Final report

Impacts of climate extremes on the productivity, nutritional characteristics and persistence of perennial legumes and mixtures

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Abstract

Perennial legumes and herbs play an important role in pasture sustainability and methane emissions reduction by virtue of their relative drought tolerance, high nutritional quality, and anti-methanogenic properties. However, their responses to predicted changes in climate are largely unknown, as is the role of management in modifying these responses. To address these key knowledge gaps, we exposed four pasture legumes, in combination with herbs and/or grasses, to year-round rainfall manipulation in combination with warming or contrasting management regimes at the Pastures and Climate Extremes (PACE) facility at Western Sydney University.

Both reduced rainfall and warming decreased pasture productivity, usually in an additive manner. Sainfoin-cocksfoot swards were the most climate-sensitive and digit-desmanthus the most climate-resistant. Although productivity of biserrula was strongly suppressed by warming and low rainfall, it produced the lowest methane *in-vitro*.

Temperate mixtures (-58%) were more affected by reduced rainfall than tropical (-44%) mixtures, with the largest losses occurring in spring. More frequent harvests (simulating grazing) decreased sward-level productivity but boosted plantain growth. In spring, frequent harvests and low rainfall strongly suppressed legumes and increased senescence, implying lower forage value. Understanding how rainfall interacts with warming and grazing helps inform pasture management decisions for improving sustainability under future climates.

Executive summary

Background

Australia is experiencing a more variable and increasingly extreme climate, with higher temperatures, more frequent heatwaves, declining cool season rainfall and longer, more intense droughts, compared to the past few decades. Climate-resilient pastures are essential for sustaining livestock productivity, yet many of the most widely used pasture species are highly sensitive to both rainfall and temperature, with climate change therefore posing a major risk to the pasture feed base that underpins the meat and livestock industry. The livestock sector contributes approximately 11% of Australia's anthropogenic greenhouse gas emissions, including through enteric methane production which is linked to forage quality and digestibility. The ability to reliably produce good quality forage under current and future climates while reducing methane emissions, is critical for the sustainability of the industry.

Multi-species pastures integrating grasses, legumes and herbs offer an opportunity to enhance climate resilience, maintain year-round productivity, reduce fertiliser requirements, and mitigate methane emissions through improved forage quality and bioactive compounds. However, the effect of more extreme climates on the productivity, nutritional quality and anti-methanogenic properties of key forage species and mixtures is a major knowledge gap, as is the role of grazing management in climate-resilience. To address this, we conducted a series of climate manipulation experiments, involving combinations of warming (+3°C), rainfall manipulation and/or grazing intensity, at the Pastures and Climate Extremes (PACE) facility, at Western Sydney University's Hawkesbury Campus in Richmond, NSW.

Objectives

The project's main objectives were to:

1. Quantify the impacts of future climates (+3°C warming and contrasting rainfall extremes) on the productivity and carbon allocation strategies of perennial legumes and grass-herb-legume mixtures across multiple seasons.

2. Compare the performance of new "opportunity" species (e.g., desmanthus, sainfoin, chicory) with legumes (e.g., lucerne) traditionally used in southern pasture systems under contrasting climatic conditions.

3. Determine the effects of climate warming and extreme rainfall conditions on plant nutritional chemistry, including anti-methanogenic properties of perennial legume and herb species.

4. Evaluate the role that grazing management can play in the climate resilience of new perennial pasture mixtures in terms of productivity, persistence and belowground carbon storage.

Methodology

Two-species mixtures comprising legume-grass and legume-herb combinations were exposed to factorial combinations of warming (+3°C) and altered rainfall regimes (high, 1003 mm y^{-1} versus low, 570 mm y^{-1}, based on local data). Tropical and temperate five-species mixtures were grown, separately, under contrasting (low/high) rainfall, and temperate mixtures were also subjected to a high/low frequency grazing treatment, simulated by harvesting.

Pasture productivity and belowground storage: Aboveground net primary production (ANPP) was quantified via periodic harvests throughout the year, with material separated to species or functional group level. Belowground net primary production (BNPP) was measured using mesh-free ingrowth cores, while non-structural carbohydrate (NSC) storage was analysed using standard laboratory procedures to evaluate relationships with post-harvest regrowth.

Forage quality: Nutritional traits - crude protein (CP), dry organic matter digestibility (DOMD), metabolisable energy (ME), neutral detergent fibre (NDF), acid detergent fibre (ADF) and water-soluble carbohydrates (WSC) - were predicted using near-infrared spectroscopy (NIRS) models developed by the NSW Department of Primary Industries Feed Quality Service; sub-samples were also analysed via wet chemistry for validation.

Anti-methanogenic potential: Methane emissions associated with the digestion of four legumes and chicory were quantified via *in vitro* fermentation assays using rumen liquor. All nutritional analyses and methane production assays were undertaken on samples produced under climate treatments.

Results/key findings

1. Legume-grass and legume-herb species pairs differed markedly in their sensitivities to reduced rainfall, with overall (24-month) productivity declines ranging from -7% (desmanthus/digit) to -35% (lucerne/phalaris, sainfoin/cocksfoot). The biggest seasonal reductions (up to -81%, sainfoin) were seen in spring.

2. Elevated temperatures mostly reduced productivity, with declines of up to -65% (biserrula) likely reflecting temperature-driven soil drying and exceedance of warm season physiological thresholds. The tropical legume, desmanthus, was however a notable exception, more than doubling its productivity under 3°C warming.

3. The combination of low rainfall and higher temperatures resulted in the lowest productivity across all temperate species, likely driven by both an exacerbation of soil moisture stress and negative effects on leaf-level physiology. The tropical species pair (desmanthus/digit) was an exception to this, with warmer temperatures offsetting rainfall-associated productivity losses.

4. Based on individual species' productivity responses to low rainfall and higher temperatures, overall climate sensitivity can be categorised as follows:
    a. High sensitivity (highest risk to graziers): Biserrula, cocksfoot#, sainfoin#
    b. Medium sensitivity: Lucerne, phalaris
    c. Low sensitivity (lowest risk to graziers): Desmanthus, digit, chicory

    # sainfoin and cocksfoot had medium sensitivity to reduced rainfall or warming alone, but were highly sensitive to their combination

5. Persistence across the two years of the study was low for chicory and sainfoin, even under high rainfall and ambient temperatures. Lucerne, digit and desmanthus were highly persistent but the latter was not abundant, reflecting its low establishment and slower growth.

6. Increases in legume/herb nutritional quality (crude protein, metabolisable energy and/or digestibility) in response to decreased rainfall (lucerne, desmanthus, chicory) or increased temperature (lucerne, sainfoin) were consistently offset by yield declines. These treatment-related trade-offs in forage quality versus quantity were smallest (i.e. least unfavourable) for chicory and desmanthus, and largest (indicating reduced quality and yield) for biserrula.

7. *In vitro* methane production varied strongly among species and climate treatments. Biserrula had by far the lowest emissions (85% lower than lucerne), confirming its anti-methanogenic potential, albeit with strong climate constraints on its productivity in our study. Desmanthus, chicory and biserrula all produced less methane under the combination of warming and low

rainfall in either spring or autumn, responses that were not associated with a decrease in fibre content.

8. Tropical mixtures were more than twice as productive as temperate ones at our warm-temperate study site, and less negatively affected by low rainfall. Their high summertime productivity may help address summer feed gaps, although the nutritional challenges (lower protein, higher fibre contents) associated with C_4 grasses would necessitate a higher proportion of companion legumes in such mixtures.

9. More frequent (simulated) grazing reduced overall productivity, with no evidence of compensatory growth in response to frequent biomass removal. The biggest effects of high grazing frequency were under wet conditions where productivity was high. Importantly, however, frequent grazing under dry springtime conditions significantly reduced seasonal sward-level biomass production, over and above the rainfall-related productivity decline. Although only a small (<10%) component of our experimental pastures, the herb plantain responded positively to frequent grazing, even in dry conditions, highlighting its value as a durable component of mixed species pastures.

10. Belowground carbon allocation was altered by reduced rainfall, resulting in higher root biomass and lower carbohydrate stores. While frequent grazing increased proportional carbon allocation to roots under high rainfall, the opposite effect was seen under dry conditions. The combination of frequent biomass removal and low rainfall also resulted in reduced rates of pasture regrowth (post-harvest), a finding that was strongly associated with low carbohydrate stores. This highlights the importance of moderating grazing pressure under dry conditions, to allow replenishment of belowground carbon reservoirs to fuel aboveground biomass production.

Benefits to industry

11. Pasture mixtures including deep-rooted legumes (lucerne, desmanthus) alongside tap-rooted herbs (e.g. chicory, plantain) appear to be a good option for increasing climate resilience and boosting productivity. Inclusion of warm-season (C_4) grasses in sub-tropical and warm temperate areas (that do not experience sub-zero winter temperatures) is also likely to boost growing season productivity. The lower nutritional quality of such grasses, relative to temperate species, may however necessitate an increase in the proportion of legumes to boost sward-level protein, metabolizable energy and digestibility, when included in mixed pastures.

12. Gains in nutritional quality (higher crude protein and metabolisable energy, lower fibre content) seen in response to warming and/or reduced rainfall for some species were largely offset by declines in pasture quantity. Given this, the best options to support livestock nutrition and intake requirements in a warmer, drier climate are likely to be those species that had the smallest treatment-related decline in productivity alongside modest increases (chicory) (or little change - desmanthus) in nutritional value.

13. Biserrula was associated with very low methane emissions compared to other legume and herb species. Although it performed poorly under low rainfall and higher temperatures, it remains a promising species for reducing enteric methane production and, by extension, increasing feed conversion efficiency in areas and years that are climatically suitable (i.e. good winter/spring rainfall, moderate spring temperatures) and in sites with well-drained, acidic soils. Alongside biserrula, chicory also seems promising for reducing methane emissions per unit metabolisable energy (as a proxy for emissions intensity relative to animal production).

14. Tropical mixtures provide a highly productive feed base that is less affected by low rainfall than temperate mixtures and can help address a summer feed gap in warm temperate regions that have sufficient summertime rainfall (e.g. northern NSW, southern Queensland, South Coast and Western Plains NSW). Targeting higher legume percentages in such mixtures can help offset the lower protein and higher fibre concentrations associated with the C_4 grass component.

15. Gains of up to 28% in the amount of available forage can be made by reducing the frequency of grazing (simulated by harvesting in this study). Such benefits can be even greater during spring (up to 51%). Reduced grazing pressure during spring resulted in large productivity and resilience benefits in our temperate mixed pastures, particularly under dry conditions. Allowing plants time between grazing events to build up the belowground starch reservoirs that drive re-growth following defoliation and/or alleviation of climate stress can improve both resilience and persistence. Prolonged periods of reduced root productivity – as was seen under frequently grazed, dry conditions - may have negative implications for soil carbon stocks. Importantly, a higher cover/biomass of grazing- and drought-tolerant herbs, such as plantain, may help offset some of the observed negative effects of frequent grazing and low rainfall on pasture productivity (e.g. by providing resilient forage and reducing evaporative water loss from exposed soil).

Future research and recommendations

16. Climate-resilient pastures should comprise mixtures that combine species with functional complementarity - such as deep-rooted legumes alongside drought- and heat-tolerant grasses and other herbs - to enhance water-use efficiency and functional resilience. Some important advances have been made in this project, but evaluation of the climate sensitivity of a wider range of candidate species - and their performance in different mixtures and proportions - is an essential next step towards providing robust recommendations for growers across the region.

17. Building on the above, tropical species have the potential to play an increasing role in more southerly, warm-temperate regions (e.g. NSW Riverina), as demonstrated by their high productivity and relatively lower drought sensitivity in the current study. Further research is needed to evaluate different combinations of species, and legume:grass planting proportions, to achieve appropriate targets for nutritional quality in such mixtures.

18. Having identified the importance of reducing grazing offtake under dry spring conditions for forage resilience, overall productivity and persistence, further work is needed to evaluate the consequences and farm-scale economics of a wider range of grazing regimes (considering both grazing intensity and timing), under varying climates. In particular, it will be important to do so at scale and with grazing animals, to complement controlled experiments that simulate grazing.

19. Noting the importance of belowground carbon stores for fuelling post-grazing regrowth, a key area for future research is to examine how repeated and/or prolonged drought cycles influence root dynamics, carbohydrate reserves, and post-stress recovery. This will deepen the mechanistic understanding of how grazing and climate interact to affect both productivity and persistence, with such knowledge having the potential to drive economic gains in terms of reduced supplementary feed requirements and reseeding costs, as well as potential soil carbon benefits.

20. Trade-offs between climate-related gains in protein content and dry matter digestibility seen in some species, and productivity decline, have not been widely evaluated and may be important for highly productive species that are of more marginal quality (e.g. some tropical grasses, and other herbs). A better understanding of how protein content, protein digestibility (ruminal and post-ruminal) and dry matter digestibility are influenced by warming and drought can enable grower adoption of warm-adapted species across temperate regions.

21. Two of the species in this study showed particular promise for their ability to reduce ruminant methane emissions (biserrula) and/or emissions intensity (biserrula, chicory). Incorporation of these species into the pasture feed base may offer a viable method for reducing farm-scale carbon emissions. However, additional research is needed into the plant chemical and structural mechanisms behind this, as well as evaluation of whether these are linear or threshold responses between plant biomass consumed and methane reduction. Further, confirming *in vitro* findings *in vivo* is key to developing a pathway for pasture-based methane emissions reduction.

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1. Background

Australia experiences high interannual variability in rainfall, a trend that, along with rising temperatures, has intensified over recent decades (CSIRO & BoM, 2024; IPCC, 2022). Climate models predict an additional 2-5°C increase by the end of the century, accompanied by more frequent heatwaves and greater inter- and intra-annual rainfall variability (BoM, 2024). South-eastern Australia has seen decreased winter and spring rainfall since the late 1990s, characterised by extended dry spells and more severe rainfall events (CSIRO & BoM, 2024). Regional climate is strongly influenced by large-scale drivers such as the El Niño Southern Oscillation (ENSO; Collins et al., 2010; McPhaden et al., 2006) and the Indian Ocean Dipole (IOD; Pepler et al., 2014; Reddy et al., 2021), with both projected to produce more extreme events under climate change (Cai et al., 2014; Lieber et al., 2024).

Rising temperatures and increasingly variable rainfall patterns are expected to intensify pasture productivity losses via direct reductions in photosynthesis, increases in evapotranspiration and greater water limitation of plant growth (Moore et al., 2021; L. Yuan et al., 2024; Yuan et al., 2019). In southern Australia, where many pasture species already operate near their thermal optima, even modest warming could markedly reduce forage productivity (Cui et al., 2018; Cullen et al., 2009). This poses a substantial risk for pasture-dependent industries and associated livelihoods, as well as the economic contribution they make to gross domestic product (ABARES, 2025; Mai et al., 2025).

Pastures dominated by perennial species with deep roots, high root-trait plasticity and substantial carbon reserves are likely to be more climate-resilient, as these traits enhance water uptake, nutrient acquisition and persistence under prolonged drought (Chandregowda et al., 2022; Volaire et al., 2020). Where possible, combining species with contrasting phenologies, such as cool- and warm-season focussed growth, can help reduce seasonal feed gaps and stabilize productivity across years (Churchill et al., 2022; Hallmark et al., 2024). Moreover, mixtures containing diverse functional groups promote sustained productivity through niche complementarity and facilitation, while maintaining forage quality under warmer, drier conditions - an essential factor for sustaining livestock performance and reducing sectoral emissions (Churchill et al., 2024; Distel et al., 2020).

High-quality forage contains more fermentable sugars, organic acids, and proteins, with an associated high digestibility and feed conversion efficiency. In contrast, under heat and water stress, forage quality typically declines due to higher stem-to-leaf ratios, greater fibre content and lower crude protein and metabolizable energy (Lee et al., 2017; Sanz-Sáez et al., 2012). Low-quality forage not only limits animal performance but also increases enteric methane (CH_4) emissions. Globally, livestock systems - including feed production, land-use change, enteric fermentation, and manure management - emit about 6.2 Gt CO_2-eq annually (~12% of global anthropogenic GHG emissions; FAO, 2022). Enteric fermentation alone contributes 2.8 Gt CO_2-eq CH_4 per year, around 77% from cattle. In Australia, enteric methane from ruminant livestock accounts for roughly 11% of total greenhouse gas emissions (by global warming potential) (FutureFeed, CSIRO, 2020). These emissions can account for up to 17 % of gross energy intake by livestock, reducing feed efficiency and amplifying global warming (Paredes, 2022).

Methane production in the rumen, driven by methanogenic archaea, is highly sensitive to diet quality and digestibility. Forage species rich in non-structural carbohydrates, lipids and crude protein are associated with lower methane yields, whereas climate-associated declines in quality may increase emissions by ~0.9 % per 1 °C warming (Lee et al., 2017). Ruminant diet composition also shapes microbial communities (Henderson et al., 2015) and fermentation pathways, with higher digestibility and feed intake improving efficiency (Hristov et al., 2013) and reducing methane intensity per unit of milk (Knapp et al., 2014) or meat (Beauchemin et al., 2022) produced. Shifts toward more water-soluble carbohydrates and fewer structural carbohydrates further mitigate methane by accelerating rumen passage rates, promoting propionate formation and suppressing methanogens (Pacheco et al., 2014).

Multi-species swards of perennial grasses, legumes and herbs offer a promising alternative to conventional low diversity/monoculture pastures in Australian grazing systems (Thomson & Albornoz, 2023). Such mixtures can reduce fertiliser demand while maintaining productivity (Jaramillo et al., 2021), enhance resilience in the face of climate variability (Lüscher et al., 2022) and outperform monocultures in persistence and yield (Nyfeler et al., 2009). Several legumes and herbs also possess anti-methanogenic properties, reducing CH_4 emissions through improved forage quality and secondary metabolites (Badgery et al., 2023; Ku-Vera et al., 2020). However, data remain limited on how these species and mixtures perform under increasingly extreme climates. Understanding their productivity, nutritional chemistry and resilience is vital for management strategies that support both economic viability and carbon neutrality.

Regular grazing can enhance pasture production by stimulating compensatory growth (Oesterheld & McNaughton, 1991; Vogel et al., 2012) and maintaining plants in a vegetative state that is associated with higher forage quality relative to reproductive-stage plants (Fenetahun et al., 2021). Regular grazing also maintains quality by limiting lignification and fibre accumulation and sustaining a favourable stem-to-leaf ratio (Bruinenberg et al., 2002; Dumont et al., 2015; Ren et al., 2016). Given that climate stress typically reduces forage productivity, drives shifts in carbon allocation, and affects forage quality, it is important to understand how the intensity of biomass removal (i.e. grazing frequency) interacts with climate to affect forage productivity and nutritional characteristics.

To address these challenges, we conducted a series of three climate-manipulation experiments at the Pastures and Climate Extremes (PACE) facility, at Western Sydney University. The first experiment evaluated productivity, forage quality and anti-methanogenic properties of legume-grass and legume-herb species pairs, under factorial combinations of rainfall (low, high) and temperature (ambient, +3 °C). The second examined the relative responses of temperate and tropical mixtures to low (versus high) rainfall regimes in terms of seasonal productivity and composition. Further, a third experiment evaluated the interactive effects of contrasting rainfall regimes and grazing frequencies (simulated via harvesting) on a five-species (grass-legume-herb) temperate pasture by quantifying productivity, nutritional quality, and persistence responses, across multiple seasons.

2. Objectives

The overall project objectives were as follows:

1. Quantify the impacts of future climates (+3℃ warming and contrasting rainfall extremes) on the productivity and carbon allocation strategies of perennial legumes and grass-herb-legume mixtures across multiple seasons.

2. Compare the performance of new “opportunity” species (e.g., desmanthus, sainfoin, chicory) with legumes (e.g., lucerne) traditionally used in southern pasture systems under contrasting climatic conditions.

3. Determine the effect of climate warming and extreme rainfall conditions on plant nutritional chemistry, including anti-methanogenic properties of perennial legume and herb species.

4. Evaluate the role that grazing management can play in the climate resilience of perennial pasture mixtures in terms of productivity, persistence and belowground carbon storage.

3. Methodology

3.1 The Pastures and Climate Extremes (PACE) field facility

3.1.1 Site description

The PACE (PAstures and Climate Extremes) facility is located at the Hawkesbury Campus, Western Sydney University, Richmond, NSW, Australia (S33.60972, E150.73833; 25 m a.s.l.). The region has a warm temperate climate with a mean annual temperature of 17.2 °C, ranging from daily means (calculated as (maximum - minimum)/2) of 18.8 - 9.4 °C in summer to 3.2 - 17.3 °C in winter. Mean annual precipitation is 727 ± 36 mm (SE), with high interannual variability (500–1,400 mm over the past 30 years).

3.1.2 Experimental facility

Figure 1. Infrastructure and design of the Pastures and Climate Extremes (PACE) experiment showing: A) polytunnel shelters, B) experimental plots inside shelters, C) ceramic heating lamp and D) schematic of plot layout and treatments within a shelter.

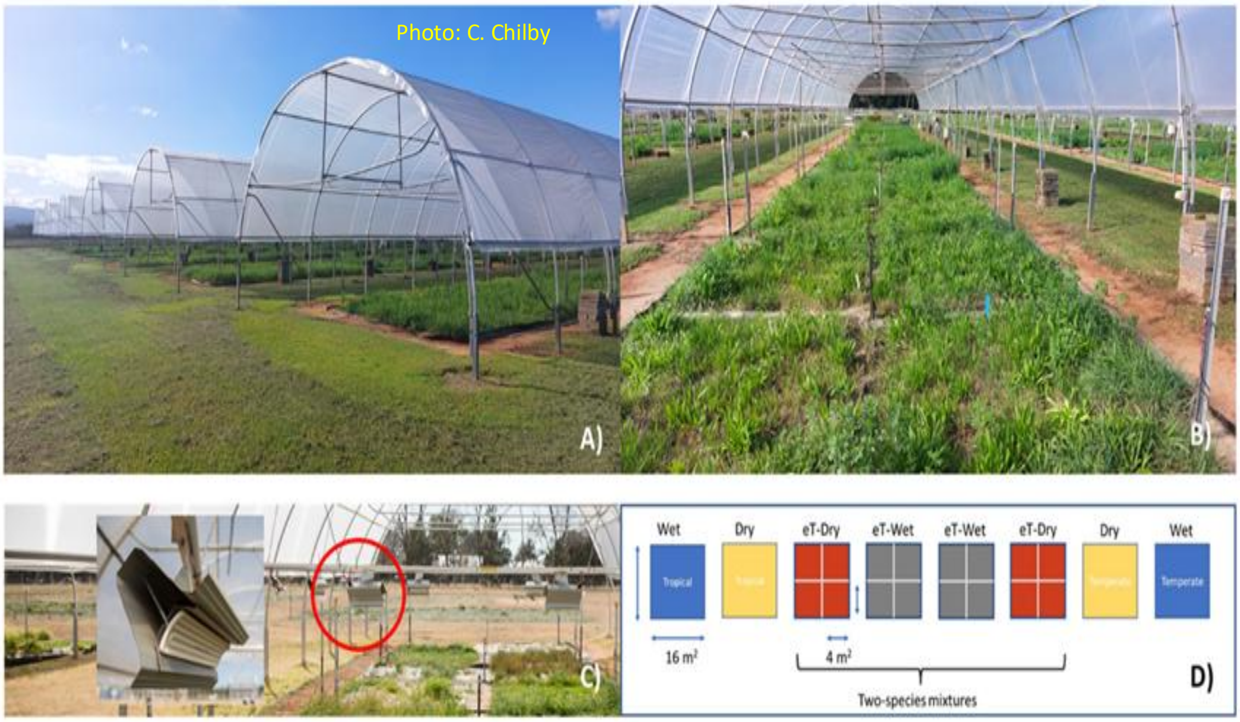


Photo: C. Chilby

The facility comprises six polytunnel shelters constructed from galvanized steel frames and covered with a single 250 µm polyethylene sheet (Solarweave, GALE Pacific Pty Ltd, Australia) to exclude ambient rainfall (Fig. 1A). Plastic coverings were replaced in November 2022, completing infrastructure upgrades for the current experimental phase. Each shelter measures 48 × 8 × 4.6 m, oriented SW–NE with open ends facing the prevailing wind. Side walls open to 1.5 m above ground to allow free air circulation and minimize shelter effects on microclimate. Each shelter contains eight plots (4 × 4 m); four dedicated to warming x rainfall experimentation and a further four to rainfall-only manipulation. Prior to sward establishment in 2022, the top 5 cm of soil was replaced with homogeneous, low-carbon soil to eliminate legacy effects that may have persisted following the PACE 1 experiment (2017-2020). Species pairs were sown into subplots (2 × 2 m), while tropical and temperate mixtures were established at the plot level (details below). Species were randomly assigned to plots and subplots (Fig. 1D). Root barriers (VercanTM, textured high-density polyethylene; Argosee Greenhouse Technology Pty Ltd, Australia) were installed to 90 cm depth between plots and 30 cm depth between subplots to minimise root intrusion. Buffer zones of 1 m (between plots) and 0.5 m (between subplots) were established to minimise inter-specific competition for light. Subplots were separated by a single row of pavers to enable access with minimal sward disturbance.

Three distinct experiments were conducted at the PACE facility, as summarised below.

3.2 Experiment 1: Factorial warming x rainfall manipulation

The warming and rainfall manipulation experiment included three temperate species pairs - chicory/biserrula, sainfoin/cocksfoot and lucerne/phalaris, established in April 2022, and one tropical pair - digit/desmanthus, sown in August 2022. All species were established at the subplot level (2 × 2 m; Table 1), with six replicates per treatment. Baseline data were collected in spring 2022, prior to initiation of warming and rainfall treatments in mid-December 2022. Seasonal productivity responses were assessed at the species level through regular harvests; data presented in this report are from December 2022 to November 2024 (i.e. 24 months of climate manipulations).

Table 1. Species pairs and cultivar details for the factorial rainfall x warming experiment.

Species pair	Species name	Cultivar
Chicory/Biserrula	*Chichorium intybus*	Puna 2
	Biserrula pelecinus	Casbah
Cocksfoot/Sainfoin	*Dactylis glomerata*	Currie
	Onobrychis viciifolia	Othello
Phalaris/Lucerne	*Phalaris aquatica*	Holdfast GT
	Medicago sativa	Sardi 7
Digit/ Desmanthus	*Digitaria eriantha*	Premier
	Desmanthus virgatus	JCU2

3.3 Experiment 2: Temperate and tropical mixtures under contrasting rainfall

This rainfall manipulation experiment comprised a temperate five-species mixture (cocksfoot, prairie grass, lucerne, sainfoin and plantain) that was sown in April 2022 and a tropical mixture (Rhodes, panic, lucerne, desmanthus and spineless burr medic), established in August 2022, in 4 x 4 m plots. Both mixtures and rainfall treatments had six replicate plots (n=24) (Table 2). Baseline productivity data were collected in spring 2020, and rainfall manipulation commenced in mid-December 2022 following sward establishment. Seasonal productivity was monitored at the species level through regular harvests, with the final harvest undertaken at the end of February 2025.

Table 2. Species and cultivar details for the temperate/tropical comparison.

Pasture type	Species	Cultivar	Common name
Temperate mixture	*Dactylis glomerata*	Convoy	Cocksfoot
	Bromus catharticus	Matua	Prairie grass
	Medicago sativa	Sardi 7	Lucerne
	Onobrychis viciifolia	Othello	Sainfoin
	Plantago lanceolata	Grasslands Lancelot	Plantain
Tropical mixture	*Chloris gayana*	Katombara	Rhodes
	Desmanthus virgatus	JCU2+Marc	Desmanthus
	Megathyrsus maximus	Gatton	Panic
	Medicago sativa	Sardi Grazier	Lucerne
	Medicago polymorpha	Cavalier	Spineless burr medic

3.4 Experiment 3: Factorial rainfall × "grazing" frequency manipulation

Grazing was simulated by biomass harvests (to a height of 5 cm above ground) undertaken at contrasting frequencies: (1) **low-frequency harvesting**, aligned with industry grazing recommendations (peak of vegetative growth; Clements et al., 2003), resulting in a total of 7 harvests and (2) **high-frequency harvesting**, triggered when sward height reached 20 cm, resulting in 21 harvests across the 21 month study. Each 16 m² temperate mixture plot was divided into two 8 m² subplots and randomly assigned to harvesting treatments. This subdivision occurred within both high (Wet) and low (Dry) rainfall treatments, making it possible to evaluate rainfall × harvest frequency interactions. Pasture production was monitored at the sward- and functional group (grass, legume, herb) level, with biomass separated at each harvest, oven-dried and weighed. Rainfall treatments commenced in the first week of December 2022 and the grazing frequency treatments commenced in June 2023; data presented are from June 2023 to the end of February 2025 (21 months).

3.5 Rainfall and warming treatments

3.5.1 Rainfall manipulation

Rainfall treatments were designed to replicate the size and pattern of rainfall events that characterize historically dry and wet years at the study site. These treatments simulate realistic extremes of low and high rainfall that are expected to occur more frequently under climate change (CSIRO & BoM, 2022). The wet regime represents the least water-limited conditions typically experienced by local pastures and provides a benchmark against which to assess performance under dry conditions. Treatments were delivered via a computer-controlled, plot-level spray irrigation system.

To define experimental rainfall regimes, we analysed 30 years of rainfall data (1992–2021) from Richmond, NSW (Bureau of Meteorology station 067105; ~5 km from the site). From this record, the five wettest years (mean annual precipitation [MAP] 1003 mm) and five driest years (MAP 578 mm) were identified (Fig. 2). Two representative years were then selected for each extreme - 1994 and 2019 (dry) and 1999 and 2021 (wet) - to develop seasonal irrigation schedules. Seasonal rainfall amounts are summarised in Table 3.

Table 3. Seasonal rainfall amounts in high (wet) and low (dry) rainfall treatments, averaged across 2023 and 2024.

	Spring	Summer	Autumn	Winter
Wet (mm)	320.6	325.1	244.0	112.9
Dry (mm)	151.0	229.4	121.8	76.1

Rainfall events were grouped into five size classes (<2, 2–5, 5–10, 10–20, >20 mm). For each season, we calculated total rainfall and the mean number of consecutive dry days between events. Events <2 mm were excluded and their totals redistributed to larger size classes, consistent with climate projections of fewer but more intense rainfall events (IPCC, 2018). The resulting irrigation schedules therefore capture seasonally explicit averages of event size, frequency and dry-day intervals for extreme dry and wet years in the local area. Rainfall treatments commenced in the first week of December 2022 (Fig. 2a).

The site's sandy loam soil (Blackendon Sand: 81% sand, 6% silt, 11% clay, ~1.8% organic matter) is characterized by rapid fluctuations in soil water content (SWC), particularly in the top 20 cm where SWC is monitored. Under the wet regime, SWC was expected to remain above 10% for most days, supporting vigorous plant growth. By contrast, the dry regime was associated with extended periods of SWC <10%, imposing substantial water deficits (Fig. 3).

Figure 2. (a) Soil volumetric water content (%) in the top 20 cm across treatments, and (b) irrigation inputs (mm) between 15 December 2022 and 28 February 2025, averaged across all species pairs. Treatment abbreviations: aT-W (ambient temperature, Wet rainfall regime), aT-D (ambient temperature, Dry rainfall regime), eT-W (elevated temperature, Wet rainfall regime) and eT-D (elevated temperature, Dry rainfall regime).

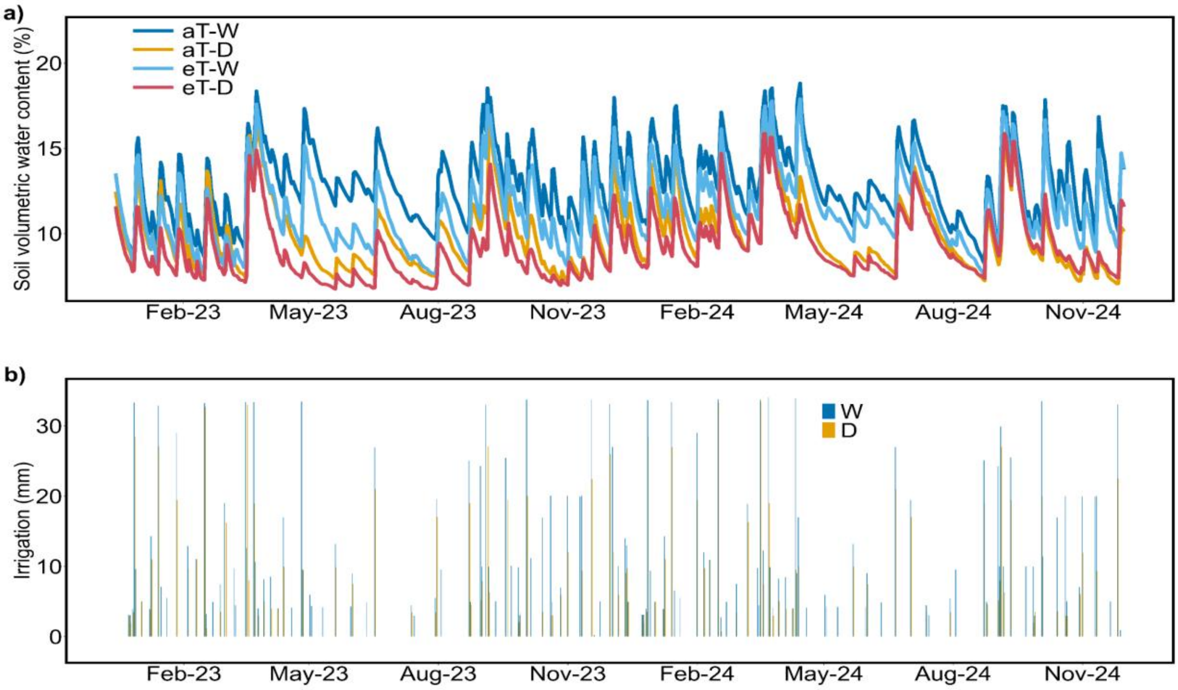
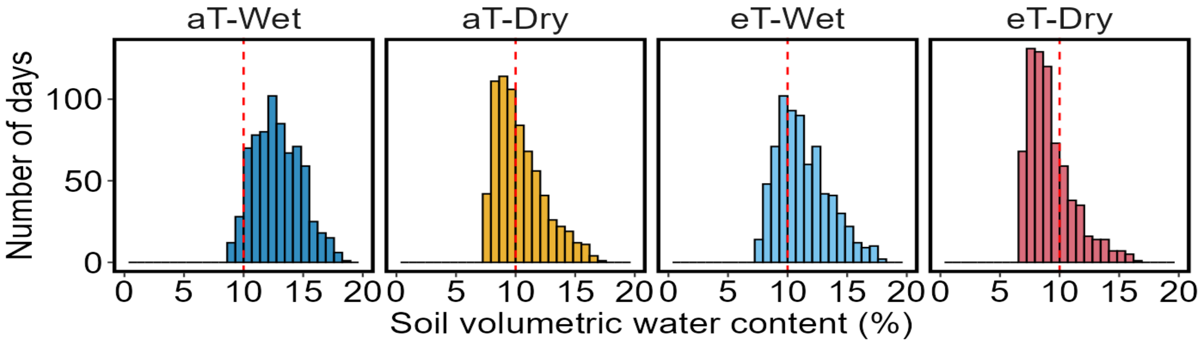


Figure 3. Frequency distribution of soil volumetric water content (%) by treatment. Treatment abbreviations: aT = ambient temperature, eT = elevated temperature, Wet = high rainfall, Dry = low rainfall.



3.5.2 Temperature manipulation

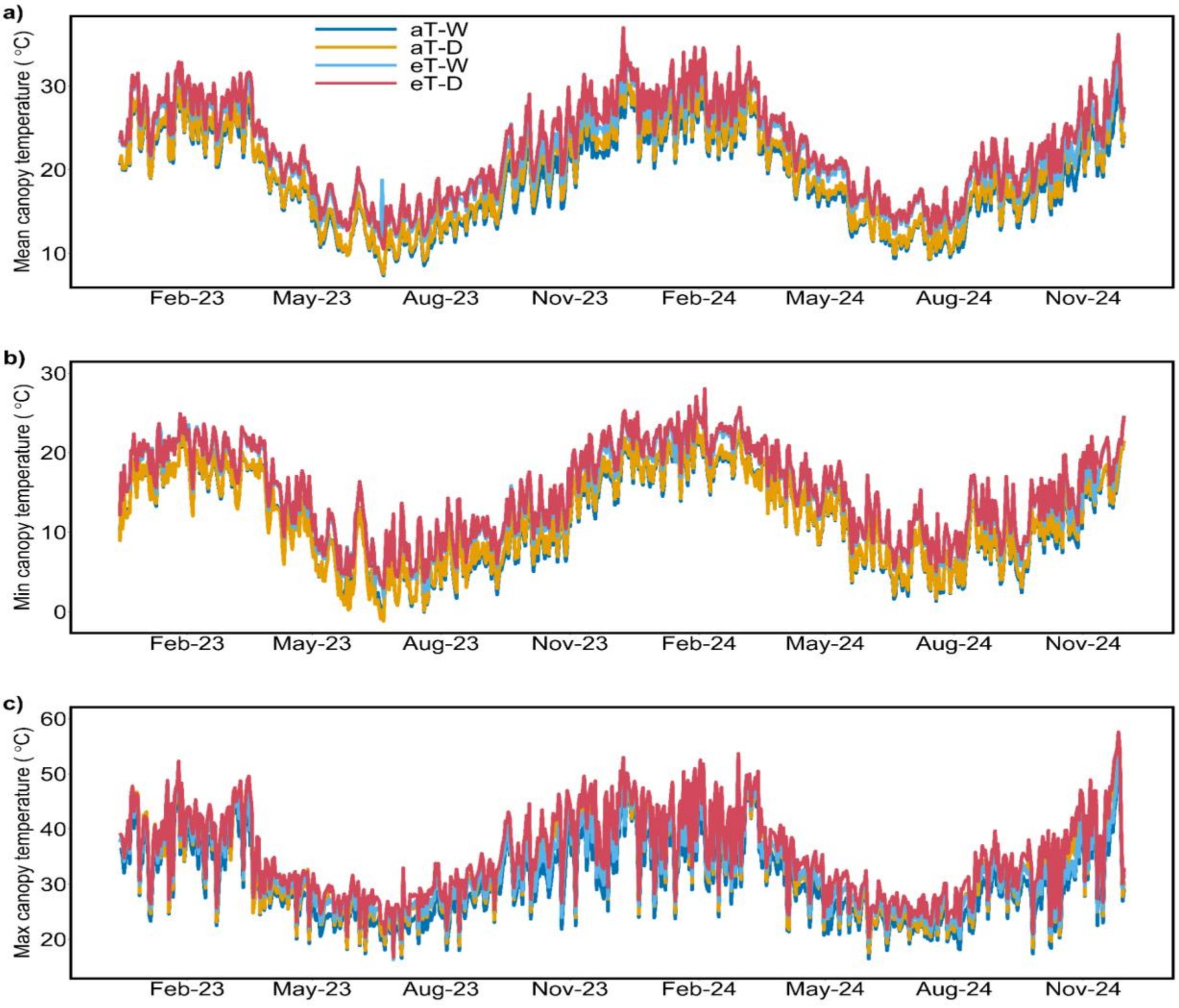
The warming treatment applied a year-round increase of +3 °C in plot surface temperature, simulating projected warming for Australia by 2080 under RCP7.0 (IPCC, 2017) and SSP3-7.0 (IPCC, 2021) scenarios.

Each 4 × 4 m plot was warmed using arrays of eight 1000 W ceramic infrared (IR) heaters (FTE 1000W; Ceramicx, Ireland) mounted 1.4 m above ground (Kimball et al., 2008; Figure 1D). Heaters were angled to provide uniform IR coverage across the four subplots, with power adjusted every minute via pulse-width modulation, controlled by a data logger (CR1000; Campbell Scientific, USA) implementing a proportional–integral-derivative (PID) control algorithm.

Surface temperatures, incorporating both plant and soil components, were recorded at 5-minute intervals using IR sensors (SI-100; Apogee Instruments, Logan, UT, USA) mounted at 3.8 m. These measurements were used in a feedback control system to regulate heating. The treatment maintained natural diel fluctuations while sustaining +3 °C above ambient plots in real time. Infrared heating primarily affected plant and soil surfaces and slightly reduced air humidity (~1%). The warming treatment commenced in mid-December 2022 and produced distinct temperature profiles, with minor secondary influences on temperature associated with rainfall treatments (Fig. 4).

3.5.3 Environmental monitoring

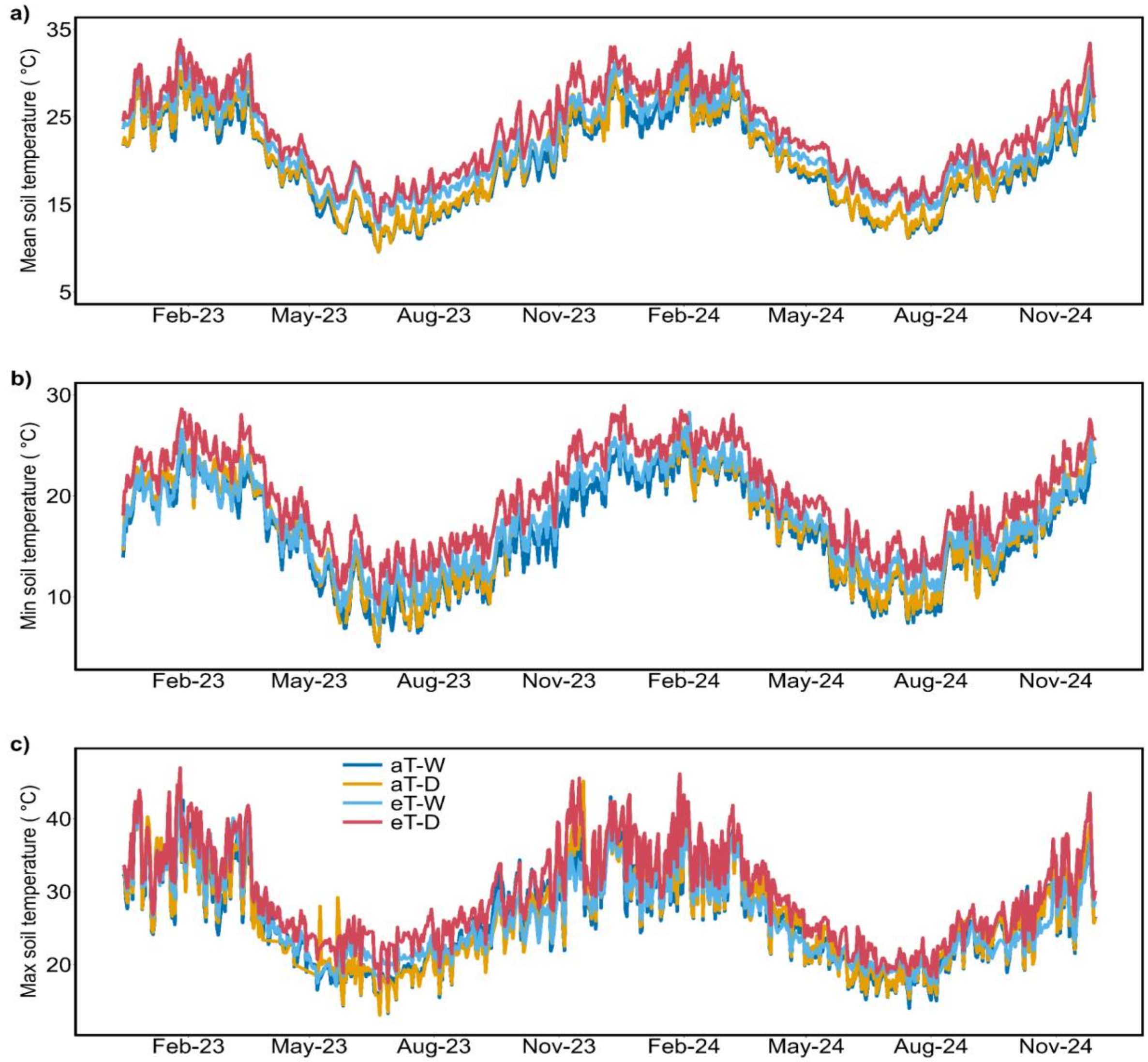
Figure 4. Plot surface temperature (a) mean, (c) minimum and (e) maximum from mid-December 2022 to 28 February 2025. Treatment abbreviations as in Fig. 2.



Prior to the start of climate treatments in mid-December, sensors were installed in each shelter to continuously monitor environmental conditions. Air temperature and relative humidity were measured every 5 minutes using sensors (Series RHP-203B; Dwyer Instruments Inc., USA) mounted inside and outside shelters at 0.6 m height in forced-ventilated radiation shields (Fig. 4).

Soil volumetric water content (0-20 cm depth; CS616, Campbell Scientific, USA; Fig. 2b) and soil temperature (5 cm depth; T107, Campbell Scientific, USA) were recorded at 15-minute intervals (Fig. 5). Photosynthetically active radiation (PAR) was measured at 5-minute intervals with quantum sensors (Apogee Instruments, USA) installed inside (3 m height) and outside (6 m height) shelters.

Figure 5. Soil temperature (a) mean, (b) minimum and (c) maximum from 15/12/2022 to 28/2/2025. Treatment abbreviations as in Fig. 2.



3.6 Aboveground net primary production (ANPP)

Seasonal aboveground productivity responses to warming and rainfall were evaluated from December 2022 to March 2025; responses of tropical/temperate plots to contrasting rainfall regimes and of temperate plots to grazing frequency and rainfall were measured from June 2023 to March 2025. Subplots were harvested to 5 cm above ground using a sickle mower and hand shears (Fig. 6). Biomass was sorted to species, oven-dried at 70 °C to constant mass and summed within and across seasons to estimate cumulative production. Harvests followed industry grazing guidelines, typically at peak vegetative growth (Clements et al., 2003) or at the end of the season.

To compare responses to climate treatments among species/ pasture mixtures, we calculated treatment effect size as:

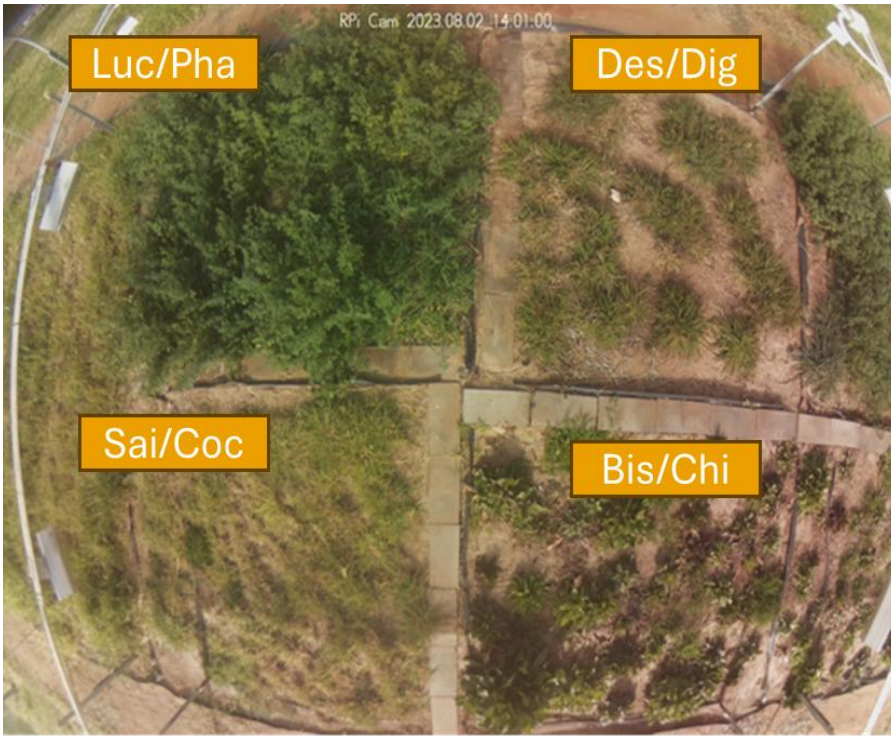
$$Effect\ size = exp\ (ln\ (\frac{Treatment}{Control}))\text{-}1$$

Figure 6. Aboveground biomass harvest at the PACE facility using a sickle mower and hand shears to measure aboveground net primary production.

3.7 Canopy greenness monitoring

Using high-resolution phenology cameras, we monitored daily pasture canopy greenness in all two-species subplots, as an index of plant growth (Fig. 7). The green chromatic coordinate (GCC), representing canopy greenness, was extracted for each species pair to assess intrinsic patterns of canopy development and the effects of climate treatments. Daily phenocam measurements provide high-temporal-resolution insights into canopy dynamics, complementing periodic harvest data.

Figure 7. Phenology camera image, taken at mid-day, to quantify subplot-level greenness.



3.8. Belowground carbon allocation

We assessed belowground carbon allocation under altered rainfall regimes and harvest frequency by measuring standing root and crown biomass, belowground net primary production (BNPP), the fraction of total (above+belowground) productivity allocated belowground (fBNPP) and non-structural carbohydrate (NSC) concentrations.

3.8.1 Standing root and crown biomass

Root biomass was sampled in September 2023 (at the start of spring) and in February 2024 and 2025 (at the end of summer) at depths of 0–10, 10–20 and 20–30 cm using a 5 cm auger. Three soil cores per replicate were composited by depth, roots separated (2 mm sieve), washed, oven-dried (70 °C, 72 h) and weighed. Crown biomass was collected at the end of spring and summer 2024 from 20 × 40 cm quadrats, trimmed of shoots, washed, oven-dried (70 °C, 72 h) and weighed.

3.8.2 Belowground net primary production (BNPP)

BNPP (g m^{-2}) was measured from September 2023 to February 2025 using mesh-free ingrowth cores (Andreasson et al., 2016). In September 2023, three 5 cm diameter × 30 cm deep holes per subplot were refilled with root-free soil (3:1 ratio of field soil to sand) compacted to reflect plot-level bulk density, marked with PVC collars, and harvested every six months. New locations were selected for each successive set of measurements. Soil was separated by depth (0-10, 10-20, 20-30 cm), composited per subplot and depth, and roots processed as above. BNPP was calculated as root accumulation over six months and was assessed for three sequential 6-month periods. Fractional belowground allocation was expressed as BNPP relative to total plant production (above + belowground, excluding crowns). Crown biomass was estimated separately within a fixed area (40 cm × 40 cm), where all crown material was collected after aboveground and root sampling, then oven-dried at 70 °C for 72 hours before weighing.

3.8.3 Non-structural carbohydrates (NSCs)

NSCs (soluble sugars + starch) were quantified in roots (September 2023-February 2024 growth) and crowns (February 2024). Approximately 15 mg of oven-dried, ball-milled tissue (MM400, Retsch GmbH) was extracted three times with 2 ml methanol: chloroform: water (12:5:3, v/v/v) to separate soluble sugars from the starch-containing pellet. The starch pellets were dried, hydrolysed with 35% perchloric acid and reacted with 5% phenol + H_2SO_4. Absorbance was measured at 490 nm using a CLARIOstar Plus spectrophotometer (BMG LabTech).

3.9 Nutritional quality and yields

During each harvest, ~50 g of subsampled biomass was frozen (-20 °C), freeze-dried and ground to 1 mm. Forage nutritional traits - crude protein (CP), dry organic matter digestibility (DOMD), metabolisable energy (ME), neutral detergent fibre (NDF), acid detergent fibre (ADF) and water-soluble carbohydrates (WSC) - were predicted using near-infrared spectroscopic (NIRS) models developed by the NSW Department of Primary Industries and Regional Development Feed Quality Service (NSW DPIRD FQS) (Table 3). To validate predictions, 10% of samples were randomly selected for wet chemistry analysis (AFIA, 2011).

Chemical analysis of NDF and ADF was undertaken sequentially, following Van Soest et al. (1991), using an ANKOM 200 fibre analyser. CP was calculated as N × 6.25 from nitrogen measured via Dumas combustion. DOMD was estimated using the pepsin–cellulase method and ME calculated as ME = 0.203 × DOMD – 3.001 (AFIA, 2011). WSC was measured via water extraction and the alkaline ferricyanide method (AFIA, 2011).

In 2024/25 (spring–summer), perennial legumes were additionally sorted into leaves and stems and their dry weights used to calculate leaf: stem ratios. For sainfoin, the rachis of compound leaves were treated as stem, rather than leaf, while those of compound leaves of other species were included with the leaf fraction.

Nutritional yields for crude protein (CPY) and metabolizable energy (MEY) were calculated by combining seasonal biomass production with corresponding forage quality parameters as follows:

$$CPY\ (kg\ per\ ha) = \frac{CP(\%\ DM)}{100} x\ Seasonal\ biomass\ (kg\ per\ ha)$$

$$MEY\ (MJ\ per\ ha) = \ ME\ (MJ\ per\ kg\ DM)\ x\ Seasonal\ biomass\ (kg\ per\ ha)$$

3.10 *In vitro* methane production of key forage species

Total gas and CH_4 production were predicted for spring 2023 and summer 2024 samples (n = 199) using NIRS, with calibration models developed from 343 freeze-dried forage samples (including all study species). These were validated against an independent set of 70 samples used to measure *in vitro* CH_4 production from 48-h fermentations with rumen liquor, following Li et al. (2025). For the latter measurements, one sample per species × season × treatment combination was randomly selected (n = 36).

Rumen fluid was obtained from fistulated cattle fed on a standardised diet of lucerne and oaten hay cubes (Multicube, NSW, Australia) at the Animal Nutrition Unit, Wagga Wagga Agricultural Institute. The fluid was transferred to pre-heated containers (39 °C) and taken to the laboratory where half was strained through coarse muslin and fine cotton, and the remainder homogenised before straining through muslin. Fluid was mixed with a buffer (1:4, v/v) and adjusted to pH 6.88. Fermentations were conducted with 1 g of freeze-dried plant material ground (to 1mm) and 120 mL buffer–rumen mixture in 250-mL ANKOM RF glass bottles flushed with N_2 to ensure anaerobic conditions. Each run included one blank and three standards (biserrula, white clover, sudan grass) with known *in vivo* digestibility that were collected from previous Department of Primary Industries and Regional Development (DPIRD) field trials. Bottles were incubated in a shaking water bath at 39 °C with automatic venting at 3 psi to prevent pressure build-up.

Total gas production was recorded throughout incubation via headspace pressure, and gas composition was determined at 48 h. Gas samples were collected through septa using syringes and analysed on an SRI 8610 MG#5 gas chromatograph fitted with thermo-conductivity detector (TCD) and using a 2-m Hayesep D column and a 1.5-m 5A molecular sieve column running high-purity helium as carrier gas. Gas yields were corrected for blanks (rumen fluid–buffer mix incubated without substrate). Methane yield was expressed as mL g^{-1} dry matter at standard temperature and pressure.

4. Results

4.1 Experiment 1: Factorial warming x rainfall manipulation

4.1.1 Aboveground net primary production of grass-legume and herb-legume mixtures in response to warming and rainfall treatments

Mean aboveground net primary production (ANPP) varied markedly among pasture mixtures, reflecting differences in inherent productivity and species-specific climate sensitivities. The lucerne-phalaris (Luc/Pha) mixture was the most productive, yielding ~18 t ha^{-1} under ambient and well-watered conditions (aT-Wet) over the 24 months of experimentation (Dec-2022 to Nov-2024) (Fig 8a and Table 4). Lucerne dominated the sward, contributing 90% of spring biomass after two years. Although productivity of both lucerne (-35.5%) and phalaris (-33.4%) declined under low rainfall (-35% at the sward level), overall productivity remained relatively high. The modest reduction under warming (-15% at the sward level; Luc -15% and Pha -26%) suggests that these cultivars function near their thermal optimum under current southeastern Australian climates (Cullen et al., 2009).

The sainfoin-cocksfoot (Sai/Coc) mixture had the lowest productivity (<4 t ha^{-1} yr^{-1}) and the greatest sensitivity to climate treatments (Fig. 8b and Table 4). The marked declines in ANPP under reduced rainfall (-35%) and warming (-41%) point to limited physiological tolerance and weak compensatory interactions between the component species. Cocksfoot, the dominant contributor to sward biomass, was more sensitive to heat (-44%) than reduced rainfall (-32%), consistent with reported thermal constraints on cool-season C_3 grasses (Loka et al., 2019; Sun et al., 2024). Sainfoin, although moderately tolerant of warming, was highly susceptible to reduced rainfall (-57%), while the combination of warming and low rainfall resulted in the largest productivity decline (-62%). These yield responses suggest that this mixture is unsuitable for warmer and drier environments. This aligns with previous studies reporting yield reductions in sainfoin under drought, though responses vary among ecotypes (Irani et al., 2015). Some populations have, however, shown greater drought tolerance (Sheppard et al., 2019; Yao et al., 2024). Given sainfoin's broad geographic range across Mediterranean to warm-temperate regions, management interventions - such as improving soil pH and nutrient status to support nitrogen fixation and pairing it with species with complementary resource-use traits - could enhance its persistence and productivity under a wider range of climates.

The biserrula-chicory (Bis/Chi) mixture experienced relatively small reductions in ANPP under both reduced rainfall (-15%; $p<0.01$) and warming (-11%; $p<0.1$) (Fig.8c and Table 4). However, since chicory dominated biomass production (~83%) in these sub-plots, overall sward responses largely reflected this species' low rainfall sensitivity (10% reduction) which is attributable to its deep tap-root system (Gardner et al., 2024). Biserrula, however, was highly sensitive to both low rainfall (-75%) and warming (-65%). As a deep-rooted cool-season annual, biserrula's early winter/spring growth phenology suggests a (summer-) drought-escape strategy. While this strategy is typical of annual species (Haling et al., 2016; Loi et al., 2005), it does not equate to drought-escape when cool-season rainfall is low. This finding is consistent with previous observations of more than 50% productivity declines under cool-season drought (Churchill et al., 2022) and underscores the importance of drought timing relative to species phenology in determining pasture resilience (Wilcox et al., 2022; Yao et al., 2024; Zhou et al., 2019). Despite its sensitivity to low growing season rainfall in the current study, it may still have good potential in areas with moderate amounts of winter/spring rainfall.

The desmanthus–digit (Des/Dig) mixture was least affected by climate treatments (Fig. 8d and Table 3), reflecting the higher thermal optima of tropical species and the superior water-use efficiency of C_4 grasses (Simpson et al., 2020; Taylor et al., 2010, 2014, 2018). While desmanthus responded positively to warming (+101%) and negatively to reduced rainfall (-35%), its low biomass contribution (<8%) limited its influence on total sward ANPP. Nevertheless, its positive warming response suggests potential for improved performance in warm-temperate environments under future climates, particularly in soils with a higher clay content.

Figure 8. Aboveground productivity responses to altered rainfall and warming in two-species pasture mixtures across two years. Bars represent annual treatment means ± SE (n=6). Inset boxes show mean production over the two-year period from Dec-2022 to Nov-2024. Inset boxes with different Letters above denote significant differences between treatments. Treatment abbreviations as in Fig. 2. Pasture abbreviations: Luc/Pha (Lucerne/Phalaris); Sai/Coc (Sainfoin/Cocksfoot); Bis/Chi (Biserrula/Chicory) and Des/Dig (Desmanthus/Digit).

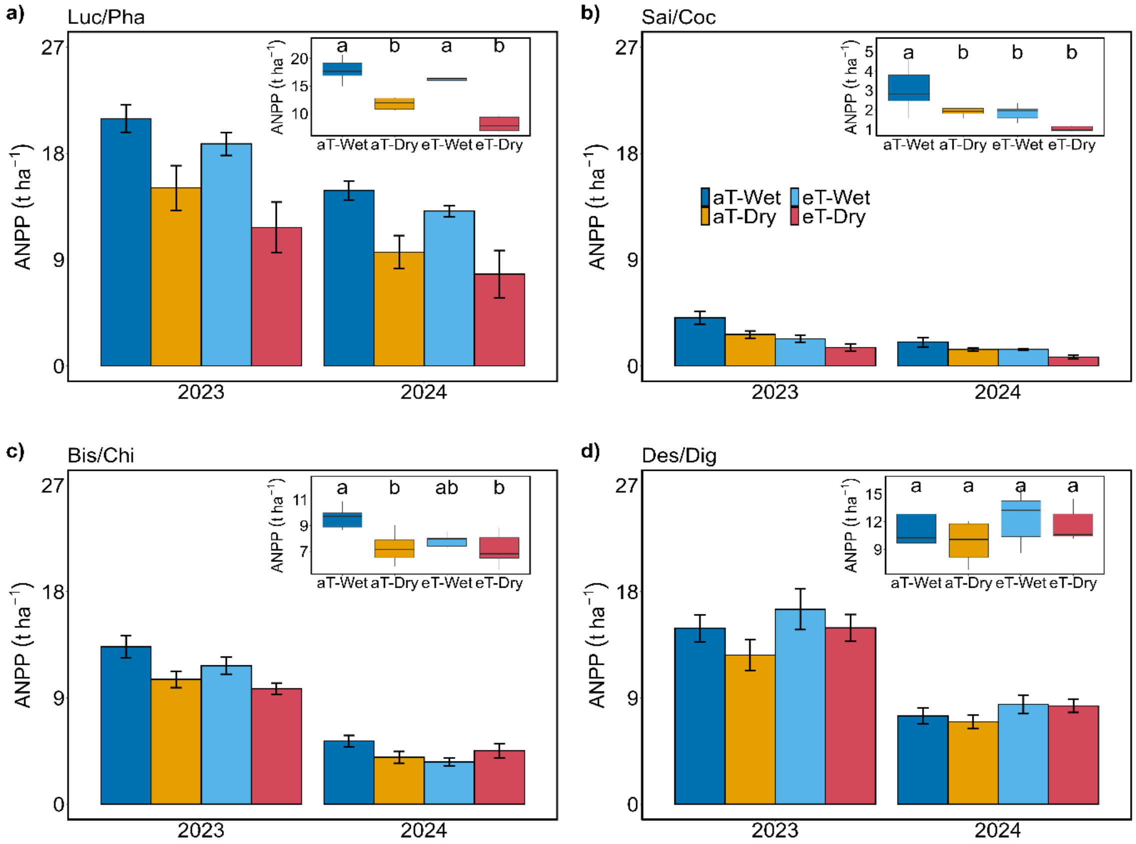


Table 4. Means (t ha^{-1} y^{-1} ± SE) and summary statistics for the effects of warming (T), altered rainfall (R) and their interaction (T*R) on pasture production by mixture and species (2023-2024).

Pasture	aT-Wet		aT-Dry		eT-Wet		eT-Dry		T	R	T*R
	Mean	±SE	Mean	±SE	Mean	±SE	Mean	±SE		p-value	
Luc/Pha	17.91	0.84	12.36	1.6	15.97	0.6	9.753	2.06	*0.092*	**<0.001**	0.797
Luc	16.52	0.89	11.44	1.58	14.83	0.59	8.823	1.96	*0.099*	**<0.001**	0.713
Pha	1.079	0.13	0.684	0.23	0.765	0.15	0.544	0.12	0.091	**0.028**	0.502
Sai/Coc	3.046	0.46	2.034	0.18	1.855	0.16	1.158	0.17	**0.001**	**0.006**	0.571
Sai	0.547	0.13	0.166	0.03	0.285	0.06	0.193	0.09	0.199	**0.016**	0.119
Coc	2.09	0.32	1.522	0.16	1.262	0.09	0.761	0.08	**<0.001**	**0.014**	0.863
Bis/Chi	9.349	0.54	7.274	0.47	7.654	0.34	7.157	0.51	*0.053*	**0.009**	*0.087*
Bis	0.681	0.18	0.157	0.04	0.228	0.1	0.066	0.03	**0.006**	**0.001**	*0.052*
Chi	7.741	0.32	6.748	0.45	7.053	0.34	6.601	0.47	0.223	**0.044**	0.423
Des/Dig	11.19	0.88	9.814	0.92	12.48	1.14	11.64	0.77	0.117	0.255	0.781
Des	0.734	0.28	0.438	0.13	1.405	0.33	0.955	0.38	**0.006**	*0.066*	0.690
Dig	10.18	0.85	9.055	1.04	10.72	1.08	10.29	0.62	0.348	0.409	0.707

Bold values indicate statistical significance at $p < 0.05$ and italics indicate marginal significance at $p < 0.1$.

4.1.1 Summary: *The effects of higher temperatures and altered rainfall regimes on mixed pastures depend strongly on the physiological thresholds, morphological traits, and dominance patterns of component species. Mixtures combining deep-rooted perennials and C_4 species with moderate heat and drought tolerance appear most promising for sustaining productivity under the warmer and drier conditions projected for southern Australia. However, it is noteworthy that climate sensitivity can still vary considerably across seasons, even among resilient species (see 4.1.2, below).*

4.1.2 Seasonal patterns in ANPP of grass-legume and legume-herb mixtures, and component species, under factorial warming and rainfall treatments

Across mixtures, there were distinct seasonal patterns in ANPP, peaking in spring for Sai/Coc, in summer for Bis/Chi and Des/Dig and remaining high throughout spring and summer for Luc/Pha (Fig. 9). The cocksfoot–sainfoin mixture also showed moderate autumn regrowth, reflecting the bimodal growth pattern typical of many species that are sensitive to high summer temperatures (Kiniry et al., 2018; Tercek et al., 2023).

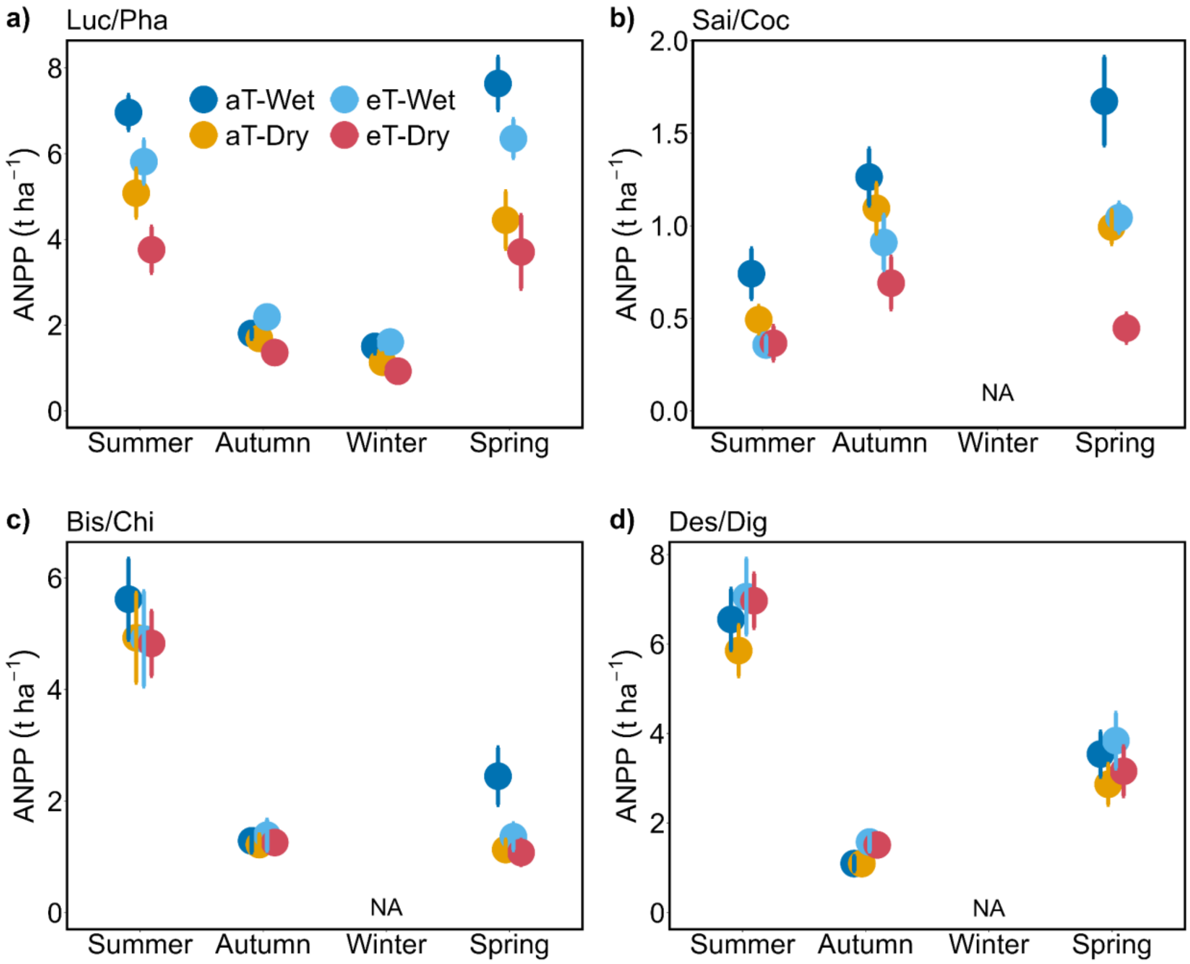
Sward level ANPP of Luc/Pha declined markedly under reduced rainfall in all seasons, ranging from 24% in autumn to 42% in spring (Fig. 9a, Table S1); high springtime rainfall sensitivity highlights the crucial role of water availability during the early part of the growing season (Marklein et al., 2020). Elevated temperature limited growth only in summer (-21%), although higher temperatures also amplified (+38%) the effect of reduced rainfall on autumn productivity, a response that may be mediated via disruption of stomatal functioning and/or photosynthesis (Oishy et al., 2025). Lucerne contributed over 90% of sward productivity, so its climate sensitivity largely dictated sward-level responses. This species' productivity declined between 27% (autumn) and 41% (summer) under low rainfall and was also suppressed under summertime warming (Table S1). Phalaris, which represented less than 10% of sward biomass, was also strongly constrained by low rainfall (-43% in winter and -59% in spring) and, to a lesser extent, also by warming (Table S1).

The Sai/Coc mixture was highly responsive to climate treatments, particularly reduced rainfall during spring, which decreased ANPP by 47% (Fig. 9b, Table S1). Warming consistently suppressed sward-level productivity across seasons - summer (-42%), autumn (-32%) and spring (-44%). This was primarily driven by cocksfoot's response to elevated temperature (-56%, -30%, -45% in summer, autumn and spring, respectively), confirming the sensitivity of this temperate C_3 grass to high temperatures, which can increase respiration and reduce photosynthetic efficiency (Hunt et al., 1996). The absence of warming benefits on winter/spring ANPP suggests that high maximum temperatures and temperature variability during late spring offset potential productivity gains (Bernacchi et al., 2023).

Sainfoin, the non-dominant partner in the Sai/Coc mixture, was particularly sensitive to reduced rainfall, with spring productivity declining by 81%. Summertime productivity was also reduced by low rainfall (-63%) under ambient conditions, but not under warming, indicating a rainfall × warming interaction (Table S1). The mitigating effect of warming may be linked to extended growth duration or enhanced root activity (Orians et al., 2019; Tissink et al., 2025). These results highlight contrasting sensitivities within the species pair: cocksfoot was primarily affected by warming, whereas sainfoin was strongly constrained by low rainfall. This example of complementarity between species could be expected to help stabilize sward productivity under simultaneous heat and moisture stress, although this was not a productive mixture under the climate and soil conditions in the current study.

The Bis/Chi mixture exhibited distinct seasonal and species-specific responses, with productivity peaking in summer (Fig. 9c, Table S1). Sward level responses to low rainfall were highest (-42%) in spring (when both biserrula and chicory were actively growing), coinciding with rapid canopy expansion and high transpirational water demand. This reduction was particularly pronounced under ambient temperature (-54%) compared with elevated temperature (-21%), reflecting a rainfall × temperature interaction whereby warming partially mitigated the effects of low rainfall during this season, as was also seen for sainfoin (above).

Figure 9. Seasonal aboveground productivity responses to altered rainfall and warming in two-species pasture mixtures, averaged across 2023 and 2024. Values are means ± SE (n = 6). No winter harvesting was undertaken for Sai/Coc, Bis/Chi, or Des/Dig as there was very low biomass at this time.



The spring through autumn growing season of chicory complements the winter-spring phenology of biserrula, and highlights chicory's dominance of summer and autumn productivity in this mixture. Chicory experienced only a modest but significant decline in springtime productivity (-22%) under low rainfall and was relatively unaffected at other times, including under warming. This likely reflects its ability to access subsoil moisture via its deep taproot (Gilgen & Buchmann, 2009). In contrast, biserrula, an annual legume, showed sharp declines in spring productivity under both low rainfall (-75%) and warming (-65%), reflecting its reliance on timely rainfall for regeneration (Goward et al., 2025). Its poor regrowth under warm, dry conditions suggests establishment challenges under future climates, particularly when competing with established perennials. However, biserrula performed well under well-watered ambient conditions, indicating its potential suitability for cooler temperate environments. Overall, the contrasting strategies of chicory and biserrula highlight the value of functional diversity and strategic species selection for sustaining pasture productivity and resilience under increasing climatic variability (Table S1)

The Dig/Des mixture (Fig. 9d, Table S1) was resistant to both warming and reduced rainfall. Reduced rainfall had little effect on ANPP, while warming actually increased productivity (autumn, +41%), reflecting the high thermal optimum and drought tolerance of the dominant C_4 grass, digit. Warming boosted digit productivity by 31% in autumn, consistent with its high physiological thermal optimum and water-use efficiency (Sage & Kubien, 2007; Taylor et al., 2014). The tropical legume, desmanthus, also responded positively to warming, with productivity increases of 136% in autumn and 123% in spring, contributing to enhanced total sward productivity (Fig. 9, Table 4). However, springtime desmanthus growth was reduced by 45% under low rainfall, indicating sensitivity to soil moisture deficits during the early part of its growing season. Notwithstanding low-temperature constraints on tropical species' viability in cooler regions, digit and desmanthus responses to climate treatments highlight the potential for tropical C_4 grass–legume mixtures to sustain forage production under the increasingly hot and dry conditions projected for southern pasture systems (Cullen et al., 2009; Vendramini et al., 2023).

4.1.2 Summary: *The biggest effects of climate treatments were in spring, where large sward-level productivity declines of temperate mixtures were seen in response to reduced rainfall, along with reductions of up to 44% (Sai-Coc) in response to increased temperature. Elevated temperatures were also detrimental for summertime productivity of Luc-Pha In contrast, warming increased autumn productivity in the tropical (Des/Dig) species pair, particularly for desmanthus, which also benefitted from higher springtime temperatures. Given the critical importance of spring (and summer) climate conditions, areas predicted to have lower rainfall and higher temperatures during the growing season are likely to experience reduced productivity of many temperate species, while warmer spring and autumn temperatures may increase the suitability for, and productivity of, tropical species within warm temperate regions.*

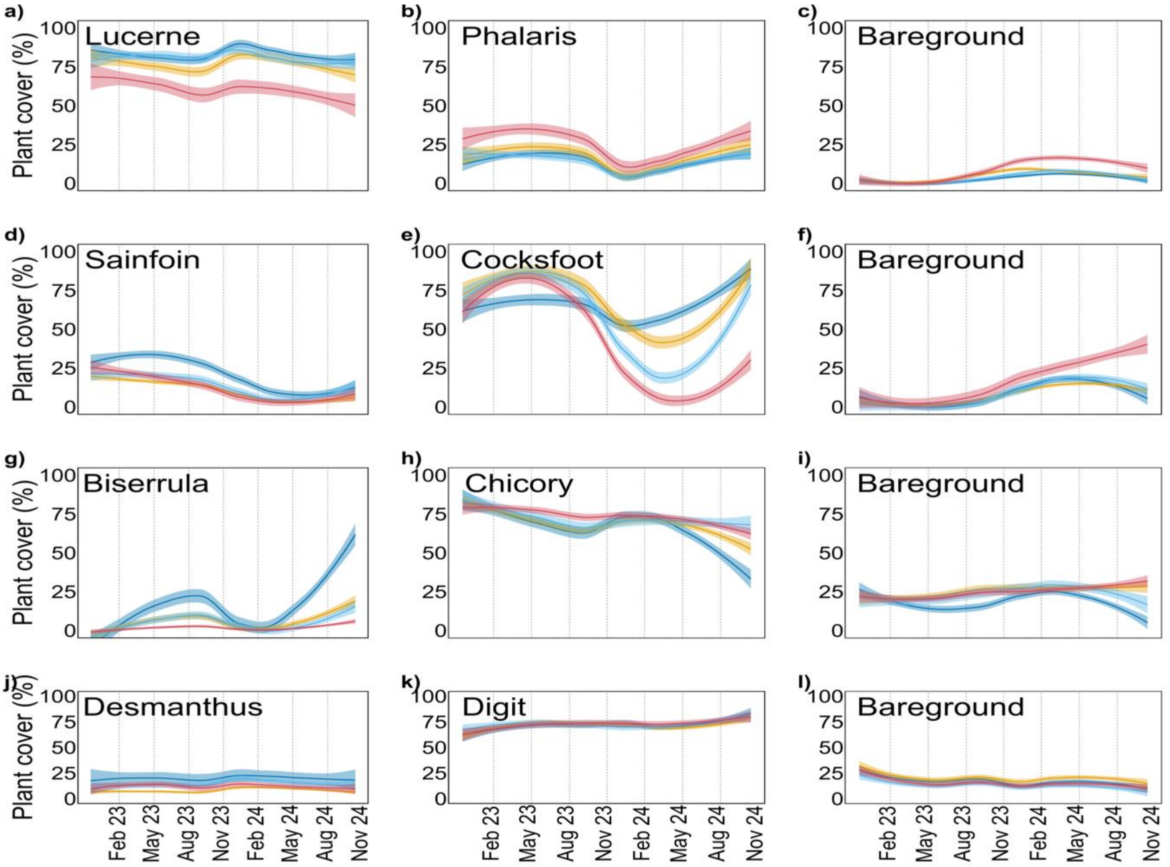
4.1.3 Species persistence under warming and altered rainfall.

Persistence was evaluated by comparing changes in species-level cover data from December 2022 to November 2024 (Fig. 10), alongside changes in productivity from a pre-treatment (2022) spring baseline to spring 2024 (Fig S1). Lucerne cover remained consistently high in well-watered, ambient temperature plots throughout the experiment, and productivity increased from 2022 to 2024 (Fig. S1b), indicating that the species was highly persistent. Warming reduced both cover and productivity, strongly so when combined with low rainfall, indicating that lucerne persistence was lower under this treatment combination. It is also noteworthy that lucerne experienced an outbreak of two-spotted spider mites (*Phytoseiulus persimilis*) in winter 2024, with mite numbers substantially higher in warmed plots, relative to ambient. This flags the important concept of climate change impacts on biotic stressors and the potential for additional, indirect consequences of warmer conditions for pasture productivity and persistence.

Phalaris established well initially, comprising ~40% of sward-level biomass (and ~30% cover) prior to treatments commencing. Although this species' cover fluctuated in line with its cool-season phenology, its peak (spring) productivity was low after two years, suggesting it was not particularly persistent, even under well-watered conditions (Fig. 10b). This may reflect either its poor competitive ability when growing with lucerne, which itself increased strongly over the first 12 months, or its inability to cope with the high summer temperatures and well-drained soils at the study site (Norton et al., 2016; Volaire, 2008).

Similar patterns of declining cover and productivity over time were also apparent for sainfoin (Fig. 10d) and chicory (Fig 10h). Despite sainfoin's strong performance in the first few months of the study, it did not appear to compete well with phalaris once the latter became established. Sainfoin may also be less well-suited to the local field conditions (sandy-loam soils, high spring/summer temperatures) than other species. Chicory's declining cover and productivity may have been hastened by the appearance of Sclerotinia root rot in several plants in the first year, and an outbreak of powdery mildew in the second year.

Figure 10. Species persistence under contrasting rainfall and temperature treatments, as represented by changes in cover over time. Each row shows the cover of the species pairs and bare ground within their plots. Colours represent treatments – Dark blue= ambient temperature (aT)-Wet; light blue=aT-Dry; yellow=elevated temperature (eT)-Wet; red=eT-Dry.



Cocksfoot maintained a fairly high level of cover (Fig. 10e) and increased its productivity (Fig. S1c) under well-watered, ambient conditions, but was less persistent under elevated temperatures, especially when combined with low rainfall. Indeed, when growing under warm, dry conditions, cocksfoot cover declined by ~50% over the two years, and was less than half that in ambient, high rainfall plots at the end of the study. The combination of poor persistence for both sainfoin and cocksfoot under warming and reduced rainfall resulted in a substantial increase in bare ground in these sub-plots over the two years (Fig 10f). The annual legume biserrula showed pronounced seasonal fluctuations in cover, reflecting its annual growth form and reliance on spring rainfall for seed germination and establishment (Revell et al., 2012). Across the two years, biserrula was persistent under wet, ambient conditions, but much less so under low rainfall, higher temperatures, and their combination (Fig 10g).

Digit maintained high levels of cover (Fig. 10k) and biomass (Fig. S1e) across all treatments, highlighting its sustained strong performance. Desmanthus was similarly persistent (Fig 10j), albeit at a lower cover than its companion grass. Its gradual increase in productivity over the two years (Fig. S1f) reflects its longer establishment time and slower growth rate than digit, consistent with other semi-arid leguminous shrubs (Archer et al., 2017).

***4.1.3 Summary:** Overall, pasture persistence was high in two of the deep-rooted perennial legumes evaluated (lucerne, desmanthus) and those species adapted to warmer climates (digit, desmanthus). Despite being deep-rooted, sainfoin was not persistent, possibly reflecting its low tolerance of the high spring and summertime temperatures experienced at the study site. Cocksfoot and biserrula persisted under well-watered, ambient conditions, but not under elevated temperatures or low rainfall.*

4.1.4 Using phenocam data to quantify climate treatment effects on early pasture regrowth following seasonal harvests.

There was strong seasonal variation in canopy greenness across all species pairs (Fig. 11), with low rainfall and higher temperatures reducing greenness, to differing extents, over the course of the study.

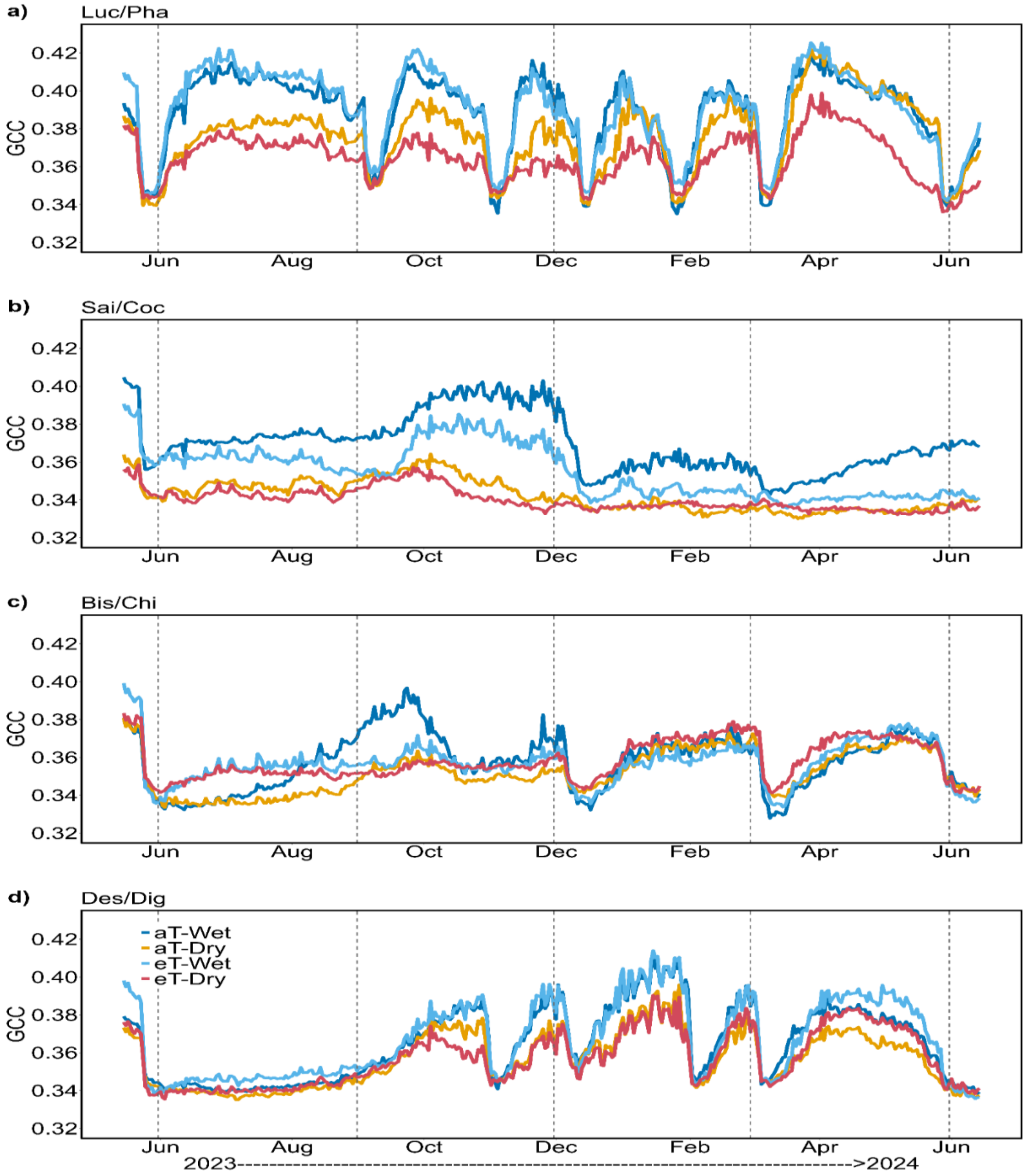
The canopy greenness metric (green chromatic coordinate, GCC) was used to track daily changes in vegetation regrowth for each species pair, for a period of 15 days following harvest events (Fig. S2). This provides insight into whether climate treatments were particularly influential in the early phase of post-harvest recovery and, by comparison with seasonal biomass data, whether early responses were sustained over time.

In the Luc/Pha mixture, low rainfall markedly constrained early canopy regrowth across all seasons (Fig. 11a), confirming the high sensitivity of this temperate mixture to soil moisture limitation. Large rainfall-related reductions in canopy re-greening were seen in winter (Fig. S2a) and under combined warming and reduced rainfall during spring, summer, and autumn (Fig. S2b-d), when evaporative demand and soil water deficit were high. Warming alone exerted little influence on early post-harvest regrowth rates under the high rainfall regime, indicating that temperature responses are likely driven by the soil drying effect of higher temperatures (Figure 2a).

There was a strong negative effect of reduced rainfall on post-harvest canopy regrowth patterns of Sai/Coc swards during winter (Fig. S2f), spring (Fig. S2g), and summer (Fig. S2h). Furthermore, under well-watered conditions, warming (eT-Wet) slowed the rate of canopy re-greening in summer, likely reflecting thermal inhibition of growth during the warmer part of the year. Phenocam data revealed poor autumn regrowth across all treatments. Given that autumn productivity (from harvest data) in these plots was at a similar level to that seen in summer (Fig. 9), this suggests that poor post-harvest regrowth in early autumn was compensated by stronger mid/late season productivity, at least in well-watered ambient temperature plots. Treatment differences were nevertheless apparent in both phenocam and harvest data for this period.

The Bis/Chi (Fig. 11c, Fig. S2k-o) and Des/Dig (Fig. 11d., Fig. S2p-t) mixtures both had negligible winter re-growth following the end of autumn harvest. The Des/Dig mixture exhibited strong regrowth during summer across all treatments, consistent with its tropical origin and adaptation to warmer conditions. There was, however, slower regrowth in dry plots indicating that moisture limitation still constrains thermally adapted species, including the productive C_4 grass, digit, which contributed strongly to canopy-level greenness.

Figure 11. Green chromatic coordinate (GCC) of species pairs from winter 2023 (June) through autumn 2024 (May) under factorial combinations of altered rainfall and warming. Values are daily averages of two measurements (11am and 12pm) across six replicates. Vertical dashed lines indicate seasonal transitions.



4.1.4 Summary: *Canopy regrowth following defoliation is highly dependent on both seasonal conditions and the combination of temperature and soil moisture availability. Low rainfall strongly constrained post-harvest regrowth across species and seasons, whereas the effects of warming were contingent on soil moisture (more negative under dry conditions) and species' thermal optima (enhanced autumn growth of tropical species). The capacity of tropical mixtures to quickly re-green canopies under warmer temperatures but not under low rainfall underscores the critical role of water availability as the primary driver of postharvest regrowth rates (i.e. grazing resilience) even for more water-use efficient species. Conversely, the strong suppression of winter and summer regrowth in* *temperate mixtures highlights their vulnerability to projected increases in both heat and moisture stress.*

4.1.5 Plant chemistry under reduced rainfall and elevated temperatures

Nutritional analyses were conducted on the five pasture legume and herb species. For legumes, all live aboveground material (leaves, stems, and flowers where present) were included in analysed samples, while only leaves were used for the herb chicory. Detailed nutritional data are presented in the appendix (Table S2) and significant treatment responses are summarised below in Table 5, and as response ratios (i.e. the magnitude of change from values obtained for plants growing under well-watered conditions and ambient temperature (aT-Wet)) in Fig. 12.

Reduced rainfall increased crude protein (CP) in some cases (desmanthus, chicory), decreased it in biserrula, and produced seasonally-dependent directional responses for lucerne (increase in summer, decrease in spring). Elevated temperature increased CP in sainfoin and chicory at multiple timepoints. Climate stresses like drought have been shown elsewhere to generally reduce nitrogen and hence CP concentrations (He and Dijkstra, 2014; Liu et al. 2023) but increases are also common, related to a reduction in plant growth resulting in a lower dilution of N with carbon-based plant fractions (Dumont et al., 2015; Grant et al., 2014). Indeed, the lower CP in chicory under ambient temperature with high rainfall in summer 2025 (Table S2) likely reflects its higher biomass production. Seasonal variability in CP was common, but lucerne and biserrula generally maintained the highest values.

Dry organic matter digestibility (DOMD) and metabolisable energy (ME) exhibited both increases and decreases in response to treatments. Reduced rainfall increased both metrics in lucerne but decreased them in sainfoin, while elevated temperature was associated with increases for lucerne and sainfoin and decreases for desmanthus. Across species, DOMD and ME were generally higher in chicory and biserrula and lower in sainfoin and desmanthus. The absolute highest values of DOMD and ME were in autumn, from chicory growing under ambient temperature, well-watered conditions.

Neutral detergent fibre (NDF; sum of hemicellulose, cellulose, and lignin components) was generally less affected by climate treatments than the more recalcitrant acid detergent fibre (ADF; cellulose and lignin), suggesting a shift in fibre composition rather than overall fibre content. Both fibre fractions are negatively associated with feed quality - while NDF influences voluntary feed such that animals eat less forage as NDF values increase, higher ADF is associated with reduced digestibility and metabolisable energy. Fibre fractions (NDF and ADF) were reduced under both low rainfall and elevated temperatures for lucerne and sainfoin, concomitant with increases in CP. In contrast, ADF increased under reduced rainfall in biserrula and chicory (though only at ambient temperature) and under elevated temperature in desmanthus and chicory. Such changes likely reflect treatment-associated reductions in the leaf:stem ratio, as stem contains relatively more cellulose and lignin and relatively less hemicellulose than leaf (Catunda et al., 2022). Lucerne generally had the highest fibre content, whereas chicory had very low fibre, likely due to the use of leaf-only samples rather than the whole plant. Notwithstanding the latter caveat, on the basis of its nutritional quality and digestibility, chicory would be a beneficial addition to pasture mixtures, and its low fibre content could buffer against increases in fibre in companion species (e.g. grasses, legume), which may otherwise reduce intake or feed conversion efficiency.

Water-soluble carbohydrates (WSCs; a measurement of the sugar content) increased under reduced rainfall in lucerne and desmanthus and under elevated temperature in sainfoin but declined in chicory.

WSCs can act as a reserve of carbohydrates and accumulate due to reduced plant growth and slower development of structural fibres (De Roover et al., 2000; Fulkerson & Donaghy, 2001; Kagan, 2022; Martínez-Vilalta et al., 2016). Where the sugars were lower, we often saw higher fibre content (both NDF and ADF), which may suggest more rapid plant development and lignification. Chicory consistently had high WSC concentrations, while sainfoin and desmanthus generally had low levels. While sugars are readily fermented in the rumen and serve as a highly digestible source of energy, excessive amounts, particularly in combination with high starch intake, can pose a risk of ruminal acidosis.

Figure 12. Response ratios of nutritional quality metrics collected during spring and summer 2024 under three climate treatments (aT-D, eT-W, and eT-D), relative to ambient, well-watered conditions. Negative values indicate a decrease, relative to ambient temperature, wet conditions and positive values indicate an increase. Biserrula did not re-grow after the spring harvest so there are no summer data for this species.

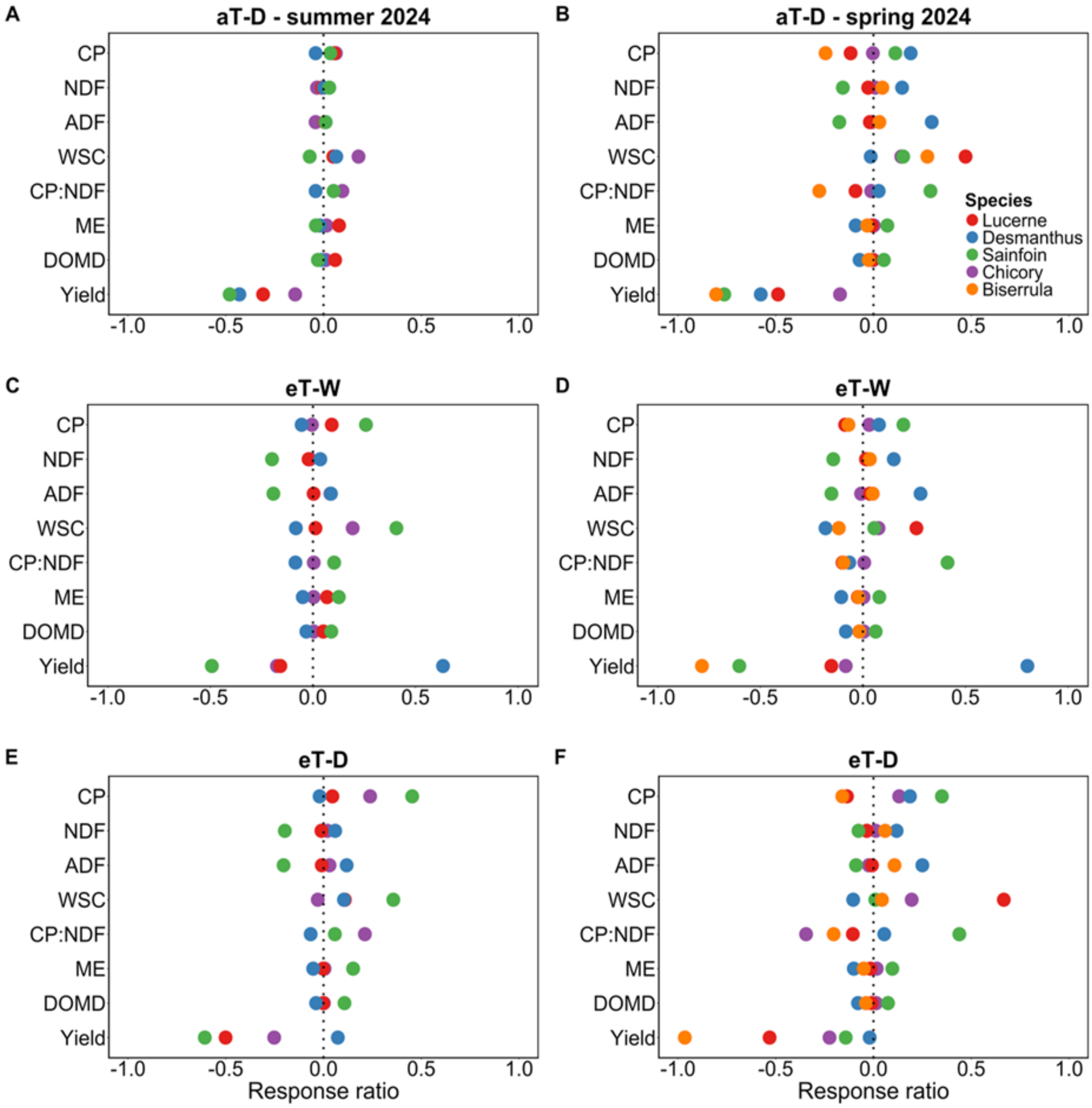


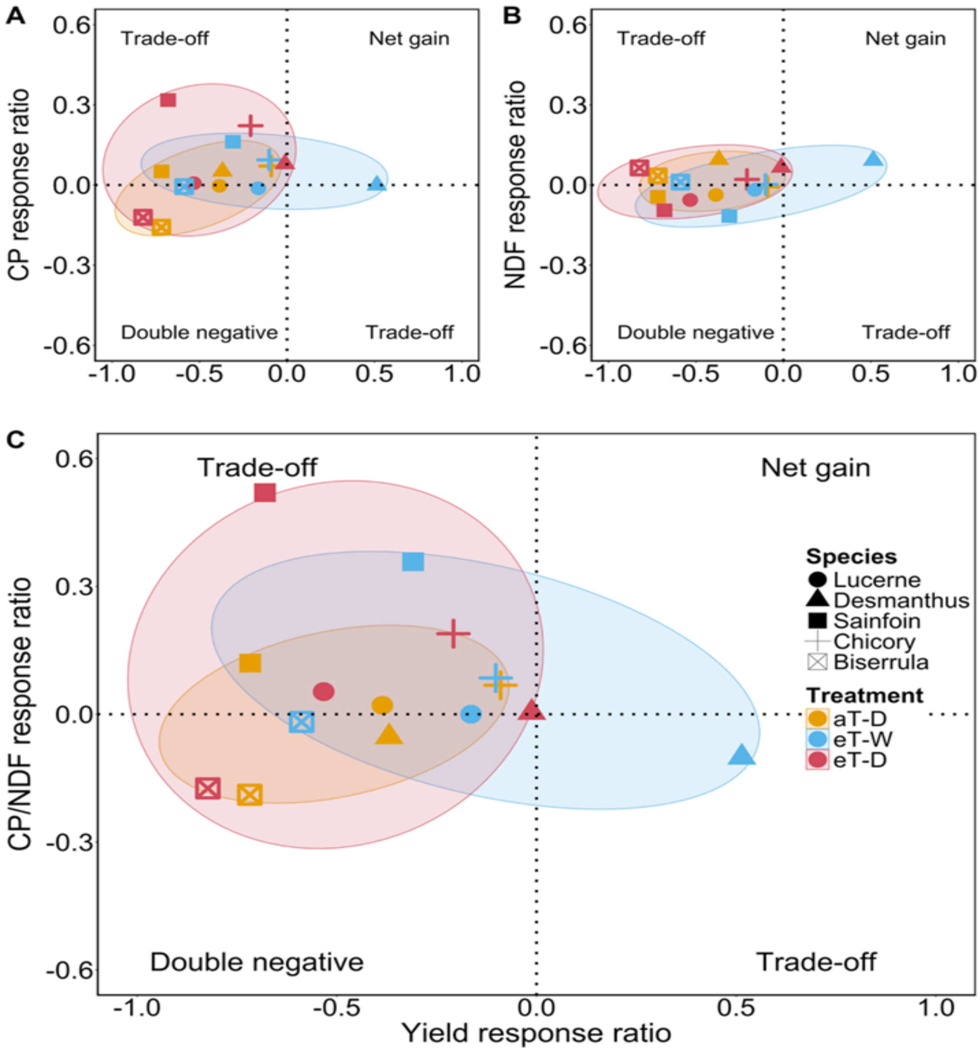
Table 5. Summary of treatment effects on key nutritional metrics (crude protein (CP), metabolisable energy (ME), dry organic matter digestibility (DOMD), neutral detergent fibre (NDF), acid detergent fibre (ADF), and water-soluble carbohydrates (WSC)). + indicates an increase (at one timepoint), ++ (at multiple timepoints), - decrease (at one timepoint), -- decrease (at multiple timepoints), +- (increases and decreases at different timepoints) under low (relative to high) rainfall or elevated (relative to ambient) temperatures, or their combination. Ns=not significant.

Species	Treatment	CP	ME	DOMD	NDF	ADF	WSC
Lucerne	Rainfall	+/- [1]	+	+	--	--	++
	Temperature	ns	+	+	-	-	ns
	Rain x Temp	ns	ns	ns	ns	Ns	ns
Biserrula	Rainfall	-	ns	ns	ns	+	ns
	Temperature	ns	ns	ns	ns	Ns	ns
	Rain x Temp	ns	ns	ns	ns	Ns	ns
Desmanthus	Rainfall	+	ns	ns	ns	Ns	++
	Temperature	ns	--	--	ns	++	ns
	Rain x Temp	ns	- [2]	- [2]	+ [3]	+ [3]	ns
Sainfoin	Rainfall	ns	-	ns	ns	Ns	ns
	Temperature	++	++	++	-	-	+
	Rain x Temp	ns	ns	ns	- [2]	- [2]	ns
Chicory	Rainfall	++	ns	ns	ns	Ns	ns
	Temperature	++	-	-	ns	++	-
	Rain x Temp	+ [3]	ns	ns	ns	- [4]	+ [5]

[1]Increase in summer; decrease in spring; [2]All treatments significantly lower than aT-W values; [3]All treatments significantly higher than aT-W values; [4]aT-D significantly lower than other treatments; [5]aT-D and eT-W values significantly higher than aT-W and eT-D values.

Given that both the amount and quality of forage are important for grazing animals, we have provided an overview of how climate treatments affect both, evaluating trade-offs (where either productivity or quality decline, but the other increases), double negative responses (where both decline) or double positive responses (net gains, where both increase). Figure 13 summarises response ratios (i.e. the magnitude of treatment effects, relative to well-watered, ambient temperature conditions) for aboveground productivity (ANPP) and the ratio of crude protein to NDF as a measure of forage quality (von Keyserlingk et al., 1996) for the five forage legume and herb species. Lucerne, chicory and sainfoin generally exhibited a trade-off in nutritional and productivity responses where forage quality increased but yield reduced (Fig. 13). Lucerne and chicory were relatively productive compared to the other species, even under reduced rainfall and warming, so this nutritional trade-off may be considered beneficial (in terms of nutritional yield, i.e. biomass x nutrient concentration), assuming pasture yield can still support good stocking rates. On the other hand, the productivity of sainfoin was generally low as well as highly sensitive to rainfall and warming treatments; increases in nutritional quality would be insufficient to maintain nutritional yield in the context of strongly reduced biomass for this species. Gains in nutritional quality were generally also observed for desmanthus, except under elevated, well-watered conditions where this reversed, with yield increasing while quality decreased (Fig. 13). As a tropical legume in a warm temperate environment, it is likely that elevated temperatures were closer to the physiological optimum for desmanthus, compared to ambient conditions. Biserrula was negatively impacted by all climate treatments in terms of both productivity and nutritional quality, emphasising its high sensitivity to changes in climate conditions, particularly reductions in rainfall.

Figure 13. Overall (multi-season) treatment response ratios for yield and nutritional quality, relative to ambient, well-watered conditions, for A) Crude Protein (CP), B Neutral Detergent Fibre (NDF), and C) their ratio (CP/NDF). Data include four timepoints for lucerne, chicory and desmanthus, three for sainfoin and two for biserrula. Negative response ratios represent a decrease relative to well-watered, ambient temperature plots while positive values represent an increase.

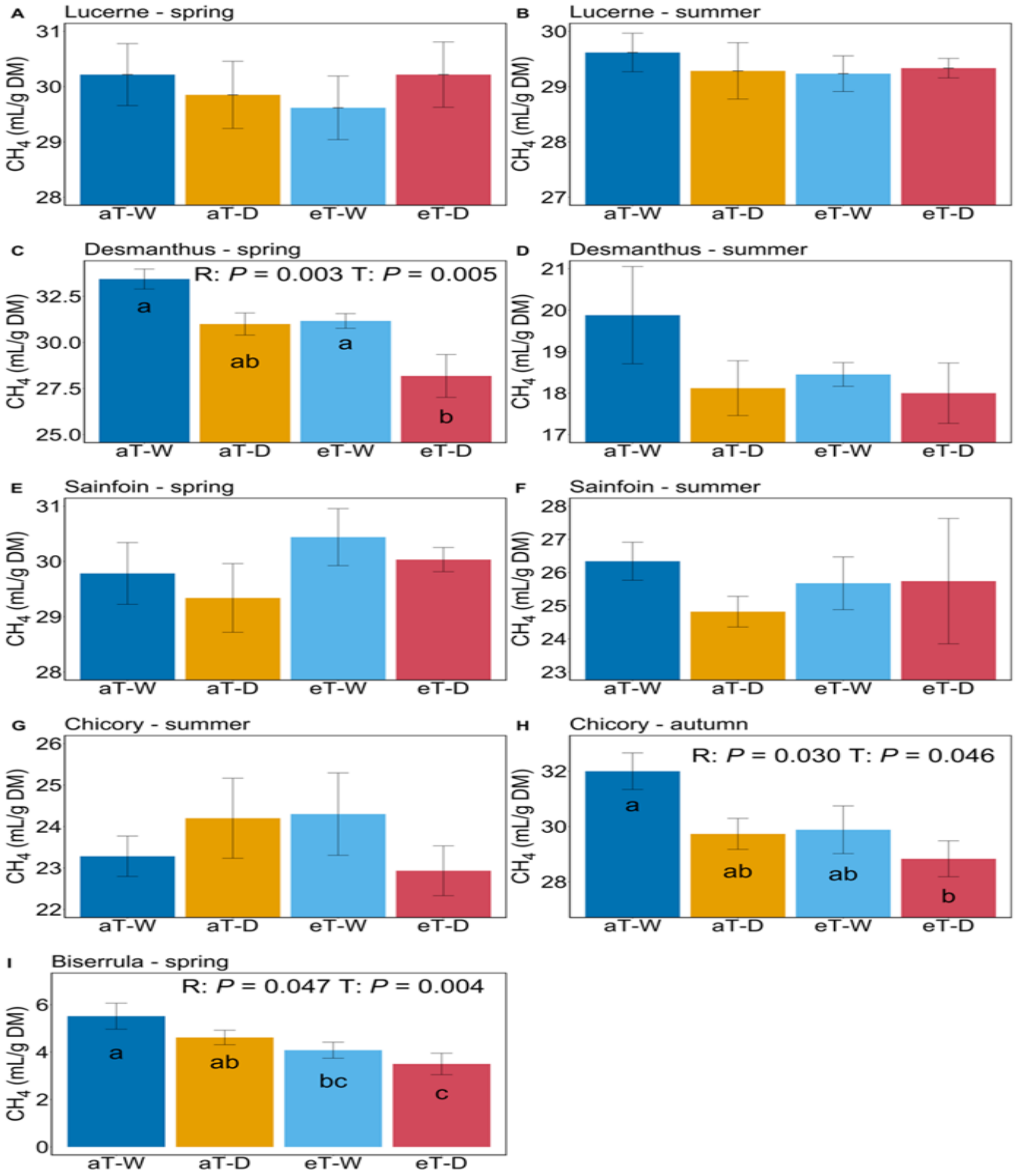


__4.1.5 Summary:__ Crude protein content generally increased in response to warming and reduced rainfall, while the impacts of climate treatments on other nutritional metrics varied in both magnitude and direction across species. Increased nutritional quality under low rainfall and/or warming for lucerne and chicory partly offset yield declines, indicating a partial trade-off between qualitative and quantitative responses to more extreme climate conditions.

4.1.6 Treatment effects on *in vitro* methane production

Methane production was predicted for 2023–2024 samples using near-infrared spectroscopy and validated with 48-hour incubations of a subset of samples. Methane production was strongly inhibited by biserrula (-85% relative to lucerne in spring; Fig. 14), as has been observed previously (Banik, et al., 2013a, b; Li et al., 2025). Further investigation is needed as to whether this *in vitro* inhibition of methanogenesis would be reproduced *in vivo*, and if the anti-methanogenic attributes of this plant can be fully harnessed given the known issues with palatability and photosensitisation (Quinn et al., 2018; Swinny et al., 2015). Previous research has indicated that sheep may be less likely to develop an aversion to biserrula if fed this species as part of a mixed diet, rather than in monoculture (Thomas et al., 2015), and further research is required to understand how biserrula's inclusion in different proportions in forage would influence its anti-methanogenic potential.

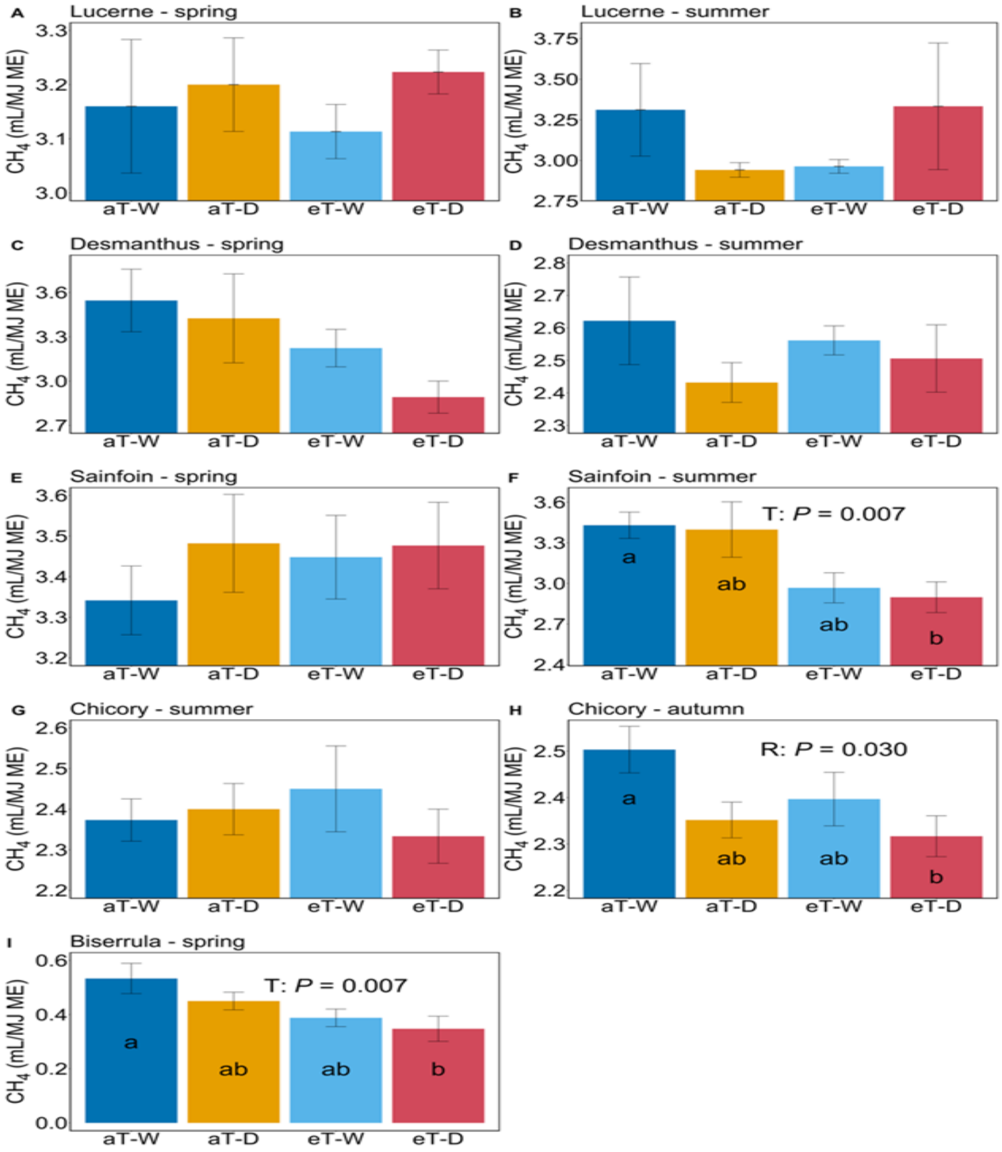
Figure 14. NIRS-predicted *in vitro* methane (CH_4) production in response to factorial rainfall and temperature treatments. Letters represent significant treatment differences indicated by post-hoc pairwise comparisons.



Seasonal variation was evident, with desmanthus harvested in summer producing less CH_4 than in spring-grown material; this coincided with lower total gas production, suggesting a general decline in fermentative capacity, likely linked to shifts in plant morphology (e.g., higher proportion of stem).

Reduced rainfall and elevated temperature each decreased CH_4 production in at least one season for biserrula, desmanthus and chicory (Fig. 14), in alignment with previous research into forages grown under climate stress (Hart et al., 2022; Riede et al., 2019). These changes are likely related to reductions in digestibility, resulting in lower fermentation, along with shifts in nutritional quality and secondary chemistry.

Figure 15. NIRS-predicted *in vitro* methane (CH_4) production, per unit metabolisable energy content, in response to factorial rainfall and temperature treatments. Letters on bar plots represent significant treatment differences indicated by post-hoc pairwise comparisons.



When expressed per unit of metabolisable energy (as a proxy for emissions intensity relative to animal production), biserrula and chicory both showed lower emissions intensity, relative to lucerne (Fig. 15). For biserrula, this reflected strong inhibition of methane production, whereas for chicory it was due to high ME content. Correlations between nutritional quality metrics and CH_4 production varied among species. For example, CH_4 production increased with digestibility (DOMD) for desmanthus, sainfoin and chicory, but no such relationship was observed for lucerne or biserrula. It is worth noting that relationships between CH_4 emissions and forage nutritional metrics may be underemphasised by *in vitro* measurements, where a homogenous (small) particle size of plant material is used.

4.1.6 Summary: *Biserrula had by far the lowest CH_4 production in in-vitro incubations, with values 85% lower than lucerne in spring. Low rainfall and elevated temperatures were associated with reduced CH_4 production for three of the five species. Methane emissions intensity (CH_4 produced per unit metabolizable energy) was low for both biserrula and chicory, relative to lucerne, suggesting that these species may be valuable for increasing feed-conversion efficiency and reducing farm-scale greenhouse gas emissions.*

4.2 Experiment 2: Temperate and tropical mixtures under contrasting rainfall regimes

4.2.1 Aboveground net primary production (ANPP)

This field experiment revealed distinct productivity and persistence responses of temperate and tropical pasture mixtures to reduced rainfall. Overall, ANPP across the two years was markedly higher in the tropical mixture (21.3 t ha^{-1} total, of which grasses were 10.35 t ha^{-1} and legumes 10.79 t ha^{-1}) than in the temperate one (total: 8.69 t ha^{-1}; grasses: 1.60 t ha^{-1}, legumes: 5.93 t ha^{-1}, herbs: 0.60 t ha^{-1}) (Fig. 16 a, b). This highlights the inherently greater productivity of warm-adapted species under current (and likely future) climatic conditions in warm temperate or sub-tropical regions within the southeast. However, both mixtures experienced substantial productivity declines under reduced rainfall, confirming soil moisture limitation as a dominant control on performance of both pasture types.

The temperate mixture was more sensitive to low rainfall than the tropical mix, with a 54% reduction in total ANPP. Productivity losses were most pronounced in legumes (-63%, Fig. 16), suggesting that water stress may have constrained nitrogen fixation (Gil-Quintana et al., 2013; Streeter, 2003) as well as shoot regrowth following harvests. Grasses were also strongly affected by reduced rainfall (-50%; Fig. 16), likely reflecting their shallow rooting strategy which has been shown elsewhere to be associated with drought sensitivity (Kou et al., 2019; Sun et al., 2024). Although the herb plantain contributed modestly to total biomass (7.8% of ANPP under high rainfall), its lower sensitivity to rainfall marginally improved its proportional contribution to plot-level biomass under dry conditions (to 9.9% of ANPP). This relative drought resistance, compared to other plant functional groups, suggests a potential stabilising role for tap-rooted herbs in mixed temperate pastures.

The tropical mixture maintained substantially higher productivity than the temperate mix, under both rainfall regimes, with a smaller overall decline (-44%) under reduced rainfall. This somewhat higher tolerance of low rainfall reflects the relatively small productivity decline (-15.6%) of the dominant C_4 grasses (principally Rhodes) that contributed 49% of sward biomass averaged across two years. Legume sensitivity to reduced rainfall (-72.3%) was similar to that in temperate plots. The smaller reduction in tropical grass biomass under low rainfall compared with temperate grasses likely reflects the higher water-use efficiency and tolerance of high summer temperatures of C_4 grasses (Osborne et al., 2008; Taylor et al., 2010, 2014).

Differences in the productivity of temperate grasses between treatment years (38% less biomass in 2024 than in 2023; Fig. 16c and e) suggest an increasing response to prolonged low water availability over time, alongside a reduction in their ability to compete for limited resources within the mixed sward. The latter is evidenced by an increasing legume biomass over time (15% more productive in the second year), likely reflecting differences in rooting strategies between plant functional groups (Chandregowda et al., 2022; Freschet & Roumet, 2017).

Interannual shifts in functional group productivity were also evident in the tropical mixture, with strong lucerne persistence (64% increase in 2024 relative to 2023 in low rainfall plots) partially offsetting grass productivity losses (61% reduction under low rainfall in 2024) (Fig. 16d and f). These patterns indicate that prolonged drought exposure may selectively favour deeper-rooted, stress-tolerant species, leading to compositional shifts that shape long-term pasture resilience and nutritional value. Further research is needed to evaluate relationships between drought sensitivity and the leaf and root traits of pasture grasses, legumes, and herbs, to identify species and cultivars with drought resistance traits.

Figure 16. Overall (2-year) productivity by season of (a) temperate and (b) tropical mixtures during 2023–2024 under wet and dry rainfall regimes, and annual means by plant functional group for 2023 (c, e) and 2024 (d, f) for temperate and tropical mixes, respectively. Inset boxplots indicate cumulative annual biomass.

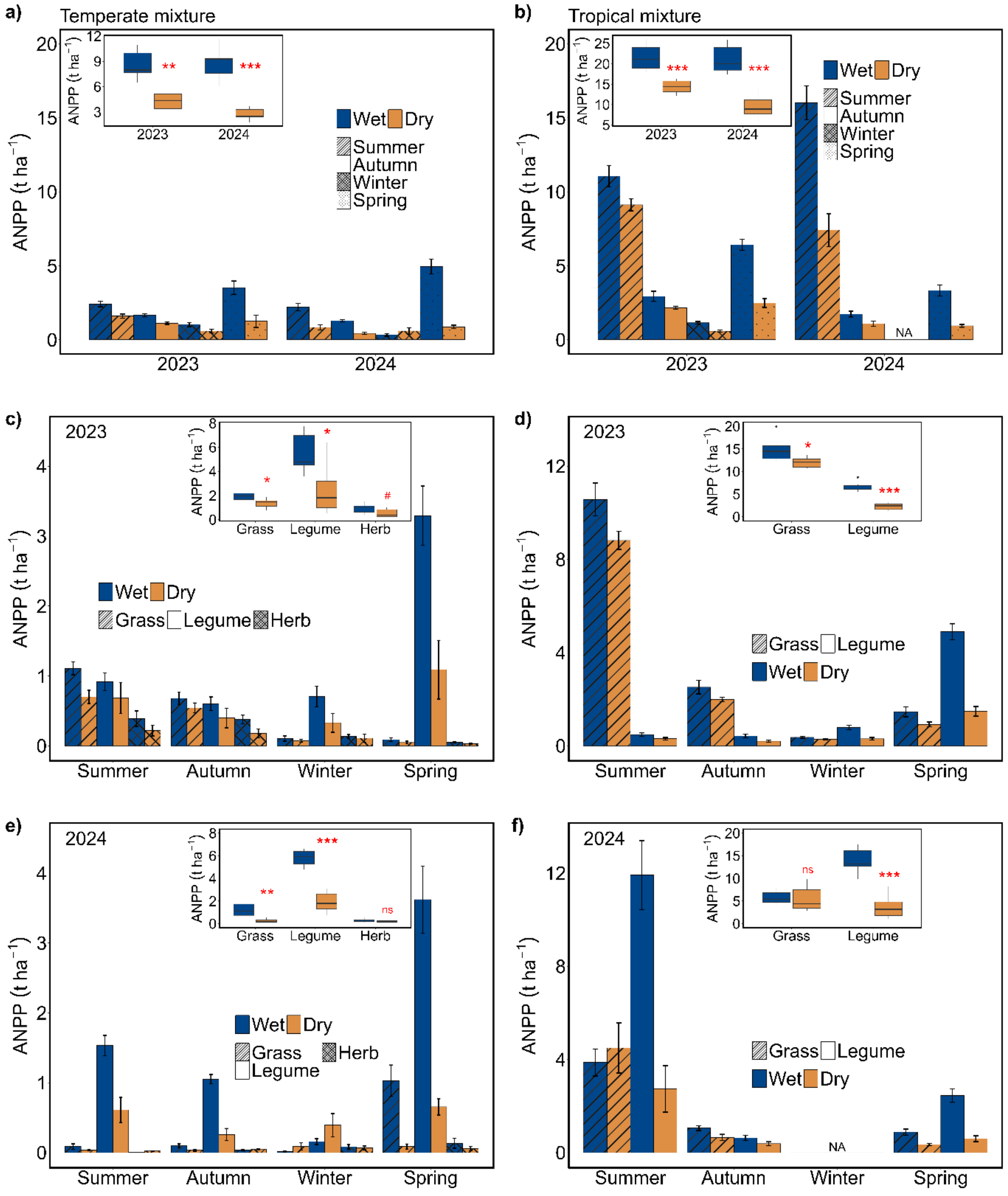
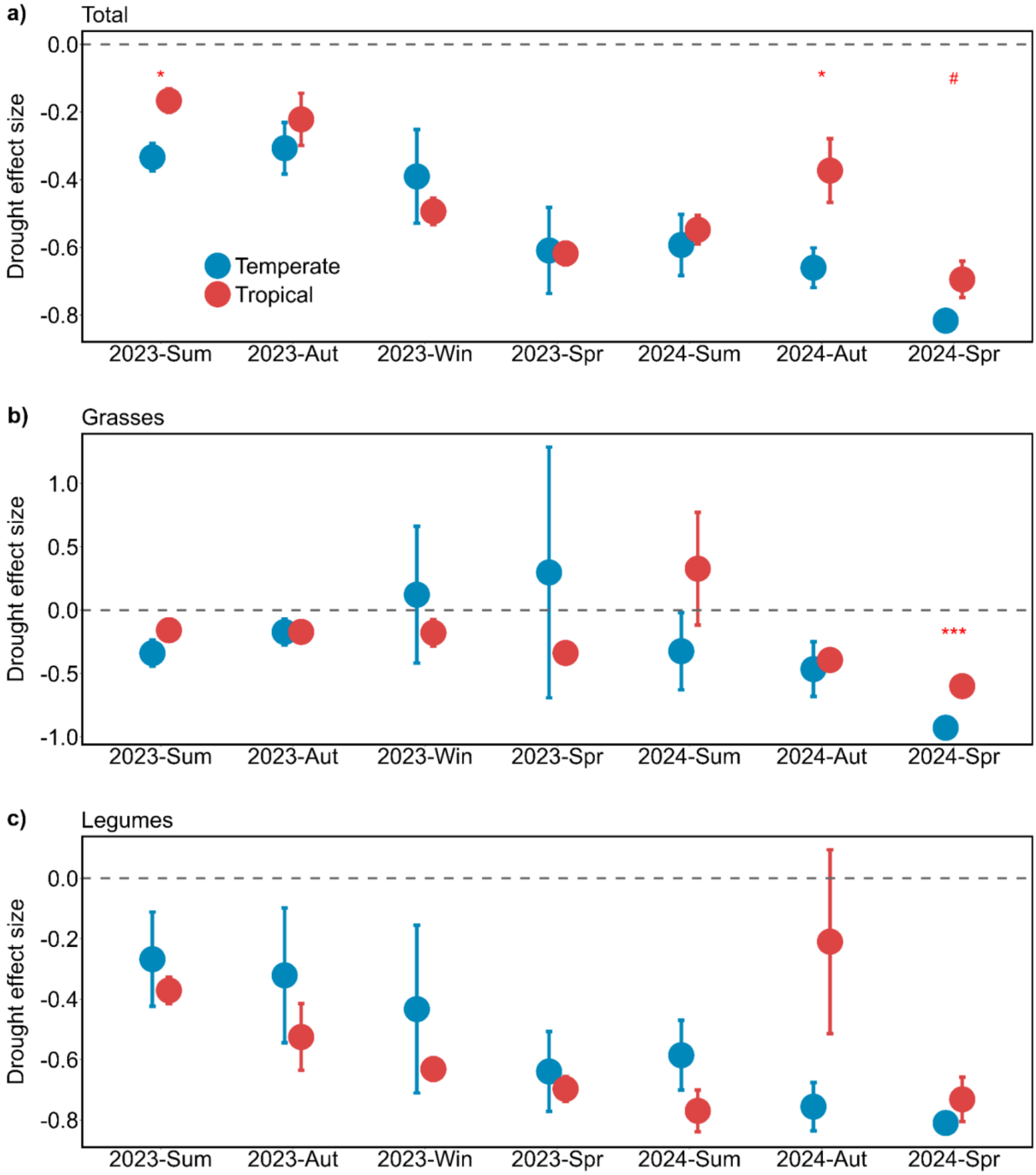


Figure 17. Drought effect size for productivity of temperate and tropical mixtures across seasons (2023–2024): (a) total, (b) grasses and (c) legumes. Asterisks denote significant differences in effect size between mixtures (*** p < 0.001; ** p < 0.01; * p < 0.05; # p < 0.10).



Seasonal analyses showed that the biggest productivity declines under low rainfall were in spring, for both mixture types (Fig. 16 and 17, Table 6); this is when rapid growth and high-water demand coincided with rising ambient temperatures and vapour pressure deficits. Springtime productivity losses of up to 75% in temperate and 65% in tropical mixtures highlight the vulnerability of early-season growth to water deficits. In temperate swards, spring productivity declines were similar between grasses (-88%) and legumes (-75%), whereas in tropical mixtures, legumes were more affected (-72%) than grasses (-46%). The smaller decline in tropical mixtures during this period underscores the adaptive advantage of warm-season species that maintain photosynthetic activity under high vapour pressure deficit and low soil moisture (Taylor et al., 2014).

Table 6. Seasonal aboveground biomass (2023–2024) under contrasting rainfall treatments in temperate and tropical mixtures.

Pasture	Season	Rainfall treatment	Aboveground biomass (tha^{-1})	±SE	Effect size	p-value
Temperate mixture	Summer	Wet	2.31	0.464	**-0.47**	**0.001**
		Dry	1.219	0.381		
	Autumn	Wet	1.468	0.194	**-0.47**	**<0.001**
		Dry	0.772	0.192		
	Winter	Wet	0.681	0.274	-0.14	0.619
		Dry	0.589	0.307		
	Spring	Wet	4.235	1.067	**-0.75**	**<0.001**
		Dry	1.062	0.630		
	Annual	Wet	12.93	0.714	**-0.54**	**<0.001**
		Dry	5.952	0.464		
Tropical mixture	Summer	Wet	13.537	0.701	**-0.39**	**<0.001**
		Dry	8.265	0.559		
	Autumn	Wet	2.336	0.189	**-0.3**	**0.01**
		Dry	1.627	0.128		
	Winter	Wet	1.069	0.144	**-0.5**	**0.009**
		Dry	0.533	0.085		
	Spring	Wet	4.875	0.293	**-0.65**	**<0.001**
		Dry	1.713	0.174		
	Annual	Wet	21.320	0.957	**-0.44**	**<0.001**
		Dry	11.897	0.998		

4.2.2 Quantifying nutritional yields under altered rainfall

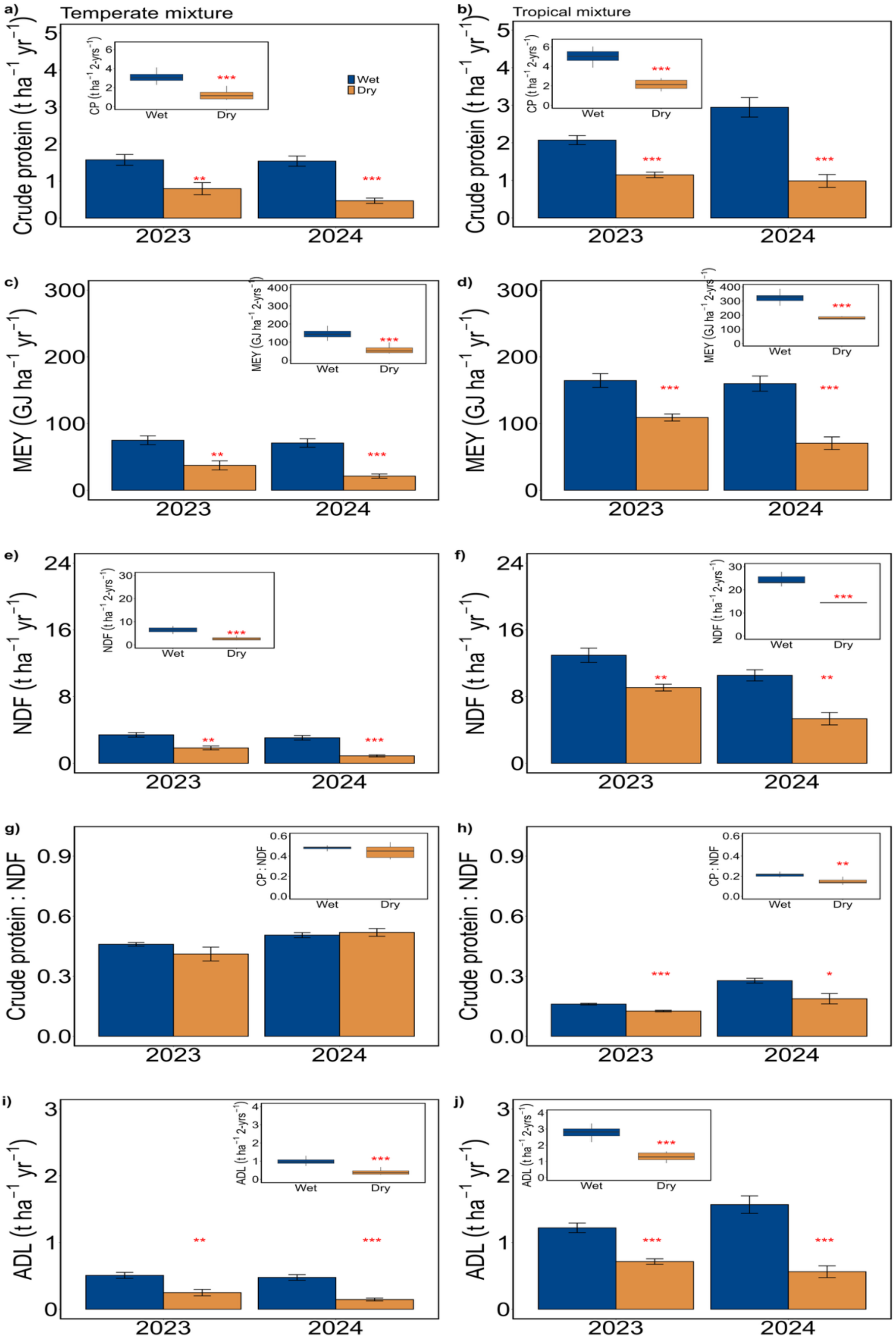
Nutritional yield was calculated by multiplying species-specific total biomass by the corresponding crude protein (CP), metabolizable energy (ME) or fibre (NDF) concentrations. For temperate species, nutritional metrics were measured in the current study, whereas for tropical species we used values from the previous PACE experiment (Table S4). It is important to recognise that forage with extreme values of key nutritional parameters will not support production regardless of nutritional yield. For example, NDF concentrations exceeding 35% can be expected to result in voluntary feed intake declines and very low concentrations (below 28%) may pose risks of ruminal acidosis, especially if diets are high in non-structural carbohydrates (Dairy Australia, 2020).

In temperate pastures, values of ME greater than 9.9 MJ kg^{-1} DM are required to support high production, 8.2 MJ kg^{-1} DM for moderate production, 7.4 MJ kg^{-1} DM to maintain dry stock and values less than 7.4 MJ kg^{-1} DM lead to weight loss of stock (Harrington et al., 1984). It is worth noting that these values reflect the overall nutritional parameters of livestock diets, and poorer quality forage can contribute to a nutritious diet if it is consumed alongside higher quality forage or concentrates.

The higher nutritional yield of the tropical mixture compared with the temperate mixture reflects the far greater productivity of the former. Substantially greater crude protein (CP) and metabolizable energy (ME) yields (+72% and +147%, respectively) indicate that tropical mixtures can provide more energy- and protein-rich forage, even under reduced rainfall (Fig. 10). However, the accompanying increases in lignin and fibre yield (ADL +183%; NDF +328%) and a low CP:NDF ratio indicate reduced palatability and digestibility, likely limiting intake and feed conversion efficiency (Fig. 18).

Low rainfall markedly reduced CP (-59.5% in temperate, -57.5% in tropical) and ME (-59.8% and -44.6%, respectively) yields in both mixtures, reflecting strong biomass responses to water limitation. The reduction in CP:NDF ratio under drier conditions, particularly in the tropical mixture (-31%), further indicates a shift toward more fibrous, less digestible forage. This pattern aligns with established physiological responses, where water stress increases structural carbohydrate investment while reducing nitrogen allocation to leaves (Catunda et al., 2022; Varol et al., 2025).

Figure 18. Nutritional yields of temperate mixtures in terms of (a) crude protein, (c) ME, (e) NDF, (g) CP:NDF ratio, (i) ADL, and for tropical mixtures (b) crude protein, (d) ME, (f) NDF, (h) CP:NDF ratio and (j) ADL. Inset boxplots show cumulative nutritional yield. Asterisks denote statistical significance (*** p < 0.001, ** p < 0.01, * p < 0.05, # p < 0.10).



Interannual and seasonal variations in forage quality were closely tied to shifts in plant functional group composition. The tropical mixture's low CP:NDF ratio during summer and autumn coincided with C_4 grass dominance, while the subsequent decline in grass abundance from 2023 (64%) to 2024 (46%) - and greater proportional legume biomass contribution - was associated with improved forage quality and higher CP:NDF ratios. Similarly, the decline of grasses in the temperate mixture across the study (from 28% to 9%) suggests that sustained legume dominance results in higher-quality forage through increased crude protein and lower fibre concentrations.

4.2 Summary: *Overall, these findings demonstrate the greater rainfall sensitivity of temperate compared to tropical pasture mixtures and highlight trade-offs between productivity and nutritional quality. While tropical mixtures provide greater biomass (and hence a greater nutritional yield) under dry conditions, a relatively high legume proportion (compared to temperate swards) is required to counteract the lower nutritional value of* C_4 *grasses in such mixtures, and thereby meet livestock nutritional requirements.*

Strategic management that favours legume persistence - such as selecting drought-tolerance traits (e.g. low SLA, greater root trait plasticity) and maintaining favourable soil pH, nutrient levels, and grazing regimes - can enhance long-term survival and nitrogen fixation, thereby improving both yield and feed quality under future warmer, drier climates.

4.3 Experiment 3: How does grazing intensity modify pasture response to low rainfall?

Plant aboveground productivity responses to reduced rainfall vary depending on species traits, trait plasticity, drought severity, and the species' climate of origin. Grazing management also plays a central role in sustaining forage supply by promoting compensatory growth and maintaining younger, non-senescent plant material. However, the effects of grazing depend strongly on the intensity, frequency, and timing of biomass removal. Intense grazing can deplete belowground carbohydrate reserves by limiting their replenishment via photosynthesis, thereby reducing forage persistence (Augustine & McNaughton, 2006; Zhou et al., 2017). While grazing tends to deplete belowground carbon reserves, drought can often increase proportional biomass allocation belowground (Cao et al., 2024; Chandregowda et al., 2022; Yu et al., 2024), thereby having opposing effects on re-growth capacity and persistence. Understanding the magnitude of impacts and how these two pressures interact to affect plant productivity and resilience is critical for developing sustainable grazing strategies under a drier future climate.

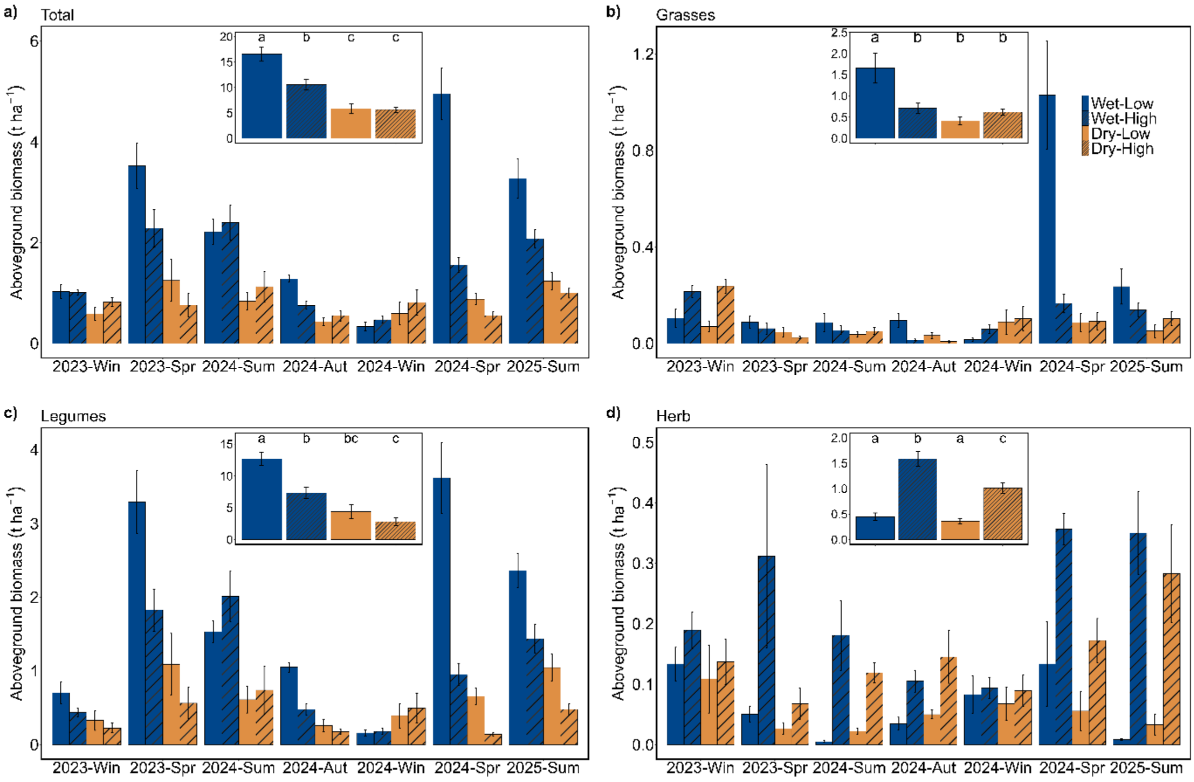
We tested the hypothesis that intense (i.e. frequent) grazing overrides drought-induced increases in the proportion of belowground carbon investment relative to total plant reserves, thereby reducing forage persistence. Specifically, we quantified aboveground production across multiple seasons and linked these dynamics to belowground carbon storage under factorial combinations of rainfall (well-watered *vs*. reduced) and harvest frequency (low *vs*. high) in a mixed temperate pasture system.

4.3.1 Aboveground biomass production

Reduced rainfall and high harvest frequency strongly affected above- and belowground production, highlighting key trade-offs between short-term forage supply and long-term persistence. Consistent with expectations, both reduced rainfall and frequent harvesting suppressed aboveground biomass, though the magnitude of response varied among plant functional groups. Reduced rainfall imposed a major constraint on productivity (-58% in Dry plots under both low (5.81 t ha^{-1}) and high (5.62 t ha^{-1}) frequency harvests), yielding far less than well-watered conditions (13.5 t ha^{-1}; mean of Wet-LF 16.6 and Wet-HF 10.6 t ha^{-1}) over the 21 months of the study. Frequent harvesting reduced productivity by 28% (8.08 vs. 11.2 t ha^{-1}), though its effects were contingent on water availability; large growth reductions were found under well-watered conditions (-36%; 10.5 vs. 16.6 t ha^{-1}) but effects on total productivity were negligible under reduced rainfall (Fig. 19a). This interaction indicates that the overall (multi-season) effects of more frequent grazing are dependent on sward productivity - and thus rainfall - rather than the other way around. It is noteworthy, however, that there was strong seasonal variation in the nature of rainfall x grazing interactions (detailed below).

Plant functional groups differed in their responses to treatments, reflecting contrasting sensitivities and adaptive strategies. Legumes were the most productive under well-watered conditions (contributing 73.8% of total biomass; 10.02 of 13.57 t ha^{-1}) but also the most sensitive to both reduced rainfall (-64%) and frequent harvesting (-41%) (Fig. 19c), possibly due to their high carbon requirements to support nitrogen fixing symbionts (Fisher et al., 2010; Lepetit & Brouquisse, 2023) Grasses also showed fairly high sensitivity, with biomass reduced by 56% under low rainfall and by 36% in response to frequent harvesting (Fig. 19b). Interestingly, under dry conditions, more frequent harvests increased grass biomass by ~49%, suggesting that they may have benefitted from reduced competition with legumes - which were strongly reduced - under this treatment combination. These results align with previous findings that moderate grazing can enhance regrowth in drought-tolerant grass species through improved light interception and nutrient turnover (Gao & Carmel, 2020; Yan et al., 2024) (Fig. 19b).

Figure 19. Seasonal variation in aboveground net primary production of temperate mixtures partitioned by functional group: a) total, b) grasses, c) legumes, d) herbs, under wet and dry rainfall regimes combined with low and high harvest frequencies. Inset panels show cumulative aboveground production over 21 months (winter 2023–summer 2025).



The perennial herb, plantain, exhibited strong compensatory growth responses (Oesterheld & McNaughton, 1991) to treatments, with biomass increasing threefold (+221%) under frequent harvesting, across rainfall regimes (+255% under wet and +179% under dry conditions). This positive response to more frequent harvesting likely reflects its basal rosette morphology, which protects meristems from defoliation and enables rapid regrowth (Merino et al., 2024). Its lower rainfall sensitivity (-32%) compared with grasses and legumes suggests that plantain could act as a stabilising component in mixed swards, buffering total productivity under combined climate and grazing pressures (Fig. 19d).

The amount of dead material produced was lower under reduced rainfall (-32%), whereas the effects of frequent harvesting were rainfall dependent - reducing dead material under wet conditions (-48%) but increasing it in dry plots (+81%). The increase in dead material under dry–high frequency harvests suggests that severe defoliation can accelerate senescence and mortality when soil moisture is limiting, further constraining canopy recovery and nutrient recycling (Ferraro & Oesterheld, 2002) (Table 7).

Table 7. Summary statistics for aboveground productivity responses to rainfall and harvesting frequency across seasons, by plant functional group. P-values were obtained from a linear mixed model using ANOVA (‘F’), with rainfall and grazing treatments and their interactions as fixed effects and shelter as a random effect.

	Aboveground production									
Treatments	Total		Grasses		Legumes		Herb		Dead	
	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
Rainfall	162.5	<0.001	26.34	<0.001	138.9	<0.001	7.378	0.007	10.81	0.001
Harvest freq.	25.63	<0.001	8.215	0.004	40.72	<0.001	54.62	<0.001	1.507	0.222
Season	29.21	<0.001	19.13	<0.001	28.69	<0.001	3.349	0.004	9.812	<0.001
Rainfall: Harvest freq.	22.67	<0.001	19.59	<0.001	12.36	<0.001	4.106	0.044	27.13	<0.001
Rainfall: Season	17.99	<0.001	14.81	<0.001	14.29	<0.001	1.825	0.098	5.775	<0.001
Harvest freq.: Season:	10.64	<0.001	13.08	<0.001	10.16	<0.001	4.172	<0.001	7.907	<0.001
Rainfall: Harvest freq: Season	5.005	<0.001	10.34	<0.001	3.876	0.001	0.831	0.547	5.006	<0.001

Note: “Season” represent seven independent seasons, from winter 2023 to summer 2025.

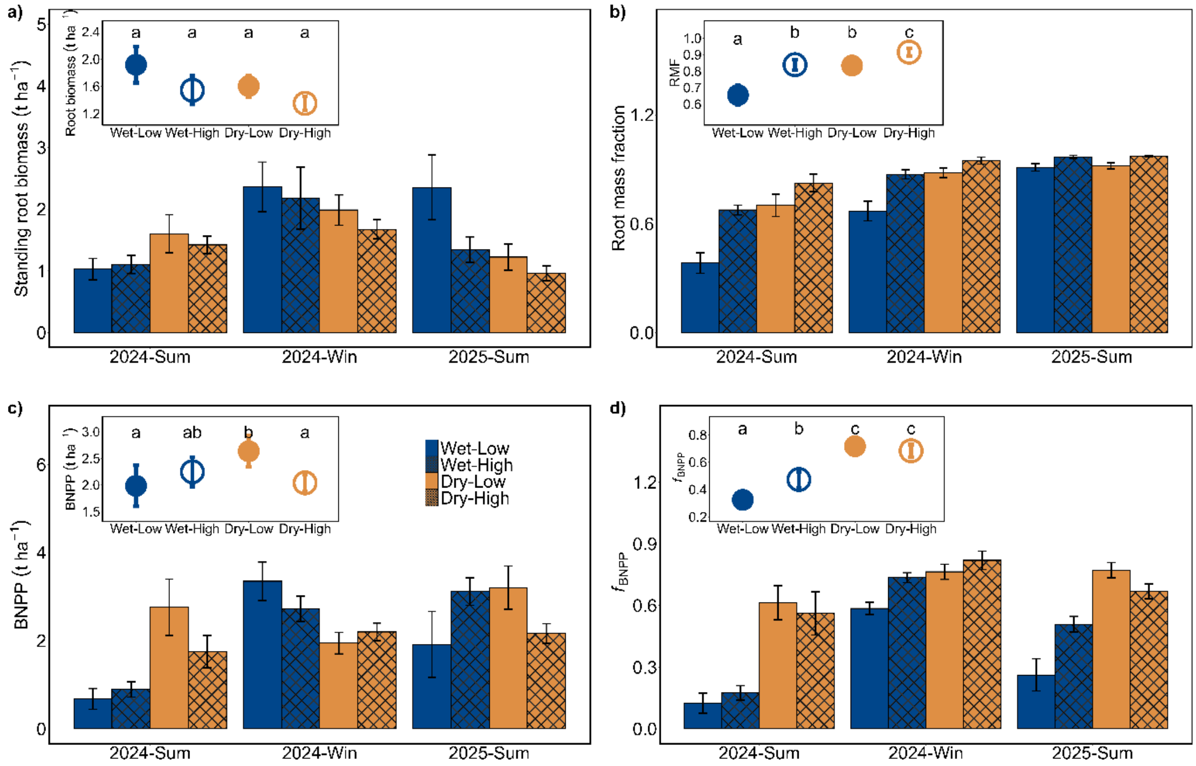
Seasonal analyses showed that spring and summer together accounted for most of the sward-level productivity (82%; 11.13 t ha^{-1}; mean of Wet-LF 13.95 and Wet-HF 8.31 t ha^{-1}), with reduced rainfall and frequent harvesting reducing yields by 66% and 35%, respectively, during this period. There was also a significant rainfall x harvest frequency interaction, whereby high (relative to low) frequency harvesting reduced spring+summer ANPP by 40% under high rainfall, and by 18% under low rainfall. Legumes produced 85% of their total (21-month) biomass during spring and summer months (8.52 of 10.02 t ha^{-1}), with frequent harvesting reducing legume productivity (relative to less frequent harvests) by 42% under wet and 43% under dry conditions over this period; the biggest reductions were seen during spring (-60% in both wet and dry plots). Grasses produced 79% of their total biomass during spring and summer months, with high frequency harvests reducing productivity (relative to less frequent harvesting) by 71% under wet conditions but increasing it by 21% under dry conditions during spring and summer months. More frequent harvesting was also associated with productivity gains for plantain, which increased spring+summer biomass by 509% under wet and by 367% under dry conditions. The seasonal differences in sensitivity to rainfall and grazing intensity across plant functional types reinforces the importance of functional diversity in maintaining sward resilience during critical growth periods. Evidence from other grassland systems likewise indicates that greater functional diversity enhances ecological stability under grazing and extreme climatic conditions (Hallett et al., 2017; Zhang et al., 2024).

4.3.2 Belowground carbon allocation

Persistence of perennial pasture species relies on belowground carbon storage, which supports aboveground regrowth following senescence, defoliation, or other disturbance events. Although species differ in their storage capacity, the latter is strongly influenced by climate conditions and management practices (Tumber-Dávila et al., 2022). Plants commonly increase root allocation under drought to enhance water uptake and reduce transpirational loss, while grazing can either stimulate or constrain root carbon allocation depending on intensity, timing and species (Wang et al., 2022). Understanding these dynamics and their interactions is critical for managing pastures under projected climate change. To investigate this, we quantified carbon allocation to roots and crowns and measured storage as non-structural carbohydrates (NSCs).

Belowground responses highlighted the pivotal role of carbon storage in plant resilience. Across treatments, standing root biomass (i.e. all roots produced since sowing) declined modestly with high frequency harvesting (Fig. 20a and Table 8), but root mass fraction increased by up to 28% (Wet-HF) (Fig. 20b and Table 8), indicating plastic adjustments in carbon allocation. While low (relative to high) rainfall tended to increase belowground allocation - an adaptive strategy to enhance water uptake and survival - frequent harvesting under dry conditions diminished this benefit, likely due to reduced assimilate availability for storage. This finding supports the hypothesis that intense defoliation overrides drought-induced root investment, constraining recovery capacity.

Figure 20. Belowground biomass allocation in a temperate pasture under dry and wet rainfall regimes with low and high harvesting frequencies across multiple seasons: (a) standing root biomass, (b) root mass fraction, (c) belowground net primary production and (d) fraction of total primary production allocated belowground.



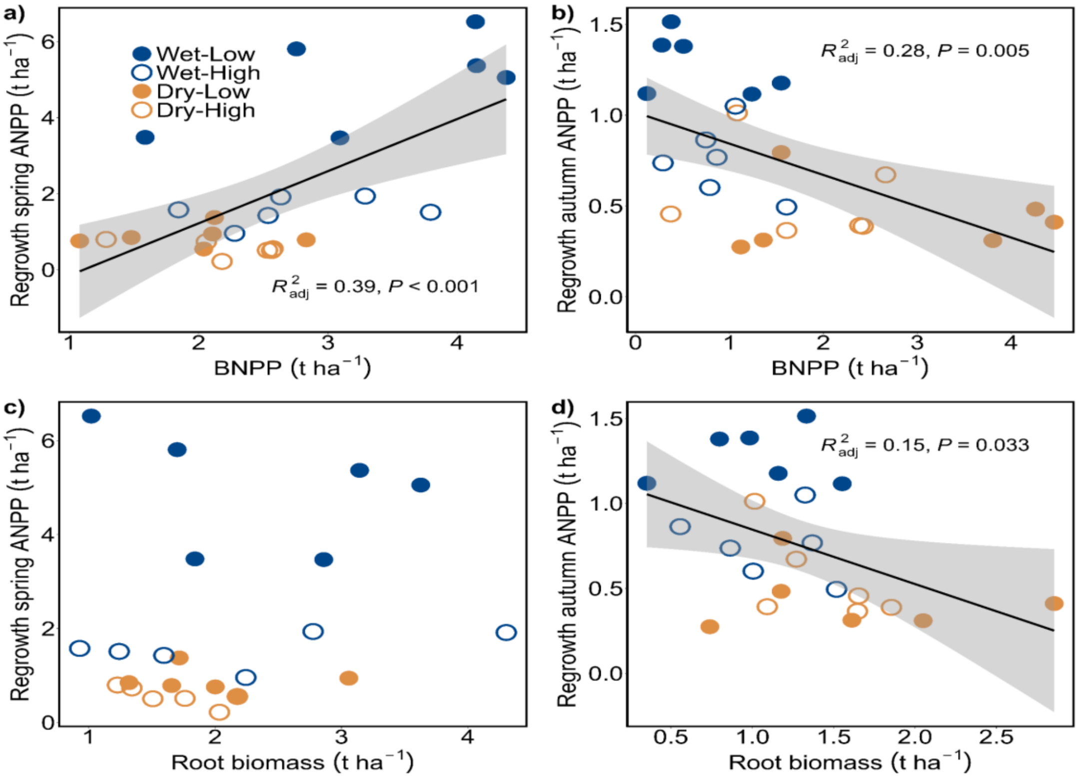
Patterns in belowground net primary production (BNPP, i.e. root material produced entirely within a specific 6-month period under treatments) further emphasized this interaction. Reduced rainfall increased the proportion of total production allocated belowground (f_{BNPP}) by 76%, whereas frequent harvesting enhanced allocation only under well-watered conditions (+46%) (Fig. 20d and Table 8). Under dry conditions, high frequency harvesting reduced BNPP (-23%), again suggesting that frequent defoliation limits carbon replenishment belowground with negative implications for long-term persistence (Fig. 20c and Table 8). Seasonal correlations between BNPP and subsequent aboveground growth showed that high BNPP in cooler seasons supports spring regrowth (R^2 = 0.39) (Fig. 21a), consistent with the role of stored carbon reserves in fuelling recovery after dormancy (Aubrey &

Teskey, 2018; Volkova et al., 2025). In contrast, autumn regrowth was negatively associated with BNPP (Fig. 21b) and root biomass (Fig. 21d) from the preceding spring–summer period ($R^2 = 0.28$), indicating preferential allocation to belowground storage, as opposed to aboveground growth, outside of the main growing season.

Table 8. Belowground biomass allocation responses to rainfall and harvest frequency treatments, across seasons. P-values were obtained from a linear mixed model using ANOVA (‘F’), with rainfall and harvest treatments and their interactions as fixed effects and shelter as a random effect.

	Belowground allocation									
	Standing root biomass		BNPP		Crown biomass		Root Mass Fraction		f_{BNPP}	
Treatments	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
Rainfall	2.329	0.132	0.911	0.343	0.809	0.374	**42.75**	**<0.001**	**98.35**	**<0.001**
Harvesting	*3.576*	*0.064*	0.501	0.481	0.575	0.452	**46.41**	**<0.001**	**3.613**	**0.062**
Season	**7.747**	**0.001**	**9.113**	**<0.001**	**4.742**	**0.036**	**79.69**	**<0.001**	**46.06**	**<0.001**
Rainfall: Harvesting	0.129	0.719	*3.398*	*0.07*	2.689	0.109	**6.988**	**0.011**	**8.929**	**0.004**
Rainfall: Season	**4.755**	**0.012**	**9.114**	**<0.001**	0.185	0.669	**11.53**	**<0.001**	**8.765**	**<0.001**
Harvesting: Season	1.075	0.348	0.345	0.709	0.039	0.844	**5.133**	**0.009**	1.013	0.369
Rainfall: Harvesting: Season	0.908	0.409	**3.868**	**0.026**	1.900	0.176	1.631	0.205	1.907	0.158

Figure 21. Pasture regrowth as a function of belowground carbon storage: (a) spring ANPP vs. BNPP, (b) autumn ANPP vs. BNPP, (c) spring ANPP vs. root biomass and (d) autumn ANPP vs. root biomass.



Crown biomass, accounting for more than half (~57%) of total belowground biomass, remained largely stable across treatments, underscoring its function as a persistent storage organ (Chandregowda et al., 2023) (Fig. S4). Root non-structural carbohydrate (NSC) concentrations provided further insight into the mechanisms associated with plant resilience: reduced rainfall increased soluble sugar content while lowering starch, indicating active starch hydrolysis to sustain metabolism under stress (Fig. 22

and Table 9) (Chandregowda et al., 2022). In contrast, crown NSCs were 80% higher than root concentrations and remained stable, reflecting their critical role as a long-term carbon reservoir. The positive correlation between autumn regrowth and both crown soluble sugars (Fig. 23b) and starch (Fig. 23d) further supports their role in maintaining persistence under repeated defoliation and water limitation (Wiley et al., 2017).

Figure 22. Belowground carbon storage in a temperate pasture mixture under wet and dry rainfall scenarios with low and high harvesting frequencies, showing (a) root soluble sugars, (b) crown soluble sugars, (c) root starch and (d) crown starch.

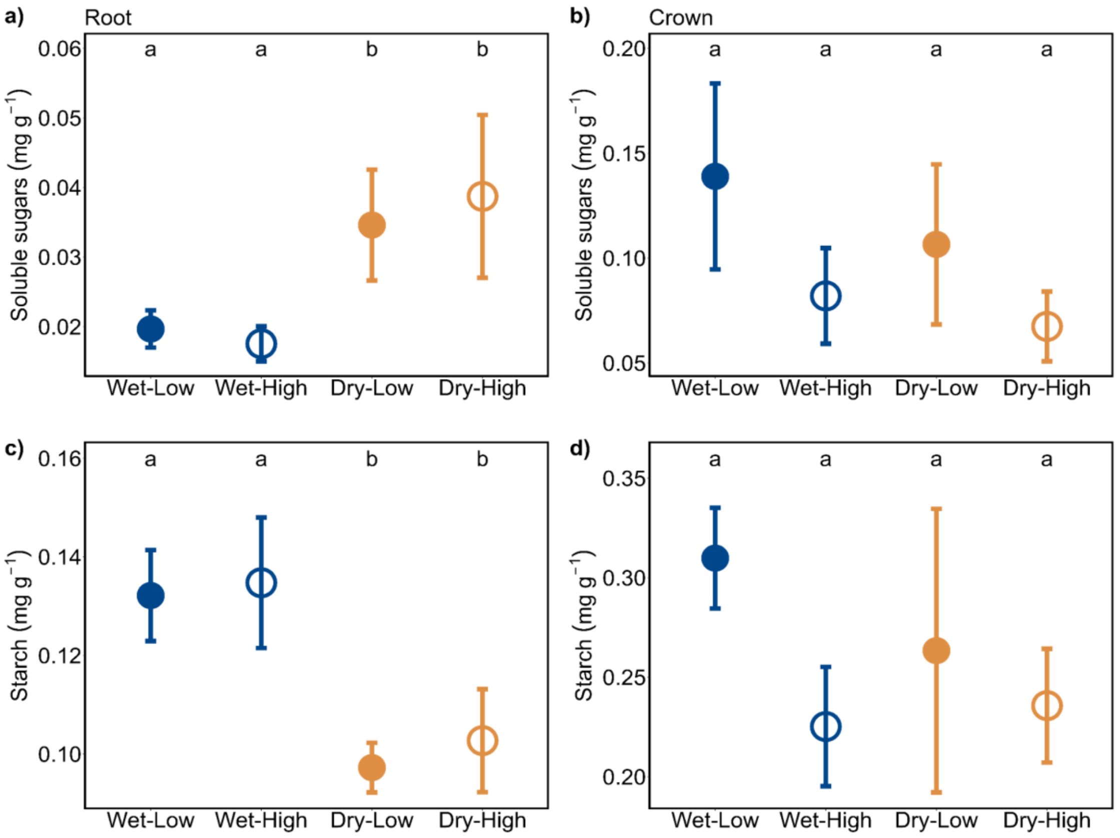
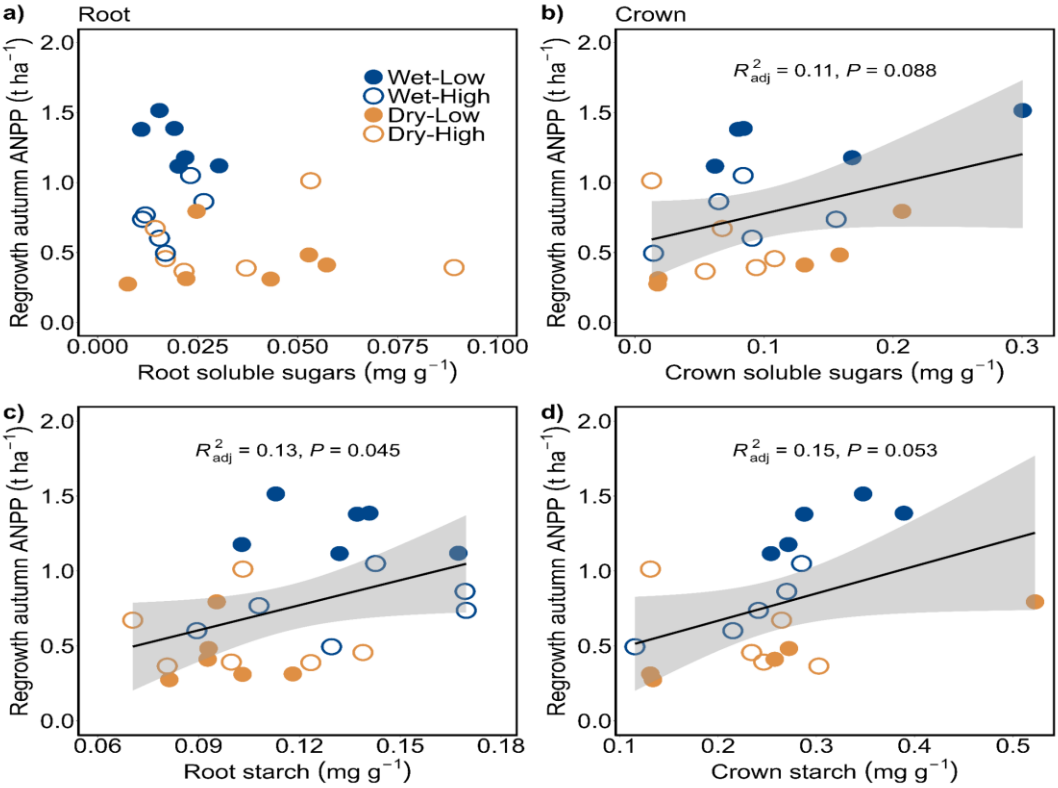


Table 9. Belowground non-structural carbohydrate concentrations in response to rainfall and harvesting frequency treatments, and their interactions. P-values were obtained from a linear mixed model using ANOVA ('F'), with rainfall and harvest treatments and their interactions as fixed effects and shelter as a random effect.

Non-structural carbohydrates		**Root**		**Crown**	
		F-value	**p-value**	**F-value**	**p-value**
Total NSC	Rainfall	1.932	0.184	0.295	0.596
	Harvest freq.	0.206	0.656	2.848	0.118
	Rainfall: Harvest freq.	0.169	0.686	0.315	0.583
Soluble sugars	Rainfall	**7.005**	**0.018**	0.498	0.493
	Harvest freq.	0.021	0.885	2.216	0.162
	Rainfall: Harvest freq.	0.209	0.653	0.077	0.784
Starch	Rainfall	**12.87**	**0.002**	0.084	0.776
	Harvest freq.	0.187	0.671	2.596	0.134
	Rainfall: Harvest freq.	0.024	0.879	0.431	0.523

Figure 23. Autumn regrowth of aboveground biomass as a function of belowground carbon storage: (a) root soluble sugars, (b) crown soluble sugars, (c) root starch and (d) crown starch.



***4.3 Summary**: Collectively, these results demonstrate that grazing intensity and rainfall interact to determine both aboveground productivity and belowground carbon dynamics. While periodic (low frequency) biomass removal can stimulate regrowth under adequate moisture, more frequent harvesting or grazing under dry conditions diminishes carbon inputs belowground (reduced root production) and plant regrowth potential, ultimately threatening sward persistence. High levels of grazing under dry conditions may, therefore, also have implications for soil carbon stocks, via its negative effects on belowground productivity. Maintaining sufficient recovery periods between grazing events, particularly during dry periods, is therefore essential to replenish belowground reserves and sustain long-term productivity. Species such as plantain, with greater regrowth capacity and drought tolerance, may serve as robust components of resilient mixed pastures that are more capable of withstanding future climate variability and grazing pressure.*

5. Conclusion

The overarching finding of this project is that rising temperatures and more extreme rainfall scenarios will present substantial challenges for maintaining productive pastures with a high nutritional value to support future livestock production. Given clear differences among species in climate sensitivity of both biomass and nutrition, a combination of compatible grasses, legumes and herbs in mixed perennial swards is essential for minimising the negative impacts of elevated temperatures and low rainfall and reducing uncertainty in seasonal feed base availability.

In our factorial warming x rainfall experiment, spring and summer growth was more sensitive to the amount of rainfall while autumn growth was more responsive to warming. The generally high productivity of the temperate lucerne/phalaris mixture, even under warming and low rainfall, highlights the advantage of pairing a deep-rooted, nitrogen-fixing legume with a perennial grass that has a complementary rooting strategy. However, this holds only where species' thermal or hydrological tolerance thresholds are not exceeded, as appears to have been the case for the sainfoin/cocksfoot mixture. The latter's low productivity and poor persistence under warming and low rainfall means that these component species are unsuitable for areas experiencing hot and/or dry conditions during spring and summer. In contrast, the climate tolerance and high productivity of the tropical digit/desmanthus mixture, and of chicory, suggest that these species may be better able to sustain biomass production and associated livestock grazing in the warmer months. Furthermore, high legume and herb protein content, digestibility and lower methane emissions intensity have the potential to (at least partially) offset the somewhat lower digestibility of the C_4 grass, digit. While the high climate sensitivity, annual life history and cool season phenology of biserrula make it particularly vulnerable to low rainfall during winter and spring, its unique secondary chemistry means it may still have a valuable role to play in ruminant methane reduction in locations where cool season rainfall and mild temperatures are conducive to this species' growth.

In the second field experiment comparing temperate and tropical pasture mixtures, rainfall reduction strongly constrained productivity, but the magnitude and consistency of these effects were governed by species' functional traits. The tropical mixture, dominated by deep-rooted summer-active lucerne and C_4 Rhodes grass, consistently outperformed the temperate grass-legume-herb mixture in both yield and persistence, reflecting the superior drought tolerance and/or water-use efficiency of warm-adapted species. Nutritional analyses showed that, compared to the temperate mixture, the tropical mixture produced substantially higher crude protein and metabolizable energy yields (i.e. biomass x concentrations) but had a higher fibre content. Low rainfall markedly reduced nutritional yield in both mixtures, with negative yield responses outstripping any benefits in terms of higher protein or lower fibre concentrations. The increased legume dominance in the temperate mixture and sustained lucerne persistence in the tropical mixture suggest that prolonged drought may favour deep-rooted, stress-tolerant species and shape long-term community resilience. Balancing legume proportions and maintaining species with contrasting rooting strategies will be essential to sustain productivity, nutritional quality and persistence under future, more variable climates.

The third experiment demonstrated that increased grazing frequency and reduced rainfall independently and interactively affect pasture productivity, carbon allocation, and persistence. More frequent grazing reduced aboveground biomass production under well-watered conditions, but not under low rainfall where soil moisture constraints on biomass were already large. The exception was in spring, when large additional negative effects of more frequent grazing were seen under low, as well as high, rainfall. Belowground responses provided insight into the carbon allocation mechanisms underlying these responses. Carbon allocation to roots was increased under low rainfall conditions, indicating adaptive investment for water acquisition. However, more frequent harvesting counteracted this benefit by reducing belowground carbon inputs and limiting non-structural carbohydrate replenishment, thereby reducing species post-grazing regrowth. If high levels of grazing are sustained over prolonged periods under dry conditions, such patterns are likely to reduce both pasture persistence and soil carbon stocks. The relative stability of crown biomass and non-structural carbohydrate pools highlights their role as persistent carbon reserves sustaining plants through climatic stress and fuelling recovery from defoliation.

The observed variation in climate resistance and grazing resilience among plant functional groups highlights the importance of functional diversity for pasture sustainability. While legumes were the most productive and most sensitive to both drought and frequent harvesting, the perennial herb plantain displayed strong compensatory regrowth and maintained productivity under the combined grazing and climate stresses. Overall, sustaining pasture productivity and persistence under warmer, drier climates will require grazing strategies that balance defoliation intensity with sufficient recovery periods, particularly during the crucial spring growth period. Incorporating resilient species such as plantain may further enhance the adaptive capacity of mixed temperate pastures growing under low or highly variable rainfall.

5.1 Key Findings

Experiment 1: temperature and rainfall manipulation

1. Warming exacerbates rainfall-driven productivity declines

The strongest productivity declines were generally seen in response to the combination of +3°C warming and low rainfall, which also had the lowest soil moisture levels across the experiment. Responses were generally additive, although there was some evidence of warming offsetting the negative effects of low rainfall (e.g., reduced rainfall decreased sainfoin productivity by 63% in summer, but warming mitigated this negative impact).

2. Species pairs varied strongly in their climate-responses

Temperate species pairs were generally more sensitive to reduced rainfall than increased temperatures, emphasising the role of soil moisture as a primary constraint on pasture productivity. Reduced rainfall decreased overall (24 month) aboveground productivity to differing extents across mixtures, ranging from relatively small declines of 7% (desmanthus/digit) or 15% (biserrula/chicory) to more substantial losses of up to 35% (lucerne/phalaris, sainfoin/cocksfoot). Yield reductions were typically biggest in spring, when low rainfall was associated with declines ranging from 18% (desmanthus/digit, not statistically significant) to 47% (sainfoin/cocksfoot, $P<0.01$).

Warming alone had marginally significant effects on overall (24-month) productivity for two of the species pairs (Luc/Pha, Bis/Chi) but was responsible for a significant 41% loss of productivity for Sai/Coc. This was attributed to lower soil moisture, driven by temperature-related increases in evapotranspiration, as well as likely exceedance of critical growing season physiological thresholds. Warming did not affect overall productivity for Dig/Des but this pair’s significantly greater autumn productivity in warmed plots likely reflects the higher optimal temperatures of tropical pasture species; desmanthus also benefitted from warming during spring.

Low rainfall consistently restricted post-harvest canopy regrowth across all species pairs and seasons, emphasizing soil moisture as the primary control on recovery. Luc/Pha and Sai/Coc were highly sensitive to low rainfall, with warming further suppressing summer regrowth under well-watered conditions. While Bis/Chi and Des/Dig sustained strong summer regrowth, they were also constrained by reduced rainfall, indicating that moisture stress can override thermal adaptation.

3. Species-level sensitivity to reduced rainfall and warmer temperatures

While it is important to recognise that individual species’ performance is a consequence of both environmental conditions (i.e. climate treatments) and competition with neighbouring species (i.e. the identity and traits of species paired together), we can tentatively summarise species’ relative climate sensitivities as follows:

Relative climate sensitivity*	Low rainfall	Increased temperature	Low rainfall AND increased temperature
Low	Chicory, Digit	Lucerne, Chicory, Digit, Desmanthus	Digit, Chicory, Desmanthus
Medium	Lucerne, Phalaris, Cocksfoot, Desmanthus	Phalaris, Sainfoin, Cocksfoot	Lucerne, Phalaris
High	Sainfoin, Biserrula	Biserrula	Biserrula, Sainfoin, Cocksfoot

**Categorisation is based on the relative sensitivity of aboveground production reduced rainfall, warming and their combination, across the two study years. Low sensitivity indicates a productivity reduction of less than 25% (or an increase), medium sensitivity corresponds to a 25-50% reduction, and high sensitivity reflects a decline of more than 50% in response to climate treatments.*

4. Increases in forage nutritional quality are offset by yield declines

Lucerne, chicory and sainfoin showed a general trade-off between nutritional quality and yield responses, where higher quality, particularly with respect to crude protein, was accompanied by reduced biomass production. For lucerne and chicory, this trade-off may be advantageous given their relatively high yields, whereas sainfoin's low productivity limits potential benefits. Desmanthus displayed a similar trade-off except under elevated temperature and well-watered conditions, where yield increased but quality declined. In contrast, biserrula was negatively affected in terms of both yield and quality, indicating high sensitivity to both rainfall and temperature. This may constrain the conditions under which biserrula can contribute to reducing methane emissions.

5. Methane suppression capacity of key legumes and chicory

Biserrula showed the greatest inhibition of *in vitro* methane production (-85% relative to lucerne in spring), confirming its strong anti-methanogenic potential. *In vitro* fermentation of desmanthus emitted less methane in summer than in spring, consistent with reduced fermentation linked to seasonal changes in plant structure (and an associated increase in indigestible fibre). Both reduced rainfall and elevated temperature decreased methane production in at least one season for each of biserrula, desmanthus, and chicory, likely due to declines in digestibility and changes in secondary metabolites. On an energy basis, biserrula and chicory showed lower methane emissions intensity, reflecting strong inhibition (biserrula) and high energy content (chicory).

6. Persistence reflects climate of origin and species traits

The tropical species (digit, desmanthus) were highly persistent, likely reflecting their higher thermal optima and, for digit, its high water-use efficiency. Among the temperate species, lucerne, a deep-rooted temperate legume, was the most persistent, even under warmer or drier conditions, while the more shallow-rooted, temperate grasses were not strongly persistent. Sainfoin did not persist well even under well-watered ambient temperatures, likely due to the combination of its low competitive ability alongside cocksfoot, and the relatively low water retention capacity of the well-drained sandy soils along with high summertime temperatures at the study site.

Experiment 2: Tropical and temperate mixture comparison

7. Tropical mixtures were more productive than temperate ones, even under low rainfall

Tropical legume-C_4 grass mixtures produced more than twice the aboveground biomass of temperate mixtures and were less affected by reduced rainfall (-54% temperate; -44% tropical); this difference was largely driven by the strong summertime productivity and high water-use efficiency of the dominant C_4 Rhodes grass. Although productivity of the summer-active cultivar of lucerne (Sardi Grazier) in the tropical mixture was significantly affected by rainfall treatment, it consistently produced more biomass than the temperate (Sardi 7) cultivar, even under low rainfall.

The biggest seasonal yield declines under reduced rainfall were in spring, with losses of up to 75% (temperate) and 65% (tropical) coinciding with periods of high vapour pressure deficit and low soil water content.

Whilst the high overall productivity of tropical mixtures was responsible for greater yields of crude protein (+72%) and metabolizable energy (+147%) compared to the temperate mixture, the high fibre content and low absolute values of CP and ME suggest that these highly productive tropical mixtures may require supplementary feeding with concentrates - or a higher target legume proportion - to meet livestock nutritional requirements.

8. Low rainfall drives shifts in composition of temperate and tropical mixtures

Despite the deep-rooted nature of lucerne, the Sardi Grazier cultivar in the tropical mixture experienced a greater proportional biomass reduction than its companion tropical grasses, across all time points. This, alongside its lower persistence compared to temperate legumes, may partially reflect increasing competition from the dominant, more water-use efficient Rhodes grass, particularly as the latter performed strongly even under low rainfall. Tropical legumes such as desmanthus, burgundy bean and stylo may well be better companion species for tropical grasses than summer-active lucerne, as long as they have opportunity to establish before such grasses dominate the canopy. In contrast, reduced rainfall was associated with a compositional shift towards legumes in temperate plots, thereby increasing sward nutritional value despite a productivity decline.

Experiment 3: Effects of grazing frequency on temperate pasture response to altered rainfall

9. Low rainfall and frequent grazing both decrease productivity (non-additively)

Reduced rainfall decreased total aboveground biomass by 58% while more frequent grazing (simulated by harvesting) was associated with a 28% productivity decline. Summed across the full 21-month study, increasing harvest frequency reduced biomass under high rainfall (-36%) but had no effect under reduced rainfall. However, during the most productive spring and summer periods, frequent harvesting significantly reduced total sward productivity under both wet (-40%) and dry (-18%) conditions.

10. Legumes are highly sensitive to low rainfall and frequent grazing

Legumes contributed most to total production but were highly sensitive to low rainfall (-64%) and frequent harvesting (-41%). Grasses declined in response to high harvest frequency under wet conditions (-57%) but not under dry conditions, so therefore increased their biomass as a proportion of the total in dry, frequently harvested plots. Changing sward composition in response to treatments was also apparent for the herb plantain*;* this species displayed strong compensatory growth, increasing productivity by 221% with frequent harvesting under both rainfall regimes. The combination of low rainfall and frequent harvests also resulted in an increase in dead biomass which, along with a decline in legumes, is likely to be associated with reduced sward nutritional quality.

11. Belowground carbon stores fuel post-grazing regrowth

Reducing the amount of rainfall altered plant carbon allocation to roots; this was evidenced by increases in belowground net primary productivity (BNPP) (+11%) and root mass fraction (+76%), indicating an adaptive response to low water availability. Root starch stores were also depleted under low rainfall conditions, suggesting carbohydrate mobilization is a key mechanism for stress tolerance. Frequent harvesting reduced carbon allocation to roots under dry, but not wet, conditions thereby limiting regrowth potential and soil carbon inputs under dry conditions. If such patterns were to persist over prolonged periods, this would likely have negative impacts on soil carbon stocks. The strong positive relationship between spring growth and the preceding season's BNPP emphasizes the role of stored carbon for regrowth of perennial species, and highlights a key mechanism by which water stress - and to a lesser extent also grazing - influences aboveground productivity and persistence.

12. Management implications

Reducing the frequency of grazing can reduce negative effects on belowground biomass and thereby boost pasture resilience and persistence. This is particularly the case in spring when the effects of frequent grazing on above and belowground productivity were high under both rainfall regimes and when the combination of dry conditions and frequent biomass offtake resulted in particularly low productivity and regrowth. Incorporating species with deep taproots, such as plantain, can enhance the adaptive capacity of mixed temperate pastures during periods of low rainfall, including under more frequent grazing.

5.2 Benefits to industry

Enhanced climate tolerance of mixed forage systems

- Identification of drought- and heat-tolerant species (e.g., lucerne, chicory, digit in this study), and compatible companion species (e.g. cocksfoot/prairie grass declined as lucerne increased in mixed pastures) guides planting decisions for sustaining productivity under future climates.

- Combining deep-rooted legumes (e.g. lucerne, desmanthus) with C_4 grasses (e.g. digit) and herbs (e.g. chicory, plantain) will improve forage availability across seasons.

- Higher legume and/or herb proportions are desirable in areas/years with low rainfall, to offset climate-related declines in nutritional quality.

Support for sustainable grazing systems

- Frequent grazing depletes plant belowground carbon stores with negative effects on regrowth (grazing resilience).

- Moderating grazing intensity - especially during dry springs - will help boost annual pasture productivity and persistence, reducing costs of re-establishment and imported feed as well as ensuring ground cover to minimise soil erosion and promote ecosystem health.

- Biserrula and, to a lesser extent, chicory have the potential to reduce ruminant methane emissions, and thereby increase feed conversion efficiency, with benefits for animal productivity and the carbon footprint of livestock enterprises.

- Inclusion of species (and cultivars) of deep-rooted legumes that maintain a good level of productivity under climate stress (e.g. lucerne Sardi 7 and Sardi Grazier, desmanthus) can help improve sward nutrition and reduce dependence on synthetic nitrogen fertilisers, lowering costs and enhancing environmental sustainability.

Long-term system stability and resilience

- Combining species with a variety of rooting strategies, photosynthetic pathways and phenologies helps enhance pasture persistence and regrowth following periods of extreme climate stress.

- Plantain and chicory performed well even under more extreme climate conditions and frequent grazing, highlighting the role these species can play in resilient pasture swards.

6. Future research and recommendations

- **Optimising species composition:** Evaluation of a broader range of mixtures with stress-tolerant legumes, deep-rooted herbs and warm-season grasses with contrasting root traits and phenology to allow identification of trait-based allocation strategies and resource use complementarity that sustain forage yield and quality. Testing wider combinations of species under a range of climate conditions is essential to identify competitive imbalances that reduce persistence and thus require remedial seeding effort.
- **Field evaluation of species performance across climate gradients:** Build on this project's experimental findings of species' climate sensitivity by evaluating the productivity and persistence of commonly used pasture species/combinations in field locations across gradients of temperature and rainfall. Using a space-for-time approach, selecting sites that represent predicted climate space for a given location (e.g. Gatton QLD as a future climate analogue for Richmond NSW) can demonstrate target species' suitability under predicted changes in seasonal temperature and rainfall.
- **Long-term persistence and recovery:** Examine how repeated drought and warming cycles influence root dynamics, carbohydrate reserves, post-stress recovery, and persistence. *Species-level* evaluation of root biomass allocation and carbon stores will help identify the physiological and biogeochemical mechanisms driving aboveground regrowth and resilience under warmer, drier conditions.
- **Climate and grazing interactions:** Given the identification of important interactions between rainfall amount, timing, and biomass offtake frequency in this study, expanding this research to different species mixtures, rainfall and grazing scenarios will enable the development of data-informed management guidelines for future, more extreme rainfall scenarios. Perennial tap-rooted herbs appear to have the ability to stabilise productivity and warrant further research.
- **Nutritional quality and methane emissions under climate stress:** A key area for further research is to undertake a more detailed evaluation of plant species with secondary chemistry that suppresses methanogenesis, including their ability to achieve meaningful reductions in CH_4 emissions when present in low and/or varying proportions in the feed base, and when growing under different climate conditions. Likewise, evaluating how lab-based measurements of CH_4 production translate to *in vivo* CH_4 generation and live weight gain is an essential next step in this research area. This research is needed to validate the viability of incorporating target species, in particular biserrula, in the pasture feed base as a method for reducing farm-level carbon emissions.
- **Adaptive management**: Test alternative grazing regimes and fertiliser strategies that respond to seasonal variability in plant carbon allocation and nutrient requirements, and support pasture persistence, under varying climates. Extend the grazing simulations undertaken so far in PACE to real grazing scenarios with cattle, that include the effects of plant selectivity, trampling and dung/urine.
- **Scaling and modelling:** Integrate empirical data into process-based and economic models to forecast regional pasture performance and profitability, and guide adaptive management strategies, under projected climate scenarios.

In summary, developing climate-resilient pasture systems requires knowledge of the species-level mechanisms driving climate sensitivity for a wider range of pasture species and an understanding of how co-occurring species interact to affect persistence over time, under differing climate conditions and management regimes. Further research in these areas will enable evidence-based recommendations for perennial species mixtures that are better adapted to warmer, drier conditions, and that can potentially play a useful role in reducing farm-scale greenhouse gas emissions.

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8. Appendix

Table S1. Means ± SE (t ha^{-1}) and results from a linear mixed-effects model showing the effects of rainfall extremes, warming, and their interaction on component species in four two-species pastures across seasons. Bold values indicate significant effects ($p < 0.05$), and italicized values indicate marginal significance ($p < 0.1$). ANPP represents the aboveground net production of each species in each season, averaged over two years across the factorial combinations of rainfall and warming treatments. Abbreviations: aT–Wet (ambient temperature–wet rainfall), aT–Dry (ambient temperature–dry rainfall), eT–Wet (elevated temperature–wet rainfall), and eT–Dry (elevated temperature–dry rainfall). Treatments: R = rainfall, T = temperature, and R * T = interactive effects of rainfall and temperature.

Pasture	Species	Season	aT-Wet		aT-Dry		eT-Wet		eT-Dry		R	T	R*T
			ANPP	±SE	ANPP	±SE	ANPP	±SE	ANPP	±SE			
Sai/Coc	Sai/Coc	Summer	0.741	0.10	0.493	0.05	0.356	0.03	0.366	0.09	*0.086*	**0.001**	*0.065*
		Autumn	1.264	0.15	1.095	0.14	0.910	0.15	0.690	0.14	0.200	**0.019**	0.863
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	1.673	0.33	0.993	0.08	1.044	0.08	0.447	0.05	**0.002**	**0.005**	0.820
	Sainfoin	Summer	0.171	0	0.063	0	0.088	0	0.105	0.1	0.142	0.495	**0.048**
		Autumn	0.325	0.1	0.128	0	0.15	0	0.123	0.1	*0.078*	0.149	0.173
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	0.214	0.1	0.039	0	0.122	0	0.026	0	**0.005**	0.234	0.358
	Cocksfoot	Summer	0.493	0.1	0.36	0	0.184	0	0.191	0	0.169	**<0.001**	0.129
		Autumn	0.939	0.1	0.967	0.1	0.76	0.1	0.568	0.1	0.493	**0.026**	0.361
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	1.128	0.2	0.679	0.1	0.698	0.1	0.287	0.1	**0.004**	**0.005**	0.884
Des/Dig	Des/Dig	Summer	6.550	0.40	5.854	0.57	7.059	0.58	6.966	0.39	0.437	0.122	0.551
		Autumn	1.095	0.17	1.094	0.10	1.576	0.17	1.512	0.15	0.801	**0.003**	0.806
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	3.541	0.37	2.866	0.31	3.842	0.52	3.157	0.39	*0.099*	0.456	0.990
	Desmanthus	Summer	0.291	0.1	0.181	0.1	0.457	0.2	0.316	0.2	0.215	0.143	0.879
		Autumn	0.103	0	0.088	0	0.226	0.1	0.224	0.1	0.839	**0.007**	0.881
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	0.34	0.2	0.169	0.1	0.722	0.2	0.415	0.1	**0.015**	**0.002**	0.446
	Digitaria	Summer	6.135	0.4	5.527	0.6	6.46	0.7	6.52	0.4	0.622	0.245	0.548
		Autumn	0.953	0.2	0.965	0.1	1.292	0.1	1.215	0.1	0.785	**0.024**	0.709
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	3.093	0.3	2.562	0.4	2.967	0.4	2.557	0.3	0.196	0.852	0.864
Luc/Pha	Luc/Pha	Summer	6.961	0.38	5.081	0.64	5.813	0.46	3.760	0.69	**0.002**	**0.041**	0.876
		Autumn	1.807	0.11	1.691	0.17	**2.192**	0.13	**1.360**	0.07	**0.001**	0.828	**0.011**
		Winter	1.504	0.10	1.137	0.25	1.607	0.12	0.925	0.19	**0.003**	0.722	0.312
		Spring	7.637	0.58	4.451	0.73	6.353	0.37	3.708	1.22	**<0.001**	0.138	0.682
	Lucerne	Summer	6.719	0.4	4.911	0.7	5.649	0.5	3.587	0.7	**0.003**	**0.047**	0.822
		Autumn	1.487	0.1	1.398	0.2	1.854	0.2	1.028	0.1	**0.001**	0.988	**0.007**
		Winter	1.125	0.1	0.847	0.2	1.247	0.1	0.708	0.2	**0.002**	0.936	0.257
		Spring	7.191	0.6	4.286	0.7	6.077	0.4	3.501	1.1	**<0.001**	0.142	0.792
	Phalaris	Summer	0.169	0	0.118	0	0.094	0	0.12	0	0.579	0.138	0.121
		Autumn	0.243	0.1	0.259	0.1	0.258	0.1	0.206	0.1	0.732	0.716	0.518
		Winter	0.314	0.1	0.193	0.1	0.208	0.1	0.105	0	**0.046**	*0.08*	0.863
		Spring	0.353	0.1	0.115	0	0.204	0	0.113	0.1	**0.001**	*0.095*	0.102
Bis/Chi	Bis/Chi	Summer	5.618	0.29	4.927	0.37	4.906	0.24	4.825	0.22	0.158	0.138	0.258
		Autumn	1.286	0.12	1.218	0.17	1.388	0.12	1.256	0.15	0.198	0.362	0.674
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	2.445	0.41	1.130	0.13	1.360	0.17	1.076	0.22	**0.001**	**0.015**	**0.026**
	Biserrula	Summer	0.003	0	0	0	0	0	0	0	NA	NA	NA
		Autumn	0.009	0	0.001	0	0.002	0	0	0	NA	NA	NA
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	0.669	0.2	0.156	0	0.226	0.1	0.07	0	**0.001**	**0.008**	*0.061*
	Chicory	Summer	5.362	0.3	4.779	0.4	4.789	0.2	4.628	0.2	0.162	0.172	0.417
		Autumn	1.227	0.1	1.151	0.2	1.361	0.1	1.194	0.1	0.118	0.248	0.547
		Winter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Spring	1.152	0.1	0.818	0.1	0.902	0.1	0.779	0.2	**0.029**	0.15	0.286

Table S2. Forage nutritional quality under factorial rainfall (R) and temperature (T) climate treatments, measured across multiple seasons and years per species between spring of 2023 and summer of 2025. Means ± standard error. aT-W: ambient Temperature, Wet; aT-D: ambient Temperature, Dry; eT-W: elevated Temperature, Wet; eT-D: elevated Temperature, Dry.

Species	Season	Treatment				p-values		
		aT-W	aT-D	eT-W	eT-D	R	T	R*T
				Neutral detergent fibre (% DM)				
Lucerne	Spring 2023	52.0 ± 1.7	52.7 ± 1.0	52.1 ± 0.8	52.4 ± 1.1	0.667	0.94	0.864
	Summer 2024	47.7 ± 2.4	47.4 ± 0.4	46.7 ± 0.7	47.2 ± 2.0	0.848	0.58	0.896
	Spring 2024	51.7 ± 0.7	50.3 ± 0.7	52.5 ± 0.7	50.0 ± 0.6	**0.003**	0.72	0.317
	Summer 2025	59.0 ± 1.1	52.2 ± 1.0	55.4 ± 1.4	49.1 ± 0.7	**<0.0001**	**0.004**	0.807
Biserrula	Spring 2023	43.7 ± 0.9	44.8 ± 1.0	43.4 ± 1.3	46.6 ± 0.8	*0.063*	0.46	0.302
	Winter 2024	41.9 ± 0.7	43.8 ± 0.7	43.3 ± 1.1	44.4 ± 1.7	0.143	0.32	0.663
Desmanthus	Spring 2023	34.7 ± 3.3	43.7 ± 2.7	39.5 ± 2.2	37.8 ± 2.7	0.237	0.657	*0.059*
	Summer 2024	42.2 ± 0.5	42.3 ± 1.0	43.8 ± 1.2	44.8 ± 1.7	0.649	0.128	0.704
	Spring 2024	30.6 ± 1.1	35.1 ± 1.4	35.3 ± 0.7	34.3 ± 1.4	0.235	0.102	**0.026**
	Summer 2025	40.0 ± 1.2	39.8 ± 1.7	42.7 ± 1.6	41.4 ± 1.7	0.612	0.195	0.761
Sainfoin	Spring 2023	41.3 ± 1.0	40.9 ± 1.8	40.2 ± 0.2	43.5 ± 1.9	0.455	0.834	0.22
	Summer 2024	38.7 ± 2.1	39.8 ± 3.0	31.0 ± 2.8	31.0 ± 1.7	0.867	**0.004**	0.901
	Spring 2024	45.4 ± 2.1	38.3 ± 1.6	38.8 ± 2.7	41.9 ± 1.0	0.475	0.347	**0.038**
Chicory	Summer 2024	27.7 ± 0.6	26.8 ± 0.6	27.3 ± 0.4	28.3 ± 0.7	0.976	0.274	*0.073*
	Autumn 2024	18.1 ± 0.3	18.1 ± 0.4	18.3 ± 0.4	18.7 ± 0.3	0.493	0.299	0.646
	Spring 2024	27.9 ± 0.5	28.2 ± 0.5	28.6 ± 0.7	28.2 ± 0.7	0.935	0.549	0.623
	Summer 2025	36.6 ± 0.4	36.4 ± 0.4	36.3 ± 0.4	37.4 ± 0.4	0.283	0.357	0.131
				Acid detergent fibre (% DM)				
Lucerne	Spring 2023	37.7 ± 1.5	38.8 ± 0.7	37.6 ± 0.6	38.2 ± 0.7	0.344	0.711	0.789
	Summer 2024	33.0 ± 0.8	33.2 ± 0.2	33.1 ± 0.4	32.7 ± 0.3	0.998	0.702	0.405
	Spring 2024	33.6 ± 0.2	33.0 ± 0.5	34.7 ± 0.3	33.3 ± 0.8	**0.018**	*0.064*	0.318
	Summer 2025	39.5 ± 1.0	34.7 ± 0.8	37.9 ± 0.9	33.2 ± 0.5	**<0.0001**	**0.039**	0.721
Biserrula	Spring 2023	25.0 ± 0.8	26.3 ± 0.7	25.2 ± 0.8	27.5 ± 0.9	**0.04**	0.305	0.493
	Winter 2024	21.8 ± 0.4	22.5 ± 0.3	22.9 ± 0.9	24.2 ± 0.7	0.163	0.107	0.637
Desmanthus	Spring 2023	20.5 ± 2.5	25.9 ± 2.0	23.2 ± 1.1	22.2 ± 1.6	0.291	0.709	0.101
	Summer 2024	25.4 ± 0.2	25.6 ± 0.8	27.6 ± 1.0	28.4 ± 1.4	0.621	**0.026**	0.822
	Spring 2024	18.3 ± 0.8	23.8 ± 1.7	23.5 ± 0.7	22.9 ± 1.5	*0.052*	**0.021**	**0.005**
	Summer 2025	25.8 ± 1.2	26.3 ± 1.5	28.0 ±0.8	27.1 ± 1.1	0.78	0.228	0.542
Sainfoin	Spring 2023	31.3 ± 0.9	31.9 ± 1.5	31.0 ± 0.3	33.6 ± 1.8	0.318	0.609	0.45
	Summer 2024	29.5 ± 1.5	29.8 ± 2.1	23.8 ± 1.9	23.4 ± 1.5	0.874	**0.003**	0.822
	Spring 2024	29.1 ± 1.2	24.0 ± 1.3	24.7 ± 2.0	26.5 ± 1.0	0.391	0.333	**0.036**
Chicory	Summer 2024	20.1 ± 0.3	19.3 ± 0.2	20.1 ± 0.3	20.7 ± 0.2	0.676	**0.005**	**0.004**
	Autumn 2024	13.6 ± 0.3	13.8 ± 0.3	13.9 ± 0.3	13.8 ± 0.2	0.929	0.614	0.534
	Spring 2024	16.6 ± 0.3	16.5 ± 0.3	16.5 ± 0.2	16.2 ± 0.4	0.53	0.53	0.875
	Summer 2025	20.9 ± 0.3	21.3 ± 0.3	21.1 ± 0.3	21.7 ± 0.3	0.114	0.325	0.935
				Crude protein (% DM)				
Lucerne	Spring 2023	18.1 ± 1.6	17.4 ± 1.2	16.5 ± 1.3	17.8 ± 1.4	0.637	0.496	0.269
	Summer 2024	19.9 ± 0.6	20.9 ± 1.3	21.7 ± 0.7	20.8 ± 0.9	0.978	0.251	0.207
	Spring 2024	22.3 ± 0.4	19.7 ± 0.6	20.3 ± 0.4	19.2 ± 0.7	**0.005**	*0.056*	0.235
	Summer 2025	14.3 ± 0.5	16.2 ± 0.3	15.1 ± 1.0	17.1 ± 0.1	**0.004**	0.144	0.944
Biserrula	Spring 2023	15.0 ± 0.7	14.5 ± 0.4	14.9 ± 0.3	14.4 ± 0.2	0.278	0.644	0.857
	Winter 2024	25.3 ± 1.2	19.1 ± 1.8	23.5 ± 2.0	21.3 ± 1.7	**0.026**	0.854	0.329
Desmanthus	Spring 2023	15.0 ± 2.0	13.7 ± 1.3	15.3 ± 0.7	16.1 ± 1.1	0.878	0.236	0.472
	Summer 2024	17.8 ± 1.1	17.1 ± 0.7	16.9 ± 0.6	17.5 ± 0.8	0.992	0.667	0.419
	Spring 2024	11.6 ± 0.4	13.8 ± 0.9	12.5 ± 0.9	13.7 ± 1.2	*0.062*	0.737	0.575
	Summer 2025	10.9 ± 0.9	13.7 ± 0.4	10.6 ± 0.5	12.8 ± 0.8	**0.0004**	0.597	0.608
Sainfoin	Spring 2023	10.5 ± 0.7	11.1 ± 1.0	10.9 ± 0.8	9.3 ± 0.7	0.81	0.644	0.242
	Summer 2024	12.0 ± 0.8	12.5 ± 1.4	15.2 ± 1.1	17.5 ± 1.0	0.154	**0.001**	0.553
	Spring 2024	13.8 ± 1.0	15.3 ± 1.6	16.5 ± 1.7	18.6 ± 0.9	0.212	**0.044**	0.807
Chicory	Summer 2024	12.9 ± 0.8	13.8 ± 0.3	12.9 ± 0.7	16.0 ± 1.0	**0.017**	0.181	0.16

	Autumn 2024	14.9 ± 0.4	15.7 ± 0.5	16.9 ± 0.7	18.5 ± 0.4	**0.029**	**0.0003**	0.532
	Spring 2024	16.4 ± 0.6	16.3 ± 1.4	16.9 ± 1.0	18.5 ± 1.0	0.413	0.104	0.254
	Summer 2025	11.8 ± 0.4	14.1 ± 0.5	14.5 ± 0.5	15.3 ± 0.4	**0.0004**	**<0.0001**	**0.022**
Water-soluble carbohydrates (% DM)								
Lucerne	Spring 2023	5.6 ± 0.2	5.8 ± 0.3	5.3 ± 0.2	5.8 ± 0.3	0.236	0.516	0.478
	Summer 2024	5.4 ± 0.2	5.6 ± 0.3	5.4 ± 0.3	5.9 ± 0.2	0.156	0.48	0.611
	Spring 2024	2.3 ± 0.2	3.4 ± 0.2	2.9 ± 0.3	3.8 ± 0.5	**0.006**	0.118	0.816
	Summer 2025	3.1 ± 0.3	3.6 ± 0.3	3.1 ± 0.2	4.0 ± 0.2	**0.016**	0.46	0.498
Biserrula	Spring 2023	9.3 ± 0.5	9.0 ± 0.2	9.4 ± 0.7	8.9 ± 0.3	0.448	0.713	0.765
	Winter 2024	5.1 ± 0.5	6.5 ± 0.9	4.5 ± 0.8	5.3 ± 0.4	0.172	0.309	0.73
Desmanthus	Spring 2023	4.2 ± 0.3	4.9 ± 0.2	3.9 ± 0.2	5.1 ± 0.3	**0.002**	0.971	0.281
	Summer 2024	4.6 ± 0.3	4.9 ± 0.3	4.2 ± 0.4	5.1 ± 0.4	**0.049**	0.43	0.321
	Spring 2024	4.2 ± 0.7	4.2 ± 0.6	3.5 ± 0.3	3.8 ± 0.3	0.738	0.237	0.681
	Summer 2025	1.9 ± 0.3	1.9 ± 0.2	1.6 ± 0.3	2.1 ± 0.3	0.304	0.78	0.414
Sainfoin	Spring 2023	6.9 ± 0.3	5.1 ± 0.5	7.2 ± 1.1	6.9 ± 0.9	0.107	0.151	0.486
	Summer 2024	6.2 ± 0.7	5.8 ± 1.0	8.8 ± 0.5	8.4 ± 0.6	0.447	**0.003**	0.898
	Spring 2024	7.1 ± 0.9	8.1 ± 0.9	7.5 ± 0.7	7.1 ± 1.3	0.598	0.833	0.301
Chicory	Summer 2024	6.8 ± 0.3	8.0 ± 0.6	8.1 ± 0.9	6.6 ± 0.5	0.807	0.935	**0.038**
	Autumn 2024	13.5 ± 0.4	12.0 ± 0.6	10.6 ± 0.6	9.9 ± 0.5	*0.056*	**0.0002**	0.426
	Spring 2024	5.0 ± 0.4	5.8 ± 0.5	5.4 ± 0.3	6.0 ± 0.5	0.13	0.441	0.889
	Summer 2025	7.6 ± 1.0	7.0 ± 0.4	7.5 ± 0.5	7.1 ± 0.5	0.574	0.888	0.965
Dry organic matter digestibility (% DM)								
Lucerne	Spring 2023	62.2 ± 1.5	61.0 ± 1.0	61.8 ± 0.6	61.1 ± 0.8	0.326	0.893	0.803
	Summer 2024	60.3 ± 3.3	63.9 ± 0.6	63.3 ± 0.4	60.2 ± 3.5	0.862	0.844	*0.075*
	Spring 2024	61.7 ± 0.3	61.3 ± 0.5	60.6 ± 0.4	61.1 ± 0.6	0.913	0.158	0.35
	Summer 2025	53.9 ± 0.9	58.7 ± 1.0	56.4 ± 1.0	60.6 ± 0.7	**0.0001**	**0.029**	0.749
Biserrula	Spring 2023	66.0 ± 0.8	65.5 ± 0.5	66.4 ± 0.8	64.5 ± 0.8	0.107	0.427	0.264
	Winter 2024	72.3 ± 0.7	70.5 ± 0.8	71.1 ± 1.4	69.5 ± 1.5	0.168	0.309	0.969
Desmanthus	Spring 2023	62.0 ± 2.7	60.8 ± 3.4	62.7 ± 1.7	62.8 ± 1.4	0.723	0.488	0.631
	Summer 2024	52.1 ± 0.8	51.5 ± 0.7	50.4 ± 0.6	50.1 ± 0.8	0.44	**0.031**	0.793
	Spring 2024	64.5 ± 0.7	59.9 ± 1.6	59.1 ± 0.8	59.4 ± 0.9	*0.082*	**0.011**	**0.032**
	Summer 2025	56.8 ± 0.8	56.2 ± 0.5	54.9 ± 0.6	56.1 ± 0.8	0.576	0.174	0.234
Sainfoin	Spring 2023	58.9 ± 0.5	56.5 ± 0.7	58.5 ± 0.8	57.6 ± 1.1	**0.012**	0.907	0.566
	Summer 2024	52.8 ± 1.2	51.3 ± 1.8	57.6 ± 1.2	58.5 ± 2.1	0.82	**0.003**	0.603
	Spring 2024	59.5 ± 1.1	62.7 ± 0.6	63.2 ± 1.6	63.9 ± 0.8	0.164	**0.046**	0.309
Chicory	Summer 2024	63.0 ± 0.9	63.6 ± 0.6	63.2 ± 0.5	63.1 ± 0.4	0.611	0.803	0.482
	Autumn 2024	77.7 ± 0.3	77.1 ± 0.3	76.2 ± 0.4	76.1 ± 0.3	0.269	**0.002**	0.439
	Spring 2024	69.1 ± 0.6	69.0 ± 0.9	69.4 ± 0.7	70.0 ± 0.7	0.629	0.32	0.592
	Summer 2025	66.9 ± 0.8	67.6 ± 0.4	67.6 ± 0.5	67.0 ± 0.7	0.989	0.925	0.32
Metabolisable energy (MJ/kg DM)								
Lucerne	Spring 2023	9.6 ± 0.3	9.3 ± 0.2	9.5 ± 0.1	9.4 ± 0.2	0.32	0.866	0.737
	Summer 2024	9.2 ± 0.7	10.0 ± 0.1	9.9 ± 0.1	9.2 ± 0.7	0.858	0.857	*0.07*
	Spring 2024	9.5 ± 0.1	9.4 ± 0.1	9.3 ± 0.1	9.4 ± 0.1	1	0.121	0.375
	Summer 2025	7.9 ± 0.2	8.9 ± 0.2	8.4 ± 0.2	9.3 ± 0.1	**0.0002**	**0.032**	0.759
Biserrula	Spring 2023	10.4 ± 0.2	10.3 ± 0.1	10.5 ± 0.2	10.1 ± 0.2	*0.091*	0.451	0.254
	Winter 2024	11.7 ± 0.1	11.3 ± 0.2	11.5 ± 0.3	11.1 ± 0.3	0.149	0.321	0.967
Desmanthus	Spring 2023	9.6 ± 0.5	9.4 ± 0.7	9.7 ± 0.3	9.8 ± 0.3	0.722	0.431	0.631
	Summer 2024	7.6 ± 0.2	7.4 ± 0.1	7.2 ± 0.1	7.2 ± 0.2	0.527	**0.029**	0.702
	Spring 2024	10.1 ± 0.1	9.2 ± 0.3	9.0 ± 0.2	9.1 ± 0.2	*0.083*	**0.012**	**0.034**
	Summer 2025	8.6 ± 0.2	8.5 ± 0.1	8.2 ± 0.1	8.4 ± 0.2	0.512	0.164	0.219
Sainfoin	Spring 2023	8.9 ± 0.1	8.4 ± 0.1	8.8 ± 0.2	8.6 ± 0.2	**0.012**	0.914	0.601
	Summer 2024	7.7 ± 0.2	7.4 ± 0.4	8.6 ± 0.2	8.8 ± 0.4	0.8	**0.003**	0.604
	Spring 2024	9.1 ± 0.2	9.8 ± 0.1	9.9 ± 0.3	10.0 ± 0.1	0.143	**0.039**	0.281
Chicory	Summer 2024	9.8 ± 0.2	9.9 ± 0.1	9.8 ± 0.1	9.8 ± 0.1	0.434	0.881	0.541
	Autumn 2024	12.8 ± 0.1	12.6 ± 0.1	12.5 ± 0.1	12.5 ± 0.1	0.268	**0.004**	0.372
	Spring 2024	11.0 ± 0.1	11.1 ± 0.2	11.1 ± 0.1	11.2 ± 0.1	0.525	0.446	0.61
	Summer 2025	10.6 ± 0.2	10.7 ± 0.1	10.8 ± 0.1	10.6 ± 0.1	0.897	0.897	0.307

Table S3. Seasonal productivity responses of temperate and tropical pasture mixtures to rainfall treatment, by functional group, averaged across 2023–2024.

Functional group	Season	Rain	Temperate (tha^{-1})	±SE	Effect size	p-value	Tropical (tha^{-1})	±SE	Effect size	p-value
Total	Summer	Wet	2.310	0.19	**-0.473**	**0.001**	13.54	0.70	**-0.389**	**<0.001**
		Dry	1.219	0.16			8.265	0.56		
	Autumn	Wet	1.468	0.08	**-0.474**	**0.001**	2.336	0.19	**-0.303**	**<0.001**
		Dry	0.772	0.08			1.627	0.13		
	Winter	Wet	0.681	0.11	-0.135	0.607	1.070	0.14	**-0.501**	**0.001**
		Dry	0.589	0.13			0.534	0.09		
	Spring	Wet	4.235	0.44	**-0.749**	**0.001**	4.875	0.29	**-0.649**	**<0.001**
		Dry	1.062	0.26			1.714	0.17		
Grass	Summer	Wet	0.597	0.06	**-0.384**	**0.032**	7.224	0.46	-0.079	0.409
		Dry	0.368	0.05			6.655	0.6		
	Autumn	Wet	0.387	0.05	**-0.258**	**0.037**	1.781	0.17	**-0.261**	**0.015**
		Dry	0.287	0.04			1.316	0.1		
	Winter	Wet	0.06	0.02	0.333	0.518	0.36	0.03	-0.208	0.138
		Dry	0.08	0.03			0.285	0.02		
	Spring	Wet	0.558	0.12	**-0.882**	**0.006**	1.169	0.12	**-0.461**	**0.002**
		Dry	0.066	0.02			0.63	0.06		
Legume	Summer	Wet	1.223	0.09	**-0.471**	**0.015**	6.195	0.75	**-0.755**	**0.002**
		Dry	0.647	0.19			1.518	0.51		
	Autumn	Wet	0.826	0.07	**-0.603**	**0.002**	0.525	0.05	**-0.451**	**0.003**
		Dry	0.328	0.11			0.288	0.06		
	Winter	Wet	0.43	0.09	-0.163	0.636	0.785	0.09	**-0.622**	**0.001**
		Dry	0.36	0.11			0.297	0.06		
	Spring	Wet	3.457	0.39	**-0.748**	**0.001**	3.673	0.29	**-0.718**	**<0.001**
		Dry	0.872	0.27			1.037	0.14		
Herb	Summer	Wet	0.195	0.06	*-0.390*	*0.086*				
		Dry	0.119	0.04						
	Autumn	Wet	0.205	0.03	-0.449	0.104				
		Dry	0.113	0.03						
	Winter	Wet	0.108	0.02	-0.185	0.586				
		Dry	0.088	0.03						
	Spring	Wet	0.092	0.04	-0.554	0.288				
		Dry	0.041	0.02						

Table S4. Nutritional values used to estimate nutritional yield across temperate and tropical mixtures. The nutritional yield of each species or functional group was calculated by multiplying its representative nutritional value (estimated during either the previous PACE1 or current PACE2 project) by its productivity.

Pasture	Species	CP	NDF	ME	ADL
Temperate mixture	Grass	13.5	57	8.42	4.8
	Lucerne	20.9	35.7	9.18	6.3
	Sainfoin	12.3	39.3	7.1	8.1
	Plantain	16.8	33.1	8.31	6.8
Tropical mixture	Grass	6.3	67.3	7.63	4.3
	Lucerne	17.2	44.3	7.71	8.8

Abbreviations: CP – Crude protein (% of dry matter; calculated as nitrogen × 6.25); NDF – Neutral detergent fibre (% of dry matter; includes hemicellulose, cellulose, and lignin); ADL – Acid detergent lignin (% of dry matter); ME – Metabolisable energy (MJ kg^{-1} dry matter).

Figure S1. Species-level biomass production prior to treatments commencing (baseline) and after two years of climate manipulation (spring 2024), as an indicator of persistence. Means ± SE are shown (n=6). Treatment abbreviations: aT-Wet (ambient temperature, Wet rainfall regime), aT-Dry (ambient temperature, Dry rainfall regime), eT-Wet (elevated temperature, Wet rainfall regime) and eT-Dry (elevated temperature, Dry rainfall regime).

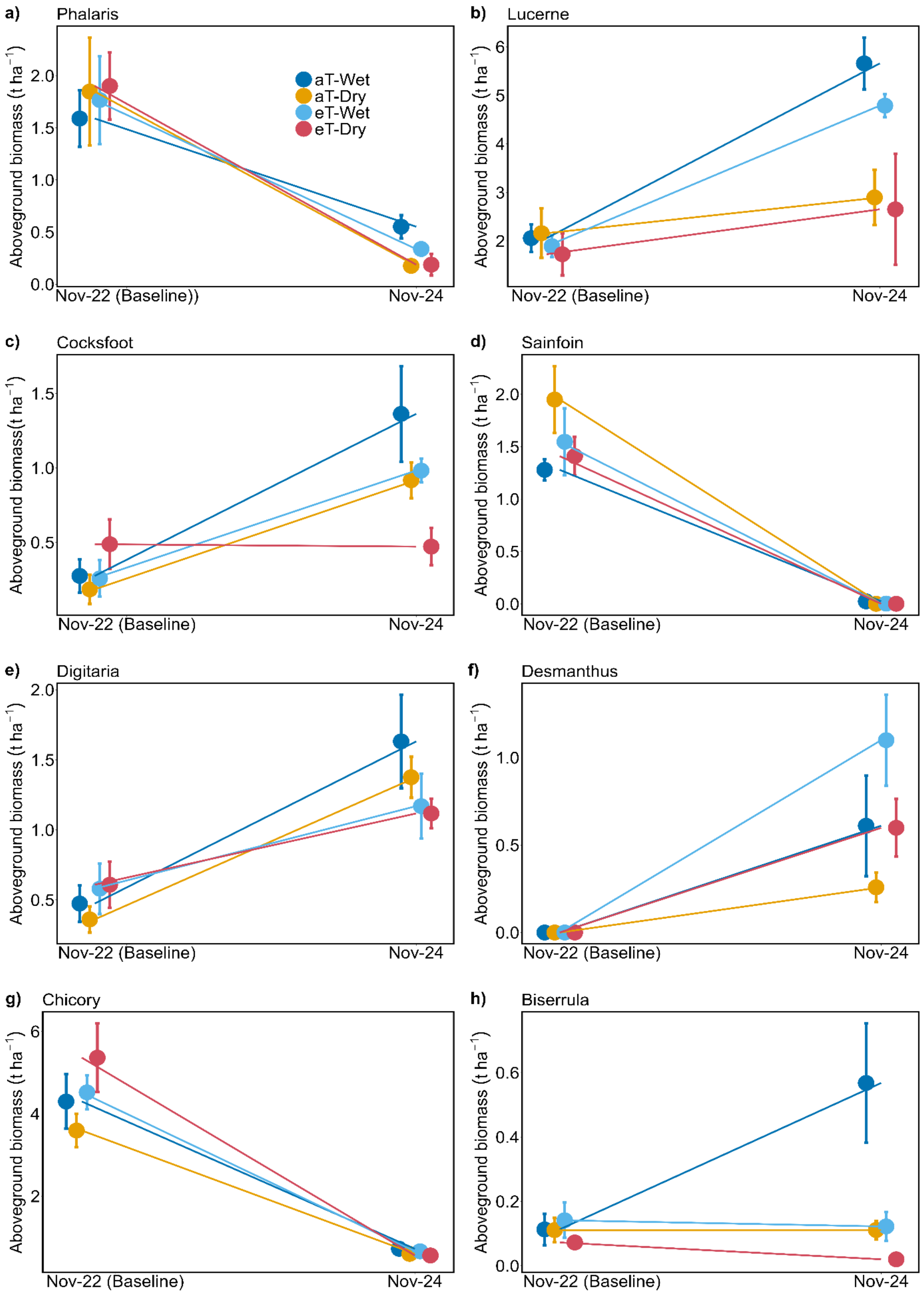

Figure S2. Regrowth dynamics of the four pasture species pairs following harvest, under factorial combinations of warming and rainfall treatments. Regrowth rates are expressed as the slope of the increase in green chromatic coordinate (GCC) over the first 15 days after harvest. Each line represents the average GCC across six shelters per treatment. Panels e, j, o, and t show overall (multi-season) average regrowth rates for each species pair. Treatment abbreviations: aT-Wet (ambient temperature, Wet rainfall regime), aT-Dry (ambient temperature, Dry rainfall regime), eT-Wet (elevated temperature, Wet rainfall regime) and eT-Dry (elevated temperature, Dry rainfall regime).

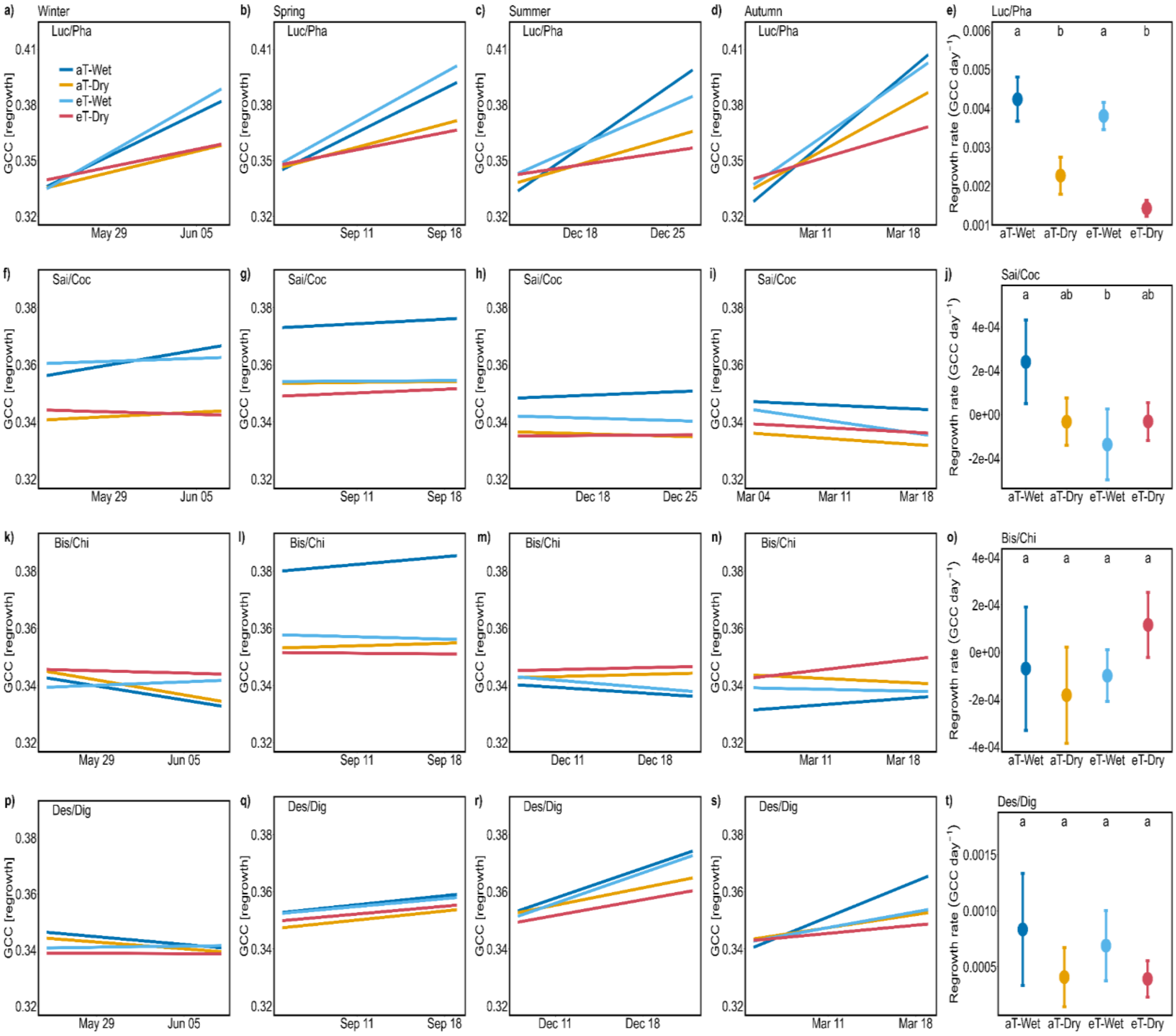

Figure S3. Relationships between green chromatic coordinate (GCC) during the first 15 days of post-harvest regrowth and seasonal aboveground production, based on least squares regressions. Treatment abbreviations: aT-Wet (ambient temperature, Wet rainfall regime), aT-Dry (ambient temperature, Dry rainfall regime), eT-Wet (elevated temperature, Wet rainfall regime) and eT-Dry (elevated temperature, Dry rainfall regime)**.**

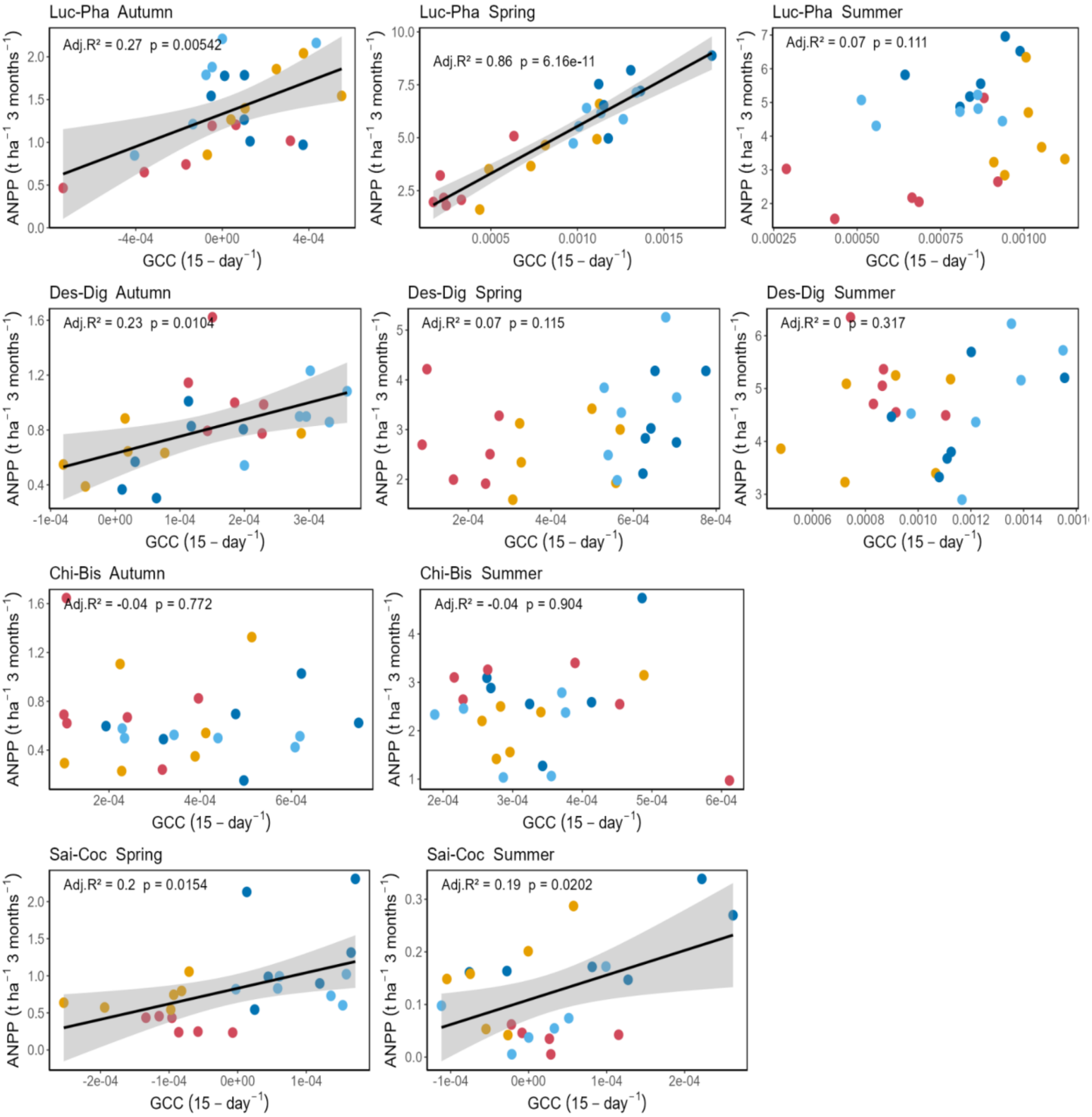

Figure S4. Biomass allocation to root crowns in a temperate pasture mixture by functional group across multiple seasons under wet and dry rainfall regimes with low and high harvest frequencies: (a) total, (b) grasses, (c) legumes and (d) herbs.