

Reconciling the Plant-Animal Interface: Convergence of Optimal Herbage Accumulation and Intake Rate by Sheep Grazing Tall Fescue

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Abstract

Aims This study evaluated the optimal herbage level from both plant and animal perspectives, through the adjustment of instantaneous herbage accumulation rate as estimated by the Gompertz curve model and short-term intake rate of sheep. *Schedonorus arundinaceus* (tall fescue) was used as an experimental model.

Methods Weekly tall fescue herbage accumulation was measured during seven growth periods initiated on monthly intervals (October, November, and December 2015, and March, April, August and September 2016) with the initiation dates arranged in a randomized complete block design with four replicates. Total herbage mass, leaf lamina mass, pseudo-stem + sheath mass, senescent mass, and sward surface height were measured each week.

Results We demonstrated that a pre-grazing sward surface height of 22.3 cm of tall fescue promoted concomitantly the maximum short-term intake rate of sheep and the instantaneous herbage accumulation rate in the spring and autumn periods. In general, the convergent point occurred after the maximum instantaneous leaf lamina accumulation rate and before the maximum instantaneous accumulation rate of pseudo-stem + sheath and senescent material.

Conclusions We suggest the existence of a convergent point in which both primary and secondary production of pastoral ecosystems could be fostered, potentially reconciling the fundamental ecological dilemma of grazing systems.

Introduction

One dilemma for pasture management oriented towards sustainable intensification (Gunton et al. 2016) and stability of yield (Conway 1987) is the ideal balance between the mass of leaves removed by grazing and the mass left as residual. The former supports high animal production, and the later supports an optimum soil-plant carbon balance (Hodgson and Da Silva 2000; Parson et al. 2011). Thus, the way in which pasture is managed has a direct influence on the maintenance of plant and animal productivity, profitability, biodiversity and mitigation of greenhouse gases in pastoral systems (Zhang et al. 2015) and desertification (Feng et al. 2015).

Plant growth can be represented by a sigmoid curve (Thornley and France 2005; Yin et al. 2003). In pasture management, the curve can adequately illustrate herbage production as a function of time, as a consequence of the management adopted (Barker et al. 2010), where the dynamics of carbon (Brougham 1955; Parson et al. 2011; Richards and Caldwell 1985) and nitrogen (Lemaire et al. 2007), morphogenesis, tillering, height, architecture (Barillot et al. 2014; Birch et al. 2003; Evers et al. 2007a, b; Verdenal et al. 2008) and nutritional value for animals (Nave et al. 2013) are implicit.

Historically, many authors have discussed the best criteria for pasture management from a plant perspective. Brougham (1956) indicate as a point of reference the criterion 95% of light interception (LI) by the sward and critical leaf area index (LAI) as the optimal moment for interruption of regrowth of temperate species in a grazing system. Da Silva and Nascimento Jr (2007) suggest the criterion of 95% LI for C4 grasses. Lemaire and Agnusdei (2000) add the importance of considering the LAI criteria and morphogenic processes and more particularly the leaf tissue flow with senescence through the leaf-life span (LLS). The plant variables mentioned above describe the processes of growth of the primary component under the influence of grazing animals, which are very important in predicting pasture efficiency and long-term sustainability under grazing (Lemaire et al. 2009). In consequence, pasture management aims at optimizing three plant tissue flows: leaf growth, intake of leaves and leaf senescence, each of these flows determining respectively herbage production, animal production and soil carbon budget.

Carvalho (2013) presented an alternative perspective for pasture management, whereby the criterion is based on the spatial-temporal scales of the plant-animal interface, represented by pasture sward surface height. From this perspective, several studies have demonstrated that there is an optimal sward structure for the maximization of short-term intake rate (STIR) of grazing ruminants (Amaral et al. 2013; Fonseca et al. 2012; Mezzalira et al. 2014; Silva et al. 2017). Therefore, this process can be understood as a concept to promote greater animal harvest efficiency, as a function of time.

Defining management strategies consistent with increased efficiency in agricultural processes is of paramount importance (Keating et al. 2010; Struik and Kuyper 2017). Thus, the main question of this work was to determine if there is a common point in pasture management that maximizes the efficiency for both the plant and animal components of pasture-based livestock production. In this study we considered that plant growth is under the effect of plant structure and time as modulator of growth and plant development processes, i.e., an auto-adaptive property of plants submitted to defoliation (Soussana et al. 2012); however, for the animal, at the plant-animal interface, the STIR can be considered an effect of the plant structure, i.e., bite mass effect (Boval and Sauvant 2019).

The purpose of this study was to evaluate the optimal point for grazing management from the plant and animal perspective, through the adjustment of instantaneous herbage accumulation rate by the Gompertz curve, proposed by Barker et al. (2010), and the maximum short-term intake rate, obtained in the study of Szymczak et al. (2020b), using *Schedonorus arundinaceus* [Schreb.] Dumort (tall fescue) as the model system.

Materials And Methods

Experimental Site

The experiment was conducted at the Canguiri experimental farm of the Federal University of Paraná, located in Pinhais city, Paraná, Brazil (25°26'30"S and 49°7'30"W). The experimental area was seeded to *Schedonorus arundinaceus* [Schreb.] Dumort cv. INIA Aurora (nomenclature suggested by Soreng et al. (2001), formerly *Festuca arundinacea* Schreb. and tall fescue as common name) was seeded at 55 kg ha⁻¹ in June 2015 using a conventional tillage method to prepare the seedbed. Nitrogen, phosphorus, and potassium were applied to the experimental area. Phosphorus was applied before sowing at 540 kg P₂O₅ ha⁻¹. When seedlings were at the 3 to 5 leaf stage, 200 kg ha⁻¹ of N and 60 kg ha⁻¹ of K₂O were applied. All fertilizations were carried out according to the soil analysis. Soil chemical analyses results of the experimental area before sowing (depth 0–0.2 m) were: 4.55% organic matter ([C organic x 1.74]/10), pH = 5.70 (CaCl₂), exchangeable aluminum = 0.00 (cmol_c dm⁻³), K = 0.11 (cmol_c dm⁻³), Ca = 5.00 (cmol_c dm⁻³), Mg = 3.10 (cmol_c dm⁻³), V (%) = 71 e P = 2,90 (mg dm⁻³). The climatic variations during the experimental conduction can be seen in Fig. 1.

The experimental area was managed under variable continuous stocking to maintain the SSH between 10 and 15 cm, beginning in September 2015 and ending five days before the initiation date of each growth period.

Treatments, experimental design and measurements

Herbage accumulation was measured during seven growth periods, with initiation dates in mid-October, mid-November, and mid-December 2015, and mid-March, mid-April, mid-August and mid-September 2016. At the beginning of each growth period, the forage was clipped to a 5-cm stubble height and allowed to grow unharvested for the remainder of the growth periods. Each growth period was started on a random new area within the herbage accumulation experimental area. The initiation dates were replicated four times in a randomized complete block design. Individual plots (experimental units) were 1 m². Thirty days before the initiation date of each growth period, N was applied at 90 kg ha⁻¹, to avoid growth restriction due to lack of N (Nelson, 2000), and before the beginning of each growth period the area was isolated to prevent animal grazing.

Sward surface height (SSH) was monitored each week using a sward stick, recording 6 points per experimental unit (Barthram 1985). Herbage mass was randomly collected from a 0.25 m² area within each experimental unit on a weekly basis. Forage samples were cut at soil level and the total herbage mass (HM) was separated into the morphological components of leaf lamina mass (LLM), pseudo-stems + sheaths mass (PSM) and senescent plant mass (SM). All samples were dried in a forced air oven at 65°C until reaching constant weight.

For the calculation of thermal time (TT), expressed in cumulative degree-days (°Cd), we used Eq. 1:

$$TT = \sum(T_{\mu} - T_b) \quad (1)$$

where T_{μ} represents the mean daily air temperature (the average of minimum and maximum temperatures). The maximum daily air temperatures during the experiment did not exceed 35°C, so the coefficient for the upper threshold temperature was considered zero (Moreno et al. 2014). In this study, 4°C was used as the T_b (Errecart et al. 2012).

In this report, we relate the patterns of herbage accumulation to bite mass (BM) and STIR by sheep grazing various SSH levels in the same experimental pasture area, which previously reported in detail by Szymczak et al. (2020b). Briefly, STIR was determined by calculating intake rate of sheep at various SSH levels using pre- and post-grazing animal weights corrected for insensible weight losses, insensible time loss, and effective eating time. Institute of Grassland and Environmental Research Behaviour Recorders (Ultra Sound Advice, London, UK) (Rutter et al. 1997) were used to record grazing jaw movements and the effective eating time, and the data were analyzed with the Graze software (Rutter et al. 2000) and used to calculate BM.

Statistical analysis

The HM, LLM, PSM and SM (means of the four experimental units sampled per initiation date) were fitted to thermal-time accumulation using the Gompertz (Eq. 2, Fig. 2) with software R (R Development Core Team, 2016). Four parameters of the model were estimated through software R, according to Barker et al. (2010):

$$H = H_{\Delta} e^{ae^{bt}} + H_{min} \quad (2)$$

where H is the herbage mass, H_{Δ} is the maximum (asymptotic) herbage mass, H_{min} is the lower asymptote for herbage mass, t is the time in thermal time accumulated and a and b were parameters that determined the shape and curvature of the Gompertz curve, respectively.

The calculation of the instantaneous herbage accumulation rate (HAR_i) was obtained by Eq. 3:

$$HAR_i = \frac{dH}{dt} = bH_{\Delta} e^{ae^{bt}} \ln\left(\frac{1}{e^{ae^{bt}}}\right) \quad (3)$$

The logistic model of Gompertz is characterized by an asymmetric curve, which increases the biological value to the forage accumulation model, because it is sensitive to changes in initial growth rates and suppression of growth (Barker et al. 2010)

Results

There was a good fit of the Gompertz model to HM, LLM, PSM and SM, in all periods, except for those beginning in March and April for SM (Fig. 2, Fig. 3 and Table 1). The coefficient of curvature (b) of the Gompertz model (equation H) for HM, LLM, PSM and SM varied during the periods of growth. For HM, the highest values of the coefficient b occurred in the periods beginning in October 2015 (0.0039), November 2015 (0.0036) and September 2016 (0.0036) and the lowest values were in the periods beginning in March 2016 (0.0025) and April 2016 (0.0044) (Table 1).

For LLM, the highest values of coefficient b occurred in the periods beginning in October 2015 (0.0060), November 2015 (0.0052) December 2016 (0.0063) and September 2016 (0.0055) and the lowest in the periods beginning in March 2016 (0.0023) and April 2016 (0.0062) (Table 1).

Regarding PSM, the highest values for coefficient b occurred in the periods beginning in August 2016 (0.0080) and September 2016 (0.0049) and lower beginning in December 2015 (0.0012) and April 2015 (0.0026) (Table 1).

The highest values for SM for the b coefficient were in the period beginning in December 2015 (0.0062) and the lowest values beginning in October 2015 (0.0011) (Table 1).

HAR_{i-max} of HM varied between 4.76 and 1.60 kg DM ha⁻¹ °C⁻¹ and HAR_{i-max} of LLM varied between 4.05 and 1.20 kg DM ha⁻¹ °C⁻¹ for the periods beginning in October 2015 and April 2016 respectively. For the HAR_{i-max} of PSM there was variation

between 0.75 and 0.38 kg DM ha⁻¹ °C⁻¹, in the periods beginning in October 2015 and September 2016, respectively (Table 1). For the HAR_{*i-max*} of SM the variation was 1.84 and 1.30 kg DM ha⁻¹ °C⁻¹ for the periods beginning in September 2016 and August 2016, respectively (Table 1).

The highest optimum total herbage mass at HAR_{*i-max*} for HM were in the periods beginning in August 2016, September 2016, April 2016 and October 2015, with values of 2889, 2848, 2160 and 2068 kg DM ha⁻¹, respectively. This HM corresponded to SSH of 23.84, 23.65, 25.26 and 24.21 cm, respectively (Table 1).

For LLM the highest values of optimum total herbage mass at HAR_{*i-max*} were in the periods beginning in September 2016, August 2016, April 2016, and October 2015 having values of 2523, 2445, 1323 and 1311 kg DM ha⁻¹, respectively. Corresponding values of SSH were 19.64, 20.48, 23.57 and 18.51 cm, respectively (Table 1).

For the PSM, the highest values of optimum total herbage mass at HAR_{*i-max*} were in the periods beginning in September 2016 and April 2016, with 3689 and 3046 kg DM ha⁻¹ and SSH of 29.61 and 29.20 cm, respectively (Table 1).

The highest values of optimal total herbage mass at HAR_{*i-max*} for SM were observed in the periods beginning in August 2016, September 2016 and October 2015, with SSH of 29.53, 31.11 and 33.16 cm, respectively (Table 1).

Discussion

Pasture growth

The HAR_{*i-max*} variation observed between growth periods may be related to differences in mean temperatures (Fig. 1) during the conduct of the experiment. According to Sun et al. (2014), the optimal growth temperature of tall fescue is between 15 and 20°C. Shoot growth rate response to temperature is first determined by response of leaf appearance rate and leaf elongation rate to temperature. Therefore, any increase in temperature leads to an increase in the proportion of assimilate used for shoot growth (Lemaire and Agnusdei 2000). Thus, in the periods beginning in October 2015, April 2016, August 2016 and September 2016, the average temperatures of 20.6, 15.5, 17.0 and 18.5°C promoted greater HAR_{*i-max*} and coefficient *b* values for HM and LLM. During the periods of November 2015, December 2015 and March 2016 there was an increase in the frequency of daily maximum temperatures above 30°C. Similar results were verified by Nave et al. (2013), evaluating growth and accumulation of herbage in a pasture with mixture of tall fescue and *Poa pratensis* L. in Columbus, OH, USA, where HAR_{*i-max*} varied with season, probably based on climatic differences (rainfall and temperature varied with the season of the year in that study).

The coefficient *b* in the Gompertz model has the effect of adjusting the slope of the curve in the exponential phase, thus, higher coefficient values represent higher herbage accumulation rates. In the case of the increase in coefficient *b* for LLM, provided by the optimal temperature range in relation to lower temperatures, an increase in the leaf elongation rate had the consequence of decreasing the phyllochron (Thomas and Stoddart 1995).

Data for the periods beginning in January, February, May, June 2016 and July 2016 were not presented in this study, as it was not possible to estimate with confidence the HAR_{*i-max*} (Supplementary Information). We attributed this to the effect of temperature, since in the summer months (mainly January and February) maximum temperatures were frequently above 30°C and in winter (May to July) there were minimum temperatures below 5°C (Fig. 1), which negatively affected the growth and development of tall fescue (Atkinson and Porter 1996; Bélanger et al. 1994; Yin and Struik 2009).

There was a poor fit of the Gompertz curve to SM in the periods beginning in March 2016 and April 2016, probably related to low senescence mass when the plants were growing under the effect of the lower temperatures (Thomas and Stoddart 1995). Leaf life span (LLS) depends on temperature, so at lower temperatures there is a long LLS and lowest rate of leaf senescence (Lemaire and Agnusdei, 2000). The effect of higher temperatures on SM can be seen in the period beginning in December 2015, when there were higher values for coefficient *b* and the optimal SM at HAR_{*i-max*} was lower than in the other months (Table 1).

The H_{min} values in the periods beginning in October 2015, November 2015 and December 2015, were probably lower than in 2016 because the tall fescue had just been established in June 2015, and as the stand established (increasing tiller number and size), the H_{min} naturally increased.

The sigmoid herbage mass accumulation curve, as observed in the tall fescue data presented here, is shaped by the interaction of the morphogenetic parameters and the interception of light and photosynthesis attributes (Evers et al. 2018; Lemaire and Agnusdei 2000) and it can be described in three stages (Parson and Penning 1988). In the first stage, there is an increase in the appearance and expansion of the leaf laminae, which leads to an increase in photosynthetic rates until they reach their maximum during the second stage of exponential growth (Parson and Penning 1988). In the third stage, there is a decrease in photosynthetic rates related to advancing development of the plants above the critical LAI, with a corresponding increase in rate of senescent material and pseudo-stem accumulation, age of the leaves, and shading of the lower leaves, thus reducing the photosynthetic efficiency of the sward (Gastal and Lemaire 2002; Li et al. 2013; Li et al. 2014; Parson and Penning 1988; Pedreira et al. 2015; Thomas 2012). The increase of LAI and height over time, causes a self-regulation process of plant architecture as a result of shade-avoidance syndrome plasticity (Aphalo et al. 1999, Chelle et al. 2007, Verdenal et al. 2008). With shading, there is a reduction in the red to far-red light ratio as well as a general reduction in light intensity inside the sward, causing hormonal changes in plant (Van De Velde et al. 2017; Yang and Li 2017). As a result, there is a change in sward morphological traits, such as leaf hyponasty, increasing sheath and leaf lamina length, elongation of the pseudo-stem/stem, tillering reduction and tiller mortality, among others (Evers et al. 2011; Gommers et al. 2013; Watanabe et al. 2005).

Animal Intake

A study conducted by Szymczak et al. (2020b) in the same experimental area as this one (same area, experimental and climate conditions and forage species), demonstrated a significant effect of tall fescue SSH on STIR of sheep. There was a quadratic response of STIR to SSH, increasing up to a SSH of 22.3 cm ($y = 5.61 \text{ g DM min}^{-1}$) and decreasing at taller SSH (Fig. 4). There was also a quadratic response of tall fescue SSH on the bite mass, with BM increasing up to a SSH of 22.8 cm (Fig. 4). The relationship between BM and STIR in the forage intake process by ruminants, evidenced in that study, is well established in the literature (Hirata et al. 2010; Laca et al. 1994; Ungar et al. 1991). Thus, BM is the main component of the forage harvesting process by the animals, which is composed of the bite volume performed by the animal and sward bulk density of the pasture herbage (Black and Kenney 1984; Hirata et al. 2010; Laca et al. 1992). At low SSH, there are restrictions on the formation of the BM affected mainly by low sward bulk density. At high SSH, the bite volume is limited by the presence of the pseudo-stem + sheath in the grazing horizons and by increasing distance of the plant organs in the sward (divarication), and thus greater time spent by the animals for the bite formation (Benvenuti et al 2008; Black and Kenney 1984; Bond et al. 2004; Burlinson et al. 1991; Fonseca et al. 2013; Greenwood and Atkinson 1977; McQueen 2000).

Mezzalira et al. (2017) found that domestic ruminants had a functional response of type IV when grazing different sward structures. The functional response of type IV, (Heuermann et al. 2011), describes the ingestive behaviour of herbivores in natural environments. In general, there is a rapid increase in the intake rate by animals as aboveground biomass increases, up to an optimum point, and then a slight decrease (Venter et al. 2018). It is based on the optimal foraging theory that states maximization of the intake rate of energy over the grazing process through decisions within different space-time scales (Charnov 1976; Pyke et al. 1977). The results of Szymczak et al. (2020b) agreed with studies that demonstrated intermediate SSH at the $STIR_{max}$ for other forage species (Fonseca et al. 2012; Mezzalira et al. 2014; Silva et al. 2017). These findings have implications at the plant-animal interface.

Plant-animal interface

The results obtained in this study suggest that the SSH corresponding to the optimum total herbage mass (i.e. HAR_{j-max}) for HM and LLM converges with the SSH at $STIR_{max}$ of sheep (Table 1, Figs. 2–4 and Szymczak et al. 2020b). For the periods beginning in October 2015, November 2015, December 2015, March 2016, April 2016, August 2016 and September 2016, the SSH at HAR_{j-max} of HM was 24.2, 21.3, 18.2, 24.5, 25.3, 23.9, 23.7 cm, respectively, which were near the SSH at $STIR_{max}$ i.e., 22.3 cm. The SSH at HAR_{j-max} of LLM was close to SSH at $STIR_{max}$ in the periods beginning in October 2015, December 2015,

March 2016, April 2016, August 2016 and September 2016, i.e., 18.5, 18.2, 18.3, 23.6, 20.5, and 19.6 cm, respectively. This meant that the net herbage accumulation rate during regrowth (after clipping) reached the maximal values at a SSH very similar to the SSH that provided maximal harvest efficiency for sheep.

The relationship can be explained by the significant increase of leaves in the sward (Figs. 2 and 3 and Table 1), promoting increased plant growth potential and harvesting by the animals, since in that SSH range the animals preferentially consume leaf mass (Baumont et al. 2004; Parson et al. 2011). From that point forward, sward structural changes occur, affecting the sheep harvest efficiency, as previously described (Sect. 4.1 and 4.2). From an ecological perspective, what is better for the animal is not antagonistic for the plant, provide that grazing intensity. Herbivores and grasses have co-evolved over millions of years (~ 23 to 5.3 Ma – from the Miocene Epoch) (Saarinen 2019), leading to several adaptive traits including body size, tooth and skull anatomy, morphophysiology of the gastrointestinal tract, behavioural characteristics of mammal herbivores (Codron et al. 2019), and grazing avoidance and tolerance mechanisms that reduce the probability and severity of defoliation of the plant, as well as mechanisms that facilitate forage growth after the defoliation event (Briske 1991). Thus, the dynamics involved in grazing can be considered as a *two-way street*, by feedback from a wide range of complex processes.

From a trophic perspective, our results suggest an alternative view to that postulated by the classical manuscript of Briske and Heitschmidt (1991), who argued that the optimization processes of interception and light conversion to biomass production and harvesting efficiency by animals cannot be maximized simultaneously. The authors argued this process as the fundamental ecological dilemma. We find a convergence between optimal SSH for plant herbage accumulation and sheep intake occurred only under optimal growth growing conditions of tall fescue, i.e., the periods beginning in October 2015, November 2015, December 2015, March 2016, April 2016, August 2016 and September 2016. For animals, the change in $STIR_{max}$ over time was more related to a drastic change in sward structure. For example, Guzatti et al. (2017) demonstrated that the $STIR_{max}$ of animals can be kept constant throughout the vegetative stage of the forage, with a decrease in the $STIR_{max}$ in the reproductive stage, caused mainly by the decreasing leaf/stem ratio. Thus, in the non-optimal periods of plant growth, the production of the system probably will be more affected by a lower stocking rate, due to lower herbage production, than to the individual performance of the animals.

Implications for pasture management

Using pre-grazing SSH of 22.3 cm (Szymczak et al. 2020b) as a management target in rotational stocking, there may be optimization of efficiency in use of light and nitrogen, tillering rate, carbon balance, and leaf appearance rate. This also may promote less instantaneous senescent material and an increase in the vegetative period of the forage in relation to the highest SSH (Evers et al. 2007a; Gastal and Lemaire 2002; Nelson 2000). From the perspective of the maximum average growth rate, Parsons and Penning (1988) suggest that the pre-grazing moment should occur between the last two phases of the curve. We presented an average growth rate curve very similar to that observed by Parsons and Penning (1988), and our results indicate that the pre-grazing point would be at point 2 of the curve. Consequently, there is a lower average growth rate at this point (sum of leaf lamina and pseudo-stems mass), and this would also result in a lower allocation of carbon to the roots (Parson et al. 2011).

According to Carvalho (2013), the depletion criterion in the “Rotatinuous stocking” system occurs when there was a 40% decrease in SSH from the pre-grazing SSH. In other words, if animals were removed from a paddock once the SSH has been reduced by 40%, the $STIR_{max}$ of the animals is maintained during the occupation period (Fonseca et al. 2012; Mezzalira et al. 2014). We hypothesize that growth rate will be maintained in the exponential phase of the curve, thus promoting a higher frequency of grazing events. Studies by Savian et al. (2018, 2020) and Schons et al. (2021) support this idea. In a long-term study, they applied this concept comparing “Rotatinuous stocking” (RN - SSH pre-grazing of 17.2 cm and SSH post-grazing of 11.9 cm) to traditional rotational stocking (RT - SSH pre-grazing of 26.1 cm and SSH post-grazing of 7.8 cm) of sheep grazing *Lolium multiflorum*. Greater total herbage production (RN = 8714 and RT = 6822 kg DM ha⁻¹) and herbage accumulation rate (RN = 52.1 and RT = 33.2 kg DM ha⁻¹ day⁻¹) and greater individual performance of the animals (RN = 0.12 and RT = 0.05 kg animal⁻¹ day⁻¹) were documented in the “Rotatinuous stocking” treatment, in which the animals began grazing a paddock at the SSH predicted for $STIR_{max}$ and removed from the paddock when the SSH had been reduced by 40%. In addition, they found

a higher leaf /stem ratio pre- (RN = 3.11 and RT = 2.64) and post-grazing (RN = 1.59 and RT = 0.76); lower light interception pre-grazing (RN = 90.6% and RT = 95.1%), higher light interception post-grazing (RN = 77.6% and RT = 62.7%) and higher non-grazed area pre- (RN = 42.2% and RT = 22.9%) and post-grazing (RN = 29.7% and RT = 3.49) for “Rotatinuous stocking”. Thus, even though there was less senescent instantaneous material at the pre-grazing point in our study (Figs. 2 and 3), they found no significant difference for the proportion of senescent material pre- and post-grazing during the vegetative stage between RN and RT. Those proportions of senescent material in RN may be related to the higher percentages of areas not grazed and by high post-grazing mass, which resulted in a guarantee of senescent flow to the soil.

For animals in this optimal pre-grazing SSH condition, high intake of highly digestible forage occurs, providing increases in feed conversion efficiency, carcass production and carcass quality and reductions in diet cost and enteric methane emissions (Savian et al. 2018, 2021; Zubieta et al. 2021), all of which are criteria that should be prioritized in grazing management strategies.

Parson et al. (1988) discuss the defoliation process, based on the growth curve of plants under different intensities of sward depletion. The authors suggested that more lenient defoliation provides a maximization of pasture productive potential, thus maintaining higher photosynthetic rates. Management strategies that prioritize lower intensity of sward depletion promote less stress on plant regrowth, since there is greater leaf area remaining after grazing, which in turn is extremely important in the carbon balance process of regrowth (Fig. 2) (Parson et al. 1988; 2011; Schons et al., 2021). Many studies demonstrate the importance of moderate grazing in pasture management for improving the performance of agricultural systems, such as efficiency, productivity, resilience (Kunrath et al. 2020, Szymczak et al. 2020a) and increased soil carbon storage (Sthal et al. 2016).

Our results suggest that the adoption of the criterion based on the intake behaviour of grazing animals has great importance from the perspective of the efficiency of the ecological processes at the plant-animal interface and system productivity. However, more studies will be needed to understand the influence of the pasture heterogeneity caused by successive cycles of grazing down by animals on the HAR_i, rate of senescent material returning to the soil and allocation of carbon to the roots.

Conclusions

The pre-grazing sward surface height of 22.3 cm in pastures of tall fescue promotes concomitantly the maximum short-term intake rate of sheep and the instantaneous herbage accumulation rate during the spring and autumn periods. Hence, we suggest the existence of a convergent point in which both primary and secondary production of pastoral ecosystems could be fostered, potentially reconciling the fundamental ecological dilemma of grazing systems.

Declarations

Author contributions

LSS conceived and designed the study, performed all experiment, analyzed the data and wrote the manuscript, AM conceived and designed the study and revised manuscript, RMS and DB analyzed the data and revised manuscript, ALGM supplied the experimental animals and revised manuscript, RFM helped on samples collection and analysis, CRL and GL revised manuscript and PCFC supplied experimental equipment and revised manuscript. All authors read and approved the final manuscript.

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Declaration of Competing Interest The authors report no declarations of interest.

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Tables

Table 1

Gompertz equations of herbage mass (H) curves and their coefficients of determination (R^2), equations of the instantaneous herbage accumulation rate (HAR_i), values of the maximum instantaneous herbage accumulation rate (HAR_{i-max}), optimal total herbage mass at HAR_{i-max} and sward surface height (SSH) at HAR_{i-max} for seven growth periods evaluated. HM, LLM, PSM and SM represents the total herbage mass, leaf lamina mass (kg DM ha^{-1}), pseudo-stems + sheaths mass (kg DM ha^{-1}) and senescent mass (kg DM ha^{-1}), respectively, of *Schedonorus arundinaceus*.

Equation H	R ²	Equation HAR _i	HAR _i max [†]	Optimal Total Herbage Mass at HAR _i max [†]	SSH at HAR _i max [‡]
October 2015					
HM y=3379e ^{6.14e0.0039x} +541	0.77	y=0.0039(3379e ^{6.14e0.0039x})ln(1/e ^{6.14e0.0039x})	4.76	2068.19	24.21
LLM y=1844e ^{7.74e0.0060x} +390.6	0.72	y=0.0060(1844e ^{7.74e0.0060x})ln(1/e ^{7.74e0.0060x})	4.05	1311.06	18.51
PSM y=601.7e ^{6.48e0.0034x} +136.3	0.72	y=0.0034(601.7e ^{6.48e0.0034x})ln(1/e ^{6.48e0.0034x})	0.75	2740.98	24.21
SM y=3196e ^{5.96e0.0011x} +0	0.82	y=0.0011(3196e ^{5.96e0.0011x})ln(1/e ^{5.96e0.0011x})	1.31	3873.48	33.16
November 2015					
HM y=3453e ^{2.61e-0.0036x} +230.7	0.78	y=0.0036(3453e ^{2.61e-0.0036x})ln(1/e ^{2.61e-0.0036x})	4.28	1482.42	21.33
LLM y=1437e ^{4.34e0.0052x} +315.9	0.68	y=0.0052(1437e ^{4.34e0.0052x})ln(1/e ^{4.34e0.0052x})	2.79	1152.26	13.92
PSM y=481.5e ^{4.24e0.0031x} +177	0.66	y=0.0031(481.5e ^{4.24e0.0031x})ln(1/e ^{4.24e0.0031x})	0.55	1601.67	21.33
SM y=2374e ^{7.14e0.0015x} -1.83	0.88	y=0.0015(2374e ^{7.147e0.0015x})ln(1/e ^{7.147e0.0015x})	1.34	3349.77	34.28
December 2015					
HM y=2359e ^{3.13e0.0033x} +498.3	0.73	y=0.0033(2359e ^{3.13e0.0033x})ln(1/e ^{3.13e0.0033x})	2.84	1663.19	18.24
LLM y=1195e ^{4.56e0.0063x} +161	0.71	y=0.0063(1195e ^{4.56e0.0063x})ln(1/e ^{4.56e0.0063x})	2.64	1224.00	18.24
PSM y=198.9e ^{6.91.2e0.012x} +349.9	0.35	y=0.0012(198.9e ^{6.91.2e0.012x})ln(1/e ^{6.91.2e0.012x})	0.64	2037.67	26.55
SM y=787.2e ^{1.74.2e0.0062x} +161.6	0.83	y=0.0062(787.2e ^{1.74.2e0.0062x})ln(1/e ^{1.74.2e0.0062x})	1.69	2504.74	29.53
March 2016					
HM y=2059e ^{3.85e0.0025x} +948.5	0.63	y=0.0025(2059e ^{3.85e0.0025x})ln(1/e ^{3.85e0.0025x})	1.88	1838.22	24.49
LLM y=1678e ^{2.31e0.0023x} +114.9	0.73	y=0.0023(1678e ^{2.31e0.0023x})ln(1/e ^{2.31e0.0023x})	1.44	1297.61	18.28
PSM y=341.2e ^{8.78e0.0039x} +258.3	0.54	y=0.0039(341.2e ^{8.78e0.0039x})ln(1/e ^{8.78e0.0039x})	0.48	1838.22	24.49
SM -	-	-	-	-	-
April 2016					
HM y=2160e ^{18.5e0.0044x} +1392	0.76	y=0.0044(2160e ^{18.5e0.0044x})ln(1/e ^{18.5e0.0044x})	1.60	2160.83	25.26
LLM y=1637e ^{31.5e0.0062x} +571.4	0.84	y=0.0062(1637e ^{31.5e0.0062x})ln(1/e ^{31.5e0.0062x})	1.20	1322.78	23.57
PSM y=608.4e ^{11.75e0.0026x} +309.5	0.63	y=0.0026(608.4e ^{11.75e0.0026x})ln(1/e ^{11.75e0.0026x})	0.58	3046.38	29.20
SM -	-	-	-	-	-
August 2016					
HM y=3524e ^{4.87e0.0033x} +1696	0.78	y=0.0033(3524e ^{4.87e0.0033x})ln(1/e ^{4.87e0.0033x})	4.31	2889.18	23.84
LLM y=1676e ^{3.87e0.0042x} +727.2	0.79	y=0.0042(1676e ^{3.87e0.0042x})ln(1/e ^{3.87e0.0042x})	2.62	2445.19	20.48
PSM y=213.2e ^{4.08e0.0080x} +489.7	0.20	y=0.0080(213.2e ^{4.08e0.0080x})ln(1/e ^{4.08e0.0080x})	0.60	2022.73	16.01

SM	$y=1254e^{16.25e0.003x}+445$	0.71	$y=0.003(1254e^{16.25e0.003x})\ln(1/e^{16.25e0.003x})$	1.30	4741.47	29.53
September 2016						
HM	$y=3387e^{5.51e0.0036x}+1493$	0.75	$y=0.0036(3387e^{5.51e0.0036x})\ln(1/e^{5.51e0.0036x})$	4.51	2848.02	23.65
LLM	$y=1887e^{6.36e0.0055x}+379.2$	0.83	$y=0.0055(1887e^{6.36e0.0055x})\ln(1/e^{6.36e0.0055x})$	3.78	2522.85	19.64
PSM	$y=212.3e^{33.37e0.0049x}+508.4$	0.21	$y=0.0049(212.3e^{33.37e0.0049x})\ln(1/e^{33.37e0.0049x})$	0.38	3688.89	29.61
SM	$y=463.1e^{20.49e0.0030x}+463.1$	0.81	$y=0.0030(463.1e^{20.49e0.0030x})\ln(1/e^{20.49e0.0030x})$	1.84	4001.36	31.11

‡ HAR_{i-max} in $kg\ DM\ ha^{-1}\ ^\circ C^{-1}$

† Optimum Total Herbage Mass at HAR_{i-max} in $kg\ DM\ ha^{-1}$

⊠ SSH at HAR_{i-max} in cm

Figures

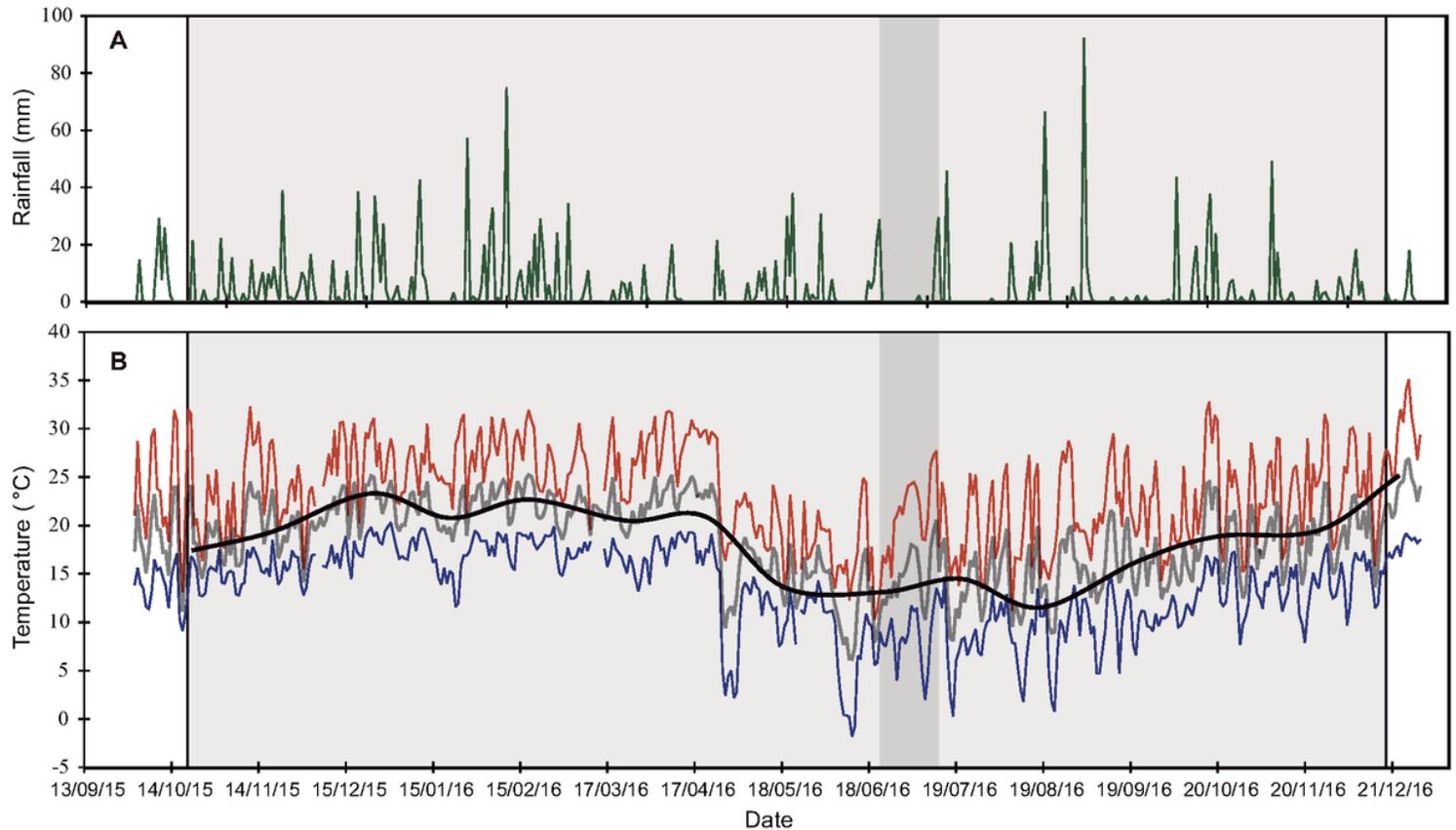


Figure 1

Daily rainfall (A) and temperature (B) during the experiments. Vertical black lines at the two corners of the graphs indicate the start and end date of experiment and the gray shaded area represents the evaluation period of experiment of study of Szymczak (2020b). Blue, black and orange lines represent the minimum, average and maximum daily temperatures, respectively.

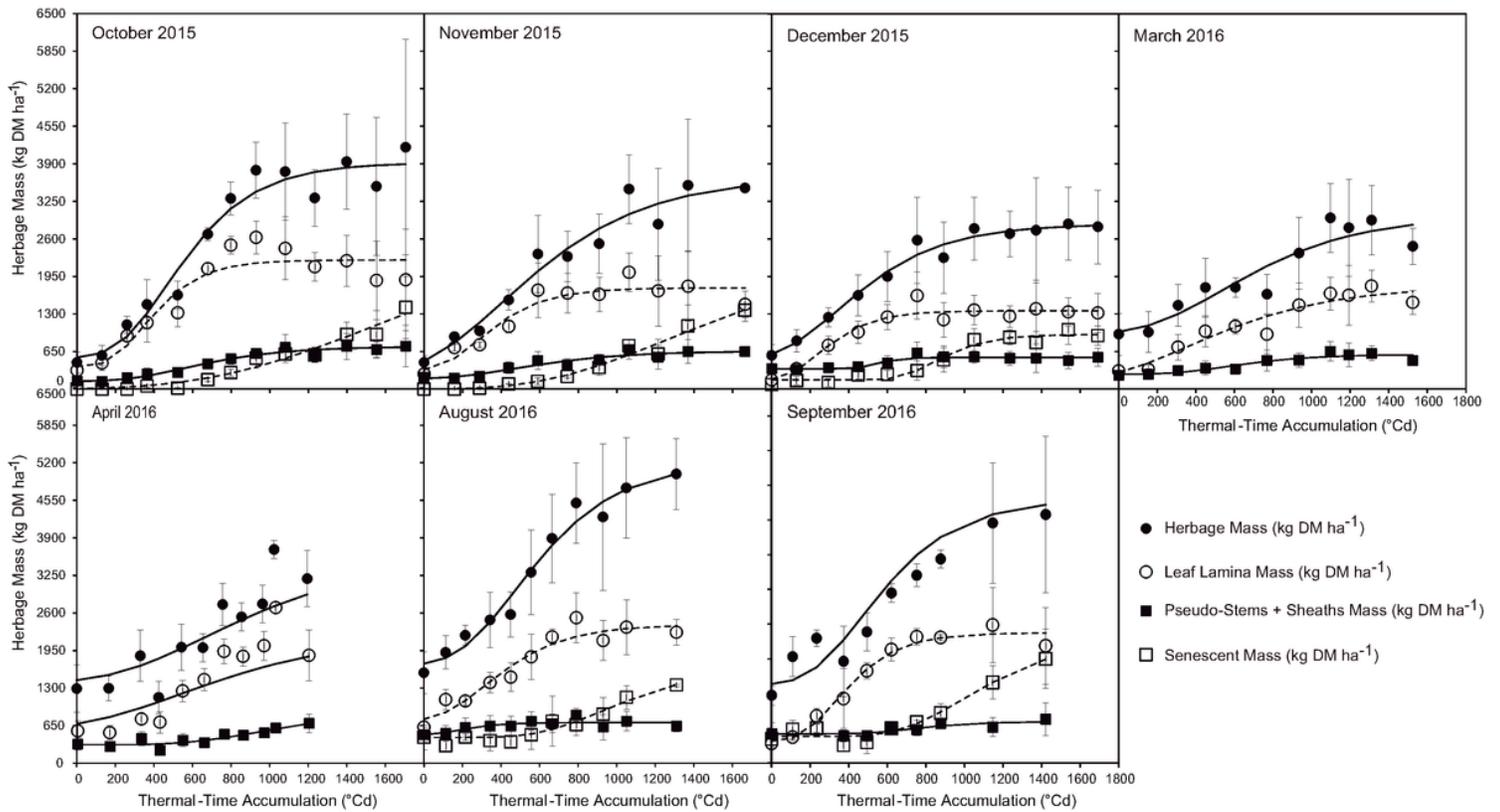


Figure 2

Average above ground herbage mass (kg DM ha⁻¹), leaf lamina mass (kg DM ha⁻¹), pseudo-stems + sheath mass (kg DM ha⁻¹) and senescent mass (kg DM ha⁻¹) of *Schedonorus arundinaceus*, for seven growth periods initiated mid-month from October 2015 to September 2016, with fitted Gompertz curves. The bars represent the standard error of the mean for each weekly sampling. The equations for each curve are presented in Table 1.

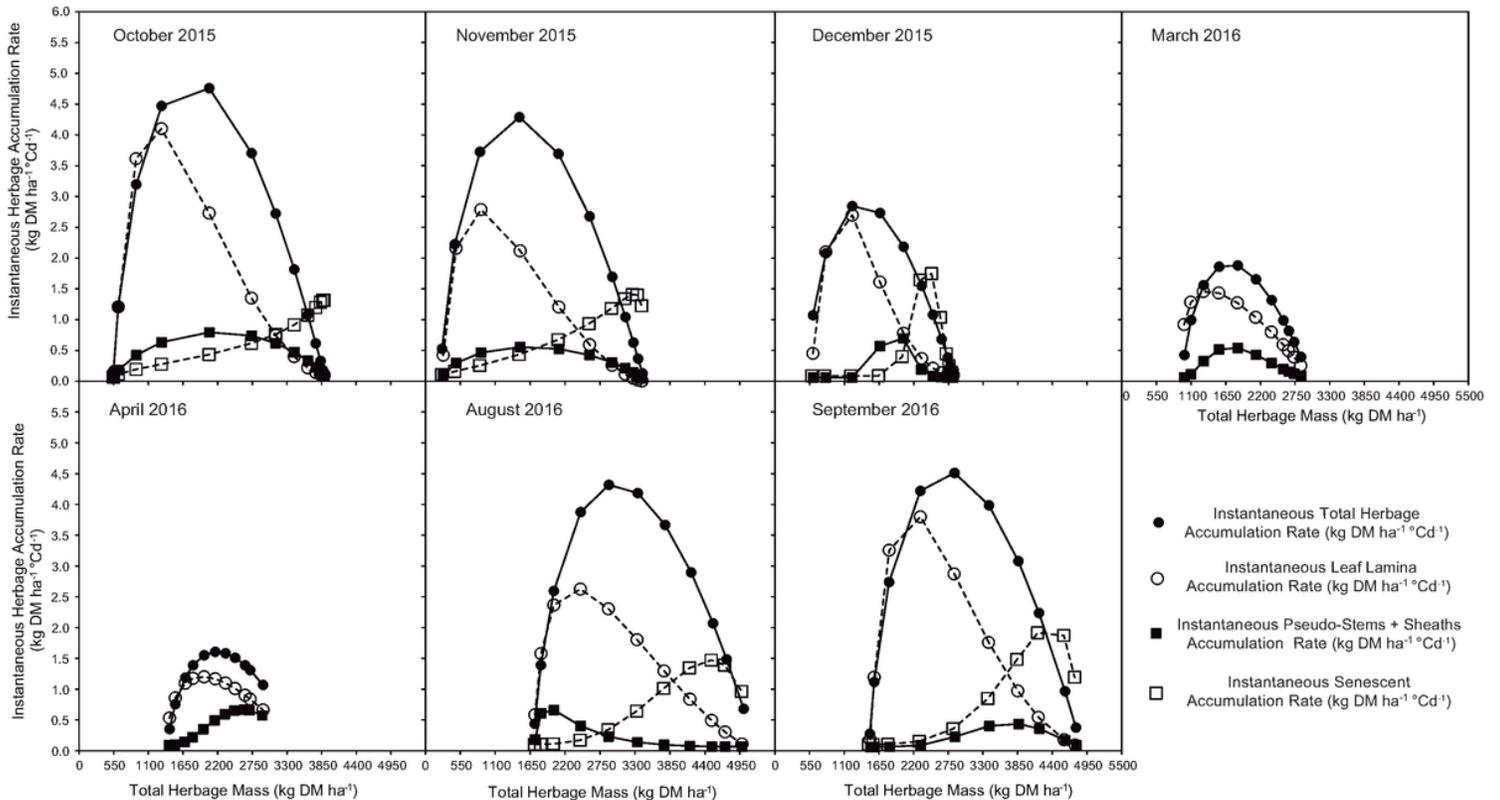


Figure 3

Instantaneous total herbage accumulation rate (kg DM ha⁻¹ °Cd⁻¹), instantaneous leaf lamina accumulation rate (kg DM ha⁻¹ °Cd⁻¹), instantaneous pseudo-stems + sheath accumulation rate (kg DM ha⁻¹ °Cd⁻¹) and instantaneous senescent accumulation rate (kg DM ha⁻¹ °Cd⁻¹), as a function of total herbage mass of *Schedonorus arundinaceus*, for seven growth periods initiated mid-month from October 2015 to September 2016, with fitted Gompertz curves. The equations for each curve are presented in Table 1.

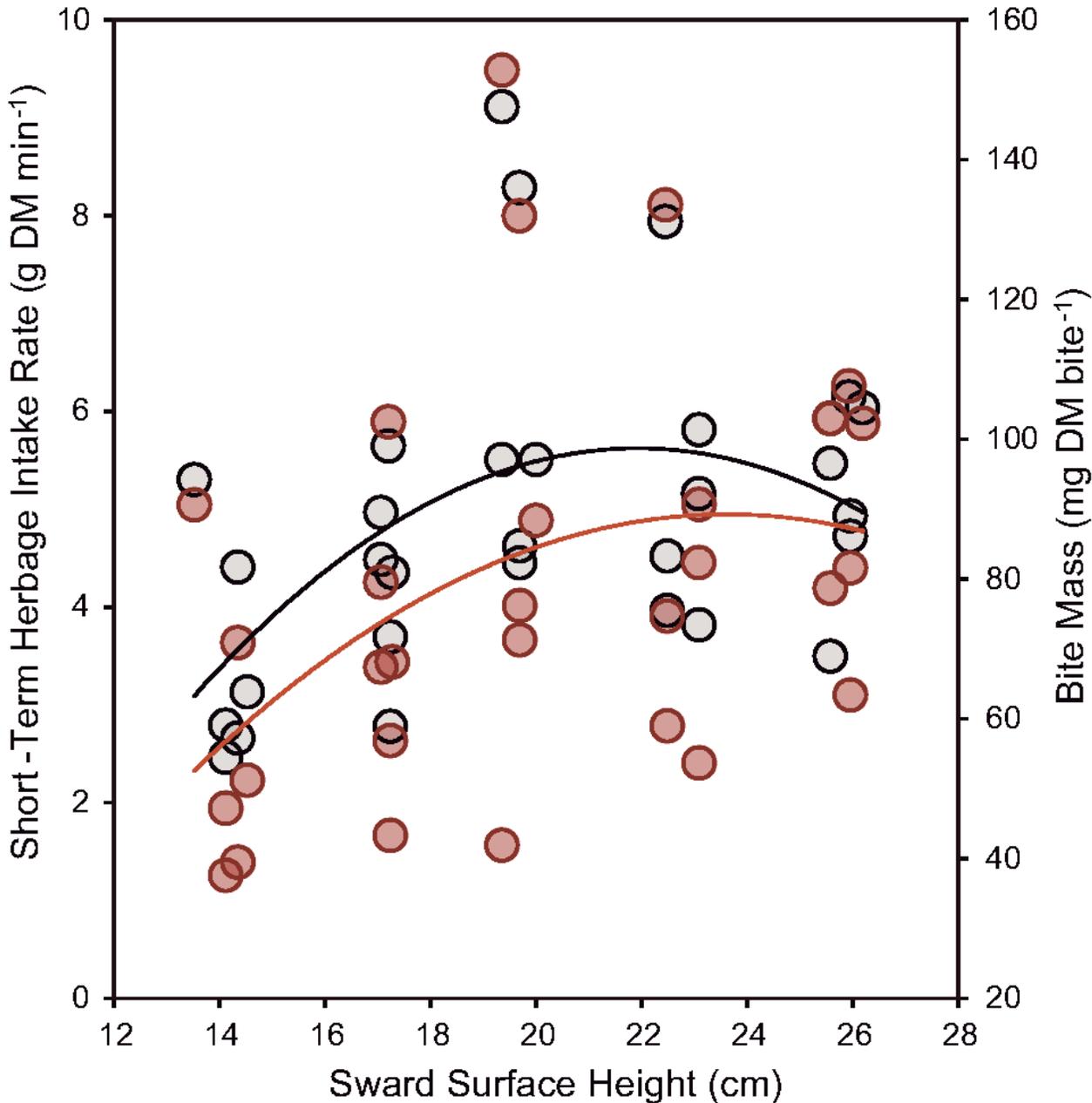


Figure 4

Short-term herbage intake rate (STIR; black; $y = -0.0346x^2 + 1.5308x - 11.334$; $R^2 = 0.7290$; $p < 0.001$) and bite mass (BM; orange; $y = -0.4797x^2 + 21.852x - 157.33$; $R^2 = 0.6693$; $p < 0.001$) of sheep as function of sward surface height (SSH), for *Schedonorus arundinaceus* [Schreb.] Dumort. (tall fescue) STIR-max = 22.30 cm. This figure is a derivative of "Tall fescue sward structure affects the grazing process of sheep" by Szymczak et al. (2020b), used under CC BY <https://creativecommons.org/licenses/by/4.0/deed.en>. This figure is licensed under CC BY <https://creativecommons.org/licenses/by/4.0/deed.en> by Szymczak, L.S.

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