

Modelling factors affecting reproductive development of perennial ryegrass in Waikato dairy pastures

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Abstract

A mechanistic model was developed to identify biological processes responsible for differences in reproductive tillering between 'Ellett' and 'Grasslands Ruanui' perennial ryegrass cultivars. In the model, a field perennial ryegrass tiller population was represented with six compartments: vegetative, emerging reproductive, mature reproductive and dead tillers (three compartments). The biological processes driving the transfer of tillers from one compartment to another were: conversion of vegetative tillers to reproductive tillers, maturation of emerging reproductive tillers, senescence of mature reproductive tillers, and death of reproductive tillers due to grazing. The model was used to analyse data from Waikato dairy pastures. This enabled some of the effects of irrigation, nitrogen, cultivar and season (weather) on the biological processes to be identified. During spring and early summer, the proportion of reproductive tillers in 'Ellett' pastures was always higher than in 'Grasslands Ruanui', regardless of treatment and year. The model explained this difference by a higher conversion rate of 'Ellett' vegetative tillers to reproductive tillers, and suggested that conversion rate is the key process determining reproductive development in perennial ryegrass. Opportunities to control reproductive tillering are discussed.

Keywords: flowering, *Lolium perenne*, perennial ryegrass, reproductive development

Introduction

Perennial ryegrass (*Lolium perenne*)-based pasture is the cornerstone of New Zealand's low cost dairying system. One aspect of managing this pasture involves controlling the reproductive development of perennial ryegrass through spring and summer to maintain feed quality (Terry & Tilley 1964) and tiller density (Matthew 1991) as biomass accumulation accelerates (Hunt & Field 1979). Options for controlling reproductive

development include timing and intensity of grazing, choice of cultivar, and applications of nitrogen or water (L'Huillier 1987; Bahmani 1999). For example, studies of reproductive tiller development in Waikato dairy pastures have shown that increased grazing pressure reduces the number of reproductive tillers through spring and summer (L'Huillier 1987), and that pastures sown with the cultivar 'Ellett' have a tendency to produce more reproductive tillers than those sown with 'Grasslands Ruanui' (Bahmani 1999). The differences between cultivars were magnified when nitrogen fertiliser was applied, whereas irrigation had no significant additional effect (Bahmani *et al.* 1997, 2001).

A knowledge of the physiological processes underlying these observations is desirable if improved management strategies are to be developed. However, the studies mentioned above did not measure responses at the plant process level. A mechanistic model provides a tool for postulating the underlying processes and then testing these assumptions against the existing data. This paper describes the development of such a model, and its application to understanding the responses of two cultivars to nitrogen and irrigation as measured by Bahmani (1999). The model described in this paper is part of a more comprehensive model of tissue flows developed for perennial ryegrass-based dairy pastures (Woodward 2001).

Materials and methods

Field data

Plots of two ryegrass cultivars were sown in autumn 1996 and were rotationally grazed with dairy cows at a farm-stocking rate of 3.2 cows per hectare over 2 years: 1996/97 (year 1, establishment) and 1997/98 (year 2). The ryegrass cultivars were endophyte-free 'Ellett' and 'Grasslands Ruanui' (referred to as 'Ruanui'), representing the modern and an older ecotype, respectively. The cultivars were treated with (+) or without (-) nitrogen (N) and irrigation (I), resulting in four treatments: -N-I, -N+I, +N-I and +N+I. Four replicates per treatment in a randomised complete block design were monitored at monthly intervals from September 1996 to January 1997 and from September

1997 to January 1998. The measurements consisted of counts of vegetative and reproductive tiller numbers within 64-mm diameter fixed frames, and were converted to percentages of total live tiller numbers. Further trial details are given by Bahmani (1999) and Bahmani *et al.* (1997; 2001).

Model structure

A field perennial ryegrass tiller population contains tillers at various stages of development, as well as dead tillers. This was represented by six compartments in the model (Figure 1). The number of tillers in each compartment was represented as a fraction of the whole tiller population. At day zero, all the tillers of the population were assumed to be vegetative. As a simplification, it was assumed that the number of live tillers in the population was constant over the study (L'Huilier 1987), and that when a tiller died it was replaced by a new vegetative tiller, which could not become reproductive in that season.

The biological processes responsible for the transfer of tillers from one compartment to another were represented by time-dependent rate functions (proportion per day) (Figure 1):

1. *Conversion* of vegetative tillers to reproductive is defined by stem elongation, and occurs at rate $c(t) = c_0 \exp(-c_2(t-t_1)) + c_1$, when $t_1 \leq t \leq t_4$.
2. *Maturation* of emerging reproductive tillers is defined by full seedhead emergence, and occurs at rate $m(t) = m_0$, when $t_2 \leq t$.
3. *Senescence* of mature reproductive tillers is defined by no green tissue remaining, and occurs at rate $s(t) = s_0$, when $t_3 \leq t$.
4. *Death* of emerging reproductive tillers is due to grazing (decapitation, pulling, trampling, pugging and fouling), and occurs at rate $g_1(t) = \gamma_1 L$, where L is the livestock density (animals/hectare) on day t .
5. *Death* of mature reproductive tillers is due to grazing, and occurs at rate $g_2(t) = \gamma_2 L$.

The shapes of these rate functions are shown in Figure 1. The 12 model parameters were given initial values based on calibration to the high stocking rate (4.28 cow/ha) treatment data of L'Huilier (1987) (Table 1).

Model fitting

In analysing the data of Bahmani (1999), the parameters c_2 , m_0 , s_0 and t_3 were fixed according to the initial

Figure 1 Model structure, showing the six tiller compartments and the transfer function shapes and coefficients.

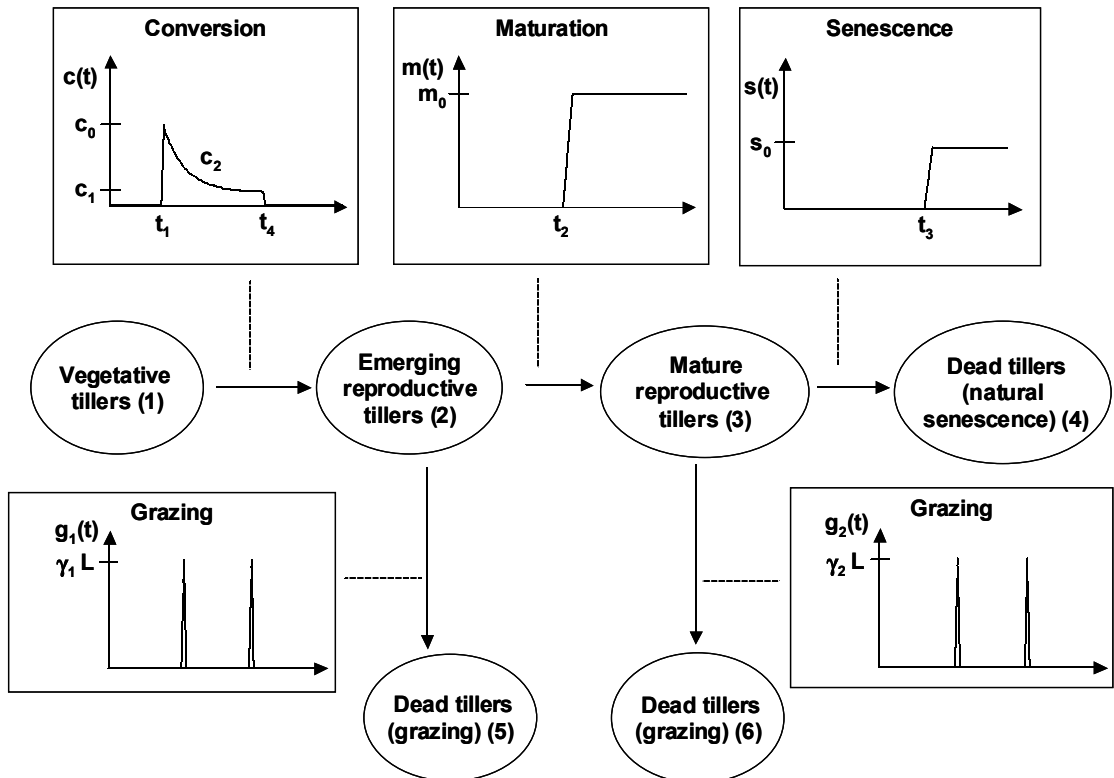


Table 1 Model parameters, and initial values based on calibration to the high stocking rate (4.28 cow/ha) treatment data of L'Huilier (1987).

Symbol	Value	Unit	Description
t_1	30 Sept	-	date of first tiller conversion from vegetative to reproductive state
t_2	2 Nov	-	date of first tiller maturation
t_3	25 Nov	-	date of first tiller senescence
t_4	10 Jan	-	date of final tiller conversion from vegetative to reproductive state
c_0	0.036	/day	conversion coefficient
c_1	0.0035	/day	conversion constant
c_2	0.078	/day	conversion function exponent
γ_1	0.016	ha/cow/day	vulnerability of emerging reproductive tillers to grazing
γ_2	0.009	ha/cow/day	vulnerability of mature reproductive tillers to grazing
L	85.6	cow/ha	livestock density on day t
m_0	0.09	/day	maturation coefficient
s_0	0.052	/day	senescence coefficient
p	0	-	fraction of defoliated reproductive tillers counted as alive by Bahmani (1999)

calibration (Table 1). Subsequent fitting confirmed these values. One parameter, p , was added to the model to account for the fraction of defoliated reproductive tillers that were counted as alive by Bahmani (1999) because they were supporting a live daughter tiller. This parameter ranged in value from 11% to 35%.

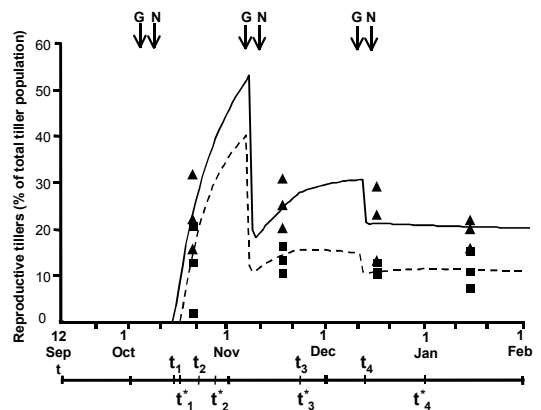
Treatments were simulated for 4 months starting on 12 September using a daily time step (Figure 2). The WinSAAM modelling software (Wastney *et al.* 1998) was used to determine the parameter values that gave the best fit of the model to the data set.

The data representing the four replicates of each treatment were fitted simultaneously, and the parameters t_1 , t_2 , t_4 , c_0 , c_1 , γ_1 , γ_2 and p were calculated for each treatment. Then the four treatments for each cultivar within each year were fitted simultaneously to determine which parameters varied significantly between treatments. As few parameters as possible were allowed to differ between treatments so that the key biological processes responsible for the observed differences in reproductive tiller proportions could be identified. A difference between treatments in one of these parameters was considered significant if the parameter value means differed by more than one standard deviation.

Results and discussion

Differences in reproductive tiller proportions between treatments and cultivars, observed by Bahmani (1999), were explained by four model parameters: c_0 , c_1 , γ_1 and p . Selected results are shown in Table 2. The differences were explained by parameters relating to conversion only, not maturation, senescence or vulnerability to grazing. This implies that regulating reproductive development requires focus toward factors that affect the conversion of vegetative tillers to reproductive tillers. These factors include genotype, environment

Figure 2 Observed and simulated proportions of reproductive tillers in the total tiller population for 'Ellett' (observation \blacktriangle , simulation —) and 'Ruanui' (observation \blacksquare , simulation ---) under +N-I in Year 2. The predicted development calendar is given for 'Ellett' (t_1 , t_2 , t_3 , t_4) and for 'Ruanui' (t_1^* , t_2^* , t_3^* , t_4^*). Timing of grazing (G) and nitrogen (N) application (30 kg N/ha at each date) are shown as ($\downarrow \begin{smallmatrix} G \\ N \end{smallmatrix}$).



and pasture management (grazing, irrigation and nitrogen application).

Genotype

Bahmani (1999) observed that the proportion of reproductive tillers was always higher in 'Ellett' than in 'Ruanui' pastures regardless of treatment and year. Modelling explained this difference by a higher conversion rate of 'Ellett', particularly later in the season (i.e., a higher c_1 ; Table 2).

Both 'Ellett' and 'Ruanui' are early flowering ecotypes. The higher propensity of 'Ellett' to flower compared with 'Ruanui' might also be genetically determined. This expressed itself from mid-October to

Table 2 Values for t_1 , c_0 , c_1 and γ_1/γ_2 obtained by fitting the model to the data of the four treatments of Bahmani (1999) simultaneously. Parameter values given with standard deviations were fitted using WinSAAM, others were fixed.

Treatment	Year	Cultivar*	t_1	c_0 (/day)	c_1 (/day)	γ_1, γ_2^1 (ha/cow/day)
-N-I	1	E	5 Oct	0.04	0.010 ^{3,4} ±0.002	0.040 ³ ±0.02
		R	5 Oct	0.04	0.004 ⁴ ±0.001	0.025±0.004
	2	E	13/19 Oct ²	0.04	0.008±0.003	0.034±0.01
		R	20 Oct	0.034±0.03	0.008±0.006	0.033±0.014
-N+I	1	E	5 Oct	0.04	0.03 ^{3,4} ±0.007	0.014 ³ ±0.003
		R	5 Oct	0.04	0.004 ⁴	0.025 ¹ ($\gamma_2=0$)
	2	E	17 Oct	0.04	0.018 ³ ±0.005	0.034
		R	20 Oct	0.044±0.011	0.001 ³ ±0.0008	0.033
+N-I	2	E	15 Oct	0.04	0.018 ^{3,4}	0.034
		R	18 Oct	0.053±0.01	0.001 ^{3,4}	0.033
+N+I	2	E	18 Oct	0.04 ⁴	0.008 ⁴	0.034
		R	20 Oct	0.02 ⁴ ±0.006	0.001 ^{3,4}	0.033

*E= 'Ellett'. R = 'Ruanui'.

¹ $\gamma_1 = \gamma_2$, except for 'Ruanui' under -N+I in Year 1.

² Adjusted within treatment across replicates

³ = parameters differed significantly from -N-I within cultivar.

⁴ = parameters differed significantly between cultivars within the same treatment.

mid-January (Figure 3). The control of reproductive development in 'Ellett' might therefore not only require careful management in early spring, but also in late spring and early summer, to maintain pasture quality and persistence throughout the season.

Season

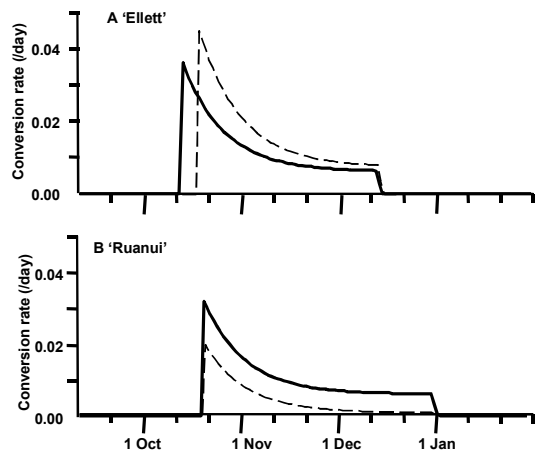
Bahmani (1999) observed that first stem elongation occurred later in Year 2 than in Year 1, regardless of treatment. The model identified this with a delayed start of conversion (i.e., a delayed t_1 ; Table 2). The model also predicted that maturation (i.e., t_2) was delayed in Year 2 compared with Year 1 for both cultivars.

The later start of reproductive conversion in spring 1997 compared with 1996 is an example of environmental effects. This response may be explained by rainfall, as June, July and August 1997 (226 mm) were drier than the winter of 1996 (421 mm) (10-year average, 415 mm). October 1997 (70 mm) was also drier than the 10-year average (115 mm). The average minimum temperature was also lower over winter 1997 than winter 1996 (3.0 versus 5.1°C). These conditions may have reduced tiller growth and, since flowering is partly controlled by tiller size, delayed flowering (Jewiss 1972).

Grazing

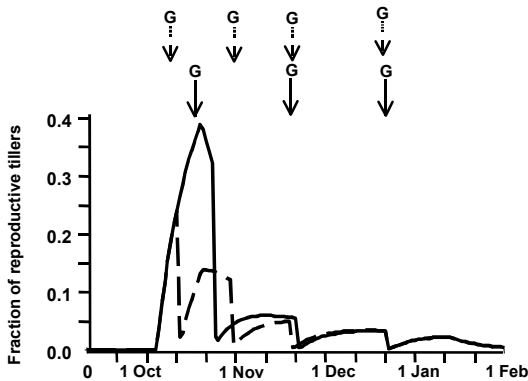
The model analysis suggested that there was no difference between the vulnerabilities of the emerging and the mature reproductive tillers to grazing. For all treatments γ_1 was equal to γ_2 in both years. The only difference was found in 'Ruanui' under -N+I in Year 1, but this could not be identified as either a cultivar or a treatment effect (Table 2).

Figure 3 Predicted pattern of vegetative tiller conversion to reproductive tillers for (A) 'Ellett' and (B) 'Ruanui' in Year 2 under -N-I (—) and +N-I (— · — · —).



The model could be used to simulate different grazing schedules to show how reproductive development might be regulated through grazing management. Making the first grazing date earlier and adding an extra grazing greatly reduced the fraction of emerging reproductive tillers according to the model simulation (Figure 4). Further modelling work and field measurement would be required to design grazing systems to optimise control of reproductive development at a farm level. In particular, reproductive tiller numbers need to be measured prior to grazing, to check model predictions that 40% or greater of tillers could be reproductive at this time (Figure 2).

Figure 4 Predicted pattern of emerging reproductive tiller proportions: (—) under the grazing schedule applied in Year 1 in Bahmani (1999) and (.....) under a simulated grazing schedule designed to minimise the number of emerging reproductive tillers predicted by the model. Dates of grazing are indicated by ↓ and ↓ respectively.



Irrigation

The effect of irrigation on reproductive tiller proportions varied between cultivars and years. ‘Ellett’ had a greater proportion of reproductive tillers under -N+I compared with -N-I in both years, whereas ‘Ruanui’ was not significantly different under -N+I compared with -N-I in Year 1, but had significantly lower proportions of reproductive tillers under -N+I in Year 2 (Bahmani 1999). Modelling suggested that the increase in reproductive tiller proportions in ‘Ellett’ was due to a significantly higher constant for the conversion function (c_1) in both years, as well as, in Year 1, a significantly lower reproductive tiller vulnerability to grazing (g_1 and g_2). The lower reproductive tiller proportion in ‘Ruanui’ under -N+I compared with -N-I was explained by c_1 being significantly lower under -N+I (Table 2).

These results suggest that irrigation could make control of reproductive development more difficult in ‘Ellett’-based pastures. However, few other published data sets exist describing the effects of irrigation on reproductive tillering in perennial ryegrass, particularly relating to temperature and irrigation interactions. The effect of irrigation on flowering needs further study, especially as irrigation is increasing in South Island dairying.

Nitrogen

‘Ellett’ and ‘Ruanui’ responded very differently to application of nitrogen (Bahmani 1999). Compared with -N-I, under +N-I reproductive tiller proportions

were greater in ‘Ellett’, whereas in ‘Ruanui’, reproductive tiller proportions were greater only until early November but lower thereafter. Modelling suggested that this response in ‘Ellett’ was due to a higher constant in the conversion function (c_1), while the response in ‘Ruanui’ was due to a significantly lower c_1 , as shown in Figure 3.

These results suggest that the application of nitrogen to Ellett in spring might compromise the plant’s perennality and persistence, whereas nitrogen might improve persistence in ‘Ruanui’.

Conclusion

This mechanistic model, when used as a tool to investigate the biological processes underlying perennial ryegrass reproductive development, highlighted how genetic, environmental, and pasture management factors affected perennial ryegrass reproductive development. This mainly occurred through changes in the rate of conversion from vegetative to reproductive tillers. Maintaining pasture quality throughout the season without compromising pasture persistence should involve the appropriate grazing management and nitrogen fertiliser practices for that cultivar. Since ‘Ellett’ ryegrass has a high propensity to flower from early spring to late summer, its use conflicts with the farmer’s objective to maintain pasture quality and persistence. Data sets describing the effects of different pasture management strategies (choice of cultivar, fertiliser application, timing, intensity, and frequency of defoliation) could be used to upgrade the model described here. Studies to track the origins and disappearance of reproductive tillers are also required to better define the processes of re-heading and disappearance. The model could then be used as a tool to assist with optimisation of pasture quality and persistence through controlling reproductive tiller development.

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REFERENCES

- Bahmani, I. 1999. Tiller dynamics and leaf growth processes of the perennial ryegrass cultivars “Ellett” and “Grasslands Ruanui” as influenced by environmental factors. Co-tutorial Ph.D. Thesis, Massey University and INPL, Nancy, France.

- Bahmani, I.; Thom, E.R.; Matthew, C. 1997. Effect 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.; 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: 121–131.
- Hunt, W.F.; Field, T.R.O. 1979. Growth characteristics of perennial ryegrass. *Proceedings of the New Zealand Grassland Association* 40: 104–114.
- Jewiss O.R. 1972. Tillering in grasses – its significance and control. *Journal of the British Grassland Society* 27: 65–82.
- L’Huillier, P.J. 1987. Tiller appearance and death of *Lolium perenne* in mixed swards grazed by dairy cattle at two stocking rates. *New Zealand Journal of Agricultural Research* 30: 15–22.
- Matthew, C. 1991. “Late control” – What is it, and why should it work? *Dairyfarming Annual* 43: 37–42.
- Terry, R.A.; Tilley, J.M.A. 1964. The digestibility of the leaves and stems of perennial ryegrass, cocksfoot, timothy, tall fescue, lucerne and sainfoin, as measured by an *in vitro* procedure. *Journal of the British Grassland Society* 19: 363–372.
- Wastney, M.E.; Patterson, B.H.; Linares, O.A.; Greif, P.C.; Boston R.C. 1998. Investigating biological systems using modelling: Strategies and software. Academic Press, San Diego, USA. 382 pp.
- Woodward, S.J.R. 2001. Validating a model that predicts daily growth and feed quality of New Zealand dairy pastures. *Environment International* (In press).
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