Article

Linking Management, Environment and Morphogenetic and Structural Components of a Sward for Simulating Tiller Density Dynamics in Bahiagrass (*Paspalum notatum*)

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Abstract: A model which describes tiller density dynamics in bahiagrass (*Paspalum notatum* Flügge) swards has been developed. The model incorporates interrelationships between various morphogenetic and structural components of the sward and uses the inverse of the self-thinning rule as the standard relationship between tiller density and tiller weight (a density-size equilibrium) toward which tiller density progressively changes over time under varying nitrogen (N) rates, air temperature and season. Water and nutrient limitations were not considered except partial consideration of N. The model was calibrated against data from swards subjected to different N rates and cutting intensities, and further validated against data from a grazed sward and swards under different cutting intensities. As the calibration and validation results were satisfactory, the model was used as a tool to investigate the responses of tiller density to various combinations of defoliation frequencies and intensities. Simulations identified defoliation regimes required for stabilizing tiller density at an arbitrary target level, *i.e.*, sustainable use of the sward. For example, the model predicted that tiller density can be maintained at a medium level of about 4000 m^{-2} under conditions ranging from weekly cuttings to an 8 cm height to 8-weekly cuttings to 4 cm. More intense defoliation is needed for higher target tiller density and *vice versa*.

1. Introduction

Grasslands are essential to human life. Our challenge is to sustain grasslands and make better use of them for agricultural production, conservation of the environment and wildlife, and other purposes (e.g., recreation and amenity). This requires understanding and predicting sward dynamics in grasslands in response to the environment (e.g., temperature and rainfall) and management (e.g., defoliation and fertilizer application).

Sward dynamics in grasslands can be mechanistically analyzed and understood by breaking down the sward into a set of morphogenetic and structural components [1,2]. This approach was taken initially for temperate forage species and later for tropical species. Based on the morphogenetic and structural mechanisms, persistence of grass (Poaceae) swards is dependent on the ability of the plant to maintain a high tiller density, which in turn depends on the longevity (rate of death) and recruitment (rate of appearance) of the tillers [3].

Bahiagrass (*Paspalum notatum* Flügge), a sod-forming, warm-season perennial, is widespread in the southern USA, and Central and South America [4]. It is also well adapted to the low-altitude regions of south-western Japan, and used for both grazing and hay [5]. This grass forms a highly persistent sward under a wide range of management [6–11]. Among tropical forage species, bahiagrass has been most detailedly studied in terms of the morphogenetic and structural components, providing a good deal of information for modeling sward dynamics of the grass [12–22].

In the present study, a model of tiller density dynamics in bahiagrass swards was built by integrating information selected from the literature. The framework of the model is a combination of interrelationships linking management, environment and morphogenetic and structural components of the sward. The model was calibrated and validated against data from swards subjected to various management conditions, and then used to explore defoliation management for sustainable use of bahiagrass swards. The aims of the study were to examine how the integrated interrelationships work as a whole and to characterize the model in comparison with previous models of tiller density dynamics in grasses. The structure and performance of the model have been partly described in Hirata [22,23].

2. The Model

The model simulates changes in tiller density by calculating tiller appearance and death, which are driven by variables relating to the sward, environment and management (Figure 1). Since the model forms a submodel of an integrated model of sward dynamics in grasslands, it requires daily herbage mass as an input from a submodel of herbage production and utilization. The model also needs mean daily air temperature, annual nitrogen (N) fertilizer rate and month of the year as inputs, and initial tiller density at the commencement of a simulation run. Water and nutrient limitations are not considered except partial consideration of N. Variables used in the model are given in Table 1.
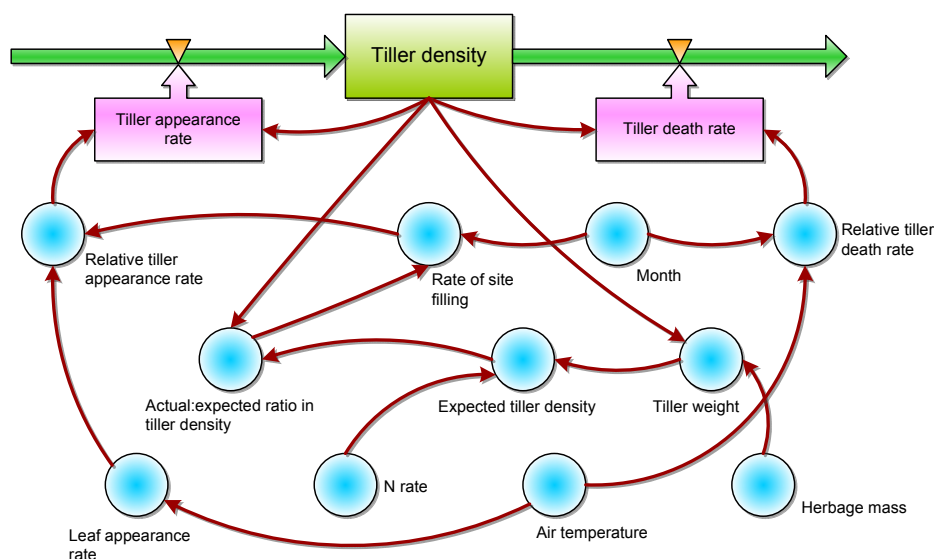
Figure 1. The framework of the model. Reproduced with permission from Hirata [23]; published by Wageningen Academic Publishers.

Table 1. Variables used in the model.

Symbol	Description	Unit
b_0	Intercept of the standard relationship between tiller density and tiller weight	log tillers m^{-2}
b_1	Slope of the standard relationship between tiller density and tiller weight	log tillers m^{-2} (log mg DM tiller^{-1})$^{-1}$
D	Tiller density	tillers m^{-2}
$D_{\text{A:E}}$	Actual: expected ratio in tiller density	fraction
D_{E}	Expected tiller density	tillers m^{-2}
F_{N}	Annual nitrogen fertilizer rate	g m^{-2} year^{-1}
F_{S}	Rate of site filling	tillers leaf^{-1}
M	Herbage mass	g DM m^{-2}
$R_{\text{leaf,app}}$	Leaf appearance rate	leaves tiller^{-1} day^{-1}
$R_{\text{tiller,app}}$	Tiller appearance rate	tillers m^{-2} day^{-1}
$R'_{\text{tiller,app}}$	Relative tiller appearance rate	tillers tiller^{-1} day^{-1}
$R_{\text{tiller,death}}$	Tiller death rate	tillers m^{-2} day^{-1}
$R'_{\text{tiller,death}}$	Relative tiller death rate	tillers tiller^{-1} day^{-1}
t	Time	day
T	Mean daily air temperature	°C
W	Tiller weight	mg DM tiller^{-1}

2.1. Rate of Change in Tiller Density

The daily rate of change in tiller density ($\Delta D / \Delta t$, tillers m^{-2} day^{-1}) is expressed as the balance between tiller appearance rate ($R_{\text{tiller,app}}$, tillers m^{-2} day^{-1}) and tiller death rate ($R_{\text{tiller,death}}$, tillers m^{-2} day^{-1}):

$$\frac{\Delta D}{\Delta t} = R_{\text{tiller,app}} - R_{\text{tiller,death}} \tag{1}$$

The two rates are written as:

$$R_{\text{tiller,app}} = R'_{\text{tiller,app}} \times D \tag{2}$$

and

$$R_{\text{tiller,death}} = R'_{\text{tiller,death}} \times D \tag{3}$$

where D is the tiller density (tillers m^{-2}), and $R'_{\text{tiller,app}}$ and $R'_{\text{tiller,death}}$ are the relative rates of tiller appearance and death (tillers tiller^{-1} day^{-1}), respectively.

2.2. Tiller Appearance

Relative tiller appearance rate is known to be the product of leaf appearance rate ($R_{\text{leaf,app}}$, leaves tiller^{-1} day^{-1}) and the rate of site filling (F_S, tillers leaf^{-1}), *i.e.*, the rate at which axillary buds develop into tillers (visible without dissection) in relation to the rate at which leaf axils are formed [24,25]:

$$R'_{\text{tiller,app}} = F_S \times R_{\text{leaf,app}} \tag{4}$$

Leaf appearance rate is expressed as a threshold response function of the mean daily air temperature (T, °C) [14]:

$$
\begin{aligned}
R_{\text{leaf,app}} &= 0 & \text{(when } T \leq 7.6) \\
&= 0.117 \times \frac{((T-7.6)/6.4)^{3.6}}{1 + ((T-7.6)/6.4)^{3.6}} & \text{(when } T > 7.6)
\end{aligned}
\tag{5}
$$

This equation shows that leaves emerge when the temperature exceeds 7.6 °C and that the leaf appearance rate attains its half-maximal response when the temperature is 14.0 °C and approaches the maximal response (asymptote) of 0.117 leaves tiller^{-1} day^{-1} at higher temperatures (Figure 2).
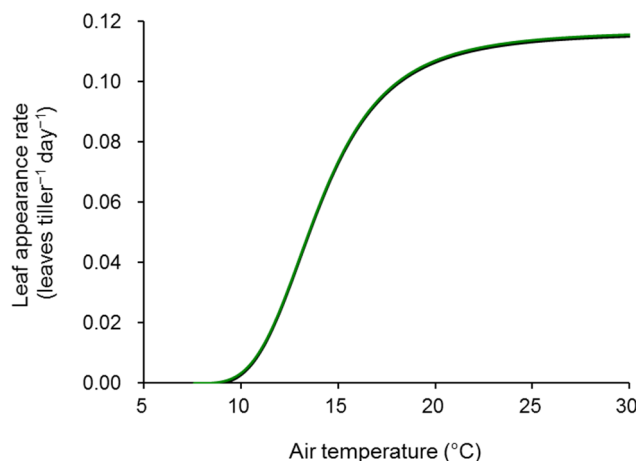

Figure 2. Relationship between leaf appearance rate and mean daily air temperature. Reproduced with permission from Pakiding and Hirata [14]; published by the Tropical Grassland Society of Australia.

The rate of site filling (F_S) is expressed as a function of the actual:expected ratio in tiller density ($D_{\text{A:E}}$), *i.e.*, the ratio of actual tiller density (D) to the expected tiller density (D_E, tillers m^{-2}), which was parameterized by revisiting the data given in Hirata and Pakiding [21] and Hirata [22]:

$$F_S = \max[0, -0.120(D_{A:E} - 1.2)] \qquad \text{(for April)}$$
$$= \max[0, -0.110(D_{A:E} - 1.2)] \qquad \text{(for May)}$$
$$= \max[0, -0.100(D_{A:E} - 1.2)] \qquad \text{(for June)} \qquad (6)$$
$$= \max[0, -0.035(D_{A:E} - 1.2)] \qquad \text{(for July–November)}$$
$$= 0 \qquad \text{(for other months)}$$

where

$$D_{A:E} = D/D_E \qquad (7)$$

Equation (6) shows that axillary buds have the potential of developing into tillers only in April–November and only when the actual tiller density is lower than 1.2 times the density expected from the standard relationship, with higher developmental rates at lower actual:expected ratios in tiller density and in April–June (April > May > June) than in July–November (Figure 3).
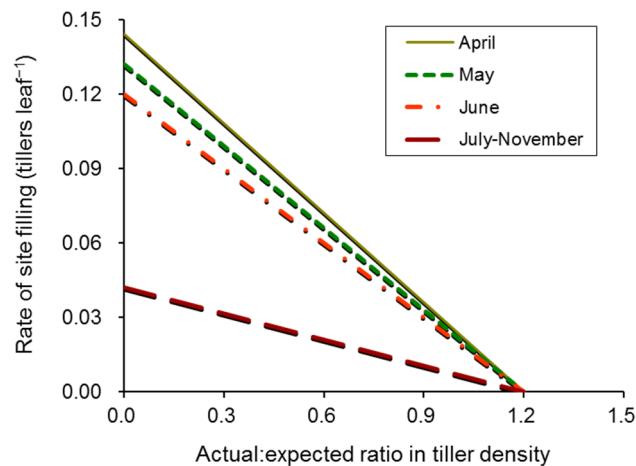

Figure 3. Relationships between rate of site filling and actual: expected ratio in tiller density.

The expected tiller density is calculated from tiller weight (W, mg DM tiller^{-1}), using the standard relationship between tiller density and tiller weight, *i.e.*, relationship in an almost stabilized sward (an equilibrium) under fixed management:

$$D_E = 10^{(b_0 - b_1 \log W)} \qquad (8)$$

This standard density–weight relationship derives from the relationship, $\log D_E = b_0 - b_1 \log W$, a reverse form of the self-thinning rule [26] in terms of *x*- and *y*-variables, which makes it possible to estimate tiller density from tiller weight. The two parameters for the standard relationship (b_0 and b_1) are influenced by annual N fertilizer rate (F_N, g m^{-2} year^{-1}) [21,22]:

$$b_0 = 4.355 + 0.0247(F_N - 5) \qquad (9)$$

$$b_1 = -0.376 - 0.0092(F_N - 5) \qquad (10)$$

Equations (8)–(10) show that the number of tillers carried on a unit land area increases as the tiller weight decreases, with a greater rate of increase at a higher N fertilizer rate (Figure 4).
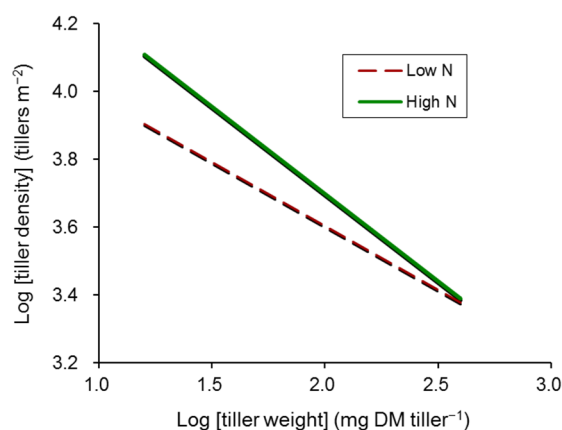
Figure 4. Standard relationships between tiller density and tiller weight. Low nitrogen = 5 g m^{-2} year^{-1}, high nitrogen = 20 g m^{-2} year^{-1}. Reproduced with permission from Hirata and Pakiding [21]; published by the Tropical Grassland Society of Australia.

Tiller weight is calculated as:

$$W = 1000 \times M/D \tag{11}$$

where M is herbage mass (g DM m^{-2}) and 1000 is a unit conversion factor from g to mg.

2.3. Tiller Death

Relative tiller death rate is expressed as a function of the mean daily air temperature [22]:

$$
\begin{aligned}
R'_{\text{tiller,death}} &= 0.00084 \times \exp(0.031 \times T) &&\text{(for spring–summer)} \\
&= 0.00020 \times \exp(0.083 \times T) &&\text{(for autumn–winter)}
\end{aligned}
\tag{12}
$$

This equation shows that the relative tiller death rate increases exponentially as the mean daily air temperature increases, maintaining higher values in spring–summer (March–August) than in autumn–winter (September–February) until the temperature reaches 27.9 °C (Figure 5).
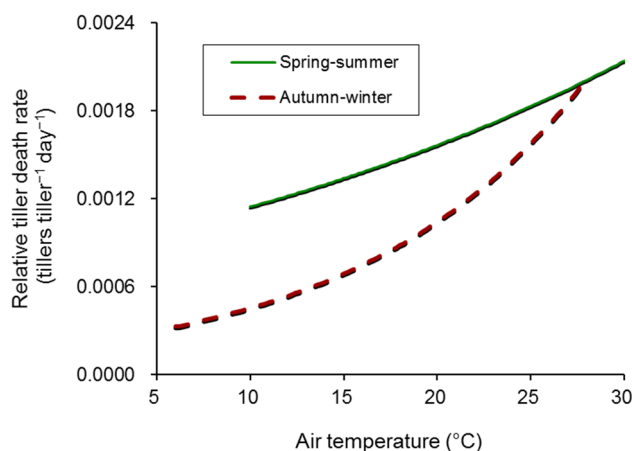

Figure 5. Relationship between relative tiller death rate and mean daily air temperature.

3. Model Performance

3.1. Calibration

The parameters for Equations (5), (6), (9), (10) and (12) were determined using a regression technique to calibrate the model. The performance of the model was first evaluated by simulating tiller density dynamics for the study from which most of the data used for calibrating the model were derived, *i.e.*, bahiagrass tiller density under different N fertilizer rates and cutting heights [18,21]. The simulations for the six experimental treatments (2 N rates × 3 cutting heights) were run for 1341 days ($t = 1, \cdots, 1341$) from 1 June 1996 to 1 February 2000. Daily herbage mass as an input (Figure 1) was estimated by interpolating data from monthly measurements. Mean daily air temperature was derived from daily records. Annual N rate was set at the actual dosage (5 and 20 g m^{-2} year^{-1} for low and high N treatments, respectively). Month of the year was calculated from the day number (t) and the initial date of simulation. Initial tiller density was set at the measured data.

Overall, the simulated tiller densities showed good agreement with the measured data, despite slight to moderate over- or under-prediction in some seasons in some treatments (Figure 6).
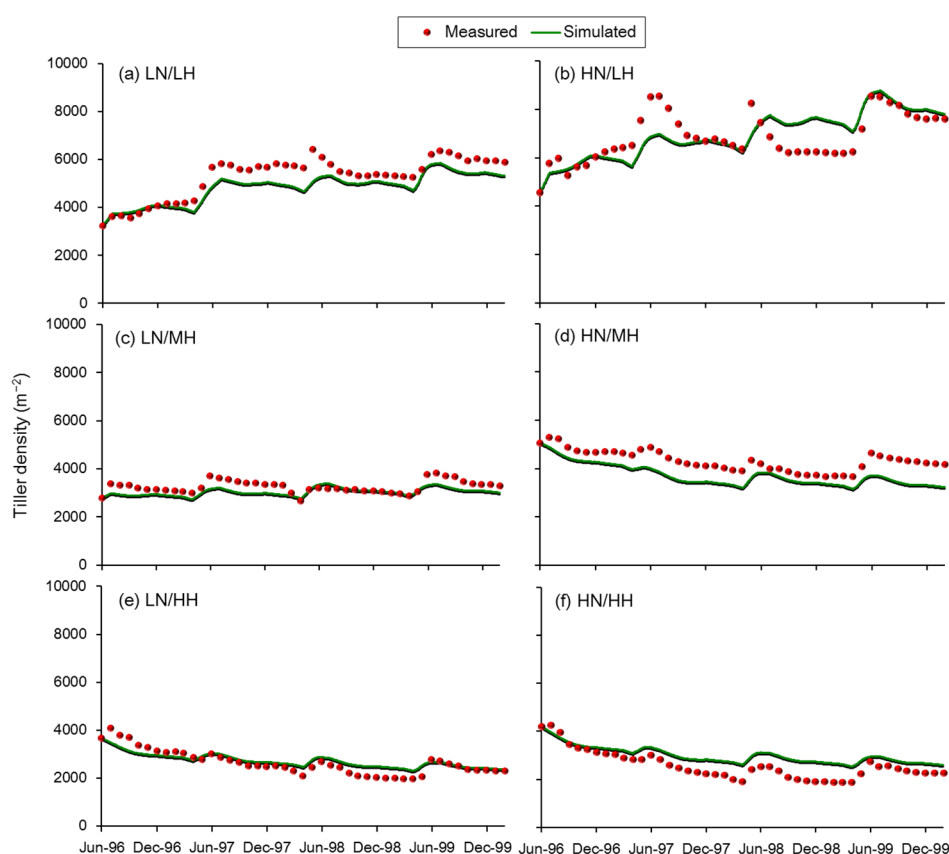

Figure 6. Measured (closed circle) and simulated (line) tiller densities in bahiagrass swards under different nitrogen rates and defoliation intensities (calibration results). Measured data derive from Pakiding and Hirata [18] and Hirata and Pakiding [21]. LN = low nitrogen (5 g m^{-2} year^{-1}), HN = high nitrogen (20 g m^{-2} year^{-1}), LH = low height (2 cm), MH = medium height (12 cm), HH = high height (22 cm) of cutting (heights above ground). Reproduced with permission from Hirata [22]; published by Research Signpost.

3.2. Validation

The model was then validated against independent data sets, *i.e.*, bahiagrass tiller density under cattle grazing [15] and under different cutting heights [10]. The simulations for the former study were run for 1462 days ($t = 1, \cdots, 1462$) from 18 May 1996 to 18 May 2000, and those for the latter study (5 cutting-height treatments) were run for 1092 days ($t = 1, \cdots, 1092$) from 30 May 1986 to 25 May 1989. Daily herbage mass was estimated by interpolating data from 2-weekly to seasonal measurements. Mean daily air temperature was derived from daily records. Annual N rate was set at the actual doses (4.5–9.7 g m^{-2} year^{-1} and 20 g m^{-2} year^{-1} for the former and latter studies, respectively). Month of the year was calculated from the day number (t) and the initial date of simulation. Initial tiller density used the measured data.

Under grazing, the simulated tiller densities showed good agreement with the measured data except some over-prediction in summer (June–August) 1997 (Figure 7). Under cutting, the simulated densities followed the measured values well over the course of 3 years, despite partial inability to follow the seasonal fluctuations within individual years (Figure 8). As a whole, the validation results were acceptable.

4. Use of the Model

As the calibration and validation results were successful, the model was used as a tool to investigate the responses of tiller density to various combinations of defoliation frequencies and intensities (heights above ground). The simulations were run for 3 years ($t = 1, \cdots, 1095$) from 1 May. Daily herbage mass was provided by a model of herbage production and utilization of a bahiagrass sward which was based on the data presented in Hirata [27,28], with no feedback from the tiller dynamics model. The mean daily air temperature (T, °C) was determined using the following equation, which approximates the long-term average of the annual cycle in Miyazaki (31°56′ N, 131°25′ E):

$$T = 17.5 + 10.5 \times \sin(2\pi(t + 9)/365) \tag{13}$$

Annual N rate was set at 10 g m^{-2}. Month of the year was calculated from the day number (t) and the initial date of simulation.
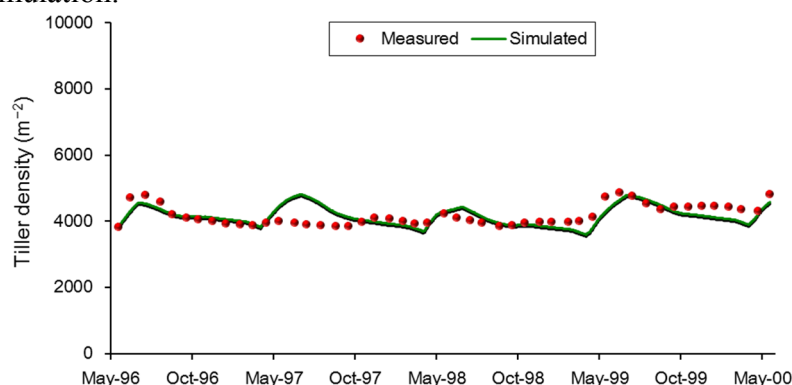

Figure 7. Measured (closed circle) and simulated (line) tiller densities in a bahiagrass pasture under cattle grazing (validation results). Measured data derive from Hirata and Pakiding [15].
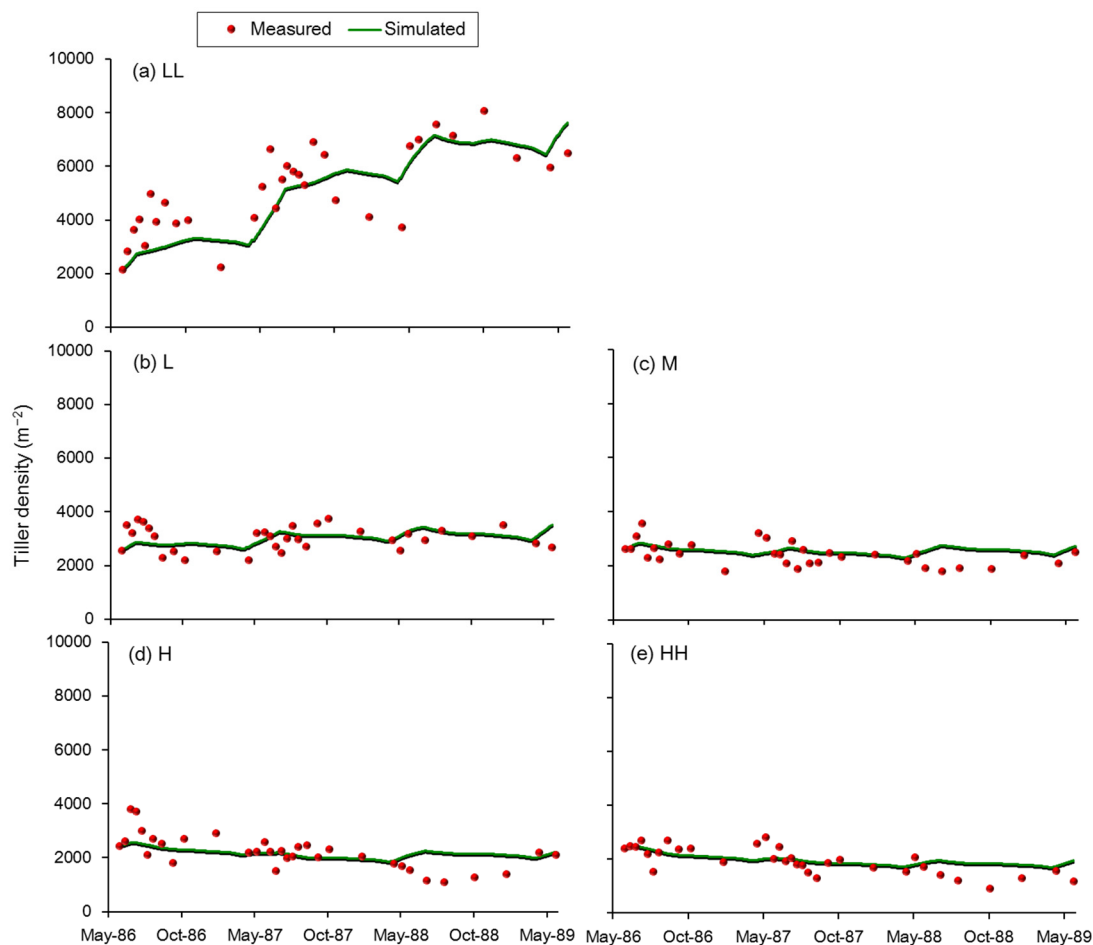
Figure 8. Measured (closed circle) and simulated (line) tiller densities in bahiagrass swards under different defoliation intensities (validation results). Measured data derive from Hirata [10]. LL = 2 cm, L = 7 cm, M = 12 cm, H = 17 cm, HH = 22 cm of cutting height above ground. Reproduced with permission from Hirata [22]; published by Research Signpost.

The simulations predicted gradual decrease in tiller density from the initial value of 4000 m^{-2} under cutting to a medium (12 cm) or high (22 cm) height, irrespective of cutting intervals ranging between 2 and 6 weeks (Figure 9). By contrast, tiller density was predicted to increase with time under a low defoliation height (2 cm), with steeper increases under more frequent defoliation.

Further simulations identified defoliation regimes (frequency and height) required for stabilizing tiller density at a low (2500 m^{-2}), medium (4000 m^{-2}) or high (6000 m^{-2}) level over 3 years, *i.e.*, sustainable use of a sward (Figure 10). The model predicted that the high tiller density can be maintained under conditions ranging from weekly cuttings to a 4 cm height to 8-weekly cuttings to 2 cm, while the low density can be maintained under conditions ranging from weekly cuttings to 19 cm to 8-weekly cuttings to 12 cm. The model also showed that maintaining the medium tiller density requires defoliation with intermediate intensities ranging from 8 cm at weekly cuttings to 4 cm at 8-weekly cuttings. Defoliation height needed decreased as the target tiller density increased and *vice versa*.
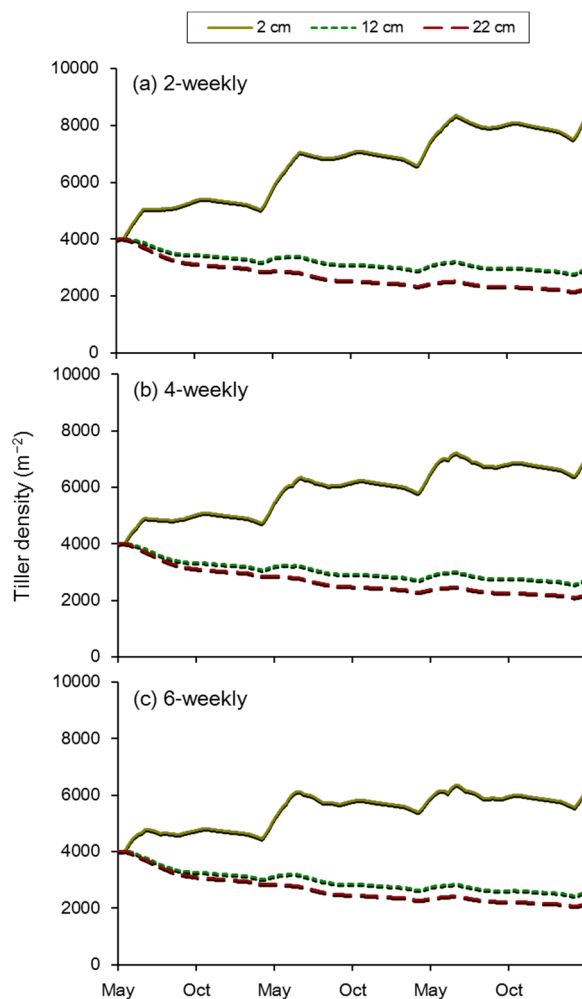
Figure 9. Predicted changes in tiller density in bahiagrass swards under various combinations of defoliation frequencies and intensities (heights above ground) at an annual N rate of 10 g m^{-2}. The initial tiller density (on 1 May) is 4000 m^{-2}.
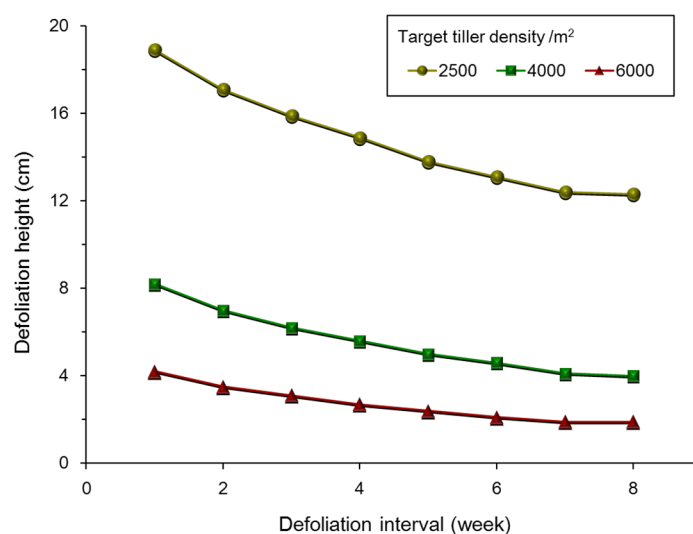

Figure 10. Predicted height (above ground) and interval of defoliation required for maintaining constant tiller density in bahiagrass swards at 2500 (○), 4000 (□) and 6000 (Δ) m^{-2} at an annual N rate of 10 g m^{-2}.

5. Discussion

Maintaining plant population density is crucial to sustainable use of grasslands for agricultural production, conservation of the environment and wildlife, and other purposes such as recreation and amenity. It has been reported that tiller density in grass swards exhibits considerable response to the environment and management [10,18,21,22,29–31]. It is therefore important to develop a model which can predict tiller density dynamics under varying environmental and management conditions.

Previous models of tiller density dynamics in grass swards described the production of new tillers (tillering) in various ways. Some defined the tiller formation rate (per unit land area or per existing tiller) directly as a function of the nutrient state in the plants (amount and concentration of assimilate, carbon (C) and N) [32,33] and leaf area index (LAI) of the sward canopy (an index of self-shading) [33]. Others described the relative rate of tiller appearance mechanistically, as a product of the leaf appearance rate and the rate of site filling (Equation (4)), and expressed the former as a function of temperature [34,35] and the latter as a function of time after defoliation [34], LAI or light transmission at ground level [34,35] and availability (amount) of C and N within the plants [34,35]. These models described the death of tillers also in various ways, relating tiller mortality (relative rate of tiller death) to the developmental stage of tillers [32], LAI [33,34], thermal time [35], assimilate supply and C and N reserves [35] and self-thinning [35].

The current model differs from the previous models mainly in that it does not include the internal nutrient state of the plants or LAI as factors influencing tiller appearance and death (Figure 1), although the positive effect of plant N and negative effect of LAI (self-shading) on tillering can be achieved indirectly by the N-dependent standard relationships between tiller density and tiller weight (Figure 4 and Equations (8)–(10)). Because of the lack of the internal nutrient state, the present model cannot predict a decrease in tillering or an increase in tiller mortality caused by the nutrient limitations within the plants, which may take place when supply of nutrients via photosynthesis and uptake from the soil are restricted due to the deficiency in soil moisture and nutrients, *i.e.*, the model can be used when the growth of plants is not limited by either water or nutrients. The model is also unable to respond flexibly to N management with varying times and rates of split applications. Incorporating the plant nutrient state into the model and linking the model to a herbage production and utilization model simulating the internal nutrient state as well as herbage mass should thus broaden the management and environmental conditions to which the model can be applied.

Furthermore, the current model uses the standard density–weight relationship (reverse form of the self-thinning rule) only for controlling tiller appearance, leaving it unused for controlling tiller death (Figure 1). This may be a reason why the simulations were not able to follow some of the drastic decreases in tiller density which often followed an increase in mid-to-late spring and/or early-to-mid summer (Figures 6 and 8). Although a previous analysis reported a poor association between the relative tiller death rate and the actual:expected ratio in tiller density [21,22], their relationship may need to be reanalyzed in more detail to find a mechanism which can be incorporated into the model.

Despite the limitations discussed above, the present model can provide important information on how tiller population density changes in response to the environment and management (Figures 6–10) based on a simple and mechanistic structure. It can therefore be concluded that the model is of

potential value as a prototype submodel for an integrated model of sward dynamics in grasslands. Refinement of the model needs to trade simplicity for complexity.

Conflicts of Interest

The author declares no conflict of interest.

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