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Morphology of tall fescue (*Festuca arundinacea*) and perennial ryegrass (*Lolium perenne*) plants in pastures under sheep and cattle grazing

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SUMMARY

The effects of contrasting management systems either of infrequent rotational grazing by town milk supply dairy cattle, or of frequent defoliation by continuously grazing sheep and beef cattle, on the morphology of independent plants and populations of 'Grasslands Roa' tall fescue in mixed pastures, were measured over 1 year (1992/93) in New Zealand. Volunteer perennial ryegrass plants were also measured for comparison.

While both species exhibited a similar pattern of clonal growth, tall fescue developed more plants of higher branching complexity than perennial ryegrass, chiefly through maintaining more connective stems, as herbage production was confined to the three youngest branching orders in both species. Greater resistance to microbial degradation of old stems through poorer quality organic matter (wide C:N ratio) compared to perennial ryegrass may be responsible for the greater complexity of fescue plants. In addition, tillering rates in tall fescue were three times lower which was offset by greater longevity and size of leaves and tillers, compared to perennial ryegrass. As a result, seasonal fluctuation in the distribution of plants among the various branching orders in tall fescue was small, producing a more stable population relative to the distinct seasonal changes in the population of perennial ryegrass plants. Grazing management had no effect on the seasonal population structure in either species.

Differences in plant structure due to grazing management were small, with only slightly more tillers on sheep-grazed than on cattle-grazed tall fescue plants. The major effect of grazing management was on dry weight or size of plant components. Cattle-grazed tall fescue plants were 120% heavier, with greater numbers and lengths of stolons and flower heads than those under sheep grazing. For the volunteer perennial ryegrass, the difference was only 65%, possibly due to competition from the more vigorous tall fescue under rotational cattle grazing.

Both species produced stolons throughout the year, although these were primarily associated with reproductive growth in spring. In tall fescue, an additional distinction was made between stolon and rhizome, the latter occurring mainly in the summer–autumn. Their possible functions in plant growth are discussed.

INTRODUCTION

Recent descriptions of the plant morphology and patterns of growth of legume and grass species in intensively grazed mixed pastures in New Zealand have revealed a remarkably similar plant structure and growth pattern between apparently contrasting species. White clover (*Trifolium repens* L.) (Brock *et al*. 1988; Hay *et al*. 1991), perennial ryegrass (*Lolium perenne* L.) (Brock & Thomas 1992; Brock & Fletcher 1993) and cocksfoot (*Dactylis glomerata* L.) (Brock *et al*. 1996) display clonal growth with regular extension at the apices and intermittent death of the older basal stems. All species form stolons, which for white clover is obligatory, being formed by extension of the terminal growing point. In perennial ryegrass and cocksfoot, stolon is only formed occasionally, either to elevate the flower head during reproduction, or to maintain the vegetative growing point in a favourable light environment near the soil surface (Brock *et al*. 1996). In grasses, stolon is formed by intercalary meristematic extension of the internode (Barnard 1964). As a consequence, most of the stolon is below the soil surface, but as the grass is the dominant component, it may form as much stolon per unit area as white clover in mixed pastures (Korte & Harris 1987; Matthew *et al.* 1989; Brock & Fletcher 1993).

Owing to its greater productivity and persistence during summer dry conditions, tall fescue (*Festuca arundinacea* Schreb.) is an alternative temperate pasture species to perennial ryegrass with potential for use in many areas of New Zealand farming (Reeves 1975; Watkin 1975). Studies in the USA have identified significant stolon formation in tall fescue (referred to as rhizomes and rooted stems; Porter 1958; Jernstedt & Bouton 1985), and since this may be an important factor in its persistence, further studies on the plant growth characteristics of this species under grazing are warranted.

To date, these plant growth studies (Brock & Fletcher 1993; Brock *et al.* 1996) have been conducted under intensive sheep grazing at Palmerston North, and have indicated that contrasting defoliation management (frequency) had little effect on plant characteristics, other than plant dry weight (DW). In order to extend these investigations, it was decided to compare the plant characteristics of 'Grasslands Roa' tall fescue and perennial ryegrass, under the contrasting conditions of a high soil fertility, high production town milk supply dairy farming at Palmerston North, and moderate soil fertility, traditional sheep and cattle grazing at Taupo.

MATERIALS AND METHODS

Sites, pastures and grazing management

The two management systems contrasted in this study were: (i) a town milk supply dairy farm (Massey University Number 1 dairy farm) at Palmerston North rotationally grazed all year round (RGDC), compared to (ii) a traditional sheep and beef cattle farm mainly continuously grazed (CGSB) (LandCorp Tahara Station), 3 km south east of Taupo (Table 1).

The soil at the Palmerston North site was a more recent, free-draining alluvial Manawatu sandy loam, gravelly phase (Dystric Fluventic Eutrochrept) (Soil Survey Staff 1992) similar to that used in previous studies of plant morphology (Brock *et al.* 1996), 1 km distant. Over the year of plant sampling, the pasture was rotationally grazed 12 times at *c.* 3-week intervals from mid-spring to mid-summer and up to intervals of 6 weeks at other times of the year. As characteristic of town milk supply farms with year-round milk production, the average stocking rate of 1·9 cows/ha was not high, and the stocking density at grazing was *c.* 118 cows/ha for 24 h.

The soil at Taupo was a Taupo silty sand, a yellow-brown pumice derived from Taupo ash (Typic Udivitrand). Pumice soils of this region are free-draining and resistant to re-wetting (Gillingham *et al.* 1974), increasing the severity of droughts which can occur from mid-summer to early winter. Large

Table 2. *Monthly and 30-year mean rainfall for Palmerston North and Taupo, New Zealand*

	Rainfall (mm)			
	Palmerston North		Taupo	
Month	1992/93	Mean	1992/93	Mean
August	110	84	144	110
September	88	82	77	94
October	86	85	91	102
November	61	73	77	90
December	167	93	149	117
January	54	66	23	83
February	44	65	65	85
March	80	73	124	77
April	54	70	35	82
May	78	94	130	94
June	103	88	172	109
July	12	93	29	112
Total	935	964	1116	1155

Table 1. *Comparison of soils and cultural practices at the Palmerston North and Taupo sites*

	Palmerston North	Taupo
Soil	Manawatu sandy loam	Taupo silty-sand
Type	(Dystric fluventic eutrochrept)	(Typic Udivitrand)
pH	6·3	6·6
Olsen P (ppm)	66	19
C:N ratio	14	18
Elevation (m asl)	33	475
Sowing date	April 1986	October 1985
Pasture sown	(Roa tall fescue 20 kg/ha, Mt Barker subterranean clover 10 kg/ha)	(Roa tall fescue 26 kg/ha, Pitau white clover 3 kg/ha, Pawera red clover 5 kg/ha)
Annual fertilizer	Longlife superphosphate (0, 10, 0, 8) 250 kg/ha	Superphosphate (0, 9, 0, 12) 125 kg/ha
Farming enterprise	Town milk supply dairy farm	Traditional sheep/beef farm

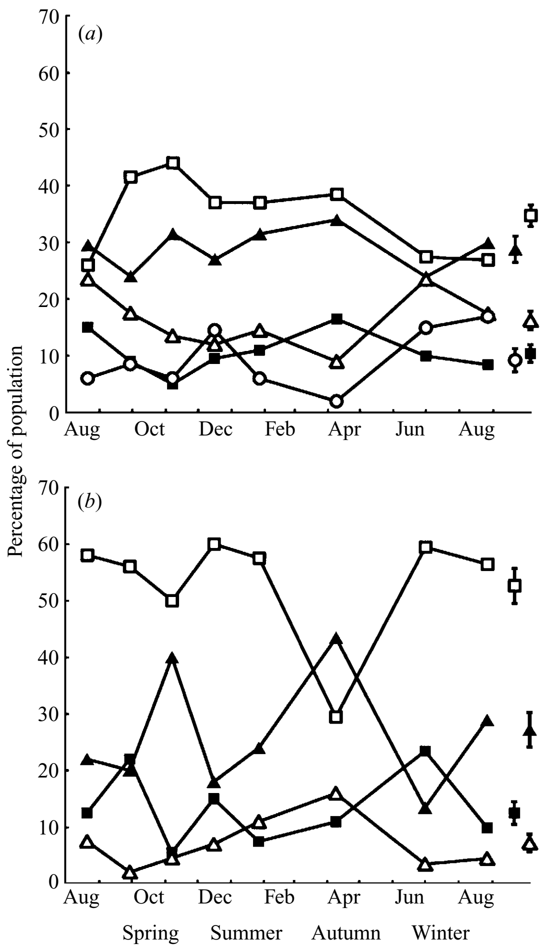

Fig. 1. Seasonal variation in the contribution of plants of various orders of branching to the structure of grass populations averaged over two sites for (*a*) tall fescue and (*b*) perennial ryegrass (■ first-order, □ second-order, ▲ third-order, △ fourth(+)-order, ○ fifth(+)-order (tall fescue only). Vertical bars are ±S.E. (15 D.F.) located at the mean for each order.

infestations of the insect pests Argentine stem weevil (*Listronotus bonariensis* Kuschel) (Prestidge & van der Zijpp 1985) and grass grub (*Costelytra zealandica* White) (Gordon & Kain 1972), combined with lower soil fertility and a small earthworm population, often results in the failure of newly sown pastures and reversion to less productive browntop (*Agrostis capillaris* L.)-dominant swards (Clare 1972; Gordon 1972; Baars *et al.* 1975). The aim of pasture management at Taupo was to graze continuously with sheep or cattle during lambing and calving from early to mid-spring (1 September to 31 October), then graze intermittently with sheep or cattle as pasture height approached 7–10 cm for the remainder of the year, saving pasture for calving or lambing by ceasing grazing from late autumn. However, in the measurement year, lack of growth due to a summer drought precluded grazing past late summer.

As no perennial ryegrass was sown at either site, all perennial ryegrass present were volunteers from buried seed or old surviving turf and were of unknown genetic background.

Pasture density

One hundred, 50 mm diameter pasture cores, were taken at random from each site on three occasions, September 1992, January 1993 and August 1993. Numbers of tillers of tall fescue, perennial ryegrass, other grass species, and growing points of white clover, other legumes and other species were recorded for each core.

Climate

Data collected from weather stations within 1 km of each site indicate that on average the Palmerston North site has mild winters (mean grass minimum temperature 2·0 °C, cf. 0·2 °C at Taupo) and cooler summers (mean maximum air temperature 21·8 °C, cf. 22·7 °C at Taupo). In the year of sampling, the climate was generally cooler than average (by 1·6 °C mean annual temperature) at both sites. Mean annual rainfall is 20% higher at Taupo than at Palmerston North (Table 2), but in the sampling year, the summer was 30% drier (late December to mid-March) at Palmerston North compared to 50% less rainfall at Taupo.

Plant sampling

Measurement of plant characteristics took place on eight occasions between August 1992 and August 1993, using the method of Brock *et al.* (1988). The RGDC pasture at Palmerston North was 6 years old, and was sampled immediately prior to grazing (every second grazing in spring and summer). Sampling of the 7-year old CGSB Taupo pasture was carried out at approximately the same time as at Palmerston North, but did not coincide with specific grazing events. On two occasions (mid-spring and early summer), the CGSB pasture was only sampled for tall fescue.

At each sampling, three turves 300 × 300 mm, located at random, were removed to a depth of 50 mm from each site. Soil was washed from each turf, and tall fescue and perennial ryegrass plants removed intact from the vegetation mat. Plants cut by the quadrat edge were discarded. In total, 40 plants of each species were taken randomly from the three turves for detailed examination in the laboratory.

The complexity of plant stem branching was classified using the method of Brock *et al.* (1988) developed for white clover. Plants with a single

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Table 3. *Effect of rotational grazing with dairy cattle (RGDC) or continuous grazing with sheep and beef cattle (CGSB) on the percentage distribution of perennial ryegrass and tall fescue tillers among eight tiller density classes (+ and − indicate values significantly higher or lower than the expected mean by chi-squared analysis on the number of values in each category)*

	Tiller density class (/m²)						Mean density (/m²)	
Species/site	0	1–2500	2501–5000	5001–7500	7501–10000	10001+	Tillers	Plants
Tall fescue								
RGDC	56·6+	27·0	8·3−	2·7−	2·0−	3·3−	1460	325
CGSB	12·7−	25·0	23·0+	15·3+	10·0+	14·0+	5140	930
Expected mean	34·6	26·0	15·7	9·0	6·0	8·7	—	—
Ryegrass								
RGDC	64·3	15·7	6·0	4·3	4·0	5·7	1900	460
CGSB	58·3	19·3	8·0	4·7	4·3	5·4	2090	470
Expected mean	61·3	17·5	7·0	4·5	4·2	5·5	—	—

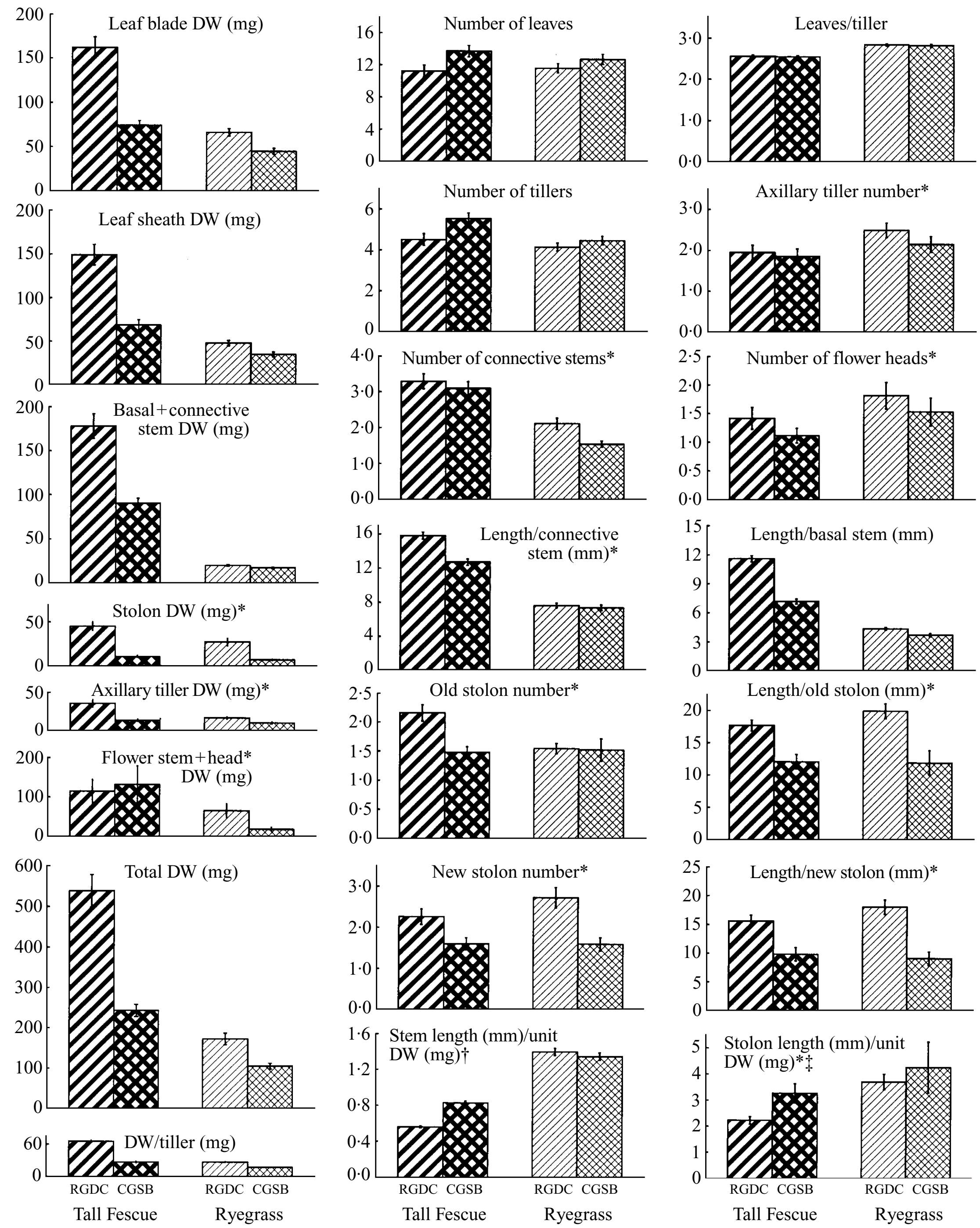
unbranched stem were classified as first-order, those with a single hierarchy of branching as second-order, those with two hierarchies of branching as third-order, and so on. Thus a third-order plant, for example, was always composed of a single primary stem and a variable number of secondary and tertiary stems. However, so that stems at the same stage of development could be compared across plant branching orders, stem hierarchies within plants were ordered by morphological position such that position 1 corresponded with the most recently formed stem hierarchy. For instance, for a third-order plant, the tertiary stems were classified as stem hierarchical position 1, the secondary stems as hierarchical position 2, and the primary stem as hierarchical position 3 (see Table 7). A total of 1200 plants (8317 stems) were described and dissected.

Plants were described using the following definitions of components (Brock & Fletcher 1993; Brock *et al.* 1996). The basic 'tiller' consisted of an active apical meristem ('growing point'), subtending leaves and stem. 'Axillary' tillers were young tillers without any discernible stem, developing in the axil of an existing leaf on the parent tiller, and still dependent on the parent tiller. Stem was categorized into several classes. 'Basal' stem was the predominant type, consisting of closely spaced nodes separated by short internodes and was situated proximal to an active growing point. Basal stems for which there was no active growing point were termed 'connective' stems, and maintained structural links between groups of active tillers in the branching system. Internodes within the basal stem that elongate by intercalary meristematic activity (Barnard 1964) to elevate the growing point either for survival or reproductive development, were termed 'stolon'. This was further classified as 'new' (soft and white, to indicate current formation) or 'old' (hard and discoloured, formed in the past) stolon. The flower head (where present), included all stem material above the node below the lowest swollen node (joint) on the flower head, once it had emerged from the leaf sheath. Remaining stem was removed from the sheath and included with stolon. Tall fescue also has the ability to form horizontal 'rhizomes' (Jernstedt & Bouton 1985) from older dormant axillary meristems below the leaf zone. These appear as rounded swellings or 'buds', and develop extravaginally as rhizomes at right angles to the parent stem. Roots were also classified as 'new' (white) or 'old' (discoloured) (Jacques & Schwass 1956).

Number and length (where appropriate) of all components was recorded for each tiller and connective stem. Numbers of buds were recorded in January (summer), April (autumn) and August (winter). Plants were then dissected into leaf blade, leaf sheath (including any unemerged leaf blade or inflorescence prior to emergence), axillary tillers, basal stem (including connective), stolon/rhizome (new and old) and flower head, and the dry weight (DW) of each fraction determined.

Data analysis

The mean characteristics of individual plant components were calculated for all stems (tillers and connective stems) classified by plant order and morphological age (see Table 7). The characteristics of each whole plant (counts and DW) were derived and the mean and standard error calculated for all time × site × species treatment combinations. The number of plants with the various components in each treatment combination was also recorded, and calculated as a percentage of the total number of plants in Tables 5 and 6 and Fig. 3. The distribution of the number of plants amongst the various plant orders was analysed by analysis of variance, and the results presented on a percentage of the population basis (Fig. 1). Pasture structure, as described by the



* For proportions of plants with this character, see Table 5; † including basal and connective stem; ‡ including old and new stolon and rhizomes.

Fig. 2. Differences between sites (management and environment) on the mean characteristics of plants of tall fescue and perennial ryegrass under rotational grazing with dairy cattle (RGDC) and under continuous grazing with sheep and beef cattle (CGSB). Tall fescue/RGDC ◪; tall fescue/CGSB ◘; perennial ryegrass/RGDC ▨; perennial ryegrass/CGSB ⊠. Vertical bars are ±S.E. (319 D.F.).

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dispersion of tillers and growing points, was analysed by chi-squared analysis on the counts of observations in the various categories, which have been expressed as a percentage of total counts in Table 3.

RESULTS

Pasture density

The rotationally grazed cattle pastures at Palmerston North (RGDC) were open and of low density (Table 3), were dominated by tall fescue, perennial ryegrass and white clover (1350/m^2), with a small contribution from other grasses (1110/m^2 e.g. *Holcus lanatus*, *Bromus mollis* and *Poa* spp.) and other species (340/m^2). There was little evidence of the subterranean clover sown at Palmerston North. At Taupo (CGSB), pastures were dominated by tall fescue, and all species were denser (white clover, 2040/m^2; other grasses, 4070/m^2; other species, 1170/m^2), but the density of perennial ryegrass was similar to Palmerston North.

Tall fescue and perennial ryegrass plant densities (Table 3) were calculated from their tiller densities and tillers/plant (Fig. 2). As there was relatively little difference in tillers/plant, plant density paralleled tiller density resulting in greater tall fescue plant density under CGSB than RGDC, while perennial ryegrass densities were similar.

Population structure

The highest order of branching encountered was seventh-order for tall fescue and fifth-order for perennial ryegrass. For analysis, as higher order plants were uncommon, these higher orders were grouped with fifth-order plants and fourth-order plants, for tall fescue and perennial ryegrass, respectively (Table 4, Fig. 1). On average, second-order plants were the most prevalent for both species, followed by third-order plants (Table 4). Both species had a similar proportion of first-order plants but tall fescue had a greater proportion of higher order plants but lower proportion of second-order plants than perennial ryegrass. Tall fescue under CGSB had higher proportions of fourth-, fifth- and higher order plants and fewer first-order plants than under RGDC.

Table 4. *Contribution of plants* (%) *of various orders of branching* (±S.E.) *to the structure of grass populations for tall fescue and perennial ryegrass under rotational grazing with dairy cattle* (*RGDC*) *or continuous grazing with sheep and beef cattle* (*CGSB*) (*fifth-order for tall fescue includes sixth- and seventh-order plants; fourth-order for perennial ryegrass includes fifth-order plants*)

	Tall fescue		Perennial ryegrass	
Plant order	RGDC	CGSB	RGDC	CGSB
1st	14±2·2	7±1·3	15±2·8	10±2·6
2nd	37±3·1	33±2·1	52±4·5	54±4·4
3rd	30±2·8	28±3·9	26±4·8	29±3·5
4th	13±2·1	20±2·1	7±2·1	7±2·6
5th	6±1·4	12±3·4	—	—

Table 5. *Percentage of plants with connective stems, stolons, flower heads and axillary tillers for tall fescue and perennial ryegrass under rotational grazing with dairy cattle* (*RGDC*) *or continuous grazing with sheep and beef cattle* (*CGSB*)

	Tall fescue		Perennial ryegrass	
Character	RGDC	CGSB	RGDC	CGSB
Connective stems	65	66	39	40
Stolons				
Old	63	27	37	13
New	47	16	44	17
Total	78	34	65	27
Flower heads	4	2	16	5
Axillary tillers	19	20	49	43

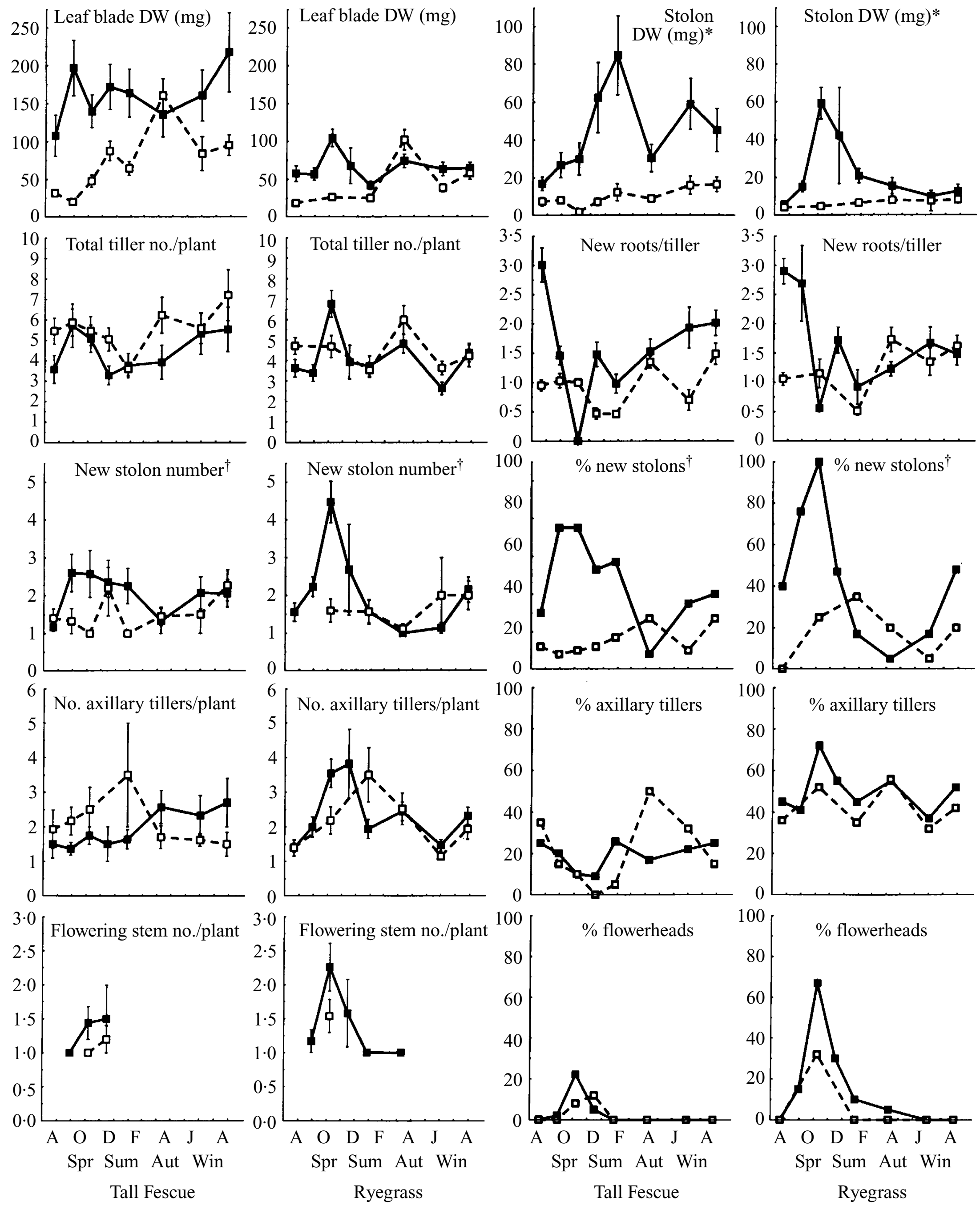
Seasonal variation in the distribution of plant orders was similar at both sites, with perennial ryegrass exhibiting greater variation (Fig. 1*b*) than tall fescue (Fig. 1*a*). Changes in perennial ryegrass distribution patterns showed two periods of variation, in late spring–early summer, and again from mid-autumn to mid-winter (Fig. 1*b*). In the first instance, first- (and second-) order plants declined while third-order increased, but in the second instance, second-order declined while the third-order plants increased.

Plant structure

Species and site

Plants were generally twice as heavy under RGDC than under CGSB, with the effect being greater for tall fescue than for perennial ryegrass (Fig. 2). Main plant components (leaf blade and sheath, basal and connective stem) followed a similar pattern, but for the smaller components, stolon was three times greater for both species under RGDC, and flower DW was lower in perennial ryegrass, particularly under CGSB.

Tall fescue plants under CGSB had more tillers than under RGDC or perennial ryegrass, but with perennial ryegrass having more leaves/tiller than tall fescue, species differences in number of leaves/plant were reduced. Numbers of connective stems and their length (Fig. 2) and the proportion of plants with connective stems (Table 5) were greater for tall fescue than perennial ryegrass. Tall fescue stems were thicker (length/unit DW) than perennial ryegrass. Number



* For proportions of plants with this character, see Table 5; † including new rhizomes.

Fig. 3. Seasonal variation in some of the mean characteristics of plants of tall fescue and perennial ryegrass under rotational grazing with dairy cattle (RGDC) (–■–) and under continuous grazing with sheep and beef cattle (CGSB) (--□--). Vertical bars are ±S.E. (39 D.F.).

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Table 6. *Proportion of tall fescue plants with rhizome buds and their mean number/plant under rotational grazing with dairy cattle (RGDC) or continuous grazing with sheep and beef cattle (CGSB)*

Season	Plants with buds (%)		Mean buds/plant	
	RGDC	CGSB	RGDC	CGSB
Summer	24	10	1·5 ± 0·27	1·0
Autumn	35	75	1·5 ± 0·25	1·4 ± 0·13
Winter	8	10	1·0	1·0

and length of stolons and the proportion of plants with stolons was greater under RGDC than under CGSB which, combined with greater stolon thickness, resulted in significantly greater stolon DW. Both species had similar proportions of plants with new stolons, but tall fescue had more plants with old stolons than perennial ryegrass. Perennial ryegrass had twice the proportion of plants with axillary tillers, and formed more flower heads than tall fescue (Table 5).

Seasonal variation

During reproductive growth in spring, perennial ryegrass under RGDC showed large increases in numbers of tillers, axillary tillers and new stolons/plant and the proportions of plants with new stolons and flower heads, but only small increases in plant DW (e.g. leaf DW) (Fig. 3). For tall fescue, the pattern was broader and lower, continuing beyond flowering into mid-summer (number of new stolons and the proportion of plants with new stolons). Under CGSB, there was little variation in spring for both species, only in autumn was there an increase in leaf DW and tiller numbers, due to lack of grazing during the drought.

Table 7. *Distribution of the number of tillers and connective stems (in parentheses) in the total population of the tall fescue and perennial ryegrass plants sampled (both sites combined), classified by morphological position within plant orders*

Morphological position	Plant branching order							Total			
	1	2	3	4	5	6	7	Tillers	%*	Connective stems	%†
Tall fescue											
1 (youngest)	68 (0)	466 (68)	552 (41)	364 (13)	119 (3)	41 (0)	6 (0)	1616	50	143	8
2		147 (80)	366 (177)	407 (92)	211 (34)	80 (14)	17 (0)	1228	38	397	24
3			48 (139)	135 (161)	114 (99)	33 (32)	19 (2)	349	11	433	55
4				12 (94)	13 (118)	20 (42)	5 (6)	50	1	260	84
5					0 (45)	7 (44)	0 (4)	7	< 1	93	93
6						0 (15)	0 (2)	0	0	17	100
7 (oldest)							0 (2)	0	0	2	100
Total	68 (0)	613 (166)	966 (357)	918 (360)	457 (299)	181 (147)	47 (16)	3250		1345	
%*	2	19	30	28	14	6	1				
Axillary tillers	6	27	75	81	31	20	4	244			
%‡	9	4	8	9	7	11	9	8			
Ryegrass											
1 (youngest)	71 (0)	743 (28)	465 (3)	108 (0)	3 (0)			1390	57	31	2
2		225 (73)	470 (82)	188 (22)	20 (1)			903	37	178	16
3			60 (93)	61 (65)	13 (3)			134	6	161	55
4				3 (38)	1 (2)			4	< 1	40	91
5 (oldest)					0 (2)			0	0	2	100
Total	71 (0)	968 (101)	995 (178)	360 (125)	37 (8)			2431		412	
%*	3	40	41	15	1						
Axillary tillers	25	239	244	117	5			630			
%‡	35	25	35	33	14			26			

* % of total tillers; † as a % of total stems (tillers + connective stem) in age group; ‡ % of tillers with axillary tillers in each branching order.

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Pattern of root appearance was similar in both species, but exhibited greater variation under RGDC than under CGSB, particularly from late winter to early summer (Fig. 3). While the number of rhizome buds forming on the bases of tillers or stems in tall fescue were low and did not vary significantly, there was a pronounced seasonal peak in the proportion of plants producing buds in autumn, particularly under CGSB (Table 6).

Tiller and stem characteristics

When stems were classified according to morphological position and plant branching complexity, few differences existed between sites for each species, but there were differences between species (Table 7). Of the stems, tall fescue had 29% classified as connective, compared to only 14% for perennial ryegrass. Most tillers were associated with second-, third- and fourth-order plants in tall fescue (77%) and with second- and third-order plants in perennial ryegrass (81%). Many of these species differences were associated with greater plant complexity in tall fescue. Over 50% of tillers were in the youngest morphological position, rising to *c*. 90% when including the two youngest positions. The proportion of connective stems increased with morphological position and plant branching order complexity, with virtually all the stems beyond the fourth morphological position being connective (85%+). Axillary tiller formation in tall fescue was low and generally evenly associated with all plant orders, but was high in perennial ryegrass over all plant orders with 35% occurring in first order plants (Table 5). Most axillary tillers (59%) were associated with the second morphological position (data not shown).

DISCUSSION

Grazing management, pasture density, plant size and morphology

The chief objective of pasture management where grazing animals must be maintained *in situ* all year, is to optimize animal feed requirements rather than maximize herbage accumulation (Brock & Hay 1993). To accomplish this and maintain high feed quality without penalizing production, the standing pasture must be maintained at between 1000 and 2500 kg DM/ha (Chapman & Clark 1984). Within these limits, method of defoliation has little effect on total production but has large effects on the number and size of plants and their components, with an inverse size/density compensation relationship operating to ensure maximum use of environmental resources (Chapman & Lemaire 1993). While differences in environmental conditions (nutrients, temperature and water) may have set different limits to total productivity at the two sites, the contrasting management systems employed at each site both aimed to optimize productivity by keeping within the optimum yield range. Management at Palmerston North opted for infrequent defoliation by rotationally grazed dairy cows as the most suitable, while Taupo used a combination of continuous grazing and short rotations with sheep and cattle. Previous grazing management studies on perennial ryegrass at Palmerston North (Brock & Fletcher 1993; Brock *et al*. 1996) showed a 75–140% greater plant DW in favour of rotational grazing over continuous grazing. As this is similar to the 65–120% differences recorded between sites for both species in this study (Fig. 2), grazing management would appear to be the major determinant of plant DW.

As a consequence of these differences in grazing management, tall fescue developed lower tiller and plant density under rotational grazing at Palmerston North, compared to more than three times higher tiller and plant density developed under continuous grazing at Taupo (Table 3). This was also reflected in individual plant DW where tall fescue plants were 120% heavier at Palmerston North (Fig. 2). In the case of volunteer perennial ryegrass (of unknown genetic parentage) the reaction was different from that of tall fescue. Comparing the two sites, perennial ryegrass tiller and plant densities were the same, and differences in individual plant DW (65%) were smaller than for tall fescue. Perennial ryegrass does not perform well in the Taupo area (Baars *et al*. 1975; Moloney *et al*. 1993), due to low tolerance of grass grub attack (East *et al*. 1980) and severe drought that can occur in these shallow, friable (hydrophobic) pumice soils (Gillingham *et al*. 1974). This would suggest that tall fescue would be more competitive in this environment and occupy more space and develop greater plant density aided by the frequent defoliation regime employed. At Palmerston North, despite the more favourable climatic and edaphic conditions, perennial ryegrass failed to respond to the same extent as tall fescue, possibly because the laxer rotational grazing management favoured the growth of larger, more competitive, tall fescue plants.

Despite such large differences generated in plant DW by grazing management, tiller characteristics of plants were little affected (Fig. 2). Within species, leaves and tillers per plant were only slightly higher under CGSB, whereas comparing species, more leaves/tiller in perennial ryegrass was counterbalanced by a higher number of tillers/plant in tall fescue. While tall fescue had more branching, perennial ryegrass produced more flower heads.

Population structure and seasonal growth processes

The clonal growth process of continual fragmentation of plants, caused by growth at the apex and death of basal stems, results in a dynamic though relatively stable population of plants distributed among the various orders of branching complexity (Brock *et al.* 1988). However, tall fescue plants had a far greater number of branches (Fig. 2) and proportion of branched plants (Table 5), resulting in a higher proportion of more complex plants than perennial ryegrass (Table 4). Nevertheless, all active growth was confined to the three youngest orders of tiller in both species (Table 7), with the higher order of branches serving as structural connections between groups of tillers.

That tall fescue plants have proportionately more stem material (old stolon, basal and connective stem, Fig. 2) and attain a greater complexity than perennial ryegrass (7th cf. 5th-order respectively, Table 7), indicates a greater persistence of older stems, possibly through differences in resistance to microbial attack and degradation. Quality of organic matter, primarily affected by C, N and P concentrations and their ratios, determines to a large extent the decomposition rates of plant material (Enriquez *et al.* 1993), and may be reflected in a slower breakdown of stem material in tall fescue than in perennial ryegrass. Turnover of tall fescue plants through the various branching orders would therefore be slower, providing a more stable population structure than in perennial ryegrass. As a consequence, this also suggests that tall fescue plants live longer than perennial ryegrass, compensating for the three times lower tillering rate (axillary tiller formation, Table 7) in tall fescue than in perennial ryegrass, and could also be related to the low proportion of plants producing flower heads (Fig. 3). However, as leaves of both species are removed at similar intervals by grazing, tall fescue tillers must have considerably greater longevity in order to maintain similar sward productivity as perennial ryegrass. Tall fescue is known to have larger tillers by producing larger leaves with a greater life span but at a lower leaf appearance rate and lower site filling rate than perennial ryegrass, all contributing to the low tillering rate of tall fescue (Norris 1982; Tavokoli 1993).

Previous studies on white clover (Brock *et al.* 1988), perennial ryegrass and cocksfoot (Brock *et al.* 1996), also revealed seasonal differences in fragmentation rate with a major period of instability during mid-spring, where accelerated decay of old stem and stolon resulted in large increases in proportions of first-order plants and a corresponding decrease in third-order plants. Greater growth over summer returned the population to its former distribution. This pattern appeared to be repeatable in most years. By contrast, the current study showed the reverse, indicating there was no spring fragmentation of plants, rather there was an increase in plant complexity possibly associated with increased post-flowering tiller formation (Fig. 1), many of which did not survive and plant complexity rapidly decreased. A similar increase in complexity of perennial ryegrass plants followed again in mid-autumn, possibly stimulated by strong growth as a result of high levels of soil mineral N which will have accumulated during the dry summer (January–February, Table 2) (Hoglund & Brock 1978) and made available by higher rainfall in March. Fewer measurements over the late summer and autumn period limit interpretation of possible causes for the changes in plant complexity at this time of the year. Unlike white clover, perennial ryegrass and cocksfoot, tall fescue showed little seasonal variation at either site. Resistance to stem decay and fragmentation, slow tillering rate and greater tiller longevity would all contribute towards a stable plant population distribution and reduce seasonal variation.

As discussed above, grazing management systems are designed to regulate feed supply quantity and quality to the grazing animal, by maintaining available herbage within a range consistent with that aim (Chapman & Clark 1984). As such, seasonal variation in canopy height or yield on offer at grazing is minimal, as reflected in the small seasonal range of leaf (and total) DW/plant (Fig. 3). The only exception was the large increase in leaf of both species during the autumn at Taupo, where because of the dry late summer, pastures had been placed under an extended grazing rotation to conserve feed, and as a consequence of the wet early autumn (March, Table 2), considerable growth had occurred before sampling in April and subsequent grazing.

The most significant feature of plant growth under seasonal influence was stolon formation, and in this the two species differed in their seasonal expression (Fig. 3). Stolons can be formed at any time of the year, but in perennial ryegrass it was closely related to reproductive development, in that the number of new stolons/plant and the proportion of plants with stolons showed a definite spring peak. This was more pronounced at Palmerston North under rotational dairy grazing where successful flower head formation was greater than under the continual grazing by sheep and cattle at Taupo. Similar results had been obtained for sheep-grazed systems at Palmerston North (Brock *et al.* 1996), which showed greater flower head formation under rotational grazing than under set stocking. In tall fescue the spring peak was lower and broader and not as clearly related to flowering, which was much reduced. Both species showed a decline in stolon activity in autumn, and an increase in late winter possibly in response to burial by treading and earthworm casting during the cool, wet winter (Brock *et al.* 1996).

Initiation of new roots may be influenced by the level and allocation of available reserves within the plant in both species. As reproductive development occurs, root growth is proportionately reduced (Troughton 1978) because of changes in assimilate partitioning between root and shoot (Parsons &

Robson 1981). A similar pattern is evident in Fig. 3. High root production in late winter had virtually ceased by mid-spring, as the increasing spring temperatures and high demands caused by the onset of reproductive growth caused a switch in allocation of reserves away from roots to the emerging flower head. This was most apparent at Palmerston North, where the rotational grazing system allowed a greater expression of growth potential compared to the tighter control of continuous grazing at Taupo at that time.

It has been reported that tillering in tall fescue has a strong seasonal pattern, with high activity in autumn in response to shorter daylength and dormancy over summer (Templeton *et al*. 1961; Kasperbauer 1990). Such strong patterns were not evident in this study and, while there was a suggestion of this pattern at Taupo for the proportion of plants with axillary tillers (Fig. 3), this could also be attributed to the improved growth conditions brought about by the change in grazing management and high soil N mediated by the rainfall pattern discussed earlier. Under dairy grazing at Palmerston North, there was little seasonal fluctuation in either the numbers of axillary tillers/plant or the proportion of plants with axillary tillers. The temperate climate of this study, may have a more uniform annual pattern of tillering compared to those reported under the greater environmental extremes experienced in continental climates of the USA (Lopez *et al*. 1967).

Stolons and rhizomes

Previous studies have indicated that perennial ryegrass (Minderhoud 1980; Brock & Fletcher 1993) and cocksfoot (Brock *et al*. 1996) can elongate the internodes of basal stem to elevate the growing point towards the top or edge of the tuft to reach a more favourable light environment to ensure survival of the tiller. Such elongation normally takes place near the tip of the stem within the zone bearing active leaves. This can occur at any time of the year, but reaches its greatest expression during reproductive growth in spring for elevation of the flower head. Vegetative expansion of tufts is largely accomplished by tillering, and is little affected by stolon formation. The propensity to form stolon is under some degree of genetic control in perennial ryegrass, and is not present in all genotypes (Harris *et al*. 1979). Tall fescue can also develop stolons, but in addition dormant axillary buds below the leaf-bearing zone can develop at right angles to the parent stem to form horizontal underground rhizomes (Jernstedt & Bouton 1985). This does not occur in all genotypes and has also been shown to be under genetic control (D'Uva *et al*. 1983). Anatomically stolons and rhizomes are identical (Troughton 1957; Heath *et al*. 1973), and are differentiated only by their orientation (D'Uva 1982, cited by De Battista & Bouton 1990). However, they tend to be expressed at different times of the year, suggesting different functions for these components. As with the other grasses, the main period of stolon formation in tall fescue commences in spring with reproductive growth, whereas the spherical rhizome buds form mainly in the late summer–autumn (Table 6) (Lopez *et al*. 1967) and their outgrowth can occur any time through to the following spring. These appear to be associated primarily with expansion, as they can extend several centimetres beyond the edge of the tuft.

In this study no differentiation was made between extended stolon or rhizome in tall fescue. Most of the new stolon category during spring–summer (September–February) would be stolon, but could include a proportion of rhizome in the rest of the year (Fig. 3). Old stolon, most surviving from the previous season, would be a mixture of both.

Growth potential as regulated by grazing management can affect stolon and rhizome development (Bouton *et al*. 1989). There were more stolons/plant and plants with stolons under RGDC at Palmerston North than under CGSB at Taupo (Table 5, Fig. 3). Similarly, there were more plants developing rhizome buds in summer under RGDC than under CGSB (Table 6). In autumn there was a dramatic reversal with more than twice as many plants under CGSB developing rhizome buds, possibly due to the long period without grazing in this system at this time, in which plants grew to a greater size (Fig. 3) and more plants developed rhizome buds. This may have been due to competition for light, as Mitchell & Coles (1955) showed that shading the base of tillers reduces tillering rate in grasses, and D'Uva (1982) found that tall fescue diverted resources away from tillering to rhizome bud formation under similar circumstances. This move to rhizome bud development in summer–autumn may also be responsible in part for the better persistence of tall fescue during drought (Brock 1982; Norris 1982), than perennial ryegrass. Growing points and tillers developing below ground as rhizomes would be protected from the high temperatures that can be experienced by growing points at or above the soil surface (Weaver 1963), similar to the effects of enhancing stolon and growing point survival by burial in white clover (Brock & Moon 1994).

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