New Zealand Journal of Agricultural Research, 2002, Vol. 45: 129–137
0028–8233/02/4503–0129 $7.00/0 © The Royal Society of New Zealand 2002

Flowering propensity of two New Zealand perennial ryegrass cultivars originating from different ecotypes

I. BAHMANI
E. R. THOM*
Dexcel
Private Bag 3221
Hamilton, New Zealand

C. MATTHEW
Institute for Natural Resources
Massey University
Private Bag 11 222
Palmerston North, New Zealand

G. LEMAIRE
Institut National de la Recherche Agronomique
Unité d'Ecophysiologie des Plantes Fourragères
F-86600 Lusignan, France

Abstract Tiller turnover at flowering is an integral component of the perennation strategy in many temperate grasses. While vernalisation and daylength requirements for flowering, and cultivar flowering date characteristics are well known, there is little information on the effects of other factors, such as N fertiliser and grazing intensity, on flowering behaviour. We compared tiller dynamics of early flowering, endophyte-free, perennial ryegrass cultivars ('Ellett' and 'Grasslands Ruanui') under two N fertiliser and irrigation levels, and dairy cow grazing. In the first flowering period after sowing (October 1996–January 1997), 'Ellett' ryegrass averaged 19.5% reproductive tillers in the total tiller population, while 'Grasslands Ruanui' ryegrass averaged 13.0%. In the second season (September 1997–January 1998), 17.1% of 'Ellett' tillers were reproductive, compared with only 7.8% for 'Grasslands Ruanui'. There was a cultivar × N interaction in summer 1997/98, with N increasing the percentage of reproductive tillers in 'Ellett', but decreasing them in 'Grasslands Ruanui'. The irrigation treatment did not affect flowering behaviour. In another study, lax grazing of endophyte-infected 'Ellett' ryegrass resulted in 7% of total tillers flowering compared with 34% under hard grazing. The importance of considering the effects of latitude on flowering behaviour is discussed.

Keywords 'Ellett' ryegrass; 'Grasslands Ruanui' ryegrass; *Lolium perenne*; reproductive tillers; vegetative tillers; grazing; latitude; nitrogen

INTRODUCTION

This paper describes two experiments. They are part of a series of studies on tillering in 'Grasslands Ruanui' and 'Ellett' perennial ryegrass (*Lolium perenne*) cultivars. One was conducted at the Dairying Research Corporation, now Dexcel, from 1996 to 1998. The hypotheses tested were that modern New Zealand perennial ryegrass cultivars exhibit seasonal patterns of tiller replacement different from those of older cultivars, and that they could, therefore, respond positively to grazing management that allowed full expression of these differences. In this experiment, 'Ellett', an early release based on the 'Mangere' ecotype, was selected as representative of modern ryegrass material, and 'Grasslands Ruanui' as representative of older material. The other experiment was conducted during 1987/88 as part of a larger research programme (Matthew 1992) and explored some possible interactions of grazing management and reproductive tillering by testing the effects of different grazing intensities on reproductive tillering of 'Ellett' ryegrass.

Other papers based on the first-mentioned experiment have shown lower DM production but higher tiller population density in the older material (Bahmani et al. 1997, 2001). These traits were a result of lower leaf elongation rate and the consequent slower recovery of leaf area index after

---

*Author for correspondence.
Email: errol.thom@dexcel.co.nz

A01037; published 30 September 2002
Received 12 November 2001; accepted 10 May 2002

defoliation in 'Grasslands Ruanui' than in 'Ellett' (Bahmani et al. 2000a). In another experiment with single plants arranged in mini-swards, 'Ellett' had a higher percentage of reproductive tillers than 'Grasslands Ruanui', and both cultivars showed a reduction in weight of reproductive tillers in response to shade, while weight of vegetative tillers was unaffected (Bahmani et al. 2000b).

Flowering behaviour of perennial ryegrass cultivars is important to agronomists and in farm practice. Studies of flowering in grasses have typically focused on vernalisation and daylength requirements for flower initiation as determinants of flowering date (e.g., Cooper 1960; Evans 1960; Templeton et al. 1961; Aitken 1974). Also important when interpreting flowering behaviour are the implications for perennation strategy. Tiller population turnover in grass swards is often very high during the flowering period. For example, diagrams of tiller cohort survival for timothy (*Phleum pratense*) in Britain show almost complete replacement of the tiller population over 1 month in mid summer (Jewiss 1966). A similar turnover event, though less pronounced, was also noted in perennial ryegrass by Colvill & Marshall (1984), Matthew et al. (1989), Hernández Garay et al. (1997), and Korte (1986). However, the data are not consistent because in the establishment year of the study by Korte (1986) and in data of Matthew (1992) for 'Grasslands Ruanui' ryegrass, no such turnover event occurred.

To rationalise these conflicting observations, Bahmani et al. (2000b), Matthew (1992), and Matthew et al. (1993) suggested that different perennial ryegrass cultivars have different perennation strategies. These should reflect differences in percentage of total tillers flowering, and in post-flowering daughter tiller production from decapitated stubs of flowering tillers. The same workers suggested that tiller population turnover associated with flowering is less strongly expressed in the first year after sward establishment than in subsequent years. To test these hypotheses, percentage of tillers flowering was monitored over two consecutive seasons in 'Ellett' and 'Grasslands Ruanui' perennial ryegrass.

MATERIALS AND METHODS

Experiment 1

The details of site, experimental design and methods, grazing management, maintenance fertiliser inputs, and insect and weed control have been reported previously by Bahmani et al. (2001). Briefly, the experiment was located at Dexcel, Hamilton, New Zealand (37°47′S, 175°19′E, 40 m a.s.l). The trial design was a $2 \times 2 \times 2$ split-plot factorial with main plots (6 × 12 m) of endophyte-free perennial ryegrass cultivars 'Ellett' and 'Grasslands Ruanui' randomly arranged in four blocks. Nitrogen (N) fertiliser (30 kg N ha^{-1}) applied as urea to half of the main plot area (chosen randomly) following each grazing, represented the subplot treatment (3 × 6 m). A total of 240 kg N ha^{-1} was applied from September 1996 to May 1997, and 180 kg N ha^{-1} from October 1997 to April 1998. Two irrigation treatments (without irrigation and with irrigation) represented the sub-subplot. Dairy cows, at a farm stocking rate of 3.2 cows ha^{-1}, grazed the plots for the first time on 24 September 1996. Grazing intervals were 29 (spring 1996), 33 (summer 1996/97), 39 (autumn 1997), 70 (winter 1997), 33 (spring 1997), 47 (summer 1997/98), and 23 (autumn 1998) days.

Measurements

Ryegrass tiller dynamics were monitored for 2 years using three fixed circular (64 mm diam.) frames per subplot, randomly located over ryegrass drill rows in September 1996. On 17 September 1996, all live tillers within each frame were counted and marked with rings made from short lengths of coloured split plastic tube (2–5 mm diam.). At each assessment, new tillers were tagged with coloured plastic tubing. At intervals of c. 30, 25, and 45 days in spring, summer, and autumn/winter, respectively, new tillers were counted and tagged. The colour of the tubing used was unique to each tagging date. Tags were removed from dead tillers and counted. Vegetative tillers were re-classified as reproductive when the first node became visible above ground level. Reproductive tillers appeared from September to January (spring to mid summer).

Experiment 2

The trial was located at Palmerston North, New Zealand (40°23′S, 175°37′E, 40 m a.s.l.) on a Tokomaru silt loam, a Argillic-fragic Perched-gley Pallic Soil in the New Zealand classification (Hewitt 1998) or a Typic Fragiaqualf in soil taxonomy (Soil Survey Staff 1990). The trial design was a Latin square with four grazing treatments applied to 10 × 10 m plots that were replicated 4 times and were located on endophyte-infected 'Ellett' ryegrass that was sown with white clover in March 1983. Selective herbicides were used to remove white clover from the pasture in July 1986. After removal of white clover, nitrogen was applied every 3 weeks as urea at 15 kg N ha^{-1}. Contrasting grazing intensities (lax, L and hard, H) were applied to two sets of treatment plots from October 1986 until October 1987. One plot from each treatment set was then changed to the opposite treatment giving LH and HL. These were implemented from 9 December 1987 to coincide with the period of reproductive growth in ryegrass. Sheep grazed the plots at variable intervals of c. 1 month in summer and 6 weeks in winter. Grazing management focused on maintaining a contrast between L and H treatments, rather than maintaining particular herbage mass targets, but in general herbage mass did not exceed 3500 and 2000 kg DM ha^{-1} for L and H treatments, respectively, with grazing residuals not below 1800 and 800 kg DM ha^{-1}, respectively.

Measurements

The primary objective of Experiment 2 was to measure seasonal root production of the contrasting lax- and hard-grazed swards (Matthew 1992). Tiller density data presented in this paper were collected as a secondary objective to help interpret the root data. At each root harvest (14 times between December 1986 and May 1988), ryegrass tiller density was determined by collecting 30, 53-mm plugs plot^{-1} (Mitchell & Glenday 1958) and counting vegetative and reproductive tillers of ryegrass and tillers of other grass species. Herbage mass estimates were also made at each root harvest from ground level cuts in three randomly chosen 0.1 m^2 quadrats plot^{-1}.

Statistical analysis

Data from Experiment 1 were analysed as a split-split-plot design using Genstat 5 (Genstat 5 Committee 1993) to determine the cultivar and N treatment effects on reproductive and vegetative tiller numbers. Square root transformation was required for some reproductive tiller number data but for simplicity means are presented on the original scale. Data from Experiment 2 were analysed as a randomised complete block design until the four treatments (L, H, LH, HL) were created, then a Latin square analysis of variance was used.

RESULTS AND DISCUSSION

Reproductive development

'Ellett' and 'Grasslands Ruanui' ryegrasses are both early flowering cultivars with similar heading dates (Tables 1 and 2).

In Experiment 1, 'Ellett' ryegrass had a higher percentage of reproductive tillers than did 'Grasslands Ruanui' from October 1996 to January 1997 (Table 1). Larger differences occurred at the same time during the second year when 'Grasslands Ruanui' produced fewer reproductive tillers than it did in the first year (Table 1). While 'Grasslands Ruanui' had a lower percentage of total tillers that flowered in the second year (7.8%) compared with the first (13.0%), a similar percentage of 'Ellett' tillers (17.1–19.5%) flowered in both years. A mechanistic model (Fiorelli et al. 2001) showed a higher conversion rate of vegetative to reproductive tillers by 'Ellett' than by 'Grasslands Ruanui' ryegrass as being the main explanation for the cultivar differences.

Ryegrass cultivars differ in the percentage of flowering tillers, or flowering "intensity". For example, Gangi et al. (1981) found c. 4% flowering in the turf ryegrass cultivar 'Pennfine' compared with 28% flowering in an early flowering forage ryegrass cultivar 'Linn'. Similarly, Wilkins (1997) recorded 47% flowering tillers in the first spring cut of 'Aberelan' compared with 58% in 'Merlinda'. What has seldom been attempted, however, is to link flowering behaviour to perennation strategy. One exception is the study of Davies et al. (1981), in which tillers appearing in summer were classified as originating from vegetative tillers, reproductive tillers, or "old buds" meaning that they were extravaginal with the point of attachment below ground and the category of the parent tiller was not easily determined. In 'S24' perennial ryegrass, these authors reported similar numbers of summer-formed tillers in each of these three categories.

Matthew et al. (1993) used the terms vegetative and reproductive pathway to describe perennation strategies in which tillering from non-flowering vegetative tillers or from the base of decapitated reproductive tillers provided the majority of new summer tillers. The distinction between the two pathways is not absolute but a matter of gradation between two extremes. The criteria for assessing the degree that reproductive pathway predominates are a higher percentage of tillers flowering, a lower percentage of spring tillers remaining as vegetative tillers in late summer, and a higher percentage of the autumn tiller population originating as daughter tillers from flowering tillers. Matthew et al. (1993) classified 'Ellett' as having a reproductive perennation pathway and 'Grasslands Ruanui' exhibiting a more vegetative pathway by comparison.

The basis for classifying 'Ellett' as having a reproductive pathway was that c. 50% of tillers, for which the parent tiller could be traced in sheep-grazed swards in early summer (10 December), were found to originate from stubs of decapitated flowering tillers (Matthew et al. 1989). In the same swards, up to 36% of 'Ellett' tillers were reproductive, and of the tillers present in mid November only 10–20% remained the following autumn (April). 'Grasslands Ruanui' swards were monitored in a different experiment the following season but in these swards only 22% of tillers were reproductive in November, and surviving November tillers formed 38% of the autumn tiller population (Matthew 1992).

In Experiment 1, the higher flowering propensity of 'Ellett' was also associated with lower survival of vegetative tillers through summer. For example, in 'Grasslands Ruanui' swards without N or irrigation applied, 32.4% of tillers surviving until summer (late February) had been present the previous September, compared with 19.6% of tillers surviving in 'Ellett' swards (Bahmani 1999). These summer tiller survival data would be inflated by c. 5% because defoliated reproductive tillers bearing daughter tillers were not recorded as dead, in contrast to the methods of Korte (1986) and Matthew (1992). Even so, the difference between the two cultivars is clear.

Despite not determining the origin of summer tillers in Experiment 1, the present results for percentage of total tillers flowering and persistence of spring tillers confirm the suggestion of Matthew (1992) that more perennation of 'Grasslands Ruanui' was achieved by a vegetative pathway than for 'Ellett', especially in the second year. However, when both cultivars were included in a single experiment in this study, the contrast between them was less marked than might have been predicted from Matthew's (1992) comparisons. This suggests that environmental or other factors contributed to the differences observed in that earlier study.

Table 1 Reproductive and vegetative tiller numbers for 'Ellett' and 'Grasslands Ruanui' ryegrass, and the percentage of total tillers that were reproductive during flowering in 1996/97 and 1997/98 (Experiment 1). NS, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; SED, standard error of the difference between cultivar means. Average SEDs are given from 1 September 1997 to 17 November 1997 (transformed data were analysed but for simplicity raw data are presented). Percentages of reproductive tillers were calculated for individual replicates before statistical analysis and so may differ from percentages calculated from the means given. For percentage of reproductive tillers on 15 December 1997 and 12 January 1998, significance levels are not given as N × cultivar interactions were significant ($P < 0.05$) (see Table 2).

	Spring 1996			Summer 1996/97		Spring 1997			Summer 1997/98	
	7 Oct	29 Oct	25 Nov	16 Dec	6 Jan	1 Sep	21 Oct	17 Nov	15 Dec	12 Jan
Reproductive tiller numbers										
'Ellett'	4.2	13.7	19.5	24.9	27.4	1.8	18.2	21.6	20.8	19.3
'Ruanui'	3.4	13.7	17.0	21.9	22.3	1.5	5.0	12.0	13.3	13.8
SED	1.07	1.27	1.79	1.70	3.46	0.84	4.96	3.35	4.40	2.76
	NS	NS	NS	NS	NS	NS	*	**	NS	NS
Vegetative tiller numbers										
'Ellett'	49.0	49.9	68.7	80.6	89.0	102.3	66.6	57.9	70.6	87.4
'Ruanui'	76.8	80.0	88.8	112.2	124.6	142.5	117.9	103.5	112.7	137.0
SED	5.08	5.89	14.55	17.20	18.22	23.37	14.53	13.74	11.73	12.68
	**	**	NS	NS	NS	NS	*	*	*	*
Percentage of reproductive tillers (%)										
'Ellett'	6.9	21.4	22.3	23.7	23.0	2.1	18.2	24.8	22.2	18.1
'Ruanui'	3.7	14.1	15.8	16.3	15.0	1.1	4.1	10.7	12.2	11.1
SED	2.40	2.75	1.87	1.62	1.21	0.99	2.12	1.00	3.06	2.20
	NS	NS	*	*	**	NS	**	***		

Effects of nitrogen fertiliser and irrigation on reproductive development

There were few effects of N on the reproductive or vegetative tiller numbers and the percentage of total tillers for either of the ryegrass cultivars over the first year (Table 2). However, 'Ellett' and 'Grasslands Ruanui' had different responses to N during the second flowering period, with cultivar × N interactions in December 1997 and January 1998 for the percentage of reproductive tillers (Table 2). In response to N, reproductive tiller numbers increased in 'Ellett' while vegetative tiller numbers showed little change, giving a greater percentage of tillers flowering with N (Table 2). By contrast, in 'Grasslands Ruanui', N produced no change in flowering tiller numbers but greatly increased vegetative tiller numbers per fixed frame. Thus, the percentage of tillers flowering was almost halved in 'Grasslands Ruanui' plots where N fertiliser was applied in the second year. McKenzie (1998) showed, in a subtropical environment, that reproductive tiller development in 'Ellett' ryegrass was promoted when 240 kg ha^{-1} of N fertiliser was applied. In a United Kingdom study by Wilkins (1995), results were similar to our findings for 'Ellett', with the mean percentage of tillers flowering in four ryegrass cultivars increasing from c. 20% at 100 kg N ha^{-1} yr^{-1} to almost 40% at 400 kg N ha^{-1} yr^{-1}, although there was no cultivar × N interaction.

It is unclear why N applied in 1997/98 increased the number of flowering tillers proportionately more than the number of vegetative tillers in 'Ellett', yet had the opposite effect in 'Grasslands Ruanui' and no such interaction in the preceding year. N fertiliser promotes vegetative tillering (Curll & Wilkins 1982; Thomas et al. 1990; Harris et al. 1996). If tillers about to flower were responsive to N for only a short period, then a flowering date by N application date interaction is a logical possibility.

Table 2 Effect of nitrogen fertiliser on reproductive and vegetative tiller numbers and the percentage of total tillers that were reproductive, during flowering in 1996/97 and 1997/98 (Experiment 1). NS, not significant; *, $P < 0.05$; **, $P < 0.01$; E, 'Ellett'; R, 'Grasslands Ruanui'; N+, with nitrogen fertiliser; N–, without nitrogen fertiliser; SED, standard error of the differences between N treatments within cultivars. Average SEDs are given from 1 September 1997 to 17 November 1997 (transformed data were analysed but for simplicity raw data are presented). Percentages of reproductive tillers were calculated for individual replicates before statistical analysis and so may differ from percentages calculated from the means given.

	Spring 1996			Summer 1996/97		Spring 1997			Summer 1997/98	
	7 Oct	29 Oct	25 Nov	16 Dec	6 Jan	1 Sep	21 Oct	17 Nov	15 Dec	12 Jan
Reproductive tiller numbers										
EN+	5.3	13.9	19.0	26.1	27.8	1.3	26.3	29.6	28.0	25.6
EN–	3.0	13.4	20.0	23.7	27.3	2.4	10.0	13.7	13.6	12.9
RN+	4.6	15.0	17.6	23.5	22.8	1.1	7.8	11.7	12.8	13.8
RN–	2.1	12.3	16.3	20.3	21.8	1.9	2.2	12.3	13.9	13.9
SED	0.91	3.43	3.18	4.66	4.87	1.11	7.73	7.98	6.06	5.26
	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Vegetative tiller numbers										
EN+	53.6	57.6	73.1	81.0	89.8	118.0	73.8	62.6	70.8	92.1
EN–	44.3	42.3	64.2	80.1	88.3	86.7	59.4	53.3	70.4	82.7
RN+	84.1	85.5	92.2	118.1	127.5	162.6	132.2	118.5	140.1	176.4
RN–	69.5	74.5	85.5	106.4	121.8	122.4	103.6	88.5	85.4	97.6
SED	10.09	11.94	12.30	8.65	9.19	25.34	15.00	15.95	17.88	22.58
	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Percentage of reproductive tillers (%)										
EN+	7.8	19.9	21.5	24.2	23.0	1.2	22.6	29.4	26.6	21.6
EN–	6.0	23.0	23.1	23.2	23.1	3.0	13.8	20.2	17.8	14.6
RN+	4.8	14.6	15.5	16.4	15.0	0.6	5.8	9.2	8.1	7.4
RN–	2.6	13.6	16.2	16.0	15.0	1.7	2.3	12.2	16.4	14.8
SED	0.72	3.26	2.25	2.01	1.94	1.10	3.74	4.85	3.43	3.25
	NS	NS	NS	NS	NS	NS	NS	NS	**	*

This is unlikely in this particular case because 'Ellett' and 'Grasslands Ruanui' differ by only 3 days in mean flowering date (New Zealand Agriseeds Ltd 1988). In the 1997/98 season (Experiment 1), the contrast in flowering intensity between the two cultivars was large compared with that reported for 'Aberelan' and 'Merlinda' by Wilkins (1997) and is probably the reason for the difference in N response, with N favouring vegetative tillering in the cultivar with low flowering propensity. Furthermore, the increase in the proportion of reproductive tillers in 'Ellett' following N application (Table 2) was associated with a decline in the tiller population (Bahmani 1999), whereas the tiller population of 'Grasslands Ruanui' increased in response to nitrogen applied during the flowering period. Thus, the response of 'Ellett' to N appears less conducive to persistence than that of 'Grasslands Ruanui'.

Since N fertiliser appeared to cause different responses in established swards, dependent on the propensity of the cultivar to produce reproductive tillers, management decisions relating to N applications should also consider ryegrass cultivar. Applying N to 'Ellett' or similar ryegrass a few weeks before flowering could be of value where high dry matter yields of lower quality forage are desired (Wilkins 1997), though possibly compromising its persistence. Conversely, for 'Grasslands Ruanui', or a variety with similar behaviour, N application at flowering could improve persistence by promoting vegetative tillering. Use of ryegrass similar to 'Grasslands Ruanui', may allow plant breeders to reduce reproductive tillering so that sward quality and animal performance is improved (Wilkins 1997) without compromising seed production potential.

The irrigation treatment did not produce differences in flowering behaviour, and so no data are presented.

Experiment 2 showed that defoliation intensity has a strong influence on percentage of tillers flowering in perennial ryegrass swards. In the first summer (January 1987), 22% of spring-born tillers had flowered under H compared with 34% under L grazing intensity. Ten months later, at the peak of reproductive growth (November 1987), there were more than 4 times the number of reproductive tillers in L compared with the H grazing treatment. Plots switched from H to L (HL) exhibited increased aftermath flowering in January 1988 compared with plots remaining under H. Conversely, plots switched from L to H grazing intensity (LH) showed reduced aftermath flowering compared with plots grazed laxly throughout (Table 3). Such large differences due to grazing intensity could account for some of the apparent inconsistencies identified above when comparing data from different experiments. Brown (1980) reported a similar effect in ryegrass seed crops, in that ungrazed crops had c. 5% more tillers flowering in the first year and 20% more tillers flowering in the second year, than grazed crops. Tiller cohort survival diagrams of Jewiss (1966) for defoliation regimes simulating frequent and infrequent cutting of *Phleum pratense* and *Festuca pratensis* suggested that less severe defoliation increased percentage of tillers flowering in these species, also. Interestingly, however, if percentage of spring tillers flowering is calculated from Korte (1986, table 6), there is little difference in percentage of tillers flowering for swards mown

Table 3 Percentage of tillers flowering in swards of endophyte-infected 'Ellett' perennial ryegrass intermittently grazed at high (H) and low (L) grazing intensities (Experiment 2). H2 denotes plots initially receiving grazing identical to the high grazing intensity plots, but designated for change to low grazing intensity. The change in grazing intensity started from 9 December 1987, after which plots were relabelled HL. Similary, L2 and LH denote change from low to high grazing intensity on the same date. SEM, standard error of the mean; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	H	H2	L	L2	SEM	*P*
24 Nov 87	6.25	8.16	31.6	36.4	2.18	***
9 Dec 87	7.05	6.92	20.9	23.8	1.63	***
	H	HL	L	LH		
29 Dec 87	1.59	2.71	4.42	3.08	0.49	*
18 Jan 88	0.75	2.95	3.21	0.48	0.51	**

frequently or infrequently (12 and 13%, respectively). Korte (1986) used 'Grasslands Nui' in his experiment, a cultivar selected from the same parent material as 'Ellett' and likely to behave similarly. Taken together, these observations suggest a possible link between tiller size and flowering propensity. Low light intensity can promote flowering in perennial ryegrass (Evans 1960), but if low light levels in lax-grazed swards of Matthew (1992) had promoted flowering, we might have expected a similar result in Korte's (1986) infrequently defoliated swards.

The influence of genotype and/or environmental and management factors on flowering behaviour of perennial ryegrass has been well recognised (Langer 1963; Jewiss 1972), with photoperiod (daylength) and temperature (vernalisation requirement) controlling the transition from vegetative to reproductive growth. Our data strengthen the view that latitude, implying variations in daylength and temperature, is an important environmental factor affecting the proportion of reproductive tillers that form on perennial ryegrass-based pastures. In Hamilton, New Zealand (37°47′S), the proportion of reproductive tillers for 'Ellett' was c. 25% in spring (November) of the second year (Table 1). Thom (1991) recorded a slightly lower figure of 18% in a mixed ('Grasslands Nui' and 'Ellett') perennial ryegrass and white clover pasture under dairy cow grazing, at the same research station. However, at a lower latitude (30°24′S) in Natal, South Africa, McKenzie (1997) reported that 'Ellett' tillers were mostly vegetative during spring (<9% reproductive) under subtropical conditions. Furthermore, in temperate climates in Palmerston North, New Zealand (40°23′S), and Lusignan, France (46°26′N), both higher latitudes than at Hamilton, reproductive tiller numbers in 'Ellett' ryegrass swards was higher (up to 36%) (Matthew 1992; Bahmani et al. 2000b) than in Hamilton (Table 1). The trend for a higher proportion of reproductive tillers at higher latitudes was also apparent for 'Grasslands Ruanui' swards (not studied in Natal), with percentage of reproductive tillers at Hamilton, Palmerston North, and Lusignan of 11, 22, and 25%, respectively. As perennial ryegrass plants require low temperature and short days to initiate floral primordia and then long days for inflorescence development (Cooper 1960), it is to be expected that ryegrass plants would receive a weaker signal to flower at lower latitudes. The comparison of field data from different experiments at different latitudes appears to confirm this.

APPLICATION

It is clear from the above results that 'Ellett' and 'Grasslands Ruanui' have different propensities to flower. The basis of the genetic difference between 'Ellett' and 'Grasslands Ruanui' is still unclear but the results are consistent with a difference in magnitude from a common vernalisation response. Standard plant breeding practices (Corkill 1949) were used to produce the cultivar 'Grasslands Ruanui'. In contrast, 'Ellett' ryegrass was the product of natural selection on a dairy farm in South Auckland, where Italian (*Lolium multiflorum*) and perennial ryegrass had been sown together from c. 1935 to 1953 (Duder 1976) as a management practice to increase the herbage biomass. Thus, it is possible that 'Ellett' has acquired genes from Italian ryegrass by introgression, increasing the propensity of 'Ellett' to produce reproductive tillers. An investigation of the genetic background of 'Ellett' ryegrass would help explain its flowering behaviour, especially if linkage to Italian ryegrass could be shown. There is wide anecdotal recognition among plant breeders that many other modern ryegrass cultivars available internationally that show high flowering propensities also have a likely origin from introgression of Italian ryegrass germplasm.

Our study shows that flowering propensity is linked to perennation strategy, with high flowering propensity linked to increased summer tiller turnover, and probably also to increased proportion of summer tillers originating from reproductive stubs. Anecdotally, the concept of differences in perennation pathway is often assumed to be synonymous with difference in persistence. This is not necessarily so. There is no *a priori* reason to expect one perennation pathway to confer greater persistence than another, although the greater tiller population turnover in the reproductive pathway implies a need for higher site filling, and therefore a greater risk of an adverse result in the event of unfavourable growing conditions occurring. However, management attuned to tiller dynamics of the cultivar in question is beneficial. In swards where the reproductive pathway predominates, tiller appearance and summer herbage production are enhanced by a less intense spring grazing regime (Matthew 1992; Hernández Garay et al. 1997). Also, we have shown that there may well be environment by cultivar interactions such as the N fertiliser by cultivar interaction reported here in Year 2.

Our studies also indicate an opportunity for further research, in that many of the observations reported above are consistent with tiller size being a major determinant of whether or not an individual tiller flowers. Reduced flowering in smaller tillers within swards was observed in a subsequent experiment (Bahmani et al. 2000b), but more detailed evaluation of the link between tiller size and flowering would be beneficial. Finally, we have shown that the effects of defoliation intensity on flowering propensity can be large, and that there also appear to be latitude effects. This will need to be kept in mind when seeking a particular outcome in terms of the degree of sward reproductive growth in spring, and also when comparing differences in flowering behaviour between different experiments.

ACKNOWLEDGMENTS

We thank the New Zealand Foundation for Research, Science and Technology for funding this research. The assistance of Helen Simons, Vicki Burggraaf, Deanne Waugh, Elizabeth Grayling, and Roslyn Watts with experimental work was very much appreciated. New Zealand Agriseeds Ltd provided the 'Ellett' ryegrass seed, and AgResearch Lincoln, New Zealand, provided the 'Grasslands Ruanui' seed used in Experiment 1.

REFERENCES

Aitken, Y. 1974: Flowering time, climate and genotype. Melbourne, Melbourne University Press. 193 p.

Bahmani, I. 1999: Tiller dynamics and leaf growth processes of the perennial ryegrass cultivars Ellett and Grasslands Ruanui as influenced by environmental factors. Unpublished co-tutorial PhD thesis, Massey University, Palmerston North, New Zealand and de I'Institut National Polytechnique de Lorraine, Nancy, France.

Bahmani, I.; Thom, E. R.; Matthew, C. 1997: Effects of nitrogen and irrigation on productivity of different ryegrass ecotypes when grazed by dairy cows. *Proceedings of the New Zealand Grassland Association 59*: 117–123.

Bahmani, I.; Hazard, L.; Varlet-Grancher, C.; Betin, M.; Lemaire, G.; Matthew, C.; Thom, E. R. 2000a: Differences in tillering of long- and short-leaved perennial ryegrass genetic lines under full light and shade treatments. *Crop Science 40*: 1095–1102.

Bahmani, I.; Varlet-Grancher, C.; Hazard, L.; Matthew, C.; Betin, M.; Langlais, A.; Lemaire, G.; Thom, E. R. 2000b: Post-flowering tillering in contrasting light environments of two New Zealand perennial ryegrass cultivars with different perennation strategies. *Grass and Forage Science 55*: 367–371.

Bahmani, I.; Thom, E. R.; Matthew, C.; Lemaire, G. 2001: Productivity of grazed perennial ryegrass dairy pastures from different ecotypes under nitrogen and irrigation treatments. *New Zealand Journal of Agricultural Research 44*: 123–133.

Brown, K. R. 1980: Seed production in New Zealand ryegrasses 1. Effect of grazing. *New Zealand Journal of Experimental Agriculture 8*: 27–32.

Colvill, K. E.; Marshall, C. 1984: Tiller dynamics and assimilate partitioning in *Lolium perenne* with particular reference to flowering. *Annals of Applied Biology 104*: 543–557.

Cooper, J. P. 1960: Short day and low temperature induction in *Lolium*. *Annals of Botany (London) 24*: 232–246.

Corkill, L. 1949: Pasture improvement in New Zealand. *Empire Journal of Experimental Agriculture 17*: 157–169.

Curll, M. L.; Wilkins, R. J. 1982: Frequency and severity of defoliation of grass and clover by sheep at different stocking rates. *Grass and Forage Science 37*: 291–297.

Davies, A.; Evans, M. E.; Sant, F. I. 1981: Changes in origin, type and rate of production of ryegrass tillers in the post-flowering period in relation to seasonal growth. *In*: Wright, C. E. *ed*. Plant physiology and herbage production. Hurley, British Grassland Society. Pp. 73–76.

Duder, F. R. 1976: Analysis of variation in a local population of perennial ryegrass (*Lolium perenne*). Unpublished DipAgr dissertation, Massey University, Palmerston North, New Zealand.

Evans, L. T. 1960: The influence of temperature on flowering in species of *Lolium* and in *Poa pratensis*. *Journal of Agricultural Science, Cambridge 54*: 410–416.

Fiorelli, C. F.; Woodward, S. J. R.; Wastney, M. E.; Thom, E. R.; Bahmani, I. 2001: Modelling factors affecting reproductive development of perennial ryegrass in Waikato dairy pastures. *Proceedings of the New Zealand Grassland Association 63*: 165–170.

Gangi, A. S.; Chilcote, D. O.; Frakes, R. V. 1981: Growth, floral induction and reproductive development in selected perennial ryegrass *Lolium perenne* L. cultivars. *Journal of Applied Seed Production 1*: 34–38.

Genstat 5 Committee 1993: Genstat 5 Release 3 Reference Manual. Oxford, Clarendon Press.

Hewitt, A. E. 1998: New Zealand soil classification. 2nd ed. *Landcare Research Science Series 1*. 133 p.

Harris, S. L.; Thom, E. R.; Clark, D. A. 1996: Effects of high rates of nitrogen fertiliser on perennial ryegrass growth and morphology in grazed pasture in northern New Zealand. *New Zealand Journal of Agricultural Research 39*: 159–169.

Hernández Garay, A.; Hodgson, J.; Matthew, C. 1997: Effect of spring grazing management on perennial ryegrass and ryegrass-white clover pastures 1. Tissue turnover and herbage composition. *New Zealand Journal of Agricultural Research 40*: 25–35.

Jewiss, O. R. 1966: Morphological and physiological aspects of the growth of grasses during the vegetative phase. *In*: Ivins, J. D. *ed*. The growth of cereals and grasses. London, Butterworths. Pp. 39–56.

Jewiss, O. R. 1972: Tillering in grasses—its significance and control. *Journal of British Grassland Society 27*: 65–82.

Korte, C. J. 1986: Tillering in 'Grasslands Nui' perennial ryegrass swards 2. Seasonal pattern of tillering and age of flowering tillers with two mowing frequencies. *New Zealand Journal of Agricultural Research 29*: 629–638.

Langer, R. H. M. 1963: Tillering in herbage grasses. *Herbage Abstracts 33*: 141–148.

McKenzie, F. R. 1997: Influence of grazing frequency and intensity on the density and persistence of *Lolium perenne* tillers under subtropical conditions. *Tropical Grassland 31*: 219–226.

McKenzie, F. R. 1998: Influence of applied nitrogen on vegetative, reproductive, and aerial tiller densities in *Lolium perenne* L. during the establishment year. *Australian Journal of Agricultural Research 49*: 707–711.

Matthew, C. 1992: A study of seasonal root and tiller dynamics in swards of perennial ryegrass (*Lolium perenne* L.). Unpublished PhD thesis, Massey University, Palmerston North, New Zealand.

Matthew, C.; Quilter, S. J.; Korte, C. J.; Chu, A. C. P.; Mackay, A. D. 1989: Stolon formation and significance for sward tiller dynamics in perennial ryegrass. *Proceedings of the New Zealand Grassland Association 50*: 255–259.

Matthew, C.; Black, C. K.; Butler, B. M. 1993: Tiller dynamics of perennation in three herbage grasses. Proceedings of the XVII International Grassland Congress, New Zealand and Australia. Pp. 141–143.

Mitchell, K. J.; Glenday, A. C. 1958: The tiller population of pastures. *New Zealand Journal of Agricultural Research 1*: 305–318.

New Zealand Agriseeds Ltd 1988: Applications accepted. *Plant Varieties Journal 1*: 5–7.

Soil Survey Staff 1990: Keys to soil taxonomy. 4th ed. *Soil Management Support Services Technical Monograph 19*. 422 p.

Templeton, W. C.; Mott, G. O.; Bula, R. J. 1961: Some effects of temperature and light on growth and flowering of tall fescue, *Festuca arundinacea* Schreb. II. Floral development. *Crop Science 1*: 283–286.

Thom, E. R. 1991: Effect of early spring grazing frequency on the reproductive growth and development of a perennial ryegrass tiller population. *New Zealand Journal of Agricultural Research 34*: 383–389.

Thomas, R. J.; Logan, A. B.; Ironside, A. D.; Bolton, G. R. 1990: The effects of grazing with and without excretal returns on the accumulation of nitrogen by ryegrass in a continuously grazed upland sward. *Grass and Forage Science 45*: 65–75.

Wilkins, P. W. 1995: Independence of dry matter yield and leaf yield among perennial ryegrass varieties differing in seasonal yield distribution. *Grass and Forage Science 50*: 155–161.

Wilkins, P. W. 1997: Improving the nitrogen-use efficiency of perennial ryegrass. *In*: Weddell, J. R. *ed*. Seeds of progress. Proceedings of British Grassland Society Conference, Nottingham, United Kingdom. Pp. 156–159.