State of knowledge in tiller dynamics

Cory Matthew [A], Mónica G Agnusdei [B], Silvia G Assuero [C], André F Sbrissia [D], Omar Scheneiter [E] and Sila C Da Silva [F]

[A] Institute of Agriculture and Environment, PN433, Massey University, Private Bag 11-222, Palmerston North 4442, New Zealand, www.massey.ac.nz

[B] Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Agropecuaria Balcarce, CC 276, 7620 Balcarce, Argentina, http://inta.gob.ar/

[C] Facultad de Ciencias Agrarias, Universidad Nacional de Mar del Plata, CC 276, 7620 Balcarce, Argentina. http://www.mdp.edu.ar/agrarias/

[D] Santa Catarina State University, Avenida Luiz de Camões 2090, Lages, SC, Brazil, www.cav.udesc.br

[E] Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Agropecuaria Pergamino, Avda Frondizi km 4.5, Pergamino, Bs As, Argentina, www.inta.gob.ar.

[F] Animal Science Department, E.S.A. "Luiz de Queiroz", University of São Paulo, PO Box 09, Piracicaba, SP 13418-900, Brazil, www.esalq.usp.br

Contact email: c.matthew@massey.ac.nz

Abstract. Persistence of sown pastures is a concern for pastoral production worldwide. Fundamentally, when a pasture does not persist the problem can be expressed in terms of inadequate new tiller production or excessive tiller death. However, the collection of data to build an understanding of sward dynamics at this level is time consuming. Tiller survival diagrams are presented for a range of temperate and tropical grass species including *Lolium perenne, Lolium multiflorum, Festuca arundinacea, Festuca pratensis, Phleum pratense*, *Bromus willdenowii*, *Cynodon dactylon*, *Brachiaria brizantha*, *Panicum maximum, Chloris gayana* and *Paspalum notatum*. It is shown that each grass has a unique perennation strategy and accordingly unique strengths and weaknesses that confer persistence or lack of persistence in different situations. There is also confusion in extension circles about the trade-off between tiller size and tiller density and how to detect a suboptimal tiller density. Grass swards respond to high herbage mass by increase of tiller size and reduction in tiller density, but reduction in tiller density is often mistaken for sward decline. A distinction must be made between size/density compensation and sward decline. Increased understanding of sward dynamics at this level should help in the evolution of management practices that improve persistence on a range of grassland types.

Keywords: Perennation strategy, flowering, biennialism.

Introduction

The persistence of grass swards can be analysed in terms of the contribution of birth and death to the change over time in tiller population density (TPD). Mathematically the population behaviour so defined can be described by matrix algebra (Matthew and Sackville Hamilton 2011) or by differential calculus equations (Louie *et al*. 1998). Simplistically the proportion of a population surviving a given time period and the birth rate of the population should total 1 for a stable population but if it is assumed that juveniles do not generate births, the birth rate required for a stable population increases sharply with lower survival. Birth and survival may also change seasonally, in which case population stability needs to be assessed over the whole annual cycle (Matthew and Sackville Hamilton 2011). A major reason for seasonal cycles of tiller birth and death is flowering and replacement tillers may be produced by either flowering or non-flowering tillers in which case the seasonal pattern of birth and death within the annual cycle is altered accordingly (Matthew *et al*. 1993). Since the collection of data for a time series of birth and death

rate data for a grass tiller population is very time consuming, published examples are uncommon, with perhaps fewer than 30 case studies published. Some unpublished data sets are also known to the authors.

Here we present selected examples and discuss the persistence strategies observed, their implications for pasture management, and questions to be resolved in plant breeding.

Selected tiller survival diagrams

Early tiller survival diagrams are those of Jewiss (1966) for meadow fescue (*Festuca pratensis* L.) and timothy (*Phleum pratense* L.). From visual evaluation, perennation in meadow fescue is strongly based on a tiller cohort produced before flowering in spring and which survives to flowering in the following spring (Fig. 1A). In contrast, persistence of timothy hinges on an almost complete replacement of the tiller population in the immediate post flowering period (Fig. 1B). For perennial ryegrass (*Lolium perenne* L.), published survival diagrams include those of Korte (1986) and Bahmani *et al*. (2003) among others. There is typically a flowering transition which is
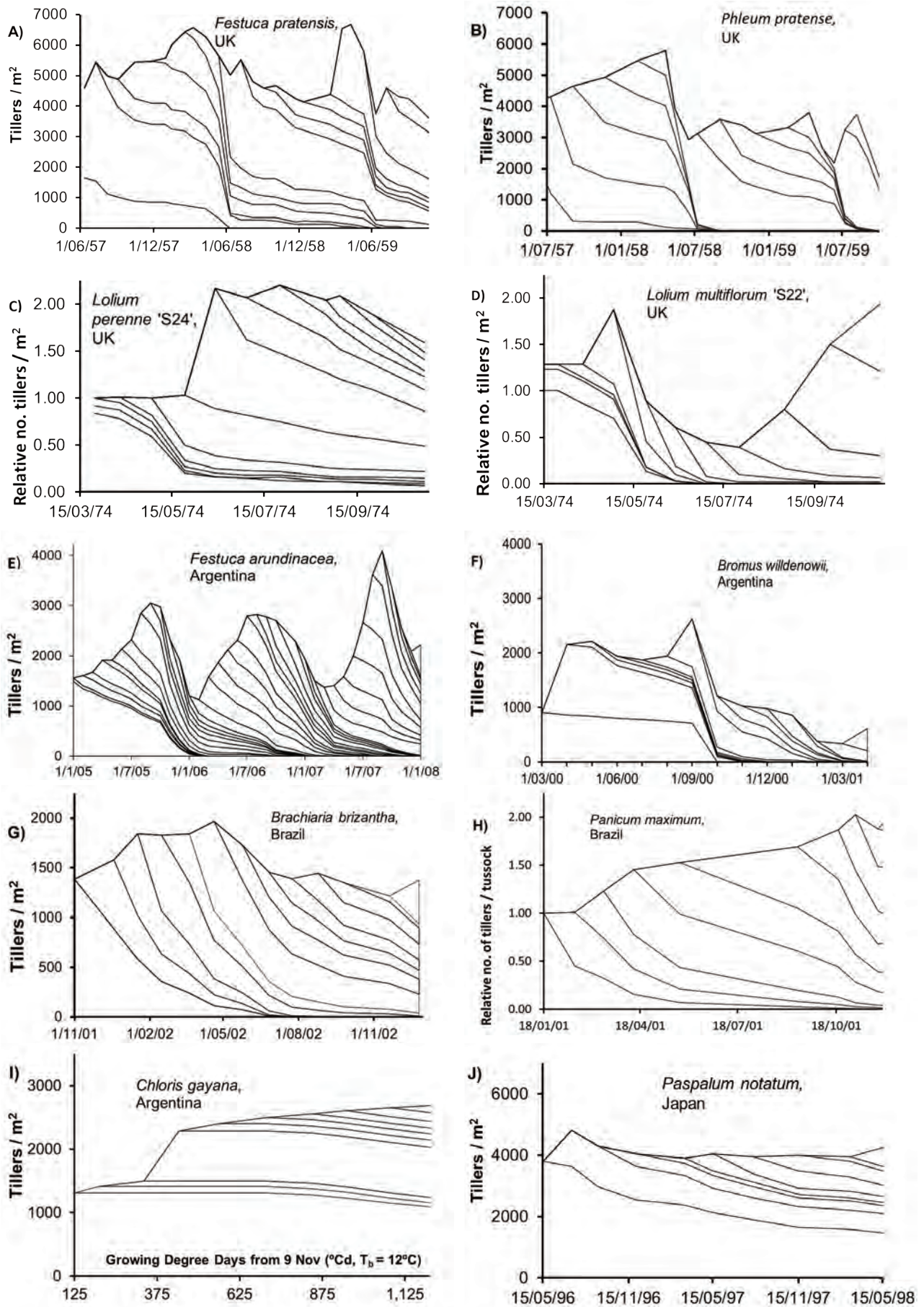
Figure 1. Tiller survival patterns for the various forage grass species discussed in the text. A – D and J are northern hemisphere sites with flowering c. June. E – I are southern hemisphere sites.

enhanced by laxer grazing management. Previously unpublished data of the late Alison Davies for 'S24' perennial ryegrass under three-weekly defoliation (Fig. 1C) shows a marked population turnover at flowering with an overall population increase. However, data from her same experiment for 'S22' Italian ryegrass (*Lolium multiflorum* L.) indicate a very high death rate of new tillers and decline in the total population through the summer months, likely attributable to the lower vernalisation requirement in Italian ryegrass (Fig. 1D). In tall fescue (*Festuca arundinacea* Schreb.), addition of cohort information to data of Scheneiter and Améndola (2012) for 'Palenque Plus' tall fescue receiving 200 kg/ha/year fertiliser N showed population increase in winter and decline in summer for each of three years (Fig. 1E). For frequently cut plots without N, tiller density had reduced to approx. 10% that of Fig. 1E) by the end of the experiment (Scheneiter and Améndola 2012). Prairie grass typically has a high proportion of tillers flowering and so a marked population turnover at the first flowering. Prairie grass often fails to re-establish a strong population after the second flowering; Figure 1F shows data for a frequent-lax defoliation regime from Scheneiter *et al*. (2008). Matthew *et al*. (2000) provide further data on Prairie grass.

In the tropical grasses, *Brachiara brizantha* cv. Marandu grown at Piracicaba, Brazil and defoliated to 20 cm exhibited a continuous pattern of tillering throughout the year (Fig. 1G), but with a fall in tiller population attributable to reduced tiller birth in June and July (which are drier as well as cooler months) and a recovery of the population with improved conditions in the November/ December period following. These swards were comparatively unresponsive to intensity of grazing, imposed as a combination of defoliation regimes varying in severity (20, 30 or 40 cm defoliation height) and frequency. However, the most intensive defoliation (10 cm) appeared to reduce the plants' ability to replace dead tillers, indicating the beginning of a degradation process (Sbrissia *et al*. 2010). Continuous tiller replacement was also observed for *Cynodon dactylon* (Carvalho *et al*. 2000) and *Panicum maximum* cv. Mombaça defoliated to 30 cm at 95% canopy light interception (Fig. 1H). For Marandu and Mombaça, the main contribution to sward leaf area formation was from 'basal', rooted tillers. Aerial tillers were small, short lived and usually associated with reproductive development of plants. However, for *Pennisetum purpureum* cv. Napier, aerial tillers played a central role in adapting to the grazing regimes imposed; rooted tillers in this species with their attached aerial tillers form tussocks which have been described as an 'integrated physiological unit' (IPU) (Paiva 2013). Generally with more frequent or lower defoliation plants will develop an increased number of smaller IPUs per unit ground area, and with less frequent or laxer defoliation the number of tillers per IPU will increase, forming larger tussocks at a lower density (Paiva 2013). This 'two tier' size/density compensation process probably allows for a greater range of LAI within a defoliation/regrowth cycle than in temperate grasses. Swards with a higher density of smaller tussocks have less stem development, younger plant tissues (higher turnover of leaves), and potentially reduced soil erosion risks (Pereira 2013). Rhodes grass (*Chloris gayana* Kunth) in miniature swards under differing defoliation regimes at Balcarce, Argentina, steadily increased in tiller

population density over the period of study in a manner similar to *P. maximum* in Figure 1H, but with distinct recruitment events (Fig. 1I) linked by the authors to light penetration to the base of the sward at defoliation (Martinez Calsina *et al*. 2012). Bahia grass swards (*Paspalum notatum* Flueggé) studied by Pakiding and Hirata (1999) in Japan were notable for extended longevity of tillers (Fig. 1J).

Size/density compensation in grass swards

Interpretation of TPD data is not straightforward. While sward degradation results in TPD decline, lower TPD is not necessarily evidence of degradation. TPD fluctuation is the mechanism by which swards optimise light interception when sward height (or defoliation regime) changes. Hence, in a sward not subject to stress-related depletion, TPD trends towards a value reflecting the environmentally sustainable leaf area index, and in normal growing conditions this value is related to herbage mass by a -0.5 power function (Matthew *et al*. 1995). It follows that the -3/2 (size/density) self thinning line for a grass sward defines the leaf area index the environment can support and the combinations of TPD and tiller dry weight that provide the environmentally sustainable LAI. TPD is therefore best interpreted by a log-scale biplot of tiller dry weight (-3/2 theoretical slope) or herbage mass (-1/2 slope), with distance from the environment reference line indicating the degree of stress or degradation (see for example Figure 6 of Martinez Calsina *et al*. 2012). However, factors like nutrient level and phenotypic plasticity also modify these relationships (Scheneiter and Assuero 2010).

The next step is to extend size/density theory to multi-species swards. In this context Yu *et al*. (2008) noted a reverse size/density effect in mixed clover-ryegrass swards, whereby size of white clover stolon units increased and their density decreased with increasing grazing intensity, indicating gap filling by clover. Similarly, Duchini (2013) found that mixed oat and annual ryegrass swards subjected to intermittent stocking exhibited a -3/2 size/density relationship when data for both species were averaged, but no relationship when considered separately. This would seem to indicate that the two species participated inter-actively in size/density compensation.

Discussion and Conclusions

The selected tiller survival diagrams (Fig. 1) show that a diverse range of perennation strategies exist among temperate and tropical forage grasses. Population recovery after tiller death at flowering is a key issue in most of the temperate grasses and is influenced by grazing regime. In all cases, any period of reduced tiller survival indicates a stress intolerance that may threaten persistence. Such vulnerability can arise from climate factors (heat, moisture deficit), defoliation management, and loss of tillers from the population through flowering. Additionally, features in some data sets suggest a 'partly biennial' behaviour in some species (Fig. 1F). In our observation, available tiller dynamics data are often overlooked by extension agencies formulating husbandry recommendations for farmers. Consideration of such data could be beneficial. For the future a formidable task presents itself to better define environmental and plant genetic influences such as flowering behaviour or a latent biennialism on persistence. However, consider the agronomic implications of produc-

ing a timothy, ryegrass, or tall fescue cultivar with the tiller dynamics of Bahia grass!

Acknowledgements

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