Analysing persistence of grass swards in terms of tiller birth and death

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Abstract

A methodology is developed to analyse the contribution to sward persistence of the processes tiller birth and tiller death, and variation in their rate over an annual cycle. The methodology is tested using previously published data for timothy grass (*Phleum pratense*). The analysis shows that high death rates of timothy tillers in summer present a problem for persistence in that tiller appearance rates required to maintain the tiller population in these conditions require tiller bud site usage statistics that are biologically unlikely in field swards. While it is not suggested that ryegrass has a naturally high tiller death rate in summer as demonstrated here for timothy, where abiotic stresses reduce ryegrass tiller survival, the same principles are likely to apply.

Keywords: Leslie matrix, *Phleum pratense*, population stability, tiller birth rate, tiller survival rate, timothy grass

Introduction

The tiller is the basic unit of production and persistence in the grass plant and Langer (1963) summarised understanding gained from 72 studies of tillering in grasses prior to that date. In the simplest studies of tiller dynamics, change over time in tiller population density is reported. Further insight can be gained by monitoring marked tillers in order to resolve change in the tiller population density into components of tiller appearance and tiller death. A third level of complexity is seen when survival of cohorts of tillers appearing over defined time intervals is monitored (e.g., Jewiss 1966). Such studies are very labour intensive and are comparatively uncommon. Two examples for perennial ryegrass (*Lolium* perenne) are reported by Korte (1986) and Bahmani *et al.* (2003). For a complete demographic analysis it is necessary to also monitor new tiller appearance for a series of age cohorts. Whereas tiller survival can be determined by repeat observations of marked tillers in fixed quadrats, determining which tillers in a fixed quadrat have produced new tillers usually requires destructive harvest of the fixed quadrat which is much more time consuming, and requires a larger number of fixed quadrats to be established for this purpose. The only such study known to the authors is that of Black (Matthew *et al.* 2000).

The work reported here was carried out between 1993 and 1997 and arose from an interest in developing a methodology for mathematical modelling of persistence in grass swards. Our approach was to define (i) the tiller population density required to capture incident light, and (ii) seasonal patterns of tiller birth and death needed to maintain the tiller population.

In addressing (i) above we considered the sward leaf area index (LAI) required for light capture, and the tiller population density needed to provide that LAI. Generally 95% capture of incident light is attained at a LAI of 3 – 4 (Simon & Lemaire 1987). The tiller population density that will provide that LAI varies with herbage mass, with fewer, larger tillers required at higher herbage mass (Matthew *et al.* 1995). Here we address part (ii) of the above persistence analysis by reporting a matrix algebra methodology to systematise understanding of implications for tiller population stability of variation in seasonal tiller appearance and survival rates.

Method and materials

Matrix modelling

To explore options for computer simulation of tiller dynamics in grass swards and possible identification of periods of seasonal instability, we used a matrix algebra method. Matrix algebra techniques for modelling population dynamics were developed by Leslie (1945), and are now well known. Briefly, Leslie's method involves a transition matrix which defines survival probabilities and birth rates for each age-group in a population, such that when this matrix is post multiplied by a column vector containing the numbers in each age-group within the population, the result is a second column vector containing the new population age structure one unit of time later. This is illustrated diagrammatically in Fig. 1 for a simple case with four age groups in the population.

In Fig. 1, $\boldsymbol{A}$ is the transition matrix of birth ($b_{i,j}$) and survival ($s_{i,j}$) coefficients for age cohorts i = 1 .. *n* and $\boldsymbol{N}_{time\ 0}$ and $\boldsymbol{N}_{time\ 1}$ are the column vectors representing the tiller numbers in each age group at successive times (Figure 1). The subscript j for coefficients *b* and *s* indicates the age group that progeny or survivors belong to at the end of the transition period. Progeny are always born into

Figure 1 Format of the matrix algebra equation for calculating tiller population at time t_1 from population at time t_0, based on reproductive rate and survival probability of tillers in each age class. A 12x12 transition matrix, ***A***, and a 30-day time step was used to describe seasonal cycles of tiller population change. Survival probabilities for each tiller age class were calculated from published data as described in the text. In the absence of published data, tiller appearance was assumed to be evenly distributed among tillers more than 1 month of age.

$$\begin{array}{cccccccc} b_{1,1} & b_{2,1} & b_{3,1} & b_{4,1} & & n_{1\ \text{time}\ 0} & & n_{1\ \text{time}\ 1} \\ s_{1,2} & . & . & . & & n_{2\ \text{time}\ 0} & & n_{2\ \text{time}\ 1} \\ & & & & \text{X} & & = & \\ . & s_{2,3} & . & . & & n_{3\ \text{time}\ 0} & & n_{3\ \text{time}\ 1} \\ . & . & s_{3,4} & s_{4,4} & & n_{4\ \text{time}\ 0} & & n_{4\ \text{time}\ 1} \end{array}$$

or: $$A \ \text{x} \ N_{\text{time}\ 0} = N_{\text{time}\ 1} \quad (1)$$

$b_{i,1}$ = rate of reproduction in age-group *i* at *time 0*. By definition, all progeny are in age-group *1* at *time 1*.
$s_{i,j}$ = probability of survival from age-group *i* at *time 0* into age-group *j* at *time 1*.
$n_{i\ time\ t}$ = numbers of tillers in each age class at a particular time. The total population, $\sum_{i=1..n} n_{i\ time\ t}$ was designated P_t.

age group 1 and survivors move from their present age group to the next, in each case. The total population P_t at time *t* thus equals the sum of the numbers in individual age-cohorts ($n_{1,t,}$ .. $n_{n,t}$) of N_t. A coefficient ($s_{4,4}$ in Fig. 1) not included in Leslie's (1945) model, was used by Usher (1972) to provide for continued survival of some members of the oldest age group. That is, with this coefficient included, n_4 (Fig. 1) represents the number of individuals four time periods old and older; without this coefficient all individuals surviving until the beginning of the fourth time period would be assumed to have died by the end of that period. The model in Fig. 1 assumes no recruitment of seedlings into the population but, if desired, an additional row and column can be inserted to define numbers of seeds formed and numbers of these germinating (Callaghan 1976).

For a square matrix A, with n rows and columns, there are n eigenvalues (λ) and associated eigenvectors (***N***) which satisfy the equation:

$$\boldsymbol{A}\,.\,\boldsymbol{N} = \lambda\,.\,\boldsymbol{N} \qquad (2)$$

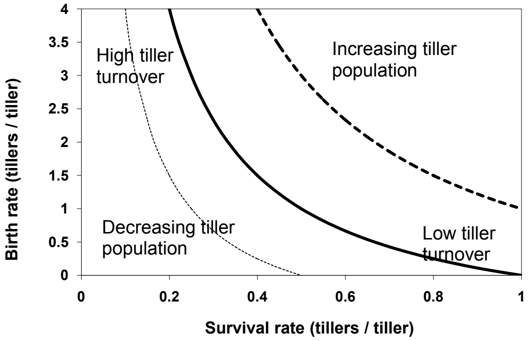
Usher (1972) noted that the first eigenvalue (λ_0) and its eigenvector are of biological interest in that they define the equilibrium that emerges if matrix ***A*** continues to operate repeatedly over successive time intervals. In this case $\boldsymbol{\lambda}_0$ is the intrinsic rate of population change (P_{t1}/P_{t0}) and the associated eigenvector (N, equation 2) defines the proportionate distribution of individuals across age-groups necessary for steady state population demography under matrix ***A***. Where the appropriate unit of time is 1 year, for example when modelling a population where young are born at a certain season every year, mean birth and death rates for each age class may be considered an intrinsic property of that age class, apart from random variation between years, in which case population stability can be assessed by solving for the eigenstructure.

Table 1 Analysis of deviance as originally calculated in 1993 for survivorship of tillers of timothy grass in data of Jewiss (1966). Statistical probabilities are not reported because the analysis did not account for repeat measures effects and software for reanalysis according to Bahamani *et al*. (2003) was unavailable. However, given the very large deviance ratio for the seasonal effect it is clear that tiller death in timothy grass has a seasonal pattern (see also Fig. 3c) that departs from 'exponential decay' of tillers in a cohort. Deviance ratios are for Type II tests. Only terms with larger deviance ratio and likely to be confirmed as statistically significant on reanalysis are reported.

Source	d.f.	deviance	Mean deviance	Deviance ratio
Season	8	1139	142	25
Year	2	64	32	5.7
Cutting	1	29	29	5.3
Flowering	2	66	33	5.9
Cutting x flowering	2	47	23	4.2
Season x year	4	105	26	4.7
Residual	145	822	5	
Total	164	4868	29	
Non-orthogonality		1451		

Since in a grass sward, tiller birth occurs continuously throughout the year, and birth rates and survival change markedly on a seasonal basis, a series of transition matrices is required to define an annual cycle of tiller dynamics. While Fig. 1 demonstrates the mathematical principles using a 4 x 4 matrix, our quantitative modelling of sward tiller dynamics used a 30-day time step and a set of 12 transition matrices of 12 rows and 12 columns for each simulation. Under this system, the ongoing survival of tillers appearing in each consecutive 30-day period is specified in 11 time steps of approximately 1 month until they are near to 1 year of age, at which point they are considered as a residual pool of old tillers, from which some tillers are also lost every month. This model assumes young tillers produce no daughter tiller in their first month of life, an assumption supported by field study (Langer 1956).

Figure 2. Sward stability diagram based on combinations of weighted average birth and survival rates per 30 days, showing isolines for P_{t1}/P_{t0} = 0.5 (declining population) (dotted line), 1.0 (stable population) (solid line) or 1.5 (increasing population) (dashed line). It should be noted that for a 10-day leaf appearance interval (30 days to three-leaf regrowth stage), the maximum possible birth rate is three tillers per tiller per 30 days.



We were also interested to simplify the stability analysis to focus on the total tiller population, P_t, rather than the age structure of the population as in Eq. 1. For the simplified situation where all $b_{i,j}$ equal b', and all $s_{i,j}$ equal s' (*i.e.* rates of reproduction and survivorship don't change with tiller age) it can be shown that $(b' + s') = P_{t1}/Pt_0$ (*i.e.* if tiller population density increases in a given month from 10 000 m^{-2} to 11 000 m^{-2}, then mean birth and mean survival expressed as fractions must sum to 1.1). To derive a more general relationship between population increase or decrease and tiller birth and tiller survival we can substitute N_{t1} above with P_{t1}, the total population, and rewrite Eq. 1 as:

$$P_{t1} = \sum_{i=1..n} n_{i\,time\,0}\, s_{i,j} + \sum_{i=a..n} n_{i,\,time\,0}\, b_{i,1} \qquad (3)$$

where n is the number of age classes in matrix ***A***, *a* is the age-class at which tillers first begin to form daughter tillers, j = min (i+1,n), and $n_{i,\,time\,0}$ is as defined in Fig. 1. If we assume that only the youngest age class does not produce daughter tillers, then dividing throughout by P_{t0} we obtain:

$$P_{t1}/P_{t0} = s'' + (P_{t0}-n_{1\,time0})/P_0 \,.\, b'' \qquad (4)$$

where s'' and b'' are weighted averages of tiller survival and birth rates, respectively, such that $s''.\,P_{t0} = \sum_{i=1..n} n_{i\,time\,0} \,.\, s_{i,j}$ and equivalently for b''. Where it can be assumed that:

$(P_{t1} - n_{1\,time\,1}) = (P_{t0} - n_{1\,time\,0})$, then the term $(P_{t0}-n_{1\,time0})/P_0 \,.\, b''$ in Eq. 4 simplifies to $s''.\, b''$, which allows equation 4, to be reduced to a more general form:

$$Pt_1/Pt_0 = s''\,(1 + b'') \qquad (5)$$

From Eq. 5 a sward stability diagram can be generated as a contour plot of isovalues of Pt_1/Pt_0 plotted on a graph of s'' against b'' (Fig. 2).

Test data set

Previously published data (Fig. 3a) of Jewiss (1966) for timothy (*Phleum pratense*), showing the survival of 12 tiller age cohorts over a 2-year period were used to test the analytical methodology. Treatment mean values, averaged over replicates, were regenerated (with permission of the original author) by enlarging the published diagrams, measuring distances from individual points to the X-axis with a ruler, and converting distances so obtained to tiller numbers per m^2.

Analysis of tiller survivorship

To identify patterns of variation in survival probability, the data were first plotted as survivorship curves showing $\log_{10}$ percentage of originally tagged tillers surviving each recording interval (Fig. 3b). In such plots, the slope for each cohort over each recording interval is a measure of the survival of that cohort over the time interval in question. (A steeper slope indicates lower survival). In the case of exponential decay with constant half-life across age-cohorts, these plots would show a series of straight, parallel lines.

Using dates of tiller counts reported by Jewiss (1966) to set up a time scale in days form the start of the experiment, Logit (survival probability)[†] as illustrated in Fig. 3b was analysed using Genstat 5.3 (Payne 1987) assuming a binomial error distribution. For such analyses, the residual deviance (equal to the residual sum of squares for errors with normal distribution) is a chi-squared testing for goodness of fit to a binomial distribution around the fitted model. A significant residual deviance value indicates that there are sources of variation not accounted for. Hence terms can be added to a regression model using an iterative approach, seeking a reduction in residual deviance.

Exponential decay of age-cohorts with constant half-life across all age-cohorts was fitted as a first step, and at this point there was a high residual deviance. Seasonal patterns were then added to the regression model using Fourier equations (Lambert 1986), and finally additional terms were incorporated using polynomial or non linear functions as appropriate to explore tiller age, flowering status and management effects. At each step, presumed non-significant terms were discarded, in order to give an 'optimal' model which had the best possible fit with the fewest parameters.

Results and Discussion

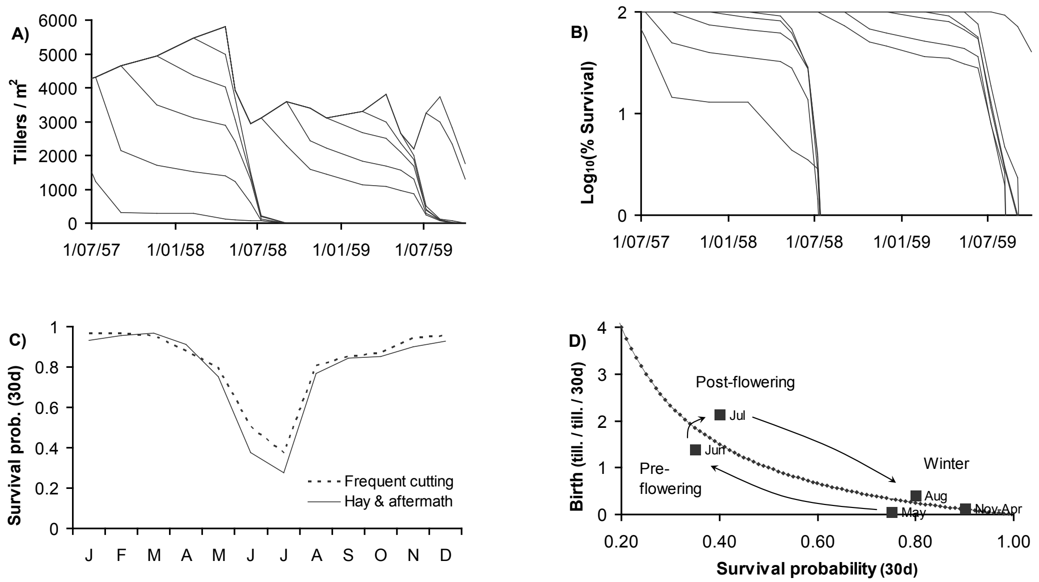
Leslie matrix simulations of tiller turnover

We produced matrix algebra simulations of annual tiller dynamic cycles for timothy, meadow fescue (*Festuca*

[†] The logit link converts 0 to 1 probability space to - to + ∞ real space.

Figure 3 **(a)** Data of Jewiss (1966) for tiller dynamics of timothy grass under a "hay and aftermath" cutting regime. The data as originally published also include a 'frequent defoliation' cutting treatment; **(b)** Survivorship of individual age cohorts for the same data set plotted as log[Present tiller number/Initial tiller number) x 100]; **(c)** Fitted seasonal 30-day mean survival probability for both cutting treatments. **(d)** Stability diagram for timothy showing seasonal change in fitted average 30-day survival probability and birth rate (tillers/tiller/30days) calculated using Eq. 5. The dotted line indicates combinations of birth and survival for which P_{t1}/P_{t0} = 1 (population constant). Further explanation is provided in the text.

Figures 3 (a – d)



pratensis), and two perennial ryegrass data sets. These are not presented here because of space constraints and issues accessing 15-year-old computer files, but essentially the models reproduced the tiller cohort survival diagrams used to generate them. The value in carrying out this work was the quantitative insight gained into differences between the respective data sets in seasonal patterns of tiller birth and death and the way differing combinations of birth and death may combine to affect population stability. Each data set modelled appeared to have a distinct persistence strategy pattern. It is not clear how much the apparent seasonal tiller birth and death rate features of each data set should be attributed to species, cultivar, environment, or other factors, but the salient conclusions for timothy grass are discussed below. A point of note was that sward behaviour tended to flip suddenly between different modes, so that often as few as three to five transition matrices could be used for several months at a time in order to compile an annual cycle, and a visually reasonable simulation of the original data still obtained. In this sense the work revealed that there are distinct seasonal phases of sward dynamics, with flowering being a pivotal time.

Quantitative analysis of tiller survivorship

Exponential decay with different half-life for different cohorts would generate straight lines with different slopes. From visual inspection of Fig. 3b it is immediately evident that the lines are neither straight nor parallel, indicating two distinct categories of departure from exponential decay, (a) a major effect of seasonal change in survival probability and (b) some indication of differences between cohorts in rate of disappearance or half-life. In both cases it would be of interest to objectively separate and statistically test the two effects. A further question is whether seasonal change in survival is constant across cohorts, or varies in some systematic way for particular cohorts or groups of cohorts. This can be tested statistically from the observation date x cohort interaction.

Analysis of deviance methodology is conceptually appropriate to the problem. However, a tiller survivorship dataset has a complex structure, usually with traditional plots (typically to explore grazing management, cultivar, or other such effects), a number of fixed quadrats within each plot to designate samples of tillers for observation, and often more than 10 different age cohorts within each fixed quadrat, for which the successive 30-day survival probability values are actually 'repeat measures' on the same experiment entities. Data sets are typically unbalanced, in that some cohorts may not appear until late in the experiment while the early cohorts may become extinct during the experiment. In this particular data set, only treatment mean values of tiller density for each cohort, for two defoliation treatments (hay and aftermath, and frequent cutting) can be recovered from the published data. To cope with such a complex data structure is a major statistical challenge.

Subsequent to the work reported here, the analysis of deviance methodology was further developed by Bahmani *et al*. (2003) to better account for the data error structure. However, we have not had the opportunity to access those algorithms to improve this analysis. For that reason we do not present probability values in Table 1, although the size of the various deviance ratios is itself informative. In particular, the seasonal effect in timothy has such a large deviance ratio that it is reasonable to assume the departure from exponential decay associated with seasonal difference in 30-day tiller survival probability to be highly statistically significant, whatever statistical model was used. For 8 months of the year from September to April, 30-day tiller survival probabilities were consistently in the range 0.8 to 0.95. For the months of June and July, the fitted 30-day survival probability was below 0.5 (Fig. 3c). The deviance ratio for the cutting effect was much smaller than for the seasonal effect (Table 1) but if significant would reflect the lower survival through the flowering period in the 'hay and aftermath' cutting regime than the 'frequent cutting' regime (Fig. 3c). The flowering effect is difficult to interpret because the flowering status of tiller cohorts and season are confounded in the data set.

Agronomy of timothy grass

If this data set is indicative, timothy swards are characterised by a period of low tiller survival in mid summer, during which the majority of the tiller population dies and is replaced by new tillers. Even without detailed analysis, this can be discerned from the original published data (Fig. 3a). However, by quantifying the seasonal change in survival probability (Fig. 3c), applying Equation 5 to calculate birth rates required considering the observed total population density changes (Fig. 3a), and plotting the seasonal survival probability and birth rate values as a trajectory on a stability diagram like that in Fig. 2, a more quantitative description of the persistence strategy of timothy grass is obtained (Fig. 3d).

The period of tiller death coincides with flowering, which is later in timothy than in perennial ryegrass, and initiated by long day length (Langer 1955). (Peak anthesis for timothy was 6th Feb. at Palmerston North, compared with 30th November for perennial ryegrass (Hill & Watkin 1975). This tiller mortality event in mid summer is likely linked to flowering of adult tillers, with replacement tillers formed from buds at the base of flowering tillers, as described for ryegrass by Matthew *et al*. (1989). Fig. 3d clarifies that after a period of comparative stability associated with high survival probability in winter, there is a much lower tiller survival rate during the pre-flowering period, with birth rate rising in compensation but only reaching levels required for population recovery in the post-flowering period. In this sense it could be said that there are 'three seasons' when considering sward dynamics of persistence in timothy: a winter stability period; a pre-flowering period when there is a risk of death rates exceeding birth rates, and a post-flowering period with continued high death rates but improved birth rates allowing population recovery.

Visual inspection of Fig. 3a indicates that during flowering in timothy it appears juvenile tillers are not exempt from the low survival probability, and may also die from competition related stress as flowering tillers develop. In support of this, Jewiss (1966) reported that spring-formed tillers generally die before flowering while still vegetative. Korte's (1986) data indicated a similar behaviour in perennial ryegrass. Where a pattern of tiller population turnover associated with flowering is strongly expressed it is a corollary that emergence of post-flowering tillers will be important to persistence. This pattern of tiller population dynamics has been referred to as the "reproductive" perennation pathway (Matthew *et al*. 1993).

For timothy this understanding of the annual tiller renewal event provides insight as to why the species is better suited to southern than northern regions of New Zealand and to higher latitudes such as Canada in the northern hemisphere. The cooler, moister conditions in Southland in summer would likely result in higher tiller birth rates through the critical tiller replacement period, than in warmer, drier conditions in Canterbury or the North Island.

An important general insight from Fig. 2 and Fig. 3b is that when 30-day tiller survival falls below 50%, tiller appearance must approach two tillers/tiller/month to maintain the tiller population. Assuming growing conditions with three leaves appearing per tiller per month, over two thirds of all tiller buds formed must initiate and grow into new tillers, whereas bud site usage in field swards is typically much lower (Chapman *et al.*1983).

By extrapolation to ryegrass, it can be seen that any event such as a drought or severe grazing, combining with moisture deficit, insect, and other stresses to cause a period of tiller death in summer might be seriously detrimental to sward persistence and farmers should be mindful about this when making decisions on summer management options. It should also be borne in mind that herbage mass on farm may fall in summer where animal feed demand (kg DM/ha/day) exceeds pasture growth. When herbage mass falls, an *increase* in tiller population density is required to maintain sward LAI, and mere maintenance of the sward tiller population would amount to a fall in LAI. Hence our analysis indicates multiple issues for grazed pastures in summer, with more tillers likely to be needed at a time when death rates are too high for this to be a realistic expectation.

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