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Dynamics of forage ingestion, oral processing and digesta outflow from the rumen: a development in a mechanistic model of a grazing ruminant, MINDY

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Abstract

Detailed representation of ingesta inflow to and digesta outflow from the rumen is critical for improving the modelling of rumen function and herbage intake of grazing ruminants. The objective of the current work was to extend a mechanistic model of a grazing ruminant, MINDY, to simulate the dynamic links between ingestive and digestive processes as affected by forage and sward features (e.g. sward structure, herbage chemical composition) as well as the internal state of the animal. The work integrates existing aspects of forage ingestion, oral physiology and rumen digestion that influence ingesta characteristics and digesta outflows from the rumen, respectively. The paper describes the structure and function of the new development, assessing the new model in terms of dynamic changes of oral processing of ingesta and rumen dilution rate under different grazing contexts. MINDY reproduces characteristics of ingesta inflow to and digesta outflow from the rumen of grazing ruminants, achieving temporal patterns of occurrence within and between meals, similar to those for grazing animals reported in the literature. The model realistically simulates changes in particle size distribution of the ingestive bolus, bolus weight and rumen dilution rate in response to contrasting grazing management regimes. The new concepts encoded in MINDY capture the underlying biological mechanisms that drive the dynamic link between ingestion and digestion patterns. This development advances in the understanding and modelling of grazing and digestive behaviour patterns of free-ranging ruminants.

Introduction

Detailed representation of digesta outflow from the rumen is critical for improving the modelling of rumen function and herbage intake of grazing ruminants. A body of empirical data and mathematical interpretation of processes determining the outflow of rumen digesta has been accumulated and summarized by Poppi *et al.* (2000) and Faichney (2005). Attempts to model outflow of rumen digesta have been diverse (Waldo *et al.*, 1972; Barboza and Bowyer, 2000; Seo *et al.*, 2009). However, models describing this process do not account for all significant sources of variation, nor do they control rumen fill and digesta flow without fractional outflow rates or retention time defined by the user (Kennedy, 2005). Moreover, most models of rumen digestion do not include the foraging process and oral processing of the forage, which is the first step of digestion. Thus, the condition in which forage is received by the rumen is neither simulated nor predicted, making these models incomplete (Prinz and Lucas, 1997).

MINDY is a mechanistic model, incorporating diurnal patterns of foraging, digestion and metabolism, dietary choice, excretion and production of a grazing ruminant (Gregorini *et al.*, 2013; 2015*b*, 2017). It is a cluster of six models, including the rumen sub-model of Molly (Baldwin, 1995, modified by Gregorini *et al.*, 2015*a*). Although MINDY includes ingestive actions and rumination time in response to animal and sward state and condition, oral processing and the resultant changes in particle size and distribution of ingesta are not included. Moreover, the current rumen sub-model in MINDY does not consider the dynamics of water ingestion with the forage (i.e. ingesta dry matter [DM]) and the fractional passage of liquid is fixed. This limits MINDY's mechanistic and dynamic capability to exploration of foraging situations where the dynamics of ingestion, modulated either passively (by sward features) or actively (by management), are expected to alter patterns of forage digestion and nutrient supply, and in turn affect animal performance and excretory (e.g. urination; Gregorini *et al.*, 2018) behaviour.

The objective of the current work was to formalize implicit interactions between ingestion and digestion processes in MINDY by including explicit representation of oral processing of

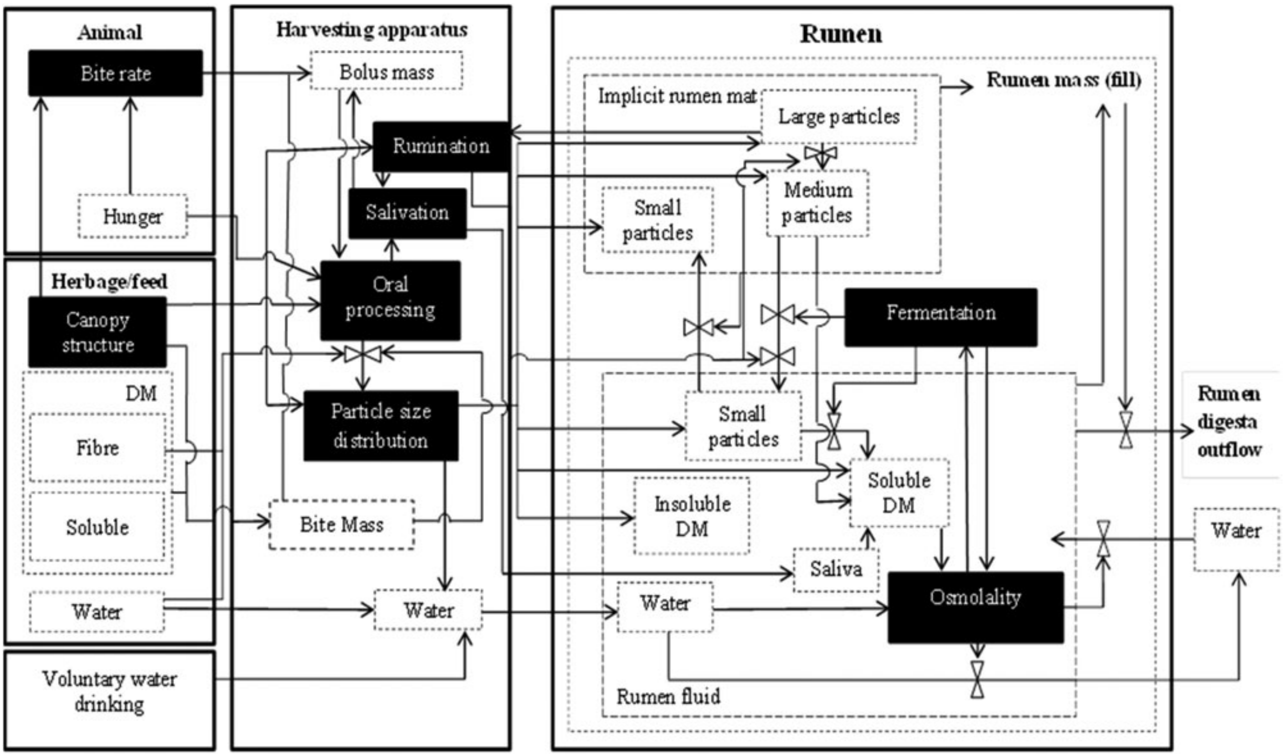

Fig. 1. Diagram (Conceptual model) of functional relationships responsible for variations in rumen digesta outflows in grazing ruminants. White boxes with solid lines are compartments; white boxes with dashed lines are pools; black boxes with solid lines are processes. Arrows indicate effects on pools, processes and fluxes are indicated by triangle valves.

ingesta and simulating, rather than setting, the fractional passage of liquid in the rumen in response to foraging context. The advances here integrate functional relationships between forage ingestion, oral physiology and rumen digestion responsible for variations in ingesta characteristics and digesta outflow rates from the rumen. The current paper describes changes in the structure and function of the model and assesses it in terms of responses to foraging conditions.

Model description and rationale

Dynamics of digesta outflow from the fore-stomach of ruminants depends on: (1) sward structure, patterns of forage intake and associated oral processing of ingesta determining particle size distribution of swallowed boli; (2) rumen function and contents and (3) regulation of flow and retention of liquid in the rumen (Pérez-Barbería and Gordon, 1998; Lechner *et al.*, 2010; Gregorini *et al.*, 2015*a*). Cattle pass large amounts of fluid through the rumen, which enhances the stratification and thereby selective retention time of digesta in the rumen (Clauss and Lechner-Doll, 2001; Clauss *et al.*, 2010). Particulate retention in the rumen facilitates ruminal digestion, while high liquid passage increases ruminal bacterial yield (Dove and Milne, 1994; Meng *et al.*, 1999; Dewhurst *et al.*, 2000; Clauss *et al.*, 2010) and serves as transport for both particulate (small) and soluble nutrients (Poppi *et al.*, 1981; Faichney, 2005). As a result, digesta outflow from the rumen is a function of fluid flow and concentration of DM in the fluid (Ulyatt *et al.*, 1984; Kennedy and Murphy, 1988). Consequently, to better represent patterns of forage intake, digestion and nutrient supply from the rumen of grazing ruminants, the passage of solids must be linked to dynamic fluctuations of particle size distribution of the ingesta and fluid outflow from the rumen.

The current work implicitly represents (1) oral processing of ingesta determining particle size distribution of swallowed boli associated with temporal patterns of feed intake; (2) dynamic regulation of flow and retention of liquid in the rumen; and (3) the association of 1 and 2 with particulate passage throughout the rumen. Modifications to the original particle size pools of the rumen model used in MINDY and related changes in digestive parameters have been presented by Gregorini *et al.* (2015*a*).

The relevant factors, pools and functional relationships are illustrated in Figs 1 and 2. The code was developed and simulations were conducted using ACSLXtreme (Aegis Technologies Group, Austin, TX, USA). Numerical integration was conducted using a fourth-order, fixed-step, Runge–Kutta method. The maximum integration interval was set to 0.001 d. Results were collected after 5 d of simulation to ensure the model had reached a stable state. The order in which the structure of model development is presented follows the natural path of forage ingestion, oral processing of ingesta, inflows of ingesta to the rumen and outflow of digesta from the rumen.

Oral processing and particle size distribution of ingesta

The distribution of ingesta through different particle size pools in the rumen is a function of ingestive actions (severing, handling and salivation) and oral processing (mastication and salivation) of a cluster of bites forming the bolus to be swallowed (Moseley and Jones, 1984; Spalinger *et al.*, 1986; Pond *et al.*, 1987; Prinz and Lucas, 1997). Particle size distribution in the swallowed bolus is related closely to forage species, sward structure, herbage

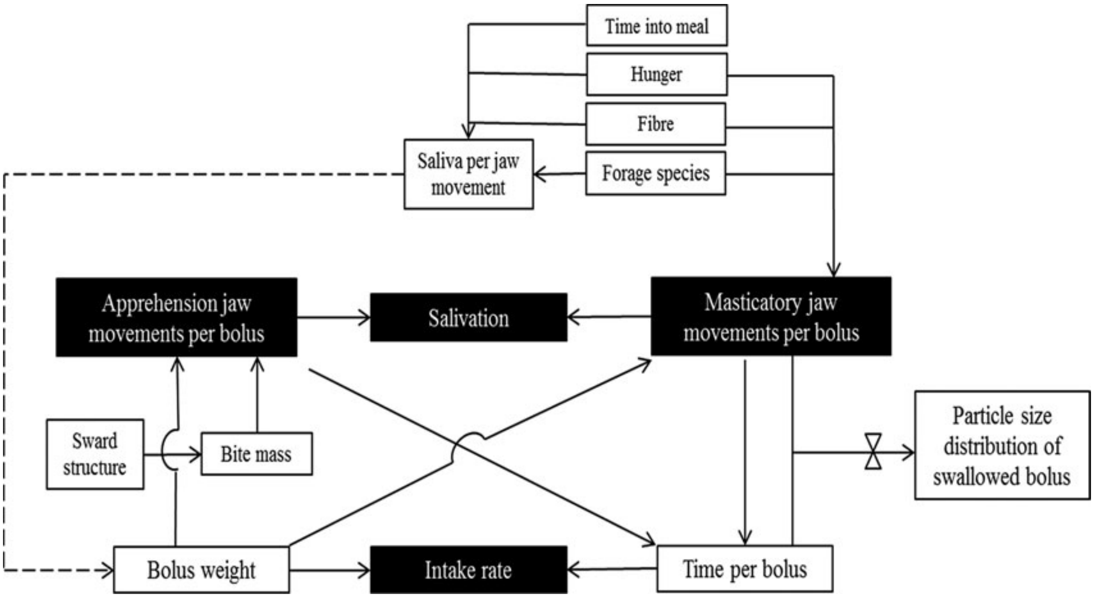

Fig. 2. A scheme of the oral processing module introduced into the MINDY cow model. Boxes represent pools or compartments and arrows represent fluxes.

chemical composition and plant phenology (Wilson and Kennedy, 1996; Poppi *et al.*, 2000; Kennedy, 2005). The drive to eat (i.e. hunger) also influences particle size distribution in the swallowed bolus (Demment and Greenwood, 1988; Greenwood and Demment, 1988; Gregorini, 2012). Hunger reduces oral processing of ingesta through a reduction in mastication as a compensatory mechanism to increase short-term forage DM intake rate (Greenwood and Demment, 1988; Demment and Laca, 1994). In addition to the severing jaw movements (bite), mastication initiates the breakdown of forage physical structure, releasing around 0.65 of the water and soluble cell contents and exposing cell walls to microbial enzymatic action (Hogan *et al.*, 1985). Ultimately, and in conjunction with a parallel salivation process, mastication determines the physical characteristics of the swallowed bolus (i.e. particle size distribution), the rate at which boli are swallowed (Bailey and Balch, 1961; Saunders, 1980; Stuth and Angell, 1982; Bailey *et al.*, 1990; Prinz and Lucas, 1997; Lucas *et al.*, 2002) and thereby the rate of digestion and nutrient availability in the rumen (Poppi *et al.*, 2000; Chilibroste *et al.*, 2007; 2008; Gregorini, 2011). Therefore, models must include oral processing and its impact on the characteristics of the bolus to be swallowed.

Oral processing of forage in the present development of MINDY is based on mastication and swallowing models of mammals (Hutchings and Lillford, 1988; Prinz and Lucas, 1997), concepts of perception/anticipation of feeding, food texture, particle agglomeration in the oral cavity and surface tension and viscosity of saliva (Prinz and Lucas, 1997), the models of chewing efficacy of Pérez-Barbería and Gordon (1998) and Shipley *et al.* (1994), and a comprehensive data set of ingestive boluses and salivation reported by Balch (1958), Prinz and Lucas (1997), Gill *et al.* (1966), Stuth and Angell (1982), Boudon *et al.* (2006) and Acosta *et al.* (2007).

Particle size of ingested herbage (and supplemental feed)

First, the model calculates the distribution of particle size of herbage harvested as pasture or consumed as supplementary food. For grazing, MINDY calculates bite depth (cm) based on sward canopy structure (see Gregorini *et al.*, 2013 for details). Bite depth depends on sward surface height (cm), and changes with herbage depletion (i.e. reductions in sward surface height). Based on a normal distribution of particle sizes per grazing stratum of the canopy (P Gregorini, unpublished data), it is assumed that the mean particle size of herbage harvested while grazing is half of the bite depth. Then the ingested particles of herbage harvested while grazing are 'allocated' to one of a set of 14 'bins' (i.e. pools), according to their size. Mesh aperture size of each bin is doubled over the range 0.0375–153.6 mm (Note: the model allows for a variable number of bins, and the range of mesh aperture size is taken from wet sieving particle size wet analyses methodology). When feeding fresh cut herbage, silages or grains, data on the ratio between small and large particles (<1.2 and >4.8 mm, respectively), known as *Psf* factor (see Baldwin *et al.*, 1987 for details) of the particular feed are provided to the model as input. Particle size distribution of ingested particles fed as supplements is then calculated using the equation of Pond *et al.* (1984) adapted for Molly by Gregorini *et al.* (2015*a*) and such a distribution of particles is then allocated to the set of the 14 'bins', according to their size.

Bolus size and frequency of swallowing

The size of the bolus to be swallowed is calculated as a cluster of a variable number of bites. During grazing, bite characteristics (mass, volume and mastication jaw movements per bolus) are variable and depend on sward structure and condition (Laca and Demment, 1991; Laca *et al.*, 1992; 1994), as well as the animal's internal state (Gregorini, 2011). MINDY accounts for those characteristics and dependencies, and in the present calculations of bolus size, mastication jaw movements according to bite mass, fibre content of the bite mass, plant species (i.e. C3, C4, herbs and legumes) and hunger level of the animal (Wilson and Kennedy, 1996; Baumont *et al.*, 2004; Kennedy, 2005; Gregorini *et al.*, 2009*b*) are also considered. Bolus size and frequency of swallowing are represented by the following calculations.

A maximum bolus size (*MaxBolusWeightFresh*, grams of fresh matter excluding saliva) was assumed, limited by the volume of the oral cavity [the oral cavity is three-dimensional; hence a linear relationship with cow weight was assumed (e.g. if a cow is X2 wide, X2 long and X2 deep, then both oral cavity and weight will be X8) (Stuth and Angell, 1982; Prinz and Lucas, 1997)]. It was also assumed that grazing ruminants maximize their short-term herbage intake rate (Bergman *et al.*, 2001; Fortin *et al.*, 2002) and thereby bolus size and swallowing rate (Stuth and Angell, 1982). Thus, in the short-term, grazing ruminants (and thereby MINDY) try to reach *MaxBolusWeightFresh*, unless extra saliva is released in the harvesting and handling actions. Faster salivation rates cause the developing bolus to disintegrate, which promotes early swallowing (Prinz and Lucas, 1997; Lucas *et al.*, 2002). The latter is supported by the results with grazing and non-grazing cattle reported by Boudon *et al.* (2006) and previous works of Gill *et al.* (1966) with cattle fed indoors.

It was assumed that salivation (*BaseSalivaPerJawMovement*, g saliva) is proportional to the number of jaw movements (severing and mastication), and is modulated by forage species (feed), time into the meal and hunger (Balch, 1958; Bailey and Balch, 1961; Gill *et al.*, 1966). Hence, greater intake rate, where a total number of severing and mastication jaw movements per unit of feed harvested is reduced, will lead to less salivation (see Boudon *et al.*, 2006). The first boluses would be smaller than those following due to extra salivation at the start of the meal. The latter increases with increasing levels of hunger (Gill *et al.*, 1966).

Bolus size and frequency of swallowing are then calculated as a function of jaw movements and time per bolus, which are derived from severing (i.e. bites) and mastication jaw movements through a feedback loop (Fig. 2) using the following set of equations:

$$\begin{aligned} \mathit{MaxBolusWeightFresh} &= \mathit{StandardCowMaxBolusWeightFresh} \\ &\quad \times \mathit{CorrectedBW} \end{aligned} \tag{1}$$

where *StandardCowMaxBolusWeightFresh* is 200 g (for a cow of 550 kg live weight). *CorrectedBW* is the empty body weight of the cow (no pregnancy and gut fill).

$$\begin{aligned} \mathit{BaseSalivaPerJawMovement} &= \mathit{BaseSalivationRate} \\ &\quad \times \mathit{JawMovementRate} \end{aligned} \tag{2}$$

$$\mathit{BaseSalivationRate} = \mathit{StandardSalivation} \times \ \mathit{BW}^{0{\cdot}75} \tag{3}$$

BaseSalivaPerJawMovement is the base amount of saliva secreted per jaw movement, severing and mastication, *StandardSalivation* is 355 g/min derived from Gill *et al.* (1966) and $\mathit{BW}^{0.75}$ the metabolic weight of the animal.

$$\mathit{TargetBolusWeightFresh} = \mathit{BolusWeightFresh} \tag{4}$$

Due to the following circular reference:

$$\left\{ \mathit{Saliva} => \mathit{BolusWeightFresh}^{=>\mathit{SeveringJawMovement}=>\mathit{Saliva}}_{=>\mathit{MasticationJawMovement}=>\mathit{Saliva}} \right\},$$

an initial and arbitrary fresh weight of the bolus (*TargetBolusWeightFresh*, g fresh matter) is used to solve for the *BolusFreshWeight* iteratively in successive approximations (REPEAT, see below).

REPEAT:

$$\mathit{BitesPerBolus} \ = \frac{\mathit{TargetBolusWeightFresh}}{\mathit{BiteMassFresh}} \tag{5}$$

$$\mathit{ActualBolusWeightFresh} = \mathit{BitesPerBolus} \times \mathit{BiteMassFresh} \tag{6}$$

$$\begin{aligned} &\mathit{MasticationJawMovementPerBolus} \\ &\quad = \mathit{DryFeedF}/\mathit{TimeIntoMealF} \times \mathit{BolusSizeF}^{\mathit{xBolusMov}} \\ &\qquad \times \mathit{BaseMastJawMovPerBolus} \\ &\qquad \times \mathit{HungerEffectOnMastication} \times \mathit{NDFF} \times \mathit{SpeciesF} \end{aligned} \tag{7}$$

$$\begin{aligned} \mathit{TotalJawMovementsPerBolus} &= \mathit{BitesperBolus} \\ &\quad + \mathit{MasticationJawMovementsPerBolus} \end{aligned} \tag{8}$$

$$\begin{aligned} \mathit{TimePerBolus} = \mathit{BitesPerBolus} \ &\times \mathit{TimePerBite} \\ &+ \mathit{MasticationJawMovementsPerBolus} \\ &\times \mathit{TimePerMastication} \end{aligned} \tag{9}$$

$$\mathit{BolusSwallowingFrequency} = \frac{60}{\mathit{TimePerBolus}} \tag{10}$$

$$\begin{aligned} &\mathit{SalivaPerMasticationJawMovement} \\ &\quad = \mathit{BaseSalivaPerJawMovement} \times \mathit{DroolingSalivaF} \\ &\qquad \times \mathit{BolusSizeF}^{\mathit{xBolusSaliva}} \times \mathit{NDFF}^{\mathit{xNDFSaliva}} \times \mathit{DryFeedF} \end{aligned} \tag{11}$$

$$\begin{aligned} &\mathit{SalivaPerSeveringJawMovement} \\ &\quad = \mathit{BaseSalivaPerJawMovement} \times \mathit{kSalivaSevering} \\ &\qquad \times \mathit{TimeIntoMealF} \times \mathit{NDFF}^{\mathit{xNDFSaliva}} \end{aligned} \tag{12}$$

$$\begin{aligned} \mathit{SalivaPerBolus} = \mathit{BitesPerBolus} & \\ &\times \mathit{SalivaPerSeveringJawMovement} \\ &+ \mathit{MasticationJawMovementsPerBolus} \\ &\times \mathit{SalivaPerMasticaitonJawMovement} \end{aligned} \tag{13}$$

$$\begin{aligned} \mathit{BolusWeightFresh} = \ \mathit{TimeIntoMealF}^2 & \\ &\times \mathit{MaxBolusWeightFresh} \\ &\times (1 - \mathit{LiquidizingSaliva} - 0{\cdot}25)/0{\cdot}25 \end{aligned} \tag{14}$$

Then,

$$\mathit{BolusWeightDry} = \mathit{BolusWeightFresh} \times \mathit{FeedDMContent} \tag{15}$$

$$\mathit{WholeBolusWeight} = \mathit{BolusWeightFresh} + \mathit{SalivaPerBolus} \tag{16}$$

where in Eqn 7, *DryFeedF* (unitless) increases saliva per mastication and number of mastications for dry feed, and decreases for moist feed (0.2 is the base *FeedDMContent*, which gives neutral effect in this equation) and is represented as follows:

$$\mathit{DryFeedF} = 1 + (\mathit{FeedDMContent} - 0{\cdot}2) \times \mathit{xFDMMastication} \tag{17}$$

xFDMMastication is the slope of the linear relationship between *FeedDMContent* and extra salivation, having a value of 0.179.

TimeIntoMealFactor is a unitless factor forcing a smaller bolus at the beginning of a meal for all foods and late in the meal for dry food, as reported by Gill *et al.* (1966). For example,

$$\mathit{TimeIntoMealFactor}_{\mathit{BeginningOfMeal}} = 1 - 300 \times (0{\cdot}025 - \mathit{TimeIntoMeal})^2 \tag{18}$$

$$\mathit{TimeIntoMealFactor}_{\mathit{RestOfMeal}} = 1 - 600 \times (\mathit{FeedDMContent} - 0{\cdot}3) \times (\mathit{TimeIntoMeal} - 0{\cdot}025)^2 \tag{19}$$

BolusSizeF is a factor (*BolusWeightDry/20*) increasing salivation during mastication as *BolusWeigthDry* increases, and *xBolusMov* (0.6, unitless) is the sensitivity of a number of mastications to bolus size. *BaseMasJawMovPerBolus* is a constant, 27, derived from the literature (Gill *et al.*, 1966; Boudon *et al.*, 2006), representing a base number of total jaw movements per bolus. *HungerEffectOnMasticaiton* (Unitless) modulates mastication in response to hunger, and it is derived as follows:

$$\mathit{HungerEffectOnMastication} = \mathit{HungerMasticationF} + (1 - \mathit{HungerMasticationF}) \times e^{e^{(-\mathit{kHungerMastication} \times \mathit{Hunger})}} \tag{20}$$

HungerMasticationF is a constant equal to 0.63. For details on the set of equations representing motivation to feed (i.e. hunger, unitless), refer to Gregorini *et al.* (2013, 2015*b*). *kHungerMastication* is a decay constant (6.8, unitless) of mastication time as a function of hunger. *kHungerMastication* can represent differences due to breed, age and dental efficacy as suggested by Pérez-Barbería and Gordon (1998). *NDFF* represents the effect [linear adjustment, according to Baumont *et al.* (2004)] of fibre on mastication and salivation and is calculated as *ActualNDF*/*BaseNDF*. Base NDF is 590 g/kg of forage DM, and actual NDF is the forage NDF content that MINDY is grazing at a particular time and space. Forage chemical composition in MINDY changes during the day and between sward canopy strata (Gregorini, 2012; Gregorini *et al.*, 2013). *SpeciesF* (1, 0.6, 0.4 and 1.4, unitless, for C3, legumes, herbs and C4 forages, respectively) is the inherent ease of breakdown (i.e. toughness) of the feed, independently of the NDF factor (Wilson and Mertens, 1995; Wilson and Kennedy, 1996).

TimePerBite and *TimePerMastication*, in Eqn 9, are calculated as follows:

$$\mathit{TimePerBite} = \mathit{TimePerJawMovementBase} \times \mathit{HungerEffectOnBiteRate} \tag{21}$$

$$\mathit{TimePerMasticaiton} = \mathit{TimePerJawMovementBase} \times \mathit{HungerEffectOnMastication} \tag{22}$$

TimePerJawMovementBase (s) is assumed to be equivalent for severing and mastication movements [$0.35 \times \mathit{CorrectedBW}^{0.125}$, (Illius and Gordon, 1987, 1992)]. *HungerEffectOnBiteRate* is a factor (unitless) reducing the time per bite (severing jaw movement) as hunger increases and is calculated as the difference between *HungerEffectOnMastication* and *kHungerBiteRate*.

In Eqn 11, *BaseSalivaPerJawMovement* is the salivation rate (g saliva per severing or mastication jaw movement). *xBolusSaliva* and *xNDFSaliva* are unitless constants, 0.595 and 0.3 respectively, representing the sensitivity of salivation during mastication to bolus size and NDF content of ingesta. The factor *DroolingSalivaF* is calculated as $\mathit{TimeIntoMealF}^{\mathit{xSalivaTimeIntoMeal}}$, where *xSalivaTimeIntoMeal* is a constant (1.77, unitless) representing the sensitivity to salivation as meal progresses.

In Eqn 12, the *kSalivaSevering* is a constant, 0.31, representing the ratio of saliva per severing to saliva per mastication movement. In Eqn 14, *LiquidizingSaliva* is the proportion of non-absorbed saliva in the bolus, and derived as follows:

$$\mathit{LiquidizingSaliva} = \{\mathit{Min}[0{\cdot}49,\ \mathit{Max}(0{\cdot}3,\ \mathit{SalivaInBolus} \times (1 - \mathit{AbsorvedSaliva}))]\} \tag{23}$$

The *SalivaInBolus* and *Absorbed Saliva* are calculated as

$$\mathit{SalivaInBolus} = \frac{\mathit{SalivaPerBolus}}{\mathit{SalivaPerBolus} + \left(\dfrac{\mathit{BolusWeigtDry}}{\mathit{FeedDMContent}}\right)} \tag{24}$$

$$\mathit{AbsorbedSaliva} = \mathit{MaxSalivaAbsorption} \times \mathit{FeedDMContent} + \mathit{MinSalivaAbsorption} \times (1 - \mathit{FeedDMContent}) \tag{25}$$

Equations 24 and 25 are biological assumptions and more data are required. However, these assumptions are supported by the fact that their incorporation in the module improved the representation of both dry feed and grazing/moist feed bolus size (Gill *et al.*, 1966; Boudon *et al.*, 2006; Acosta *et al.*, 2007). Saliva plays a role (reducing target bolus size) only when its proportion in the bolus is above 0.3 and does not seem to go beyond 0.5 of the bolus, presumably because the bolus would become 'too liquid' (Prinz and Lucas, 1997; Lucas *et al.*, 2002).

Particle size distribution of ingesta in the swallowed bolus

Particle size distribution is derived from particle sizes of ingesta in the masticated and salivated swallowed bolus, *MasticationJawMovementsPerBolus*, and *kComminute(i)*. The latter is the proportion of the content of each bin that is halved upon one mastication jaw movement and therefore moves (is transferred) to the next smaller 'bin', assuming that the breakdown is proportional to the particle size.

$$kComminute\ (i) = kComminuteMin + (kComminuteMax - kComminuteMin) \times \frac{BinMinMeshSize(i)}{BinMinMeshSize\ (14)} \quad (26)$$

KComminuteMin and *KComminuteMax* are functions of ease of particle size breakdown, which depends on the fibre content of the feed and plant species. Note that *kComminute*[1] represents *kComminuteMin*, but is not in use (nothing leaves the smallest particle bin) and *kComminute*[14] represents *kComminuteMax*.

The model then predicts the *SwallowedDistribution (i)*, which is the distribution (proportion) over the 14 bins totalling to 1. It is the final particle size distribution of ingesta after X number of mastications per bolus, i.e. bolus particle size distribution. The *SwallowedDistribution* is then collapsed into three proportions of particle sizes to feed the three particle size pools in the rumen (Gregorini *et al*., 2015*a*), *LPart*, *MPart* and *Spart* (large, medium and small particle size, respectively). The critical size for particles to escape from the rumen has been observed to be 1.2 mm (Poppi *et al*., 1981), so *SPart* represents the proportion of particles of 1.2 mm or less, while *MPart* and *SPart* represent the proportion of the particles between 1.2 and 4.8 and 4.8 mm or greater, respectively.

The particle size distribution of swallowed ingesta boluses ($P_{SwallowedLPart}$, $P_{SallowedMPart}$ and $P_{SwallowedSPart}$) is used with the DM intake rate (*FdRat*):

$$FdRat = BolusWeightDry \times BolusSwallowingFrequency \quad (27)$$

and nutrient fractions of the feed to calculate insoluble nutrient flow ($f_{SwallowedLPart}$, $f_{SallowedMPart}$ and $f_{SwallowedSPart}$) into each of the three particle size pools flowing into the rumen:

$$f_{SwallowedLPart} = FdRat \times P_{Swallowed\ LPart} \times (f_{StFd} - f_{StSFd} + f_{HcFd} + f_{CeFd} + f_{PiFd} + f_{LgFd} + f_{AiFd}) \quad (28)$$

$$f_{SwallowedMPart} = FdRat \times P_{Swallowed\ MPart} \times (f_{StFd} - f_{StSFd} + f_{HcFd} + f_{CeFd} + f_{PiFd} + f_{LgFd} + f_{AiFd}) \quad (29)$$

$$f_{SwallowedSPart} = FdRat \times P_{Swallowed\ SPart} \times (f_{StFd} - f_{StSFd} + f_{HcFd} + f_{CeFd} + f_{PiFd} + f_{LgFd} + f_{AiFd}) \quad (30)$$

fStFd, fStSFd, fHcFd, fCeFd, fPiFd, fLgFd and fAiFd represent the fractional proportions of total starch, soluble starch, hemicelluloses, cellulose, insoluble protein, lignin and insoluble ash, respectively. These inputs are as described previously (Hanigan *et al*., 2006; 2013). The inclusion of starch and insoluble protein in the *LPart* pool is a deviation from the original description by Baldwin (1995), which seems warranted given that the pool represents both the ruminal mat and also, to a certain extent, non-fermenting fractions of feed which may be caused by a delay in nutrient wetting after food enters the rumen. Also, an insoluble protein associated with the cell wall is not subject to fermentation until it is released from the cell wall matrix (Jung and Allen, 1995).

Particle sizes, pools and passage through the rumen

As described before, *LPart*, *MPart* and *SPart* flow into the rumen after ingestion and oral processing; both processes depending on sward state and condition, forage species and the internal state of the animal. This inflow of particles feeds the three-pool scheme in the rumen of MINDY (see Gregorini *et al*., 2015*a* for detail of this development in Molly). Each particle size pool in the rumen is subjected to variable rates of rumen digesta outflow and differential degradation.

Passage of *MPart* and *SPart* are assumed to be a fractional function of the liquid passage rate and the concentration of particulate DM in ruminal liquid. Initial fractional passage rates (*kPMpart* and *kPSpart*) were set to 0.1 and 0.75 at prevailing particulate DM concentrations per litre of total liquid passed. Initial assessment of the use of values closer to 1 for *kPSpart* resulted in non-biological rumen functions. The use of these values (<1) is supported by observations that particulate matter is retained and not freely flowing with the liquid phase even in cattle consuming lush herbage (Clauss *et al*., 2006; 2010, 2011; Lechner *et al*., 2010). Implicitly, this reflects the sieving action of the mat, the inability of particles to migrate to the region of the omasal orifice as rapidly as the fluid phase, or a mechanical action within the omasum or abomasum that acts to retard particle flow. Passage of particulate matter from the rumen, *PPart*, is represented as a weighted average passage rate:

$$PPart = \frac{QMPart}{QMPart + QSPart} \times kPMPart + \frac{QSPart}{QMPart + QSPart} \times kPSPart \quad (31)$$

where *QMPart* and *QSPart* are the rumen pools (kg) of *MPart* and *SPart*, respectively.

Because of the large differences in passage rates for the two pools, shifts in the distribution of bolus particle sizes due to either the sward features or its interaction with the internal state of the animal (e.g. hunger), ingestion pattern and oral processing will have significant effects on ruminal retention times and thus diet digestibility. In the model, a portion of the microbes is associated with particulate matter. Therefore, increased passage rates associated with reduced particle size will also result in greater passage rates of attached microbes.

Liquid passage from the rumen

At first glance, predicting liquid passage through the rumen seems relatively simple, being equal to the sum of water and salivation inflows, fluid outflow and the net balance of fluid across the rumen wall. However, the significant variations of particle size distribution and flow of saliva with individual ingestive boluses in response to feed and oral processing (Gill *et al*., 1966; Pérez-Barbería and Gordon, 1998), passage rate of particles and rumen fermentation pattern within and between meals (Gill *et al*., 1999; Gregorini, 2011, 2012), as well as diurnal fluctuations of rumen pools and fluid outflows (Dove *et al*., 1988; Gill *et al*., 1999; Taweel *et al*., 2004), indicate that predicting this phenomenon is complicated and needs a more mechanistic and dynamic approach. Based on the model of ruminal water balance (l/day) incorporated into Molly by Argyle and Baldwin (1988) and modified by Gregorini *et al*. (2015*a*), the passage of liquid through the rumen, *RumenLiquidOutflow* (l/day), was represented more mechanistically and dynamically as follows:

$$\mathit{RumenLiquidOutflow} = \mathit{RumenDigesta} \times \mathit{fLiquidOutflow} \times (1 - \mathit{RumenDM}) \tag{32}$$

and rumen *DilutionRate* (%/h), known as the fractional passage of liquid, was calculated as:

$$\mathit{DilutionRate} = \frac{\mathit{RumenLiquidOutflow}}{\mathit{RumenLiquidVolume}} /24 \tag{33}$$

$$\begin{aligned}\mathit{RumenLiquidVolume} = {} & \mathit{RumenLiquidInflow} \\ & - \mathit{RumenLiquidOutflow} \\ & + \mathit{OsmWater}\end{aligned} \tag{34}$$

The inflow of liquid to the rumen, *RumenLiquidInflow* (l), is the sum of water ingestion (moisture content of the feed) and water imbibed. The latter is described in detail by Gregorini *et al.* (2018), in a parallel development of MINDY to simulate diurnal patterns of urination and drinking. *RumenLiquidInflow* also includes saliva, as a product of severing bites and oral processing (as described before), plus salivation while ruminating and resting as described in Gregorini *et al.* (2013) and Gregorini *et al.* (2018). *OsmolalWater* (l, Eqn 35) is the water flowing in and out of the rumen through the rumen wall as a response to the difference between *RumenOsmolaity* and blood osmolality (López *et al.*, 1994). *RumenOsmolality* represents ruminal milliosmolality and blood milliosmolality is 280, plus the intercept of Eqn 35, 20 l/day. *RumenOsmolality* is calculated as the molar sum of soluble carbohydrate (Cs), ammonia (Am), VFA (Acetic, Ac; Propionic, Pr; Butiric, Bu), lactate (La), amino acids (Aa), and soluble ash (As) divided by *RumenLiquidVolume* (in ml). Moles of soluble ash were calculated by dividing the weight of soluble ash by the molecular weight of sodium bicarbonate and multiplying by an osmolality factor of 1.7, which was derived empirically. The remaining metabolites are predicted from the rumen of MINDY. Water moves from the rumen to blood when *RumenOsmolality* is <225 and the reverse when it is >225.

$$\mathit{OsmolalWater} = 70 \times [(\mathit{RumenOsmolality} - \mathrm{BloodOsmolality}) \times 1000] + 20 \tag{35}$$

In Eqn 32, *RumenDigesta* (kg) is the sum the rumen DM and liquid [(assuming a density of rumen liquid of 1), *RumenLiquidVolume,* litres)] contents. Ruminal fluid outflow has been reported to be dictated by total rumen content (Okine *et al.*, 1989; Chilibroste, 1999; Schettini *et al.*, 1999). *RumenDM* is the proportion of DM of the rumen digesta and *fLiquidOutflow* is a multifactorial function described as follows:

$$\begin{aligned}&\mathit{fLiquidOutflow} = \\ &\mathit{fLiquidOutMin} + \\ &\frac{\mathit{fLiquidOutMax} - \mathit{fLiquidOutMin}}{\{1 + e^{[(\mathit{kLiquidOutCurvature} \times (\mathit{kRumenInflection} - \mathit{RumenLiquidVolume}/\mathit{CorrectedBW})]}\}} \\ &\times \mathit{RumenDMF} \times \mathit{BehaviorF} \times \mathit{PregnancyF} \times \mathit{SerotoninF}\end{aligned} \tag{36}$$

fLiquidOutMin and *fLiquidOutMax* in Eqn 38 represent the lower (0.052) and upper (0.4) fractional (proportion/h) of liquid passage rate through the rumen. *kLiquidOutCurvature* (179, unitless) is a constant controlling the curvature of the sigmoid dependency of fractional liquid passage rate on *RumenDigesta*. *kRumenInflection* is also a stabilizing constant (0.13), representing the proportion of the rumen liquid volume flowing out of the rumen around which rate of liquid passage is growing fastest. *RumenDMF* is a factor representing how much to slow down *fLiquidOutflow* when the rumen is 'dry', giving a value of 1 when the *RumenDM* equal 0.14 (*RumenDMBase*), or a value of 0.89 when *RumenDM* reaches its driest point (~0.18, *RumenDMUpper*) and drinking is triggered [see Gregorini *et al.* (2018) for details on the representation of drinking behaviour in MINDY]. Simply, *RumenDMF* represents the slowing down of the liquid passage rate as the rumen becomes drier and is calculated as follows:

$$\begin{aligned}&\mathit{RumenDMF} = \mathit{RumenDMFMin} + (1 - \mathit{RumenDMFMin}) \\ &\quad \times \mathit{Max}\{0, [\mathit{Min}(1, \ \mathit{RumenDMUpper} - \mathit{RumenDM})]\}/ \\ &\quad (\mathit{RumenDMUpper} - \mathit{RumenDMBase})\end{aligned} \tag{37}$$

As demonstrated by Balch and Campling (1962) digesta does not flow through the rumen with the rumen in stasis. See also Owens *et al.* (1998), which indicates, as suggested by Deswysen *et al.* (1987), Ulyatt (1983) and Wilson and Kennedy (1996), that ruminal contractions are necessary for digesta to pass through the rumen (Thiago *et al.*, 1992; Gill *et al.*, 1999). Seo *et al.* (2007) compiled data from 19 experiments, showing that frequency of rumen contractions differs with behavioural activity: eating, ruminating and idling, had 1.56, 1.12 and 1.13 rumen contractions per min., respectively. Thus, *BehaviourF* is a representation of this behavioural modulation. *BehaviourF* takes the values of Seo *et al.* (2007) divided by 1.56. This modulation factor helps to represent fluctuation of liquid outflow from the rumen (and particulate matter carried in it) throughout the day, as response to feeding management and or diet that alter behavioural (i.e. eating time, ruminating and idling) time budgets.

The *PregnancyF* (unitless) and *SerotoninF* (unitless) in Eqn 36 are factors representing the effect of pregnancy stage on rumen capacity and the effect of serotonin on motivation to eat and peristaltic movements of the rumen. The former accelerates *RumenLiquidOutflow* during eating as the gravid uterus increases in volume, causing a faster liquid passage rate of digesta. This is supported by the results of Vanzant *et al.* (1991), who reported a faster passage rate of the rumen liquid for pregnant and lactating than for non-lactating cattle at the same forage digestibility; by the report of Hanks *et al.* (1993), who showed that pregnancy leads to a greater particle passage rate, a shorter ruminal and total gastrointestinal retention time in cattle; and by the results of Coffey *et al.* (1989) and Gunter *et al.* (1990) with sheep, showing increments of particle passage rates with advancing pregnancy.

$$\mathit{PregnancyF} = \frac{1}{\left(\dfrac{1}{\mathit{GravidUiterusWeight}}\right)^{\mathit{kPregnancyRumen}}} \tag{38}$$

where *kPregnancyRumen* (0.61, unitless) is a constant controlling the acceleration of liquid passage rate as the foetus grows (due to increased pressure on the rumen).

SerotoninF is calculated as follows:

$$SerotoninF = 1 + kLiquidSerotonin \times (1 + Serotonin) \qquad (39)$$

where *kLiquidSerotonin* is a constant (0.5, proportion), representing the proportional change of liquid passage rate due to serotonin fluctuations. In MINDY, *Serotonin* (0–1, unitless) is a proxy of the effect of the diurnal fluctuations of serotonin and its effect on feeding motivation and rumen function (Gregorini, 2011, 2012). The effect diurnal fluctuation of light intensity on the hypothalamic suprachiasmatic nucleus has been hypothesized to be related to the secretion of melatonin (Gregorini, 2012). Diurnal fluctuations in melatonin release (greater during the dark and lower during light periods) have been documented in domestic and wild ruminants (Gregorini, 2012). Melatonin is synthesized from tryptophan derived from serotonin, which explains the diel rhythmic patterns of serotonin depletion during the late afternoon to early evening and replenishment from dawn onwards. Increased levels of serotonin may inhibit the reward functions at the mesolimbic system, diminishing motivation to feed (Pittroff and Soca, 2006). Serotonin has also been related to gastric emptying dynamics in ruminants through the effects on cholecystokinin release (Pittroff and Soca, 2006). Serotonin has been related to reductions in gastric emptying by augmenting the secretion of, and response to, cholecystokinin (Hayes *et al.*, 2004; Li *et al.*, 2004). Cholecystokinin reduces the intensity and frequency of the reticulum-rumen contractions (Bruce and Huber, 1973) and reduces the opening size of the pyloric orifice, increasing the retention time of digesta in the rumen and satiety signals from it, thereby reducing ingestion rates (Pittroff and Soca, 2006). Therefore, rhythmic diel variations in serotonin depletion counteract the effects of cholecystokinin. This phenomenon is supported by the results of Dove *et al.* (1988) with grazing ewes, who reported the fastest digesta flow during and immediately after the dusk grazing.

$$Serotonin = \left[\frac{(DielRythm + 1)}{2}\right]^{kSerotonin} \qquad (40)$$

$$CircadianRythm = Sine \times Pi \times [2 \times Pi \times (RelativeTime - DielRythmLag)] \qquad (41)$$

where *kSerotonin* is 1.81 (unitless) modifying the sine wave shape. *RelativeTime* is the time of day (d) relative to the time of sunrise and sunset (d); and, *DielRythmLag* is a constant, 0.045 (d) set to 1 h to create a delay due to build-up time of serotonin and melatonin during day/night, respectively.

Illustrations

The present work focuses on formulating and describing the structure and function of the new development in MINDY, with a preliminary conceptual validation (Rykiel, 1996) conducted for different feeding scenarios. Validation means that the model is acceptable for its intended purpose because it meets specified performance requirements (Rykiel, 1996). The purpose of the present development was to integrate existing knowledge of interactions between ingestion and digestion processes in MINDY by including explicit oral processing of ingesta and simulating – rather than setting – fractional passage of liquid in the rumen as a response to behaviour/ foraging context. The context for the model is a foraging ruminant. The theoretical model performance was assessed subjectively, as suggested by Rykiel (1996), by MINDY's ability to simulate realistic patterns of oral processing of ingesta in response to various grazing scenarios, commonly present in intensive pastoral dairy farms.

For illustrative purposes, MINDY was confronted with: (1) herbage of contrasting forage species, only differing in *SpeciesF* (a proxy for forage species toughness); (2) a period of restriction in available grazing time, with or without a maize grain meal before allocation of a new pasture strip; and (3) a factorial arrangement of herbage allowances and sward surface heights. In other words, the goal was to illustrate how MINDY's diurnal patterns of ingestion and oral processing of ingesta are sensitive to the toughness of herbage, hunger and sward structure, and how, would that change digesta outflows dynamics from the rumen. In all simulations, the outputs required from MINDY were: intake rates, masticatory behaviour, ingestive bolus weight, particle size distribution in the bolus and rumen dilution rate.

The effect of forage species with contrasting features for oral comminution

The distribution of ingesta through different particle size pools in the rumen digesta is a function of ingestive actions and oral processing forming the swallowed bolus (Moseley and Jones, 1984; Spalinger *et al.*, 1986; Pond *et al.*, 1987; Prinz and Lucas, 1997). Thus, forage species, sward structure, herbage chemical composition and plant phenology are key factors determining particle size distribution of the swallowed bolus (Wilson and Kennedy, 1996; Poppi *et al.*, 2000; Kennedy, 2005). Although this phenomenon is well documented in the literature and some models have attempted to include it implicitly (Sauvant *et al.*, 1996; Baumont *et al.*, 2004), there is a lack of information on the effect of plant-related comminution properties (e.g. toughness) on patterns of bolus size, particle size distribution, intake rate and rumen dilution rate. The current work simulated a scenario where MINDY [initialized as a pregnant Friesian dairy cow (500 kg liveweight) was in mid-lactation (150 days in milk)] strip-grazing monoculture swards of *Lolium perenne*, *Medicago sativa* and *Pennisetum clandestinum*. All swards had a height of 30 cm and herbage mass of 3000 kg DM per ha. The grazing area allocated to MINDY was 100 m^2 and pasture was allocated after the morning milking (08:00 h).

Figure 3 presents MINDY's diurnal patterns of ingestive bolus particle size distribution, bolus weight, mastications per bolus, bolus swallowing frequency, rumen dilution rate and herbage intake rate. These results indicate different ingestive-oral processing dynamics as a function of forage species. This dynamic in turn determines the variations in intake pattern and rumen dilution rate among forage species.

As constraints in forage comminution increase, i.e. *Medicago sativa*, *Lolium perenne* and *Pennisetum clandestinum*, respectively, the proportion of swallowed large particles (*FLPartSwal*) increases, with a significant reduction of the proportion of medium and small particles in the swallowed boluses (Fig. 3, a–c). These results are supported by the classical works of Poppi *et al.* (1981), McLeod and Minson (1988), Luginbuhl *et al.* (1989) and Bailey *et al.* (1990), who studied the particle size reduction during mastication of different forages (C3, C4 and legumes) and plant parts (leaf and stem) by cattle and sheep. The within, and between, meal variations in bolus particle size distribution reveals the capabilities of MINDY to simulate the

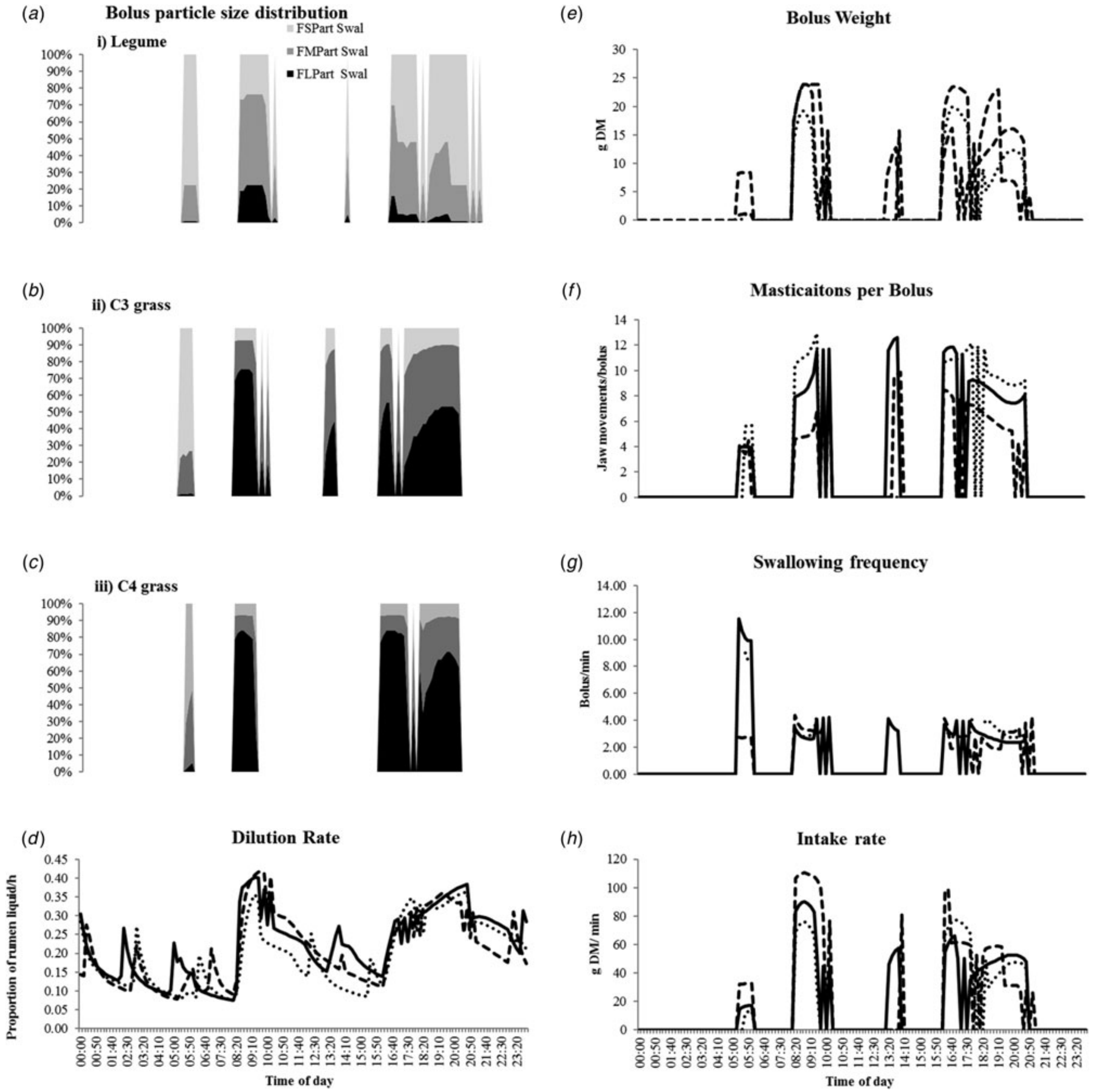

Fig. 3. Predicted effect of herbage toughness, i.e. *SpeciesF*, on ingestive (swallowed) boluses particle size distribution, boluses weight, mastications per bolus, bolus swallowing frequency, rumen dilution rate and herbage intake rate. In a–c: FLPartSwal, FMPartSwal and FSPartSwal are large, medium and small particles, respectively. In d–h: Solid line is *Lolium perenne*; dotted line is *Pennisetum clandestinum*; and dashed line is *Medicago sativa*.

effect of these plant characteristic throughout the day, in conjunction with grazing management and the internal state of the animal. Mastication dynamic within a meal is also a function of an animal's motivation to feed (Gregorini, 2011) and diurnal arrangement of meals, thus it also depends on grazing management (Gregorini, 2012), as presented in the next section.

MINDY predicts differences in bolus size (DM) according to forage species (Fig. 3e). These model outputs are consistent with the reports of Kennedy and Murphy (1988), Wilson and Kennedy (1996) and Kennedy (2005), reporting the effect of forage species on mastication dynamics. Both bolus size and mastication dynamics determine the bolus swallowing frequency (Prinz and Lucas, 1997). Swallowing frequency reflects one of the main ingestive constraints to herbage intake, which is posed by comminution characteristics of forages, as demonstrated by MINDY's intake rate dynamic and diurnal pattern of herbage intake (Fig. 3h).

Ruminal contractions increase almost exponentially with eating rate (Freer and Campling, 1965) and accelerate liquid and particulate passage rates through the rumen as demonstrated by Okine *et al.* (1989), and reported and modelled by Seo *et al.* (2007). Thus, in conjunction with oral processing, herbage intake pattern has a major influence on digesta outflow from the rumen (Gregorini *et al.*, 2008; Gregorini, 2012), as indicated by MINDY's rumen dilution rate outputs (Fig. 3d). Liquid flowing out of the rumen is the medium by which solids flow out of the rumen

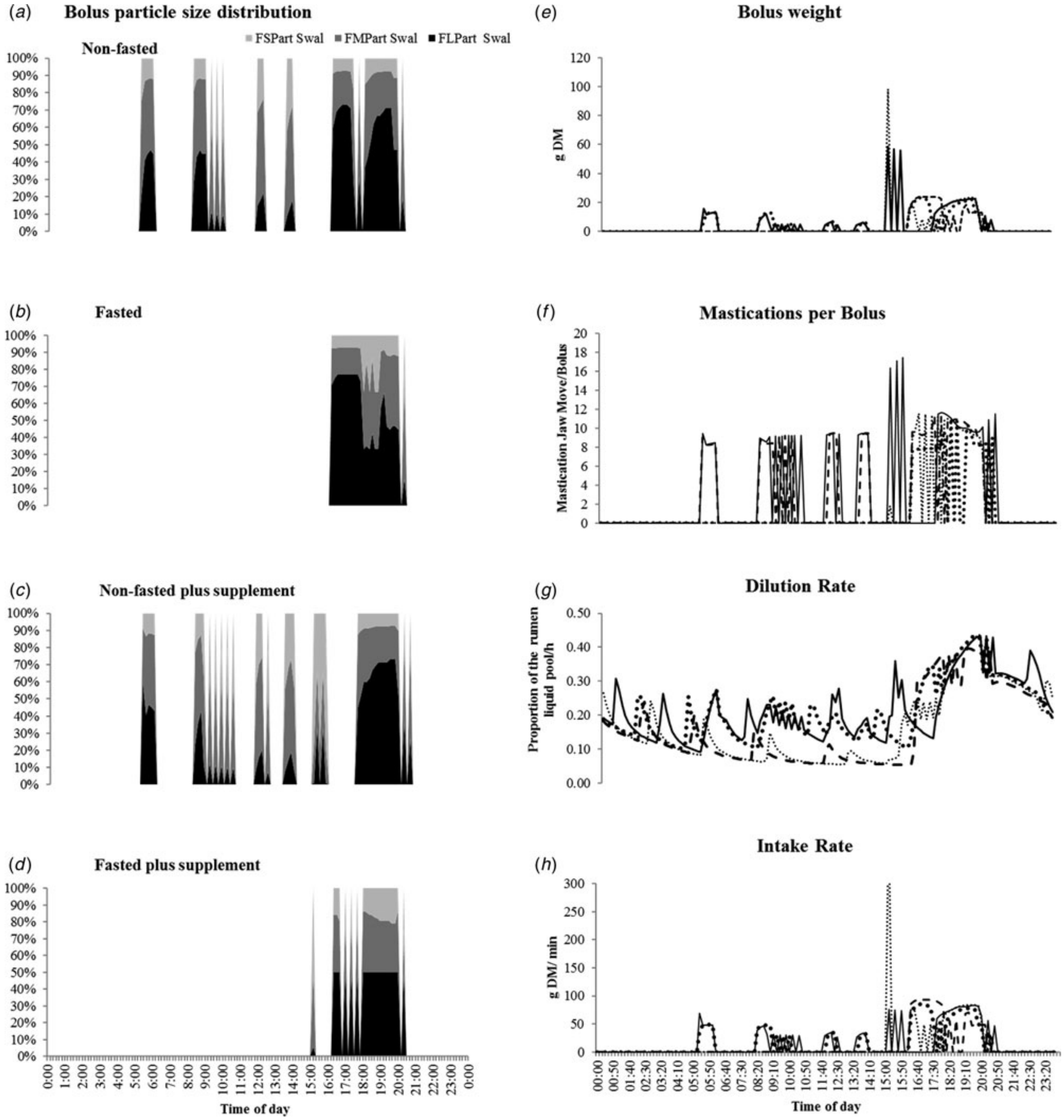

Fig. 4. Predicted effect of hunger (fasting) as modulated by feeding management (supplementation, cracked maize grain), on diurnal pattern of swallowed boluses particle size distribution, boluses weight, mastications per bolus, intake rate and rumen dilution rate. Left panel (a–d): FLPartSwal, FMPartSwal and FSPartSwal are large, medium and small particles, respectively. Right panel (e–h): Doted line is pasture allocation at 8 am; Dashed line is pasture allocation at 4 pm with stand-off between milkings; Solid line is pasture allocation at 8 am with a meal of 3 kg DM of cracked maize grain during the afternoon milking; and Small dotted line is pasture allocation at 4 pm, with stand-off (fasting time off the pasture) between milkings and a meal of 3 kg DM of cracked maize grain during the afternoon milking.

and is the way particle outflow was modelled in the current development of MINDY and the latest development of Molly (Gregorini *et al*., 2015*a*). The present results of these modelling illustrations support the concept that forage species, as characterized by chemical and biomechanical features, influence ingestion and thereby digestion dynamics, which influences herbage intake and its patterns and thereby rumen fermentation patterns. The latter is of particular interest from environmental (e.g. enteric methane emission, N excretion), nutritional (nutrient supply to the host animal) and animal welfare (minimal total discomfort and rumen health) standpoints (Gregorini *et al*., 2017).

The effect of hunger on oral processing of ingesta and rumen dilution rate

In a review of behavioural adaptations of dairy cows to changes in grazing management, Chilibroste *et al*. (2015) concluded that most of the available information focusing on short-term ingestive responses (i.e. herbage intake rate) lacked essential links with the internal state of the animal, i.e. hunger, and post-ingestive behaviour such as rumen function. Hunger level influences feeding motivation (Forbes and Gregorini, 2015). The latter modulates the dynamics of ingestive tactics, including intake rate and mastication, and consequently digestive patterns within and between meals. Hungry animals reduce mastication (i.e. oral processing) to increase herbage intake rate, swallowing boluses with larger particles and thus increasing rumen retention time of digesta (Greenwood and Demment, 1988; Chilibroste *et al.*, 2007; Gregorini, 2011).

To evaluate MINDY's oral processing of ingesta and digesta outflow from the rumen in response to hunger, four scenarios were simulated where MINDY [initialized as a pregnant Friesian dairy cow (500 kg liveweight) was in mid-lactation (150 days in milk)]: (a) Non-fasted, strip-grazing a sward of *Lolium perenne* with a surface height of 30 cm and an herbage mass of 3000 kg DM per ha, allocated 100 m^2 after the morning milking (08:00 h); (b) Fasted, strip-grazing the same sward as in (a) but allocated 100 m^2 after the afternoon milking (4 pm) for only 4 h; (c) Non-fasted plus supplement, strip-grazing the same sward and being fed three kg DM of maize grain during the afternoon milking; and (d) Fasted plus supplement, strip-grazing the same sward as in (b) and being fed 3 kg DM of maize grain during the afternoon milking. Figure 4a-g present the effect of hunger (as set by scenarios a–d) on MINDY's diurnal patterns of ingestive bolus particle size distribution, bolus weight, mastications per bolus, rumen dilution rate and herbage intake rate. These results indicate different dynamics in the oral processing in response to hunger, which in turn results in variations in intake pattern and rumen dilution rate.

As hunger levels increase, i.e. from scenario c, to a, to d and b, the proportion of swallowed large particles (*FLPartSwal*) increases, with a reduction of the proportion of small particles in the swallowed boluses. These results are supported by Greenwood and Demment (1988) and Chilibroste (1999), who report an increase in the particle size of forage flowing into the rumen of beef and dairy cattle, respectively, as a response to increments in fasting periods, i.e. hunger. Figure 4g helps explain these differences, which are especially marked at the beginning of the meal after the afternoon milking. The 'hungrier' MINDY 'felt' before a meal, the fewer mastications per ingestive bolus were made. This phenomenon is also evident during supplement consumption. The boli were heavier and much less masticated in scenario d than c. Gregorini *et al.* (2009*b*) reported a marked reduction in oral processing jaw movements including mastication as hunger level of dairy cows foraging *Dactylis glomarata* increased. These and similar results reported by Gregorini *et al.* (2007) for beef cattle grazing *Cynodon dactilon* swards support these outputs of MINDY.

Oral processing, and thereby particle size of ingestive boluses, and eating activity have a strong influence on rumen digesta outflow. Daily mean digesta passage rates through the rumen in scenarios c, a, d and b were, 0.249, 0.218, 0.255 and 0.207 kg of dry digesta per hour, respectively; while daily mean rumen dilution rate was 0.214, 0.210, 0.163 and 0.160 of the rumen liquid pool per hour, respectively. The diurnal patterns of the different rumen dilution rates are evident in Fig. 4g, where marked differences exist between fasted (slower) and non-fasted scenarios. The particular scenario d illustrates the links between oral processing (boluses particle size, eating activity) rumen peristaltic movements and digesta outflow from the rumen. Although MINDY was fasted for 20 h, by the time it was allocated to the pasture, it had just consumed 3 kg of maize at the greatest rate (it was 'hungry') with the lowest masticatory rate and heaviest boluses; collectively, reducing hunger and motivation to graze (especially at the beginning of the meal) as shown in Fig. 4h. Because of this reduced hunger level, each grass bolus was masticated more (Fig. 4f) compared with the other scenarios, and boluses with a lower proportion of large and greater proportions of medium and small particles (Fig. 4a-d) were swallowed. Moreover, almost all of the time at pasture was spent grazing, but slower at the beginning of the meal (as a response to a lower level of hunger). Both scenarios help explain the rumen dilution rate dynamic during the meal, and the faster (compared with the other scenarios) solid digesta outflow rate during eating and daily mean (Fig. 5).

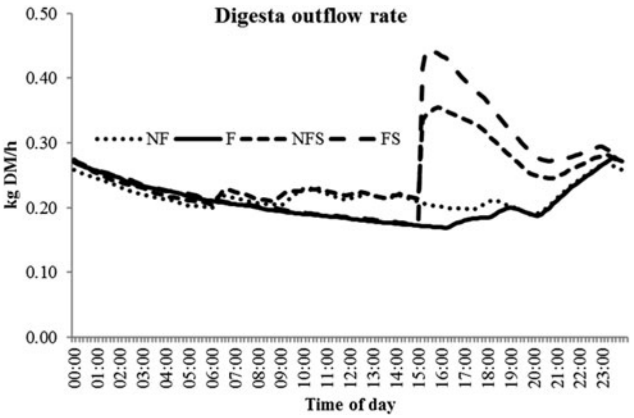

Fig. 5. Predicted effect of hunger (Fasting) as modulated by feeding management (cracked maize grain supplementation) on diurnal pattern of rumen digesta outflow rate. Small dotted line is pasture allocation at 8 am; Solid line is pasture allocation at 4 pm with stand-off between milkings; Small dashed line is pasture allocation at 8 am with a meal of 3 kg DM of cracked maize grain in the afternoon milking; and Dashed line is pasture allocation at 4 pm, with stand-off (fasting time off the pasture) between milkings and a meal of 3 kg DM of maize in the afternoon milking.

Together, these results show that MINDY, as in real ruminants (Laca *et al.*, 1994), reduces mastication as a compensatory mechanism to increase intake rate, but swallows longer/larger particles of herbage, as shown with cattle by Chilibroste (1999) and Greenwood and Demment (1988), which, in turn, increases rumen retention time of digesta and slows down the rumen dilution rate as hunger increases. Such slowing down of rumen dilution rate is supported by Gregorini *et al.* (2008) for beef cattle and Gregorini *et al.* (2017) for dairy cows.

The effect of herbage allowance and sward surface height

The new developments in MINDY include the addition of oral processing and the resultant changes in bolus particle size distribution, along with mechanistic and dynamic water ingestion and the fractional passage of liquid through the rumen. Collectively, they enhance the model's capability to explore foraging situations where the dynamics of herbage ingestion and oral processing is expected to alter patterns of intake and digestion, as well as nutrient supply to the host animal from the rumen. This development, in turn, improves simulations in which variations of animal performance and nutrient excretion are expected to be modulated, passively, by sward features, or actively by grazing management (Gregorini *et al.*, 2018). These hypotheses were challenged by setting a factorial arrangement of scenarios between four herbage allowances [25, 30, 35 and 40 kg DM (above-ground)/cow/day]

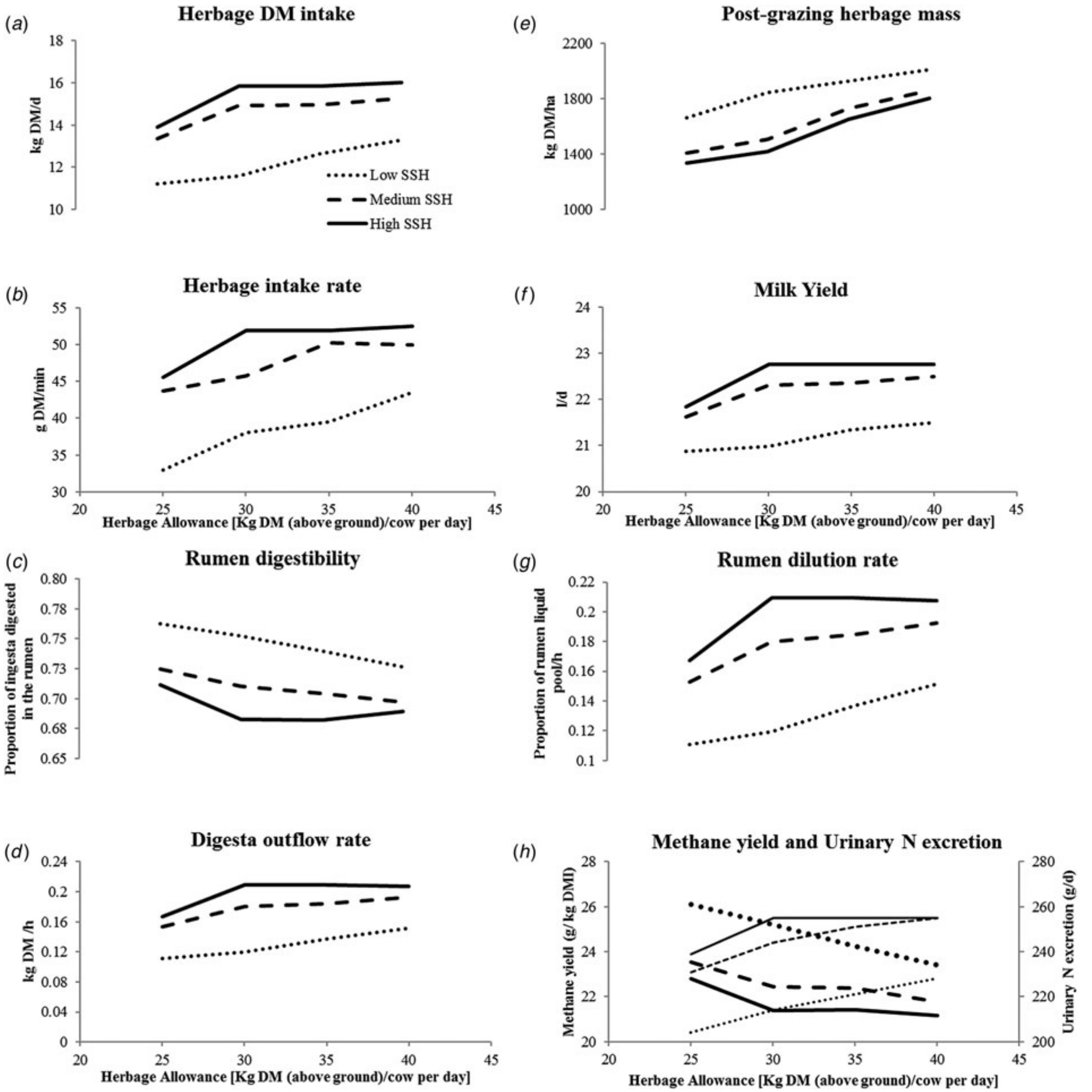

Fig. 6. Predicted effect of herbage allowance (kg DM above ground/cow/day) and sward surface height, on (a) herbage DM intake, (b) herbage intake rate, (c) rumen digestibility, (d) Digesta outflow rate, (e) post-grazing herbage mass, (f) milk yield, (g) rumen. Low (dotted lines), 15 cm; Medium (dashed lines), 22.5 cm and High (solid lines), 30 cm sward surface height (SSH) as extended tiller height. (h) Methane yield (thick lines) and urinary N excretion (thin lines) at Low (dotted lines), Medium (dashed lines) and High (solid lines) SSH.

and three sward surface height (15, 22 and 30 cm, extended tiller height). In each scenario, MINDY [initialized as a pregnant Friesian dairy cow (500 kg liveweight) in mid-lactation (150 days in milk)] strip-grazed a sward of *Lolium perenne* with a herbage mass of 3000 kg DM/ha, allocated after the morning milking (08:00 h). Herbage allowances were created by changing the daily area allocated to MINDY: 83,100, 116, and 133 m^2.

Figure 6a-h present the effect of herbage allowance and sward surface height on daily herbage intake, rumen function, methane yield and urinary N excretion. These results indicate:

First, that increasing the herbage allowance leads to greater herbage intake with a variable diminishing response but lower grazing efficiency (Fig. 6a and e, respectively). This response was expected, being well-known (Pérez-Prieto and Delagarde, 2012; 2013). The variability of such a response depended on the sward surface height, indicating that at the same herbage allowance with the same herbage mass, sward structure (i.e. sward canopy height) will determine herbage intake, its rate and harvesting efficiency. The current results suggest that increments in sward surface height, at the same available herbage mass, can increase herbage accessibility and facilitate the harvesting process, leading to greater intake rates and daily herbage intakes. Such a response relates to changes in sward canopy structure and vertical distribution of herbage mass and its morphological components. These outputs of the model are supported by literature reporting investigations of the functional response of large ruminants under relatively homogeneous swards (Laca *et al.*, 1992; 1994; Demment and Laca, 1994; Gregorini *et al.*, 2009*a*; 2011; Carvalho *et al.*, 2015).

Secondly, digestive (and excretory) responses are linked strongly to ingestive patterns and grazing management. Green leaf content is the sward component that promotes herbage intake (Burns and Sollenberger, 2002) because the amount of green leaf is better correlated with bite than herbage mass *per se* (Wade and Carvalho, 2000). Moreover, accessibility to leaves is closely related to the N content of herbage consumed in each bite (Bailey *et al.*, 1996; Drescher, 2003). According to Waite (1963) the upper strata of the sward canopy is removed first; therefore, the quantity and quality (e.g. protein content) of the diet selected and eaten by grazing cattle depends on the level of herbage depletion and sward structure (Chacon and Stobbs, 1976). In MINDY, increments of sward surface height at the same herbage mass lead to a square (rather than triangular with the base at the bottom) distribution of herbage mass in sward canopy, increasing the leaf content of the upper grazing strata. Moreover, in MINDY, quality of herbage and leaf content of the sward canopy strata diminish from top to bottom (for details see equations in Gregorini *et al.*, 2013). Thus, and as reported in the literature (Wade and Carvalho, 2000), in temperate swards, increments in herbage allowance and leaf accessibility (e.g. through an increment in sward height, Gregorini *et al.*, 2009*a*) would increase leaf proportion in the diet. The latter is supported by the reduction in grazing efficiency (Fig. 6e) and thus increments if herbage DM (Fig. 6a) and thereby N intake rate.

Although an increased herbage allowance increases DM intake and its rate, it reduces rumen digestibility. The latter is explained by the faster digesta outflow from the rumen (Fig. 6d) and rumen dilution rate (Fig. 6g). These relationships are documented in the literature (Poppi *et al.*, 2000) and show the benefits of this new development in MINDY. Reductions in rumen retention time diminish methane yield, which adds to the benefits of greater milk production (Fig. 6h). However, and as a product of greater N intake, urinary N excretion increases (Fig. 6h). The magnitude and pattern of this trade-off varies, and quite significantly, with sward surface height. Thus, the three-dimensional arrangement of herbage mass should not be ignored in managing grazing and or selecting forage cultivars with low N. The latter is important for temperate grazing systems; known by the excess of N supply to inefficient N users such as cattle (cattle use of N rarely exceeds 0.30; Dijkstra *et al.*, 2013; Gregorini *et al.*, 2016). In these systems an excess of urinary N load onto pastures increases N leaching, leading to pollution of water resources.

The pollution swapping between methane emission and urinary N excretion is always present (Dijkstra *et al.*, 2011; Gregorini *et al.*, 2016), but increments in the environmental impact of increased methane yield are easily offset by reductions in urinary N excretions (Dijkstra *et al.*, 2013; Gregorini *et al.*, 2017). Moreover, increments in herbage allowance and accessibility reduce rumen digestion (Fig. 6c) and thereby fibre digestibility, the cheapest source of nutrient in pastoral systems. Within this context, the present model outputs suggest that, at the same herbage mass and allowance, increments of sward surface height of forage species with similar chemical composition should be re-considered and further evaluated.

Summary and conclusions

The model development presented in the current paper makes explicit the functional relationships among direct and indirect controls of ingestion and rumen digestion. Although additional statistical evaluations are required, and more data may be needed to further define some parameters, MINDY theoretical validation indicates that patterns of herbage intake and oral processing of ingesta are reproduced realistically, achieving the sensible (and realistic) effect on rumen digesta outflow from a grazing dairy cow consistent with basic knowledge reported in the literature. The model's representation of those functional relationships allows simulating grazing management and its effects more comprehensively and realistically. Therefore, the new concepts encoded in MINDY capture many of the underlying biological mechanisms that influence and link the effect of ingesta oral processing and digesta outflow from the rumen. MINDY's new development can then help in advancing the understanding and nutritional ecology of foraging, grazing patterns and their management for environmental protection. Previous modelling efforts on forage ingestion and digesta outflow from the rumen have been either purely empirical or not comprehensive enough to include these more complex concepts. Therefore, this current iteration of MINDY represents a step forward, but the model offers promise as a heuristic tool for feed intake and grazing process research and as an informative tool for grazing and cow management decisions.

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