parameters (e.g. low recovery function, plant senescence) available in the DairyMod-SGS, given the difficulty of measuring those parameters in the field. However, more pasture-specific parameters would improve the model performance, especially under suboptimal and low-temperature stress conditions (where the minimum air temperature drops below the plant base temperature).

7.3.3 Limitation of DairyMod-SGS and implications

It is important to acknowledge the limitations when using the DairyMod pasture model and to interpret its results with a clear understanding of its scope and potential inaccuracies in certain scenarios. Further, comprehending the limitations of the model proves valuable for both its future applications and model development. The model exhibited limitations in capturing the initiation of the plant reproductive phase and lacked explicit simulation of phenological shifts (i.e. accelerated growth rate, changes in carbon partitioning during flowering and stem elongation, which decrease the leaf: stem ratio) in all three perennial tropical pastures. Consequently, relying solely on the model outputs to drive management decisions could result in compromises to both pasture quality and utilisation, and negatively impact farm productivity. This is particularly relevant to the modelled herbage accumulation in the summer. However, additional functions and parameters (i.e. partitioning and senescence fluctuations between phenological phases, plant storage organs dynamics) in APSIM Next Generation (Bosi et al. 2020a) and CROPGRO (Brunetti et al. 2021) have shown better simulations of perennial tropical pasture phenology and partitioning for *Piatã* palisade grass and *Megathyrsus maximus* cv Tanzania and Mombaça, respectively. Therefore, this limitation can be addressed in future developments of the DairyMod-SGS model, to better describe the phenology of perennial tropical pastures, capturing the leaf and stem partitioning and translocation of resources, especially during the reproductive phase.

In addition, DairyMod-SGS exhibited limitations in appropriately handling plant persistency (i.e. plant density over time) and capturing the associated reductions in pasture growth rate under suboptimal growing environments (Mediterranean and desert). Consequently, the model tends to significantly overestimate pasture biomass in these environments, despite the lower pasture growth recorded in the field. Therefore, the model outputs need to be cautiously interpreted under these suboptimal conditions. The failure of the model to simulate plant persistence could be due to a lack of model functions to define the initial sward conditions for each pasture regrowth (e.g. plant energy reserves, pasture residual weight and composition (leaf, stem and dead materials)) (Cullen et al., 2008). Overall, the present study suggests that efforts must be made to develop additional functions in the model (Bosi et al. 2020a; Brunetti et al. 2021) to define the pasture residual compositions and plant reserves that will allow DairyMod-SGS to better simulate stubble dynamics, regrowth after each defoliation, and plant persistence.

7.3.4. Model validation in Sri Lanka

Chapter 6 in this thesis used AgMERRA (Ruane et al., 2015) gridded climate data, due to the lack of long-term observed climate data availability across multiple sites in Sri Lanka (Nisansala et al., 2020). Out of the several reanalysis climate databases that utilise comprehensive methods and covariates, AgMERRA was identified as a potential data set to use in Chapter 6, and these grided data have been previously used to substitute the measured climate data in several modelling studies in Sri Lanka (Gunarathna et al., 2019; Gunarathna et al., 2020; Wimalasiri et al., 2020). The effective resolutions of different parameters in AgMERRA are 0.25° for rainfall, 0.50° for temperature and 1.0° for solar radiation, however, the data may not capture the full range of climate variability that occurs at local scales and may not accurately represent the microclimate conditions at some sites. In addition, a classical validation of the model using independent data was not performed before the application of the model. This was due to the absence of pasture biomass data as a result of BM, GP and RR not being previously tested in Sri Lanka. However, given the high model accuracy under broader model testing environments including similar tropical conditions to Sri Lanka (Chapter 5), it was assumed that the validated model was robust enough to capture the soil and climate variability and subsequent plant responses under Sri Lankan conditions.

7.4. Recommendation for future studies

7.4.1. Model validation for grazing scenarios

The DairyMod-SGS pasture model defines the grazing parameters in terms of plant digestibility (digestibility of live NDF under non-limiting water (%) and digestibility of dead NDF (%)) and relative grazing preference, which defines the relative grazing weighting for leaf over stem (leaf weighting parameter and stem weighting parameter) as affected by plant morphology (Johnson, 2008). While the digestibility parameters of BM, GP and RR were identified in the present thesis (Chapter 4), the rest of the grazing parameters were not evaluated. In addition, the carbon partitioning and senescence of plant materials are influenced by the management (cut-and-carry vs grazing) (Bosi et al., 2020a) and the effect of animal trampling and grazing on pasture structure and productivity need to be better understood before applying the model in grazing scenarios (Bosi et al., 2020a). While the overarching objective of Chapter 5 was to parameterise and validate the DairyMod-SGS model for tropical pastures in cut-and-carry systems, the present study did not attempt to test the model under grazing conditions. Further, long-term biomass data under grazing management are still limited for these tropical pastures. Overall, the parameterised and validated DairyMod-SGS model for BM, GP and RR can be potentially used under grazing conditions without major changes to its present parameters, however, validation using independent grazing data sets is recommended in future. This future work, together with the findings of this thesis, will broaden the applicability of the model to plan pasture management and estimate the forage available to the animal in both cut-and-carry and grazed pastures.

7.4.2. Farming system modelling

This thesis has comprehensively explored three improved tropical pastures (BM, GP and, RR) in terms of nutritive value and agronomic performance, and developed the DairyMod-SGS pasture model to be able to use as a tool to explore the likely performance of these pastures in different environments. Overall, an improvement in the quantity and quality of tropical pastures can substantially increase milk production. In addition, feeding systems that reduce the seasonality of forage production could significantly improve farm production and profitability, as pasture can usually be supplied at a lower cost per kg of DM compared to purchased feed such as concentrates (Chapman et al., 2008a, b). Therefore, it is important to further extend these findings to the whole farm system to understand the potential consequences in terms of farm production and economy. Systems models have been used elsewhere for similar purposes (Chapman et al., 2014a; Chapman et al., 2008a; Chapman et al., 2011) but they have largely been used under temperate pasture systems. Specifically, connected multiple simulation tools can be used to achieve these objectives in a series of simulations and modelling approaches. These tools can be a biophysical pasture growth model (parameterised and validated DairyMod-SGS in the present study) to generate tropical pasture growth data from basic climate, soil, and plant parameters; a dairy production model (e.g. DairyPredict (Walker et al., 2014) or UDDER (Larcombe, 1989)) to generate estimates of milk production based on energy partitioning within the cow as influenced by farm management practices (stocking rate, calving pattern, feeding plan, supplement feeding, grazing management, etc.) and animal genetic potential (lactation curve, animal live weight); and a financial analysis program (e.g., DairyPredict or Red Sky (http://www.redskyagri.com)) to estimate operating profit and return on assets based on typical farm input costs (feed cost, supplement cost, herd cost) and product prices (milk price and livestock sales, by-products), and other variable costs. Therefore, such whole farm system modelling is recommended in the future to account for the integrated outcome of the improved tropical pasture options on dairy farm production and financial performance. With the findings of this thesis, farm system modelling can better help farmers to develop feed budgeting and feeding decisions, which ultimately improves dairy production.

7.6. Conclusions

Introducing improved tropical pastures, along with defoliation management that considers the pasture-specific physiological and morphological parameters, can substantially increase the yield and nutritive value of tropical pastures. Importantly, the climate acts as a key variable that needs to be accounted for, as it significantly impacts on both the pasture production and the nutritive value of the herbage. In addition, a parameterised and validated pasture model (e.g. DairyMod-SGS) has the capacity to be used as a tool for the intensification of pasture-based livestock production systems in the tropics, by exploring the newer pastures in terms of their likely yield, seasonality and suitability under different management systems. While Gatton panic and Rhodes grass Reclaimer have high potential to improve livestock production, *Brachiaria* Mulato II showed significant promise as an improved livestock forage option for dairying in tropical and subtropical areas including Australia and Sri Lanka. The practical outcome of this thesis provides confidence in pasture species selection and identifies the responses to different pasture management decisions, however future studies in the context of the whole farm system are required to identify the likely impact on dairy production and economics.

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Appendix

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Preliminary results of parameterisation of DairyMod pasture model for tropical pasture; *Brachiaria*

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Abstract: Exploring improved tropical forages is considered to be an important approach in delivering quality and consistent feed options in tropical and even subtropical regions under changing climate scenarios. Pasture modelling has been an effective tool in simulating pasture growth and obviating expensive field research under a range of soil, climate, and management strategies. Many models lack parameters for tropical pasture species, hindering their use in tropical regions. This study aims to adapt the generic parameters in the DairyMod pasture model to parameterise and evaluate the model for the tropical pasture species *Brachiaria ruziziensis x B. decumbens x B. brizantha* 'Brachiaria Mulato II' (BM). Data were collected from plots of BM established at in the Gatton Research Dairy (27° 54´S, 152°33`E), Queensland, Australia to parameterise the model. Model evaluation was performed through various statistical indices for accuracy and precision. Canopy structure and carbon partitioning, photosynthesis and respiration, senescence and leaf appearance parameters were mainly modified from the generic C_4 grass parameters in the model. Results showed that, species specific parameters setup for BM in the model simulated the total above ground yield (R^2=0.92), leaf (R^2=0.97), and LAI (R^2=0.93) at a reasonable accuracy. Stem production also ranged under acceptable level except the second defoliation due to decrease cutting height. Despite these reasonable simulated results, model tended to underestimate the stem production. Reasons could be higher variation of residual weight across the seasons and model failure to explicitly capture the plant physiological changes like anthesis, accelerated growth rate and increased stem production associated with tropical pasture phenological developments. Results suggest that the developed BM parameters in DairyMod are further required to be tested under range of locations and seasons to improve the model.

Keywords: *Brachiaria Mulato II, DairyMod, tropical pastures, simulation models*

1. INTRODUCTION

Warm-season perennial grasses (tropical grasses/ C_4 grasses) are the dominant forages used in tropical and subtropical regions (Cooke et al. 2020) and the presence of C_4 grasses is projected to be increased in areas where such grasses are not presently occupied due to the effect of a changing climate (Sage and Kubien, 2003). However, the scarcity of consistent quantity and quality livestock feed is as a major constraint faced by tropical dairy farmers. One of the main approaches to address the feed scarcity and deliver quality feed on a consistent basis has been to develop improved forage options and evaluate for their yield, nutritive value, and impact on animal productivity parameters (Hall et al. 2007 and Ayele et al. 2012). Intensification with improved forages can take two forms as introduction of new forage varieties on-farm to the existing feeding or integrate forage options with new feeding practices in the production system (Paul et al. 2020). Pasture modelling has been an effective tool in simulating pasture growth and complementing expensive field research by predicting the likely performance of forage species under a range of soil, climate, and management strategies (McCown et al. 2002). There are a number of different simulation models including EcoMod & DairyMod SGS (Sustainable Grazing Systems), APSIM (Agricultural Production Systems Simulator), GrassGro, DairyNZ Whole Farm Model, and CROPGRO. Despite the importance of pasture modelling in forage-based dairy production, models are infrequently used in the tropics and the greatest limitation is the lack of data and knowledge about the physiological and physical processes plant growth (Hoogenboom, 2000). According to Andrade et al. (2016), there are a few empirical models to predict the growth and herbage accumulation of genera, *Brachiaria,* however they are location specific and limit the model extrapolation as they have not considered the underlying physiological principles for a given plant growth. Due to the genotypic dependent physiological behaviours, different pastures carry their optimum growing conditions, responses to water and nutrient requirements. When species-specific physiological processes are well understood, especially for species that are new to a region, they can be synthesized using mechanistic models (Boote et al. 1998) for improving tropical pasture modelling.

Therefore, this study was undertaken to estimate the species-specific parameters required for DairyMod, then calibrate and evaluate these parameters using the field data to successfully predict the growth of the tropical pasture, BM.

2. DAIRYMOD PASTURE MODEL

DairyMod is a mechanistic biophysical pasture simulation model that models pasture growth, utilisation by grazing animals, their growth and production, water, and nutrient dynamics with different pasture management options like irrigation, fertiliser application, and defoliation (including cutting and grazing) management (Johnson, 2008). The pasture growth module is central to DairyMod (Johnson, 2008). Compared with other biophysical models, DairyMod is a dedicated pastoral dairy system model (Li et al. 2011). The model has predicted the growth dynamics of temperate forage species across a range of climates, soil types, and management under conditions in Australia and New Zealand, and outside of Oceania (Argentina, South Africa) but limited applications are reported for the tropical and subtropical species. According to the Johnson et al. (2008), the model has the flexibility to simulate tropical pasture species (DairyMod version 5.8.2 system defaults; generic C_4, native C_4, native C_4 low quality and Rhodes grass) and further Johnson et al. (2008), Cullen et al. (2008) and Perera et al. (2020) have shown DairyMod can realistically simulate the C_4 pastures (Rhodes grass, native C_4 grasses) growth and herbage accumulation under contrasting edapho-climatic and management conditions in subtropical Australia.

3. METHOD

3.1 Study location

This research was conducted at the Gatton Research Dairy (27° 54´S, 152°33`E, 89 m msl) Queensland, Australia. Climate is characterized to be subhumid and subtropical with long hot summers (28- 33°C) and short mild winters (6-10°C) with an annual average rainfall of 763 mm. Tropical pasture, Brachiaria Mulato II (*Brachiaria ruziziensis x B. decumbens x B. brizantha)* was established sowing seeds at a rate of 8 kgha^{-1} as 0.1 ha plots in October 2019 using a randomized complete block design, replicated four times. Data collection was carried out from 11 November 2020 to 06 May 2021.

Climate data

The climate data (daily rainfall, maximum and minimum temperature, wind speed and humidity) for the experimental period were obtained from the automatic weather station setup in the experimental site. Solar radiation for the experimental period were acquired through the University of Queensland, Gatton weather station located 0.9 km from the experimental site.

Soil data

The soil at the experimental site was characterized as a black vertosols, a self-mulching, seasonally cracking clay soil (clay>35%) (Isbell, 2016). Topography was estimated as nearly flat (slope<0.5%). Soil physical, chemical characteristics for the experimental plots (depth 0-10 and 10-30 cm) were extracted from the analysed field soil samples (cores were sampled on 28 September 2020). Soil profile data collected by Powell (1982) and APSoil database (APSoil *ver*. 7.20) were used to complete the missing data.

3.2 Brachiaria Mulato II data

Biomass data

Herbage mass were quantified at 28±2 days harvesting intervals using quadrat (0.5 m×0.5 m) cuts (*n*=4) clipped to 15 cm (first cut) and 10 cm (subsequent cuts) residual height from 19 November 2020 to 06 May 2021. Randomly selected tillers for each plots were evaluated just before every harvesting and categorized to (vegetative or reproductive) based on the phenological stage of the tiller (seed head presence or not). 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 pasture plots was destructively sampled to ground level after each harvesting, to determine the mass and composition. The subsamples of both above harvested and residual were separated into its morphological components (leaf (lamina only), stem (leaf sheath and stem), dead material and flowers) for compositional analysis. Hand dissected components were dried separately at 60°C for 48 hrs to determine the dry weight. The dry weights of the subsampled components were used to calculate leaf, stem, dead material, and flower composition of quadrat area (0.25 m^2) and subsequently extrapolated to calculate the DM yield (kg ha^{-1}).

Randomly selected subsamples of fresh leaves were scanned for area using the flatbed scanner and analysed using the ImageJ software (Easlon and Bloom, 2014). Leaves were dried separately at 60°C for 48 hrs to determine the dry weight to calculate the specific lead 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 total leaf area index (LAI).

After each harvesting, plots were mulched to 10 cm residual height to achieve the equal regrowing conditions. All plots were irrigated during the experimental period using hand shift allowing pastures to grow under non limiting water conditions. Fertiliser CK77 (13.3% nitrogen (N), 2.2% phosphorus (P), 13.5% potassium (K), 19.6% sulfur (S) was applied on 23 November 2020 before starting the measurements at a rate of of 40 N, 6.6 P, 40.5 K , and 58.8 S kg ha^{-1}. Urea (46 %

N) and CK77 were applied on 18 January 2021 and 19 February 2021 at a rate of 69 N kg ha^{-1} and 26 N, 4.4 P, 27 K and 39.2 S kg ha^{-1} respectively. Plots were sprayed with Titan450 (2,4-D, Isopropylamine) for weeds (Johnson grass) at a rate of 2 kg ae ha^{-1} on 11 December 2020 and 7 January 2021.

Canopy light interception

The spatial average of PAR (Photosynthetically Active Radiation) was measured at immediately before each harvest using MQ-301 light meter (Apogee Instruments, Inc, USA). In each plot, 2 readings of incoming PAR (PAR_i) above the canopy level and 8 readings of transmitted PAR (PAR_t) at ground level (placing the quantum sensor bar closer to the soil between the clumps) were taken. Measured canopy PARs were used to calculate the fraction of PAR intercepted (LI) by the canopy and subsequently the light extinction coefficient (k).

Leaf photosynthesis

The rate of net photosynthesis was measured on 11 February 2021 and 12 February 2021 at pre-harvest stage with a portable photosynthesis meter, model LI-6400XT with brad 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 pre-set auto programs leaf net photosynthesis was recorded once per plot (n=4) at a series of PAR levels (2000, 1500, 1000, 500, 250, 120, 60, 30, 15, 0 PPFμmol^{-1} mol^{-1}m^{-2}) with a reference CO_2 concentration of 400ppm. Similarly, net photosynthesis of leaves in two plots (n=2) were measured under range of CO_2 concentrations (50, 100, 200, 300, 400, 700, 800, 1200, 1500, 1700 ppm) at a reference light condition of 1000 PPFμmol^{-1} mol^{-1}m^{-2}. All photosynthesis measurements were taken at 30°C leaf temperature inside the chamber (reflective of the ambient temperature at the trial site). Measured data were used to parameterise the light and CO_2 response curves in DairyMod leaf photosynthesis submodule.

3.3 **Model parameterisation**

Generic C_4 parameters in DairyMod version 5.8.2 was used as the starting point and modifications were done following the directions of Hunt and Boote (1998) and Johnson (2008). Brachiaria Mulato II species specific parameters were derived from the experimental data and relationships reported in literature (mainly temperature, senescence, and N partitioning parameters). Experimental conditions (mulching, N fertilisation, irrigation) during the data collection period were included in the Management submodule. Soil characteristics were defined in the soil module and soil initial conditions were adjusted based on the soil data and local weather conditions. All simulations were carried out in 1 ha paddock at an average of 3.078 t ha^{-1} residual weight (measured average residual weight). All the simulations were carried out with soil carbon and N dynamic implemented.

3.4 Model evaluation

Simulated total biomass, leaf weight, stem weight, LAI were compared with observed values for the model performance. Model was evaluated for the accuracy and precision. Observed/simulated ratio, mean observed and simulated, liner regression between observed and simulated data (R^2), root mean square error (RMSE), were considered as the statistical indices. All analysis were performed in R statistical computing software (R version 4.0.5) using the package ‘Metrics’ (Hamner and Frasco, 2018).

4. RESULTS AND DISCUSSION

4.1 DairyMod parameterisation

Leaf and canopy photosynthesis

The model was parameterised using the data collected from an irrigated experiment assuming the plants were growing under no limiting water and N conditions and allow the calibration for ideal conditions. Canopy photosynthesis and respiration lie as the core of the pasture sub-model and acts as the main primary source of carbon. The pasture sub-model describes the leaf gross photosynthesis as a function of PAR (µmol CO_2 (m^{-2} leaf)$^{-1}s^{-1}$)), leaf N, temperature, and CO_2. Species-specific photosynthesis and respiration parameters for BM were estimated using the non-rectangular hyperbola described by (Johnson, 2008) (Figure 1). The rate of single leaf gross photosynthesis at saturating PAR (P_{max}) was estimated to be 28.95±0.98 µmol CO_2 m^{-2} s^{-1} and respiration at reference conditions was 2.41±0.33µmol CO_2 m^{-2} s^{-1}. Photosynthetic response to CO_2 at saturating CO_2 and at double ambient CO_2 were estimated to be 1.17±0.015 and 1.10±0.015 (unitless) respectively.

Temperature response to the rate of single leaf gross photosynthesis at saturating PPF (P_{max}) is defined in the model with two temperature variables, minimum and optimum temperature at ambient CO_2. Default values (12°C and 35°C) were modified to 15°C and 33°C based on the results reported by Pequeno (2014) and Moreno (2017) for BM. The leaf N concentration effect on the photosynthesis was kept as default for C_4 grasses with 3 and 4 N% for optimum and maximum leaf N respectively (Moreno, 2017). Light interception and attenuation by the canopy in the model are explained by the k and the value was set to 0.48 based on the measured light interception (LI) data and Moreno (2017) also reported similar k value (0.49) for BM.

Canopy structure and carbon partitioning

Measured biomass data excluding the reproductive phases were used to calculate the canopy structure and carbon partitioning in the model. Specific leaf area and number of live leaves per tiller were set to 22 $m^2 kg^{-1}$ DM and 4 respectively based the measured data. Plant senescence parameters were adjusted based on the values reported by Pequeno (2014) and Moreno (2017) for *Brachiaria* species assuming values do not significantly vary between cultivars within the same species. Leaf appearance and temperature response explain in the model with minimum leaf appearance interval and minimum temperature and temperature for maximum leaf appearance rate. These values were not measured during this study and adopted from Pequeno (2014), Moreno (2017) and Bosi et al. (2020) studies related to *Brachiaria*.

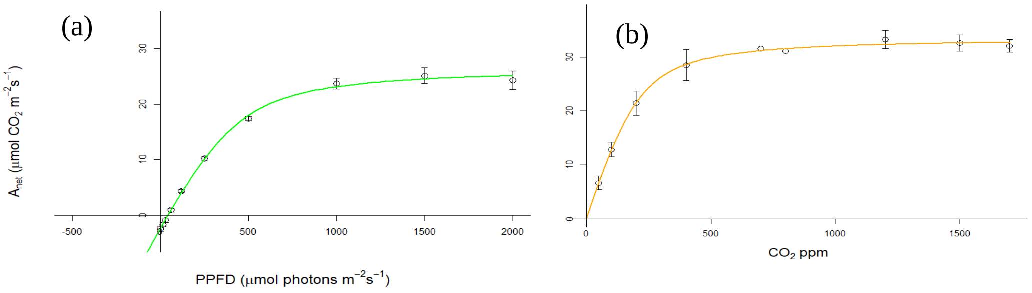

Figure 1: Species-specific photosynthetic light response (a) and CO_2 response curve (b) of Brachiaria Mulato II fitted by non-rectangular hyperbola function for the estimation of leaf photosynthetic parameters (A_{net}; Net carbon assimilation µmol CO_2 $m^{-2}s^{-1}$, PPFD; Photons flux density µmol photons m^{-2} s^{-1}).

Low temperature stress

Tropical pastures are reported to have considerable low growth rate during the cooler months of the year due to the low temperature stress and same results were observed in this study during late April to early May (late autumn). DairyMod explains the low temperature stress by ‘full stress’ and ‘initial stress’ temperatures. Therefore, defaults values (3°C and 7°C) for tropical pastures were modified to 5°C and 11°C based on measured biomass accumulation data in last season (late autumn).

4.2 Model evaluation

Parameterised DairyMod pasture model for Brachiaria Mulato II simulated total yield, leaf, stem, and LAI with reasonable accuracy (Table 1 and Figure 2). Total above ground biomass was predicted with greater accuracy than the leaf and stem yield. However, it is evident that stem productions was poorly predicted in model and it had largely underestimated compared to measured data.

Table 1: Summary of the statistics for the simulations of Brachiaria Mulato II calibration dataset collected from Gatton Research Dairy, Queensland, Australia from December 2020 to May 2021(total weight, leaf, and stem weight are expressed in DM , LAI; Leaf area index, *n;* number of observations)

Statistical indices	**Calibration data**			
	Total ($kg\ ha^{-1}$)	Leaf ($kg\ ha^{-1}$)	Stem ($kg\ ha^{-1}$)	LAI ($m^2\ m^{-2}$)
Observed mean	5718.30	2629.93	1665.45	6.20
Simulated mean	5791.64	2984.73	1970.57	6.57
Obs/Sim	0.90	0.92	0.53	1.05
RMSE	341.13	577.14	608.04	1.11
R^2	0.92	0.97	0.08	0.93
n	5	4	4	4

The variability of stem accumulation in Figure 2 (c) and lower R^2 is explained due to the changed cutting height (15cm to 10cm). However, overall poor stem simulation in the model could be due to the variation of residual weights in the paddocks wherein model only accommodated an average residual weight across all harvestings. In addition to the residual variation, model does not capture the plant phenological development and fail to explicitly simulate the phenological changes (Cullen et al. 2008) (anthesis, accelerated growth rate and increased carbon partitioning to stem) especially during the reproductive phase.

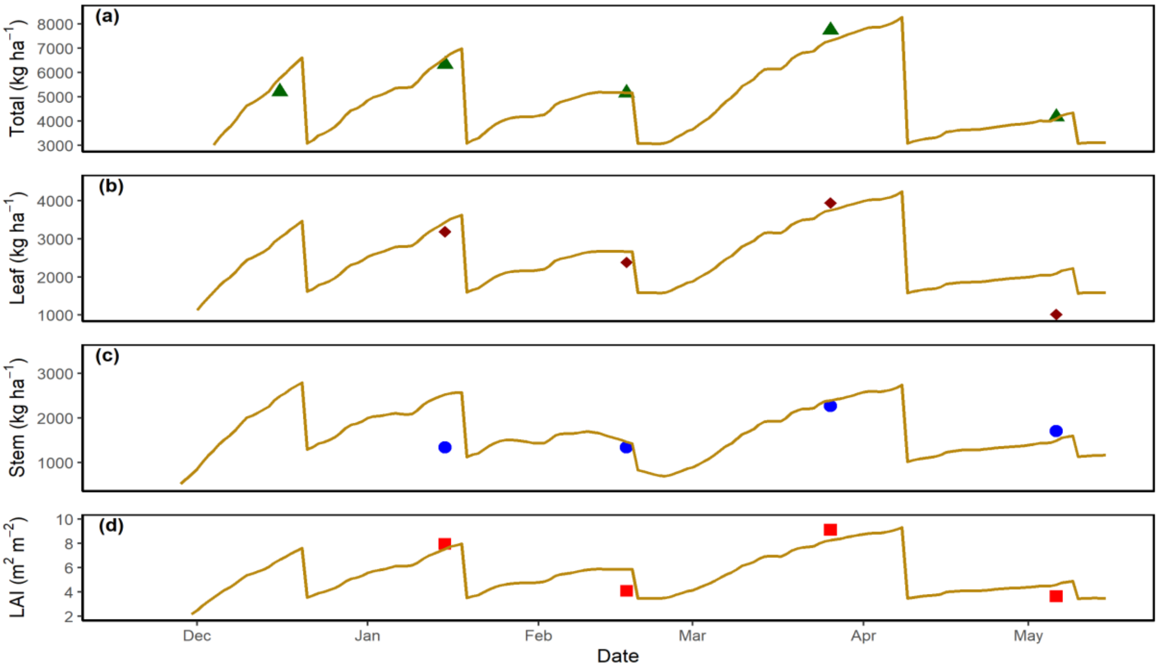

Figure 2: DairyMod simulated (lines) and (a) observed total yield (triangles), (b) leaf yield (diamonds), (c) stem yield (circles), (d) Leaf area index (LAI) (squares) of Brachiaria Mulato II in Gatton Research Dairy, Queensland, Australia from December 2020 to May 2021.

5. CONCLUSION

Simulation results revealed default C_4 generic parameters can be successfully used as starting point for setting up new tropical pastures in DairyMod. Parameterised pasture model for BM predicted the total above ground biomass and leaf yield at each harvesting point with a reasonable accuracy (R^{2}=0.92 and 0.97). However, validation of the model with larger datasets under different edapho-climatic and management conditions is required to further test the model.

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DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the candidate and the candidate's Primary Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of candidate:	Jayasinghe Mudiyanselage Priyanath Jayasinghe
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Jayasinghe, P., Ramilan, T., Donaghy, D. J., Pembleton, K. G., & Barber, D. G. (2022). Comparison of nutritive values of tropical pasture species grown in different environments, and implications for livestock methane production: A meta-analysis. Animals, 12(14), 1806.

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Date:	02-May-2023
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In which chapter is the manuscript /published work: Chapter 4

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Jayasinghe, P., Donaghy, D. J., Barber, D. G., Pembleton, K. G., & Ramilan, T. (2022). Suitability evaluation of three tropical pasture species (Mulato II, Gatton Panic, and Rhodes Grass) for cultivation under a subtropical climate of Australia. Agronomy, 12(9), 2032.

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Candidate contributed to data collection, model parameterisation, validation, data analyses and manuscript writing.

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