

Using leaf regrowth stage to define defoliation interval for diverse pastures of complementary species (*Lolium perenne* L., *Bromus valdivianus* Phil., *Dactylis glomerata* L. and *Trifolium repens* L.)

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Abstract

Diverse pastures of complementary species (DPCS) comprise species that fulfil different agroecological niches, resulting in growth asynchrony and complementarity of functional roles. It is expected that DPCS have a greater capability to tolerate and perform under increasingly extreme climate events, providing a potential alternative for New Zealand pastoral systems. In the present study, DPCS comprised *Lolium perenne* L., *Bromus valdivianus* Phil., *Dactylis glomerata* L., and *Trifolium repens* L. The leaf regrowth stage [LS; *L. perenne* (2.5-3.0LS), *B. valdivianus* (3.5-4.0LS) and *D. glomerata* (3.5-4.0LS)] is proposed to be an applicable method of defoliation management for DPCS due to a potential overlapping of the defoliation interval. The seasonal and annual herbage mass accumulation and botanical composition of DPCS and their respective single-grass and *T. repens* pastures under the LS criterion were assessed. The annual yield did not differ among pastures (average 20.26 t dry matter (DM) ha⁻¹). However, significant differences were found within seasons, with DPCS exhibiting asynchronous growth among species that reduced the seasonality of herbage accumulation and invasion by volunteer species. *Lolium perenne*, *B. valdivianus* and *D. glomerata* were shown to be complementary grass species, presenting growth asynchrony and an overlapping defoliation interval that optimised production, indicating that defoliation based on LS criterion is a suitable management for DPCS.

Keywords: *Bromus valdivianus*, *Dactylis glomerata*, *Lolium perenne*, grazing systems, growth asynchrony, seasonality

Introduction

New Zealand's intensive dairy pastoral systems rely on pastures mostly comprised of *L. perenne* and *T. repens* (ryegrass-based pastures). The persistence of these pastures is compromised by low summer rainfall, low water-holding capacity soils, shallow-rooted systems, high grazing intensity resulting in pugging and pasture pulling, and susceptibility to diseases and weed invasion (Clark 2011). In addition, under the current climate

change scenario, an unpredictable seasonality of herbage growth in ryegrass-based pastures is predicted, expressed as more frequent peaks and troughs of production (Keller et al. 2021). In diverse pastures, the different species often present seasonal activity perceived as relatively higher growth rates in one given season. Consequently, there is a greater probability that the pasture will present a higher seasonal herbage mass accumulation, pasture persistence and survival, mainly in periods of environmental constraints (Brophy et al. 2017; Bakker et al. 2021). Pastures based on species diversity can be a key alternative to cope with feed shortages caused by periods of soil water deficit (summer drought) in temperate and humid-climate ryegrass-based pastures (García-Favre et al. 2022) due to stabilisation in herbage production (Lüscher et al. 2022)

For sown ryegrass-based pastures, such as those in New Zealand, appropriate defoliation targets (i.e. herbage mass targets based on animal intake requirements, post-grazing targets) and fertilisation (maintenance macronutrients and nitrogen (N) application) are required to optimise production, quality and persistence (Hernández Garay et al. 2000; Hazard et al. 2001; Lee et al. 2008; Harris et al. 2010; Edwards and Chapman 2011). However, these factors *per se* do not guarantee the success of a diverse pasture. The complexity of sown mixtures resides on a common "drift" over time, in which many of the desired species disappear within a few years of intensive grazing management (Sanderson et al. 2007). Diverse pastures of complementary species (DPCS) are pastures that combine species of asynchronous growth (e.g., winter and summer activity) and different functional roles (i.e., deep- and shallow-rooted species, prostrate and erect growth habits) that complement each other within the same pastoral ecosystem. The present study will explore some of these aspects for a DPCS comprising *L. perenne*, *B. valdivianus*, *D. glomerata*, and *T. repens* defoliated according to the grass species leaf-regrowth stage (LS) criterion. The LS defoliation criterion is a plant-based defoliation interval, where the minimum limit is associated with the replenishment of plant

water-soluble carbohydrate (WSC) reserves after the previous grazing event, and the maximum limit of the defoliation interval is associated with the onset of senescence (Fulkerson and Donaghy 2001; Turner et al. 2006; Chapman et al. 2012; Gatti et al. 2017; Ordóñez et al. 2021). It is well established for monocultures of *L. perenne* (2.0-3.0LS) (Donaghy and Fulkerson 1997; Fulkerson and Donaghy 2001), *B. valdivianus* (4.0LS) (Ordóñez et al. 2021) *D. glomerata* (4.0LS) (Turner et al. 2006), and has been recently assessed in binary mix swards of *L. perenne* (2.5-3.0LS) and *B. valdivianus* (3.5-4.0LS) (García-Favre et al. 2022).

In order to maximise the pasture growth efficiency and persistence of a diverse pasture, it is necessary to understand the complementarity of morpho-physiological traits, the growth asynchrony of the species, the ecological and agricultural function of the species within the pasture and the practical criteria for optimal defoliation of the individual species. Currently, there is a lack of knowledge regarding using LS as the defoliation criteria in DPCS and its effects on the phenotypic plasticity, physiological readjustments, and solute distribution of the individual species within the diverse pasture. Based on the aforementioned research, a seasonal LS range for the optimal defoliation of each species was utilised in the present study, with an adjustment in spring to maintain pasture quality (see later). It is hypothesised that DPCS presents a dynamic composition in time and space, given by the species' growth asynchrony, and the complementarity of the species' functional roles as an active response to the changing environmental constraints. *Lolium perenne*, *B. valdivianus* and *D. glomerata* are expected to present a temporal overlap of their respective optimum LS interval. The present study aimed to assess seasonal and annual herbage mass accumulation, seasonal growth rates and seasonal botanical composition of *L. perenne*, *B. valdivianus* and *D. glomerata* defoliated according to their respective LS intervals as DPCS and single-grass pastures.

Material and Methods

Site and experimental setup

The study was undertaken at Massey University's Dairy 1 (Palmerston North, Manawatu, New Zealand) from 15 June 2021 to 14 September 2022, with the approval of Massey University Animal Ethics Committee (Approval number 21/24). On 24 November 2020, the area was sprayed out with N-(phosphonomethyl) glycine (glyphosate WeedMaster® G360) at 6 L ha⁻¹ and Thifensulfuron-methyl (Harmony® 50 SG) at 30 g ha⁻¹ to control weed seed bed and population. From 10 to 18 December 2020, the area was ploughed, power harrowed and levelled. On 18 December 2020, mixtures (Mix) of *L. perenne* (Lp), *B. valdivianus* (Bv)

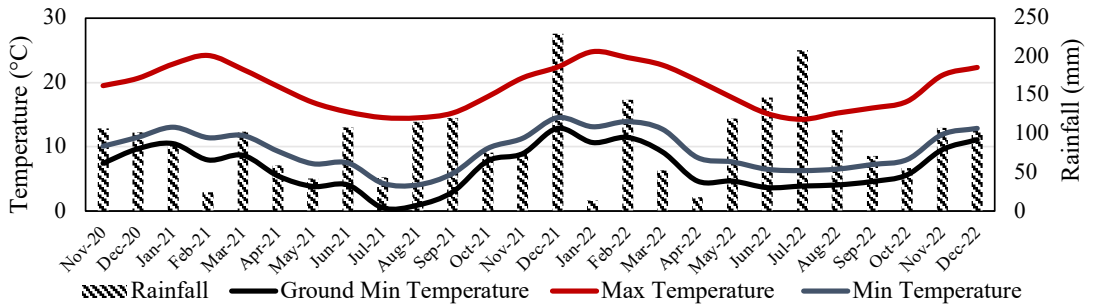
and *D. glomerata* (Dg) and their respective single-grass pastures (Mono) were established. *Trifolium repens* (Tr) was sown at the same rate in all pastures (Table 1). In December 2020, the area was irrigated for one day with a mobile gun sprinkler to ensure a successful establishment. Following this, the pastures were rainfed.

The soil type is Manawatu silt loam over sand (Landcare Research National Soil Data Base, Lab. No SB10036). The results of soil chemical analysis (0-15 cm soil depth) collected on 26 February 2021 indicated 5.60 pH CaCl₂ (0.01 M (1:2.5)), 3.33% organic matter content, 29.0 Olsen P (mg L⁻¹), 0.21 exchangeable K (me 100 g⁻¹), 6.80 exchangeable Ca (me 100 g⁻¹), 1.35 exchangeable Mg (me 100 g⁻¹), 13.0 cation exchange capacity (me 100 g⁻¹), 64.0% total base saturation content, 3 extractable organic sulphur (mg kg⁻¹) and 10.03 carbon:nitrogen ratio. The area received annual maintenance fertilisation on 1 March 2021 and 17 March 2022, at 500 kg ha⁻¹ and 400 kg ha⁻¹ of Superphosphate + Se (0% N, 22.5% P, 0% K, 27.5% S and 50% Ca). Post-grazing nitrogen fertilisations were applied as Urea in July 2021, November 2021, January 2022, August 2022, and November 2022, each at 30 kg N ha⁻¹. The climate is classified as Marine West Coast - Cfb (Köppen climate classification). The rainfall and temperatures during the experimental period are shown in Figure 1 (NIWA/AgResearch Weather Station, ~800 m from the field site).

From June 2021 onwards, the seasonal interval for defoliation was determined according to the LS criterion of each species and applied to both monocultures and mixtures (also referred to as diverse pastures of complementary species – DPCS) (Table 1 and 2). These resulted in six experimental treatments (Table 1): MonoLp (defoliated at *L. perenne* LS), MonoBv (defoliated at *B. valdivianus* LS), MonoDg (defoliated at *D. glomerata* LS), MixLp (defoliated at *L. perenne* LS), MixBv (defoliated at *B. valdivianus* LS), MixDg (defoliated at *D. glomerata* LS). In the MixLp, for instance, the *L. perenne* plants are the targeted species (α) and thus justified defoliation based on the *L. perenne* LS interval, whereas the *B. valdivianus*, *D. glomerata*, and *T. repens* neighbouring plants are the companion species. The study was arranged in a randomised complete block design, with three blocks (n=3), each with the six pasture treatments in 20 m x 20 m plots. Dairy cows grazed the plots on a one-day grazing event basis (10-15 animals per plot depending on herbage allowance) until the pasture reached an undisturbed height of 5 to 8 cm from ground level.

Leaf regrowth stage, herbage mass accumulation and botanical composition

The LS of the target species (α) and companion species

Figure 1 Monthly rainfall, ground minimum, air maximum and minimum temperatures (November 2020 to December 2022). Bars indicate rainfall; lines indicate temperatures.**Table 1** Establishment description of the four pastures species composition and sowing rate, cultivars and resulting experimental treatments once defoliation criteria were applied.

Pasture species composition (sowing rates, kg.ha ⁻¹)	Cultivars	Experimental treatments (defoliation criterion)
Lp + Tr (20 + 6)	<i>L. perenne</i> cv. Maxsyn + <i>T. repens</i> cv. Weka	1 - MonoLp (LpLS)
Bv + Tr (50 + 6)	<i>B. valdivianus</i> cv. Bareno + <i>T. repens</i> cv. Weka	2 - MonoBv (BvLS)
Dg + Tr (15 + 6)	<i>D. glomerata</i> cv. Greenly II + <i>T. repens</i> cv. Weka	3 - MonoDg (DgLS)
Lp + Bv + Dg + Tr (10 + 15 + 12 + 6)	<i>L. perenne</i> cv. Maxsyn + <i>B. valdivianus</i> cv. Bareno + <i>D. glomerata</i> cv. Greenly II + <i>T. repens</i> cv. Weka	4 - MixLp (LpLS) 5 - MixBv (BvLS) 6 - MixDg (DgLS)

was assessed on nine randomly chosen mature tillers of each grass species per plot on the day before each grazing event. The herbage mass was measured pre- and post-grazing by cutting to ground level three randomly placed 0.1m² quadrats in each plot. The samples were dried for at least 72 hours in a forced-air oven at 60°C and weighed to determine their dry matter (DM). The apparent accumulated DM (season or year) was the sum of apparent herbage growth per grazing, calculated as the difference between the pre-grazing DM at the current grazing event and the post-grazing DM of the previous grazing event. The botanical composition was assessed at every second grazing event. Two sub-samples from the herbage mass samples were randomly taken separately to be fractionated into individual components of *L. perenne*, *B. valdivianus*, *D. glomerata*, *T. repens*, dead material and volunteer species (every other species that was not the original sown species of each treatment). The separated materials were oven-dried at 60°C and weighed.

Statistical analysis

Data distribution was verified for the residual normality (Shapiro-Wilk's test) and homogeneity variance (Chi-square test) (PROC Univariate). Subsequently, data were analysed by one-way analysis of variance (ANOVA), using the LSD test to define differences among pasture treatments (PROC Glimmix) on the Statistical Analysis

System (SAS 9.4). The statistical model had the fixed effect of the experimental treatments stated in Table 1 and the random effect of block. Statistically significant differences were considered at $p \leq 0.05$.

Results

Leaf regrowth stage

The defoliation criteria applied resulted in 16 grazing events for MonoLp and MixLp, 15 for MonoBv and MixBv, and 14 for MonoDg and MixDg. The α species of the six pasture treatments achieved the target seasonal LS interval (Table 2), and the companion species presented variations in the LS within each respective diverse pasture treatment. In the MixLp, *B. valdivianus* was defoliated earlier than the target LS interval in winter 2021 and summer 2021-22, while the *D. glomerata* was mostly defoliated earlier than the target LS interval, except for spring 2023. In the MixBv, most companion species were defoliated within their respective optimal LS interval, with *D. glomerata* defoliated earlier than the target LS interval in autumn and winter 2022. In the MixDg, the *L. perenne* was defoliated later than its optimal LS interval in both winters (Table 2).

For all DPCS, the seasonal average LS of *L. perenne*, *B. valdivianus* and *D. glomerata* did not differ in spring 2021, autumn 2022 and spring 2022 ($p > 0.05$) (Table 3). Significant differences were found during winter 2021,

Table 2 Pasture treatment, pasture species composition (Spp), seasonal leaf regrowth stage interval for the defoliation of each pasture treatment according to the α species (winter, summer, and autumn; spring), and seasonal average leaf regrowth stage of each pasture species at the defoliation event.

Pasture treatment	Spp *	Seasonal LS interval for defoliation		Seasonal average of species LS					
		Winter Summer Autumn	Spring †	Winter 2021	Spring 2021	Summer 2021-22	Autumn 2022	Winter 2022	Spring 2022
MonoLp	Lp α	2.5 – 3.0	2.25 – 2.75	2.7	2.4	2.6	2.7	2.8	2.6
MonoBv	Bv α	3.5 – 4.0	3.0 – 3.5	3.8	3.2	3.7	3.7	3.9	3.4
MonoDg	Dg α	3.5 – 4.0	3.0 – 3.5	3.8	3.2	3.5	3.7	3.4	3.2
MixLp	Lp α	2.5 – 3.0	2.25 – 2.75	2.6_C	2.5_C	2.6_C	2.7_C	2.6_C	2.5_C
	Bv _{CSpp}			3.3 _E	3.1 _C	3.2 _E	3.6 _C	3.5 _C	3.3 _C
	Dg _{CSpp}			3.2 _E	2.9 _E	3.2 _E	3.4 _E	3.0 _E	3.2 _C
MixBv	Lp _{CSpp}			3.0 _C	2.5 _C	2.6 _C	2.6 _C	2.8 _C	2.6 _C
	Bv α	3.5 – 4.0	3.0 – 3.5	4.0_C	3.0_C	3.6_C	3.6_C	3.8_C	3.4_C
	Dg _C			3.7 _C	3.1 _C	3.5 _C	3.4 _E	3.3 _E	3.4 _C
MixDg	Lp _{CSpp}			3.3 _L	2.7 _C	2.9 _C	2.7 _C	3.1 _L	2.5 _C
	Bv _{CSpp}			4.2 _L	3.2 _C	3.6 _C	3.7 _C	4.0 _C	3.4 _C
	Dg α	3.5 – 4.0	3.0 – 3.5	3.7_C	3.2_C	3.6_C	3.5_C	3.6_C	3.1_C

Lp: *L. perenne*, Bv: *B. valdivianus*, Dg: *D. glomerata*; α : targeted species that determined each defoliation event (defoliation criterion = α_{LS}); LS: leaf regrowth stage; CSpp: companion species; C: correct LS of the species according to the season; E: earlier than the correct LS of the species according to the season; L: later than the correct LS of the species according to the season. *All pastures have *T. repens* in their composition. † LS range was slightly anticipated to alleviate detriments in pasture quality due to flowering stems.

Table 3 Leaf regrowth stage for *L. perenne*, *B. valdivianus* and *D. glomerata* within each pasture at the moment of defoliation (*L. perenne* on MixLp, MixBv and MixDg; *B. valdivianus* on MixLp, MixBv and MixDg; *D. glomerata* on MixLp, MixBv and MixDg) in winter 2021, spring 2021, summer 2021-22, autumn 2022, winter 2022, spring 2022.

Species within each pasture	Seasonal average LS per species					
	Winter 2021	Spring 2021	Summer 2021-22	Autumn 2022	Winter 2022	Spring 2022
<i>L. perenne</i>						
MixLp	2.6 c (± 0.06)	2.5 (± 0.41)	2.6 b (± 0.34)	2.7 (± 0.21)	2.6 c (± 0.48)	2.5 (± 0.75)
MixBv	3.0 b (± 0.17)	2.5 (± 0.32)	2.6 b (± 0.19)	2.6 (± 0.45)	2.8 b (± 0.23)	2.6 (± 0.35)
MixDg	3.3 a (± 0.35)	2.7 (± 0.57)	2.9 a (± 0.68)	2.7 (± 0.61)	3.1 a (± 0.48)	2.5 (± 0.39)
Significance	***	NS	*	NS	**	NS
<i>B. valdivianus</i>						
MixLp	3.3 c (± 0.51)	3.1 (± 0.21)	3.2 b (± 0.52)	3.6 (± 0.24)	3.5 c (± 0.56)	3.3 (± 0.41)
MixBv	4.0 b (± 0.08)	3.0 (± 0.37)	3.6 a (± 0.29)	3.6 (± 0.27)	3.8 b (± 0.16)	3.4 (± 0.42)
MixDg	4.2 a (± 0.28)	3.2 (± 0.77)	3.6 a (± 1.41)	3.7 (± 0.38)	4.0 a (± 0.37)	3.4 (± 0.08)
Significance	***	NS	*	NS	**	NS
<i>D. glomerata</i>						
MixLp	3.2 b (± 0.03)	2.9 (± 0.44)	3.2 c (± 0.38)	3.4 (± 0.75)	3.0 c (± 0.34)	3.2 (± 0.65)
MixBv	3.7 a (± 1.58)	3.1 (± 0.70)	3.5 b (± 0.21)	3.4 (± 0.25)	3.3 b (± 0.84)	3.4 (± 0.28)
MixDg	3.7 a (± 0.29)	3.2 (± 0.88)	3.6 a (± 0.44)	3.5 (± 0.52)	3.6 a (± 0.46)	3.1 (± 0.33)
Significance	*	NS	**	NS	**	NS

LS: leaf regrowth stage. Letters that differ within columns for the same species indicate values that are significantly different; * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, NS = non-significant (>0.05); following each species LS least square mean, is the (\pm) standard error of the mean.

summer 2021-22, and winter 2022, when the chronophysiological pattern consistently presented the earliest LS in the MixLp and the latest in the MixDg for the three species within the DPCS.

Dry matter accumulation, seasonal growth rates and botanical composition

The total annual (2021-22) accumulated DM was similar for all treatments ($p > 0.05$), with an average of 20.26 t DM ha⁻¹. Nonetheless, significant differences in accumulated DM were found within seasons (Table 4); MixLp was always among the pastures with the higher seasonal production (6 seasons), followed by MixBv and MixDg (4 seasons). The MonoBv had the lowest accumulated DM in winter 2021 and was among the lowest accumulated DMs in winter 2022; MonoLp was among the lowest accumulated DMs in both summers. The Mono Dg was among the lowest accumulated DMs in summer 2021-22 and winter 2022. In both springs, MonoBv and MonoLp were among the lowest accumulated DMs.

The herbage growth rates graphs are shown as pairs of treatments with the same species defoliation criteria (α_{LS}), and significant differences were found between the treatments (Figure 2). The MixLp had greater growth rates than MonoLp in both springs (42% and 23%), in summer 2021-22 (14%) and autumn 2022 (38%). The MixBv had greater growth rates than MonoBv in both winters (70% and 41%) and autumn 2022 (44%). The MixDg had greater growth rates than MonoDg in autumn 2022 (79%) and winter 2022 (72%). All DPCS had a better post-summer performance, represented by a slower decline in growth rate towards autumn.

The *L. perenne* percentage in MixLp was significantly higher than in the other two DPCS in both springs, representing 47% and 46% of its sward, compared to 37% and 28% in MixBv and 24% and 34% in MixDg (Figure 3). Overall, the presence of *L. perenne* in the mixed swards remained at around 30% throughout the seasons. During summer 2021-22, MonoLp had significantly less *L. perenne* percentage than MixLp, MixBv and MixDg and had a significant peak at 33% of volunteer plant species' presence in the sward. In summer 2021-22 and spring 2022, MonoBv had significant peaks of volunteer plant species. Across seasons, MixLp, MixBv and MixDg had at most 5% of volunteer plant species. The *B. valdivianus* percentage in MonoBv, MixLp, MixBv and MixDg dropped from winter 2021 until summer 2021-22, from 61% to 18% in the MonoBv, and around 30% to 5% in the DPCS. After the summer period, *B. valdivianus* percentage recovered in MonoBv, tripling its presence in the sward by winter 2022. However, it did not recover in the DPCS and remained around 5% after the summer 2021-22. The *D. glomerata* percentage in the DPCS increased

from summer 2021-22 until spring 2022. In MixBv and MixDg, the average *D. glomerata* percentage in the sward became five times greater, while in MixLp three times greater. The *T. repens* percentage showed to be overall higher in monocultures than in DPCS in both winters and summer 2021-22.

Discussion

Determining the multiple species to compose a diverse pasture is challenging, as the decision will be "situation-specific" (climate, soil type, pasture utilisation), as defined by (Pembleton et al. 2015;. Furthermore, increasing species number within a pastoral ecosystem requires a strategy to define appropriate defoliation management "rules" that will not favour one or two species over another (Pembleton et al. 2015; Donaghy et al. 2021). Although complex and yet to be fully unfolded, the combination of both aspects underpins the performance and persistence of a diverse pasture. Once the aforementioned aspects are fulfilled, the utilisation of diverse pastures is a suitable option for producers targeting better pastoral productivity and persistence under extreme climatic events (Finn et al. 2013; McCahon et al. 2021; Lüscher et al. 2022).

The LS criterion used as defoliation management has been validated for some single-grass pastures, including *L. perenne*, *Festuca arundinacea* Schreb, *Bromus willdenowii* K., *B. valdivianus* and *D. glomerata* (Fulkerson and Donaghy 2001; Turner et al. 2006; Chapman et al. 2012; Gatti et al. 2017; Ordóñez et al. 2021). Its potential suitability in mixed swards brings a new perspective to the grazing management of diverse pastures (García-Favre et al. 2022). In the present study, the implementation of LS for target species (α) as a criterion to define the optimal defoliation interval for monocultures and DPCS was achieved in all seasons and proved to be a practical criterion to manage the frequency of defoliation for DPCS. The MixBv had most of companion species being defoliated within their target LS range, except for autumn and winter when *D. glomerata* was defoliated slightly earlier than recommended. This showed an overlapping of the optimum defoliation intervals for the three species throughout much of the year (Tables 3 and 4).

However, in a DPCS, there may not always be a specific defoliation interval that exactly matches the optimal LS range for each individual species in the mixture. Across the year, in the MixLp, *B. valdivianus* was defoliated earlier than its optimal LS interval in winter and summer, and *D. glomerata* during the whole year; thus, *L. perenne* LS (α) frequency for defoliation does not always coincide with the targeted *D. glomerata* LS interval (companion species), and partially for *B. valdivianus* LS interval (companion species). On the other extreme, the MixDg defoliated under the *D.*

Table 4 Seasonal (winter 2021, spring 2021, summer 2021-22, autumn 2022, winter 2022, spring 2022) and annual (2021-22) apparent accumulated dry matter of pasture treatments (MonoLp, MonoBv, MonoDg, MixLp, MixBv, MixDg) subjected to the LS defoliation criteria.

Pasture	Apparent accumulated DM (t DM ha ⁻¹)									
	Winter 2021	Spring 2021	Summer 2021-22	Autumn 2022	Annual 2021-22	Winter 2022	Spring 2022	SEM season	Signific.	
MonoLp	3.33 a (±0.32)	5.45 bc (±0.37)	6.90 c (±0.36)	2.98 ab (±0.49)	18.67 (±1.08)	2.56 abc (±0.16)	6.30 c (±0.26)	0.20	***	*
MonoBv	1.86 c (±0.19)	4.75 c (±0.54)	9.23 ab (±0.34)	1.99 b (±0.19)	17.82 (±0.79)	2.23 bc (±0.21)	6.57 c (±0.34)	0.50	*	*
MonoDg	3.50 a (±0.24)	6.54 ab (±1.16)	7.40 c (±0.69)	2.24 b (±0.18)	19.68 (±2.15)	1.69 c (±0.25)	8.07 a (±0.29)	0.55	*	*
MixLp	3.67 a (±0.18)	7.71 a (±0.49)	7.86 abc (±0.06)	4.11 a (±0.35)	23.35 (±0.47)	2.81 ab (±0.16)	7.81 ab (±0.12)	0.42	*	*
MixBv	3.15 ab (±0.14)	5.68 bc (±0.74)	9.44 a (±0.90)	2.86 ab (±0.34)	21.13 (±1.80)	3.21 a (±0.11)	6.67 bc (±0.44)	0.29	*	*
MixDg	2.68 b (±0.07)	6.72 ab (±0.38)	7.55 bc (±0.27)	4.00 a (±0.81)	20.94 (±0.70)	2.90 ab (±0.55)	7.96 a (±0.48)	1.17	NS	*
SEM season										0.36

Letters that differ within columns indicate values that are significantly different; * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, NS = non-significant ($p > 0.05$); following each pasture treatment least square mean, is the (±) standard error of the mean; SEM season: standard error of the mean per season.

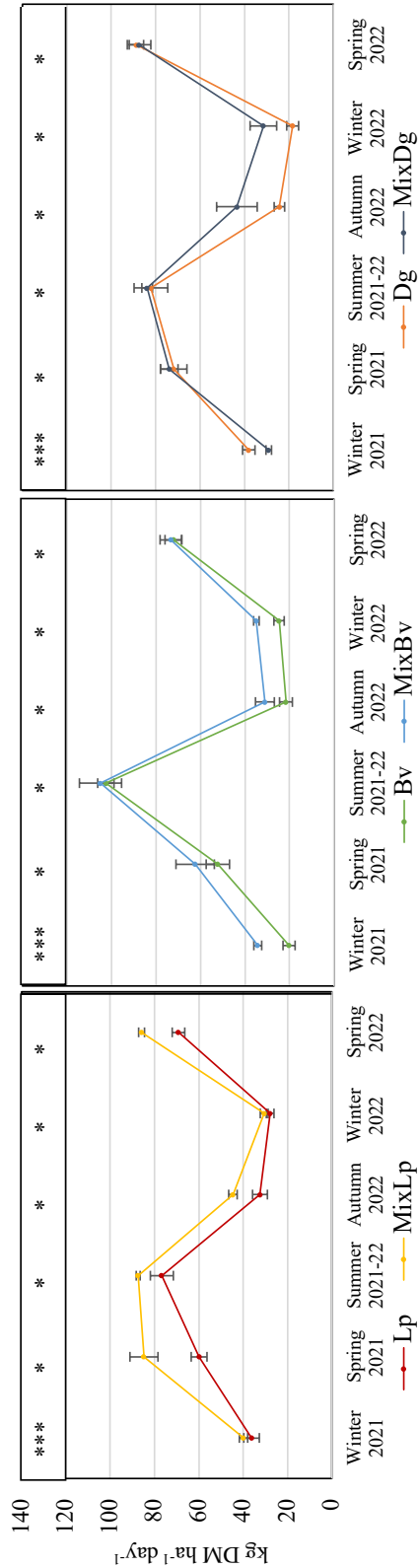


Figure 2 Average daily growth rate of MonoLp, MixLp, MonoBv, MonoDg and MixBv, MonoDg and MixDg in winter 2021, spring 2021, summer 2021-22 and autumn 2022. The figure was split according to the dLS of the same species to facilitate the visualisation of growth rate lines. The vertical bars indicate (±) S.E.M. within the same season for the six treatments. Levels of significance are indicated per season as: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, NS = non-significant ($p > 0.05$).

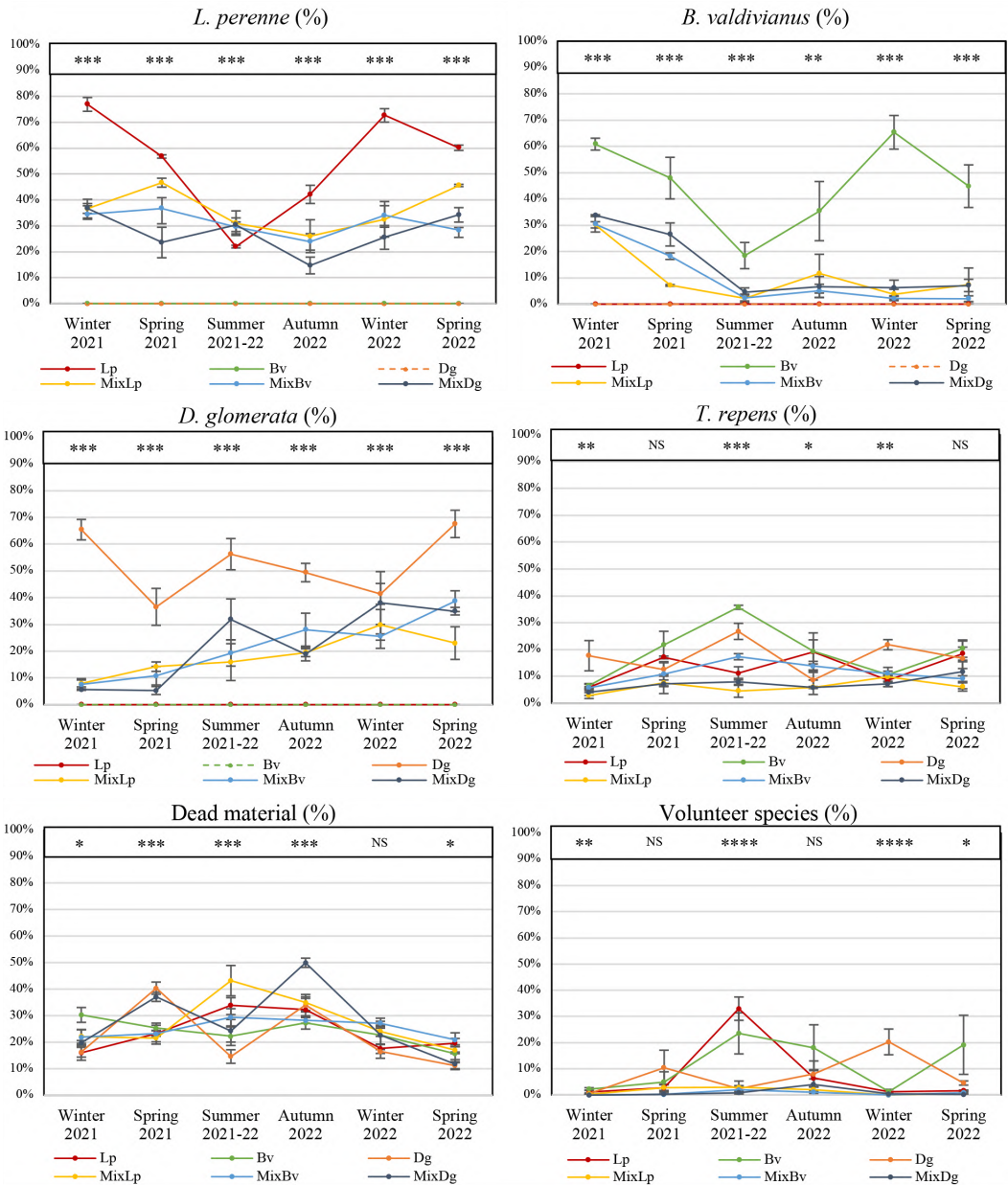


Figure 3 Average percentage of individual components in the botanical composition of MonoLp, MonoBv, MonoDg, MixLp, MixBv and MixDg during winter 2021, spring 2021, summer 2021-2022, autumn 2022 and spring 2022. The vertical bars indicate (±) S.E.M. within the same season for the six treatments. Levels of significance are indicated per season as: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, NS = non-significant.

glomerata LS (α) frequency had its companion species defoliated later than its optimal LS range, at 3.3 and 4.2 LS, respectively, for *L. perenne* and *B. valdivianus*. For MixLp and MixDg, it is possible to hypothesise that the few events in which the companion species were defoliated slightly earlier or later than their targeted LS range suggested a potential trade-off amongst the feed quality, seasonal productivity and water soluble carbohydrate reserves; that is, a faster rotation towards the minimum interval limit (*L. perenne* LS) in exchange to seasonal productivity and WSC reserves of the companion species, or a longer rotation towards the maximum interval limit (*D. glomerata* LS) in exchange for feed quality, and still allowing the four species to perform while functioning as a diverse pastoral ecosystem.

The annual apparent accumulated DM of DPCS and monocultures did not differ; the high accumulated DM for the first year ($\mu = 20.26$ ton DM ha⁻¹) can be associated with (a) management practices based on morpho-physiological plant responses morpho-physiological plant responses [i.e., the leaf-regrowth stage defoliation criteria (plant-focused management; Pembleton et al. (2015); Donaghy et al. (2021))] and residual stubble heights of 50-80 mm and/or post-grazing targets of 1000-1500 kg DM ha⁻¹ (Lee et al. 2008; Chapman et al. 2012), and plant nutritional requirements [strategic nitrogen application and maintenance fertilisation (Whitehead 2000), as detailed in the material and methods section]; (b) optimal climatic conditions for herbage growth due to La Niña weather pattern occurring in Manawatu in 2021-2022 [warmer summers and milder winters with precipitation around 900-1300 mm year⁻¹, reliable and distributed throughout the year – (Mosley 2000)]. However, the growth rate of monocultures presented a greater fluctuation from one season to the next (i.e., spring 2021 to summer 2021-22 for MonoLp and MixLp), which depicts a less even distribution of the DM accumulated during the year (Table 4 and Figure 2).

The enhancement of the ecosystem diversity in mixed pastures can be related to improved water use efficiency, broader genetic variability and local adaptation, N leaching mitigation, and higher grassland production (Minns et al. 2001). Nevertheless, not the addition of species *per se*, but the complementarity of different species morpho-physiological traits (i.e., winter and summer active, shallow and deep rooting, frost, flood or drought tolerance or survival) results in persistence and, potentially, seasonal or annual overyielding. In the present study, the complementarity of *L. perenne*, *D. glomerata*, *B. valdivianus* and *T. repens* traits were expressed as asynchronous growth across the year, leading to a more consistent DM accumulation with less seasonality. The presence of winter- and summer-active

species within the same pasture largely explains the greater seasonal growth rates of the DPCS compared to their respective single-grass pastures. In a two-year field study, García-Favre et al. (2022) found similar patterns of asynchronous growth using the same LS criteria as the present study, in mixtures of *L. perenne* and *B. valdivianus* (*L. perenne* LS = 2.5-3.0LS and *B. valdivianus* LS = 3.5-4.0LS). In their study, in the mixture defoliated at the *L. perenne* LS, *B. valdivianus* was defoliated slightly earlier than the proposed interval (3.2LS), whereas in the mixture defoliated at the *B. valdivianus* LS, *L. perenne* was defoliated slightly than the proposed interval (3.1LS); notwithstanding, both mixed pastures accumulated 15% more annual herbage mass and showed greater persistence over time (tiller population dynamics). Other studies had shown similar results when, by the end of a production year, the diverse mixtures may not always have over-yielded in comparison to monocultures or simple mixtures, but presented a more even seasonal distribution of the accumulated DM (Sanderson et al. 2007; Descalzi et al. 2020)

Another beneficial result of DPCS over single-grass pastures in the present study was their ability to withstand invasion by volunteer species. During the study period, MixLp, MixBv and MixDg had around 5% of volunteer plant species presence, while seasonal peaks (~20%) were common in MonoLp, MonoBv and MonoDg (Figure 3). This corroborates a study with monocultures and mixtures of timothy (*Phleum pratense* L.), smooth meadow grass (*Poa pratensis* L.), red clover (*Trifolium pratense* L.) and *T. repens* in Canada and Northern Europe, in which the mixed swards had less than 5% of weed presence, against 10-20% and 35-60% presence in the grass and legume monocultures, respectively (Sturludóttir et al. 2014). Anecdotally to the higher presence of volunteer species, a significant decrease in the sown grass was observed (MonoLp and MonoBv in summer 2021-22, MonoDg in winter 2022, and MonoBv in spring 2022), up to an extreme in which MonoLp had significantly less *L. perenne* percentage (22%) than in MixLp, MixBv and MixDg (average of 30% among DPCS). This event was associated with the aggressive invasion of volunteer spring- and summer-active species (*Rumex obtusifolius* L., *Paspalum dilatatum* Poir.) and volunteer winter-active species (*Poa annua* L.). The reduced presence of volunteer species in mixtures can be a side effect of enhanced niche competitiveness and consequent soil resource depletion, termed “resource use complementarity” (Knops et al. 1999; Naem et al. 2000). A secondary explanation attributed to this reduction is the “sampling effect”, which is illustrated by the larger probably that at least one of the selected species will be at the peak of competitiveness, therefore

reducing chances of non-desired species succession (Aarsen 1997; Huston 1997). Another study suggests that both processes may occur concomitantly in diverse pastures (Tracy and Sanderson 2004), which may be the case in the current study.

The botanical composition graphs depicted the species population's seasonal fluctuations (Figure 3), which have been associated with (a) competition (for *T. repens*), (b) environmental conditions (for *B. valdivianus*), (c) opportunistic relations (for *D. glomerata*) and (d) defoliation effects (for *L. perenne*). The legume persistence in legume-grass swards can be affected by establishment issues, livestock grazing selection, treading and resource competition for light, water and nutrients (Brock and Hay 2001). In the present study, the *T. repens* percentage was higher in monocultures than in DPCS (Figure 3). The limited *T. repens* presence in the diverse pastures may result from severe interspecific plant competition (Annicchiarico et al. 2014) by three highly competitive grass species (*L. perenne*, *B. valdivianus* and *D. glomerata*) with increased tiller population density and greater height. In spring 2021 and summer 2021-22, the intensified rainfall events in the Manawatu region (La Niña) resulted in saturated soil conditions for weeks. *Brome* spp. are known for their low tolerance to flooding, being recommended for freely drained soils (Stewart 1996; López et al. 1997), and during this wet period, the *B. valdivianus* presence drastically declined in all treatments (Figure 3). Further, as the *B. valdivianus* percentage significantly decreased, the *D. glomerata* percentage simultaneously increased, showing an opportunistic overtake of one species by another. Lastly, the grazing management effect was observed in the *L. perenne* percentage within the DPCS treatments. In the MixLp, the *L. perenne* LS rotation resulted in 16 grazing events (over six seasons), while the MixDg under *D. glomerata* LS rotation completed 14 grazing events. The faster grazing rotation within the MixLp treatment resulted in significantly higher *L. perenne* percentages in both springs. The morphological traits of both species may explain this; *D. glomerata* has larger tillers than *L. perenne*, and during the spring growth peaks, longer intervals between grazing events could favour *D. glomerata* tillers to become even greater in size, resulting in higher competitiveness through shading and resource depletion.

Introducing more than one or two species into pastoral systems has been previously debated (Tilman 2001; Woodward et al. 2013; Martin et al. 2020; Jaramillo et al. 2021). Reid (1994) proposed the introduction of more grass species, with an emphasis on the genus *Bromus*, into temperate, humid-climate pastures that are commonly composed of one grass component (e.g. *L. perenne*, *Festuca arundinacea*

Shreb., *D. glomerata* or *Phalaris aquatica* L.). A meta-analysis of Isbell et al. (2015) with data from over 46 experiments assessing implications in plant diversity showed that the ecosystem resilience to a broad range of climate events increased as the number of species in the pasture increased. Notwithstanding, the challenges related to increasing the plant diversity in productive grassland areas are not fully elucidated in regards to the "situation-specific" conditions (climate, soil type, pasture utilisation), species number and types (Pembleton et al. 2015) and appropriate defoliation criteria (Donaghy et al. 2021) that aims for high productivity and persistence of all species present in a given diverse pasture. Evidently, there is no panacea for this situation since it requires different species combinations for different climates, soil types and feed utilisation aligned to the most suitable management criteria.

The present study showed that DPCS defoliated according to the LS criterion was successful in achieving a high annual DM yield, reduced seasonality and lower susceptibility to invasion by volunteer species. *Lolium perenne*, *B. valdivianus* and *D. glomerata* showed to be complementary grass species, presenting growth asynchrony and an overlapping interval for defoliation. Further studies are needed for more detailed information about seasonal species population fluctuations and their impacts on feed quality and plant persistence. The hypothetical basis of the present study has the potential to be applied to other grass species in a diversified pastoral ecosystem, given that the combined species present complementary traits.

Conclusions and practical implications

The diverse pastures of complementary species (DPCS) presented less seasonality than the single-grass pastures due to growth asynchrony (i.e., winter and summer activity), with a more even yield distribution throughout the year. Within DPCS, a common defoliation interval that optimised production was observed, with the optimal LS range for *L. perenne* (2.5-3.0LS), *B. valdivianus* (3.5-4.0LS) and *D. glomerata* (3.5-4.0LS) frequently overlapping. The LS criterion was a suitable management tool for DPCS and can be considered successful due to high annual yield, reduced seasonality of yield, and lower susceptibility to invasion of volunteer species.

Diverse pasture of complementary species defoliated according to LS, as proposed in the present study, can become an important alternative for grazing systems in Manawatu, and for other New Zealand regions with more severe summer water restriction events (i.e., Waikato, Hawke's Bay and Canterbury). The hypothetical basis of the study (DPCS defoliated according to the LS criterion) has the potential to be

applied to diversified pastoral ecosystems of other climates and soil types; nonetheless, the combined species must present complementary traits. Further studies are necessary to assess the quality parameters of DPCS defoliated according to the LS criterion.

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