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Early summer pasture control: what suits the plant?

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Abstract

Plugs of sheep-grazed, ryegrass-dominant pasture were transplanted to a glasshouse, in order to make detailed studies of tiller appearance from the base of flowering tillers in late spring-early summer. In 2 experiments, cutting treatments which reduced the opportunity for transport of assimilate from parent flowering tillers to daughter tillers markedly reduced both numbers of daughter tillers formed and their size. In one of the studies, proportion of radioactive carbon dioxide fed to flowering tillers, but recovered from daughter tillers, was 7.0%, and this transported radiocarbon appeared to be delivered preferentially to leaf elongation zones of young tillers. There appear to be fundamental differences in tillerbehaviour between 'Grasslands Ruanui' ryegrass and 'Ellett' ryegrass. The implications for farm practice are briefly discussed.

Keywords ryegrass, tiller dynamics, radiocarbon, summer pasture production, pasture persistence

Introduction

In several recent New Zealand studies of tiller dynamics in ryegrass swards (Korte 1986; L'Huillier 1987; Matthew *et al.* 1991), the highest tiller appearance rates observed occurred in early summer (November-December). There is evidence that most tillers in this early-summer tiller appearance surge are daughter tillers from the stubs of flowering tillers (Matthew et al. 1989a), and that such daughter tillers can draw assimilate from theirparent tillers (Colvill &Marshall 1984; Hampton *et al.* 1987).

These observations suggest that *some* seedhead formation in early summer might be beneficial to a ryegrass sward. In a lax-hard grazing management which allowed some seedhead formation until 7 December, pasture growth rate increases were observed (Matthew *et al.* 1989b). By contrast, conventional spring-summer grazing management practice has concentrated on removal of seedheads to promote tillering and pasture quality (Hughes 1983).

This paper reports parts of 2 experiments designed to test the hypothesis that daughter tiller formation in ryegrass swards in early summer is encouraged by the presence of immature seedheads.

Methods

Both experiments were conducted at Massey University. Plugs of perennial ryegrass dominant pasture were transplanted from sheep-grazed field swards to glasshouse pots in September 1989. Plugs transplanted were circular, 80 mm diameter, and 100 mm depth. At transplanting all live ryegrass tillers were tagged to enable subsequent identification of new tillers.

Experiment 1

Plugs were from a 'Grasslands Ruanui' ryegrass-dominant sward. Transplanted cores were allowed to grow on undefoliated until November when a 2 x 2 factorial regime of 2 cutting heights and 2 cutting dates was applied to 28 pots (7 replicates). The cutting heights were 20 mm or 100 mm (LO or HI, respectively) and the cutting dates 1 or 17 November (E or L, respectively). After the initial cutting, pots were trimmed fortnightly to the original cutting height. At the imposition of cutting treatments three flowering tillers approaching head emergence were randomly selected and marked and tillers appearing since September tagged.

The 3 marked flowering tillers perpot were harvested on 12 December. At harvest, number andweightof tillers were determined separately for the following categories:

1. Primary tillers formed during the interval between the September and November taggings (Existing daughter tillers, EDT).
2. Secondary tillers formed from EDT during November/December (Existing daughter secondary tillers, EDST).
3. Primary tillers and their secondary tillers formed on the main axis at ground level or below ground during November/December (New daughter tillers, NDT. These tillers were mostly primary tillers and secondary tillers, if present, were usually small).

4. Primary aerial tillers and their secondary tillers formed from the main axis during November/ December (Aerial tillers, AT).

Experiment 2

Plugs were from an 'Ellett' ryegrass-dominant sward. In this experiment only the individual tillers selected for monitoring of subsequentdaughtertillerformation were cut, the surrounding tillers remaining uncut.

The experiment comprised 24 pots (6 replicates of 4 treatments). The treatments were (1) flowering tillers cut at ground level (2) flowering tillers cut at the flag leaf node (3) flowering tillers uncut, allowing seedhead development; and were imposed on 3 November. Treatment 1 was applied to two tillers in every pot, and treatments 2 and 3 were each applied to 2 tillers in 12 pots.

For treatments 2 and 3, radioactive carbon dioxide ($^{14}CO_2$) was fed to the marked flowering tillers to monitor the extent of assimilate transportation from parent tillers to their daughter tillers. A detailed account of the experimental technique has been given elsewhere (Matthew 1990), butbriefly. tillersreceiving $^{14}CO_2$ were enclosed in plastic envelopes sealed with a clip-seal and plastic sealing compound. Lactic acid (diluted with water to 20% v/v) was injected into a pocket in the plastic envelope, followed by ^{14}C-sodium carbonate, and the reaction between the dilute lactic acid and the sodium carbonate slowly released $^{14}CO_2$ into the plastic envelope. When geiger counter readings showed that radioactivity had transferred to the plant (usually about 2 hours) the plastic envelope was removed.

Treated tillers were harvested on 24 November, using tiller classification categories as for experiment 1. The delay of approximately 3 weeks between feeding of $^{14}CO_2$ and harvest was to allow time for distribution of ^{14}C-labelled photosynthesis products within the plant. On harvest. tillers were dried and weighed and ^{14}C radioactivity measured by liquid-scintillation counting, using a method adapted from Jeffay & Alvarez (1961).

Some tillers in spare pots were also fed $^{14}CO_2$, and harvested 5 days later for autoradiography. Autoradiography captures a visual image of radioactivity distribution on x-ray film, and information from autoradiography was used to gain information on distribution of ^{14}C within labelled tillers. in addition to counting of ^{14}C-activity as above.

Statistical analysis

For experiment 1, tiller data tended to be positively skewed, and so they were log transformed. Statistical significance results are therefore presented as the least significant ratio (LSR) between two treatment means (Steel & Torrie 1981). Dataanalysed werethemeansfor the tagged tillers in each pot.

For experiment 2, log transformation was not required. Because of the unbalanced design, means and standard errors for each category of marked tiller, calculated using means for the two tillers per pot as the experimental unit, are presented. Degrees of freedom are 19, 9 and 9 for means for treatments 1, 2 and 3, respectively.

Results

Experiment 1

The number of new daughter tillers produced was lowest for the LOxE treatment (Table 1), whereas either a laxer defoliation or a 17 day delay in cutting markedly increased daughter tiller formation per seedhead, relative to the LOxE treatment. Differences in daughter tiller weight (Table 1) need to be interpreted with caution because trimming of pots would have removed some material from developing daughter tillers. Even so, the results show the same pattern of difference in tiller weight across treatments as for tiller number.

Table 1 Numbers and total weight (mg) of daughter tillers formed (per tiller) from reproductive tillers of Ruanui ryegrass under differing spring defoliation regimes.

Category of daughter[1]		Cut 1 November (E) LO	HI	Cut 17 November(L) LO	HI	LSR 5%
2 EDST	Number	1.5	6.7	6.3	7.1	1.8
	Total Wt	10	52	108	125	2.3
3 NDT	Number	0.8	1.9	2.2	2.1	1.4
	Total Wt	9	22	62	58	1.5
4AT	Number	0.3	1.0	0.6	1.2	1.5
	Total Wt	0.7	8.1	5.8	24.0	2.3

1 Data for Category 1 (EDT) representing tiller formation under common defoliation during the pm-experimental period not presented. For explanation of abbreviations see text.

Table 2 Effects of cutting height[1] on total weight and number of new daughter tillers (NDT) and existing daughter secondary tillers (EDST) formed from flowering tillers.

	Cutting height					
	Ground level		Flag leaf node		Seedhead uncut	
Tiller category	NDT	EDST	NDT	EDST	NDT	EDST
Total weight (mg)	34.10	20.40	122.00	58.40	46.70	39.40
SE of mean	7.70	10.10	13.00	15.20	14.00	18.40
Number of tillers	1.80	1.90	4.20	5.60	2.30	3.30
SE of mean	0.18	0.57	0.48	1.18	0.33	0.74

1 Results are averaged for 2 levels of light (Matthew 1990).
2 Average individual tiller weight can be computed as weight of new tillers/number of new tillers.

Experiment 2

The weight and number of daughter tillers formed from flowering tillers were greatest when tillers were decapitated at the flag leaf node (Table 2), and were markedly reduced by either cutting seedheads at ground level or leaving the seedheads intact (Table 2).

Of radioactive carbon dioxide fed to parent flowering tillers actually recovered, 7.0% had been transported to daughter tillers, but the quantity recovered from daughter tillers was reduced from 3.99 to 2.01 kBq* ($P<0.01$) where seedheads remained intact (Matthew 1990). Also, autoradiography of tillers harvested 5 days after ^{14}C feeding indicated that transported radioactivity was concentrated in segments of daughter tiller leaves which would likely have been elongation zones at the time theradioactive carbon dioxide was fed to the parent tillers (Matthew 1990). Average specific activity for 3 such leaf segments measured was 124 Bq/mg, as compared to 34 Bq/mg for segments from different parts of the same leaves. Values for leaves of parent tillers actually fed radioactive carbon dioxide, and harvested 28 days later, averaged 117 Bq/mg for 48 tillers measured (Matthew 1990).

In comparing the results from experiments 1 and 2 it was noted that, while manipulation of flowering tillers resulted in similar daughter tiller responses in both experiments, the tiller dynamics of the responses appeared to be different (Table 3). In experiment 1 the response was more strongly expressed through secondary tillering of September and October-formed tillers. Inexperiment 2 theresponse was more strongly expressed through new daughter tiller formation at nodes above EDT. This is shown in the different ratios for NDT:EDST (Table 3).

Table 3 Ratios of NDT:EDST for tiller number and tiller weight in experiments 1 & 2.

Treatment	Experiment 1 LOxE	LOxL	HIxE	HIxL
Tiller weight	0.87	0.62	0.53	0.66
Tiller Number	0.51	0.28	0.35	0.30

Treatment	Experiment 2 Ground level	Flag leaf node	Uncut
Tiller weight	1.67	2.09	1.19
Tiller Number	0.95	0.75	0.97

* 1 Bq = 1 radioactive disintegration per second

Discussion

In experiment 1, the 4 treatments imposed (LOxE, LOxL, Hide, HIxL) represent a gradation in the opportunity for translocation from a seedhead to its developing daughter tillers. The results support the view that where there was greater translocation from parent to daughter tillers, whether of products from current photosynthesis or from mobilisation and redistribution of stored carbohydrate, both the number and size of daughter tillers formed was increased.

Similarly, theresults fromexperiment alsosupport the view that daughter tiller formation from a flowering tiller is enhanced by greater translocation from the parenttiller. Where theparenttillerwasremovedentirely, or translocation from parent to daughter tiller was reduced by allowing competition from the developing seedhead, the number and size of daughter tillers formed was again reduced. In both experiments the magnitude of the responses indicated that daughter tillers developing at the base of flowering tillers were extremely sensitive to changes in the way theirparent tillers were defoliated.

Although the total amount of carbon transported from parent tillers to daughter tillers was only a small proportion of the total taken up by the parent tillers, the factthattheassimilatetransportedfromparenttodaughter tillers was delivered preferentially to leaf elongation zones, and also to the youngest tillers (Matthew 1990) would make this transported assimilate very effective in assisting the daughter tillers to rapidly become self sufficient. Assuming almostnolossesof ^{14}C by respiration after 4 days, as observed by Danckwerts & Gordon (1987), the specific activity values of 117 and 124 Bq/mg for parent and daughter tiller leaves, respectively, show that levels of ^{14}C in leaf elongation zones of daughter tillers, shortly after labelling, were similar to those in leaves of parent tillers fed ^{14}C.

That carbohydrate from parent tillers is important for daughter tiller formation is supported by evidence from earlier studies (Davies 1977; Colvill & Marshall 1984; Hampton *et* al. 1987; Davies 1988), as is the finding that imported assimilate may be concentrated in smaller daughter tillers (Clemence & Hebblethwaite 1984). In this study the possibility of reciprocal translocation from daughter tillers to parent tillers was not investigated. However, studies by both Clifford *et* al. (1973) and Hampton *et al.* (1987) suggest that it can be safely assumed that the flow of assimilate from parent tiller to daughter was much greater than that from daughter tiller to parent.

The difference between experiments 1 and 2 in the category of tiller most strongly influenced by the presence of the flowering tillers cannot be interpreted with certainty because of the lack of appropriate experimental controls, but may indicate a fundamental difference in behaviour between Ruanui and Ellett ryegrasses. Differences in tiller behaviour as reported in Table 3 would be expected to occur if, at tiller initiation, tiller buds in Ellett ryegrass were able to develop their vascular connection with their parent tiller (Bell 1976) more quickly than buds in Ruanui ryegrass. In this case, the younger, higher tiller would not only receive a larger allocation, enabling faster development, but would also leave less assimilate to pass down to older, lower tillers. There is some anecdotal evidence to support this hypothesis (C. Matthew, unpublished data), however, it is emphasised that there could be other possible explanations for these data in Table 3.

The possibility that different grass species, and even different cultivars may have fundamentally different tillerdynamicsrequiresfurtherinvestigation. Preliminary data from studies in progress at Massey University suggest that daughter tiller formation from flowering tillers is a major factor determining swardpersistence in prairie grass, Yorkshire fog, and some ryegrasses. but less important in Ruanui ryegrass and tall fescue. Such information should lead to better understanding of the optimum grazing strategies for particular species and cultivars.

Implications for farm practice

A number of points need to be considered in applying the above results to farm practice. The flowering tillers manipulated in this glasshouse study represent just one category of tillers in the sward, and to attempt to achieve similar manipulation by grazing management would mean that only a proportion of the flowering tillers received the desired treatment. Even so, this study indicates that, contrary to popular belief, allowing some seedhead formation on ryegrass swards in early summer is likely to encourage tillering, and could therefore explain previous observations (Matthew *et* al. 1989b) of higher summer pasture productivity after a lax-hard spring grazing regime. Pasture persistence would also probably be improved. Conversely, a chemical suppression of daughter tiller formation from flowering tillers could improve yield in grass seed crops.

The recommendation that allowing some seedhead formation would likely improve tillering and summer pasture growth would not be easy to accommodate in grazing systems. Seedhead formation does produce a greater quantity of total dry matter (Matthew *et al.* 1986), but at the cost of decreased quality for animal nutrition (Hoogendoom 1987). Therefore, additional seedhead growth would be unwelcome on sheep-beef properties where control of the summer pasture surplus is often difficult.

Itmaybepossibleondairyfarms, however, to devise a grazing strategy which would effectively delay for 2-3 weeks, removal of developing seedheads on aproportion of the farm. On the basis of the likely effects on tillering, such a 'late control' grazing strategy might help overcome the thinning out of ryegrass pastures, which is a commonly reported problem on dairy properties.

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