

Structure and dynamics of grazed vegetation

Carol A. Marriott^{a*}, Pascal Carrère^b

^a Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB15 8QH, UK

^b Inra, Unité d'Agronomie, Site de Crouël, 234, Av. du Brézet, 63039 Clermont-Ferrand, France

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Abstract — The relationship between vegetation and grazing herbivores is dynamic; the structure and quality of vegetation affect the diet of grazing herbivores and, in turn, the components of grazing (defoliation, excretal return and treading) affect the structure and species composition of the vegetation. Both the vertical and horizontal distribution of vegetation are important in understanding plant-animal interactions in grazed plant communities. Mechanisms which confer grazing resistance, through avoidance and tolerance strategies, are discussed. The difficulties in addressing scaling issues at the plant-animal interface are addressed; measurements or events at a small scale cannot be directly extrapolated to a larger scale. Moreover, integration of small-scale functions could result in counter intuitive results at the larger scale. The role of modelling in exploring spatio-temporal heterogeneity in plant-animal interactions is developed. Such models allow the exploration of a large number of hypotheses which cannot be tested under experimental conditions because of logistical, time and money constraints, and provide a framework in which to better understand grazing systems. As a management tool, models have value in their predictive capacity and ability to simulate the complex situations in grazed plant communities. © Elsevier / Inra

grazing resistance / heterogeneity / plant competition / plant-animal interactions / scaling

Résumé — **Structure et dynamique de la végétation pâturée.** En conditions pâturées, la relation entre la végétation et l'animal est dynamique. La structure et la qualité de la végétation affecte l'ingestion par l'animal et, en retour, les composantes du pâturage (défoliation, restitutions et piétinement) modifient la structure et la composition floristique du couvert végétal. En conséquence, la prise en compte des distributions verticale et horizontale de la végétation sont déterminantes pour une meilleure compréhension des interactions entre la plante et l'animal. Les mécanismes qui confèrent une résistance au pâturage, à travers des stratégies d'évitement et de tolérance sont discutés, de même que la difficulté d'identifier des échelles d'étude pertinentes pour chaque fonction de l'interface plante-animal. En effet, les mesures réalisées ou les événements ayant lieu à une échelle fine (< m²) ne sont pas directement extrapolables aux échelles plus larges. De plus, l'intégration des fonctions identifiées à une échelle fine peuvent conduire à des résultats contre-intuitifs à des échelles plus larges. Le rôle de la modélisation comme instrument d'exploration de l'hétérogénéité spatio-

* Correspondence and reprints

Tel.: (44) 012 24 31 86 11; fax: (44) 012 24 31 15 56; e-mail: c.marriott@mluri.sari.ac.uk

temporelle de l'interaction plante-animal est développé. De tels modèles autorisent l'exploration d'un grand nombre d'hypothèses, qui ne peuvent l'être en conditions expérimentales à cause de contraintes logistiques, temporelles ou financières, et fournissent un cadre de travail à l'intérieur duquel nous obtenons une meilleure compréhension du fonctionnement du système pâturé. En tant qu'outils de gestion, ou d'aide à la décision, les modèles ont une valeur dans leur capacité prédictive et dans la capacité de simuler des situations complexes dans des couverts pâturés. © Elsevier / Inra

compétition entre plantes / échelles spatiale et temporelle / hétérogénéité / interactions plante-animal / résistance au pâturage

1. INTRODUCTION

The structure of vegetation is the arrangement in three-dimensional space of plant components, individual plant parts or species at a fine scale, and species or plant communities at a larger scale (field scale). Under grazing, herbivores interact dynamically with the vegetation; the structure and quality of vegetation affect the diet of grazing herbivores [24] and, in turn, the components of grazing (defoliation, excretal return and treading) modify vegetation structure and species composition.

Plant populations in grazed mixed species communities are highly heterogeneous; individual plants differ in their size, age, growth rates and reproductive capacity [11]. There are patterns, in both vertical and horizontal dimensions, in the distribution of individual plants and the biomass and architecture of their shoot (and root) systems, and in herbivores' foraging behaviour and the distribution of grazing bites, which cover a range of scales from centimetres to several metres (*table 1*) [19, 62]. The processes involved in creating these patterns are intra- or inter-specific plant competition, seed dispersal

Table 1. The spatial dimensions of plant-herbivore interactions (adapted from Noy-Meir [47]) show that vertical structure (V) has a great impact on small scale (short term) processes and horizontal structure (H) is important at all scales.

Pattern	Dimension	Scale	Process
Distribution of individual plants	H	cm-m	Competition within/between species Seed dispersal and establishment
Canopy size and architecture	V, H	cm-m	Competition for light
Root system size and architecture	V, H	cm-m	Competition for water/nutrients (environmental heterogeneity)
Size and distribution of grazer bites	V, H	cm-m	Differential defoliation by strata/patches (intensity and probability)
Pattern of herbivore foraging	H	m-km	Differential defoliation by site (preference/ selection, animal memory, landscape features)
Grazing management system	H	0.1–10 km	Differential defoliation by paddock (stocking rate) Indirect effects of treading and excretion

and establishment, differential defoliation by site, patch or vertical strata, and excretal return. These processes, which occur at different spatial and temporal scales, all contribute to the heterogeneous nature of grazed ecosystems.

Measurements of sward state (e.g., herbage mass, root mass, sward height and canopy structure, botanical composition) give an instantaneous assessment of sward conditions at a given scale and at one point in time. Such measurements are repeated to provide information on sward changes over time in response to previous events or management, but generally they fail to consider the role of spatial patterns in vegetation. Recent advances in spatio-temporal models of community dynamics have shown that spatial patterns play a crucial role in determining persistence and coexistence of species [20]. Therefore pattern description is necessary for fully understanding plant-animal interactions. Many studies have described the functioning of different aspects of grazing systems at a small scale, and then developed dynamic hypotheses on the functioning of the whole system. The problem of scale-confusion arises, and the impossibility of developing a theory at a given scale and applying it to larger one simply by changing units.

The aims of this paper are to describe vegetation structure and the current understanding of its dynamics under grazing, and to show the potential benefits of modelling studies done at different spatial and temporal scales in such complex systems.

2. STRUCTURE OF GRAZED VEGETATION

2.1. Vertical structure

Canopy structure describes the distribution of above-ground parts of plants and their geometry (spatial and angular distribution); it has a major influence on patterns of light interception and photosynthesis. The

ability to capture light resources, by positioning leaves in the upper strata of the vegetation, where light quality is high, is regarded as one strategy by which plants can compete successfully with neighbours [11]. However, this increases their vulnerability to grazing. Many responses of vegetation to grazing can be explained by the vertical gradients of light intensity and defoliation within the canopy [47]. These gradients create a trade-off for plants between competitive success in capturing light and avoidance of defoliation risk. Tall, erect plants capture most light, but are more vulnerable to defoliation and lose more leaf tissue than prostrate plants. From a plant perspective, vertical structure in terms of a biomass gradient is most important, because the functional aspect is the position of photosynthetic organs. But from an animal perspective, offtake has a quantity and also a quality component, and gradients in terms of digestibility are also pertinent.

2.1.1. Biomass

Within a vegetative sward, leaves are mainly in the upper layers of the canopy and leaf sheaths and dead material are mainly in the lower layers. There is a general relationship for temperate pastures in which bulk density ($\text{g}\cdot\text{m}^{-3}$) decreases with increasing height above ground level and dead plant material and litter tend to be concentrated at the base of the sward [29]. However, time of year and management cause variations in this relationship. For example, in grass-clover pastures, the vertical distribution of clover varied with different timing of silage conservation cuts, time of year and the clover variety [3]. In reproductive swards, culms and pseudostems are in the upper layers and, in the case of lenient grazing, this residual structure could persist from one year to another, modifying the senescent tissue distribution in the sward.

2.1.2. Digestibility

Canopy structure is a major factor in the foraging strategy of grazing herbivores [45] and affects the amount of herbage eaten [59]. The arrangement of plant components within a sward canopy means that the digestibility of successive layers of herbage is likely to decline with increasing proximity to ground level, depending on previous management [30]. For example, in a continuously stocked sward with a high stocking rate there is likely to be a steady change in digestibility from the top to the bottom of the canopy, because senescent material accumulates below the height of defoliation. However under an extensive grazing regime, senescent or reproductive material can accumulate in the layers close to the canopy surface, and maximum digestibility will occur in the layers beneath the surface strata in which green leaf material is concentrated. Thus senescent material and reproductive structures not only limit photosynthesis by shading green tissues but also limit the defoliation of green leaves by acting as a barrier, and the quality of the diet of herbivores is diluted.

2.1.3. Architectural plasticity of plants

Many species can modify their canopy architecture in response to defoliation. A prostrate stature or decumbent canopy is more resistant to grazing because less biomass is accessible to herbivores, and a greater amount of photosynthetic and meristematic tissue remains for regrowth after grazing. Morphotypes adapted to grazing [49] are characterised by a large number of small tillers, with reduced leaf number and blade area. In newly sown pastures, morphological adaptations to grazing are rapid. Larger plants of ryegrass and white clover are found under rotational compared with continuous grazing [14]. When grazing pressure is increased, grass leaves are less erect [43] and clover plants are more fragmented [9].

2.1.4. Grazing resistance strategies

The trade-off between competitive success in capturing light and avoidance of grazing risk has led to the conceptual framework of grazing resistance [8], which describes the mechanisms enabling plants to survive and grow in grazed systems. It can be divided into avoidance and tolerance components. Grazing avoidance relies on morphological and biochemical mechanisms that reduce the probability and intensity of grazing. Grazing tolerance is based on morphological attributes and physiological processes which allow the plant to promote growth after defoliation. Since grazing-induced selection primarily affects architectural attributes of plants, avoidance rather than tolerance strategy may make the greatest contribution to grazing resistance in the short-term, but tolerance may be more important in the longer term. Indeed grasslands with a long history of grazing tend to be dominated by grazing tolerant species [44].

2.2. Horizontal structure

In the horizontal plane, the grazing system can be viewed at many levels of integration and complexity, all of which are relevant for studying its dynamics. Three key levels can be identified when considering plant-animal interactions: the patch level, the community level and the landscape level. Within a community the main components of spatial pattern are the total amount of each patch type, the mean size of patches, mean inter-patch distances, variance in patch sizes, variance in inter-patch distances and connectivity between patches (*figure 1*, [26]). Van der Maarel [64] associated vegetation dynamics with spatial scale and added a temporal scale: internal dynamics (plant fluctuations, gap dynamics) at the patch level, between patch dynamics (cyclical dynamics) at the community level and successional dynamics at the landscape or



Figure 1. A hypothetical vegetation mosaic of five species showing their different amounts and spatial arrangement, indicated by differential shading.

regional scales. The hierarchy of these spatio-temporal processes means that grazing systems can be remarkably stable at one spatio-temporal scale in spite of important fine-scale spatio-temporal changes [28, 62].

2.2.1. Spatial aggregation of species

The spatial pattern in species composition is affected by: 1) environmental heterogeneity; 2) the size, growth form and dispersal distance of plant species; and 3) herbivore foraging behaviour, which creates spatial heterogeneity in the actual grazing pressure experienced by plants. The horizontal distribution pattern of individual plants or population units of different species at a given scale can modify the rate and direction of vegetation change at larger scales [38, 47]. Since plants interact primarily with their immediate neighbours, theory suggests that aggregation of species in plant communities into patches of individual species should reduce interspecific relative to intraspecific competition. Different species will compete only along the patch margins, and this should increase the likelihood of coexistence. This is supported

by experimental observations, e.g., aggregating *Poa annua* into patches reduced its competitive effect on *Senecio vulgaris* [5, 6]. Marriott et al. [39] showed that clover stolon extension at the edges of different sizes of grass/clover patches was 31–99% greater than that inside patches, so both patch size and density of patches as well as patch number will determine the spatial structure of the sward over time. Because of the considerable degree of species dynamics at the scale of a few centimetres (i.e., intra-patch) [62] the spatial structure of grassland is entirely reshuffled over a period of several years [28] and patches of high clover and grass abundance persist for only 1–3 years [13]. Such patchiness is essential for field-scale stability of legume-based pastures [55, 56].

The distribution of plant species in mixtures can be fine-grained or coarse-grained. The spatial grain can affect how species are defoliated by large herbivores, and selective defoliation within a patch is possible only if the size of the patch is greater than the size of the animal bite. The extent to which herbivores can modify bite dimensions to accommodate different selection

opportunities is not fully understood [54]. Clark and Harris [16] showed that sheep could be more selective in ingesting clover from grass/clover swards with a patchy rather than intimately mixed distribution of clover. However, De Faccio Carvalho et al. [22] found no difference in the probability of defoliation of clover growing in strips or in well mixed swards, indicating that the horizontal distribution of clover did not affect its pattern of defoliation by sheep. This may be due to differences in methodology or treatment differences in clover content.

Variation in patch size distribution of the vegetation may have profound effects on the utilisation of the resource by grazers. The foraging behaviour of individuals or groups of animals can create spatial non-uniformity of defoliation within extensively managed grassland and allow the development of patches of species or groups of species which have different defoliation intensities and frequencies. For example, defoliation intensity of species with a similar frequency of presence in two vegetation

communities in mountain pastures differed between the plant communities and between grazing systems (cattle only or mixed cattle and horses; *figure 2*) [48]. The existence of patchiness means that individual plant responses to defoliation can only be scaled up to the landscape level if there is information on patch and community scale patterns.

2.2.2. Excreta patches

Excretal return seems to be implicated in the spatial variability of species in grassland through the dual mechanisms of differential growth (input of nutrients) and selective defoliation (avoidance of excretal patches) [25].

Urine deposition creates patches with higher levels of soil and plant N than surrounding areas [37], increased rates of nutrient cycling [23] and altered species composition [41]. There are effects on canopy structure; increased dry matter production in urine patches results from both increased

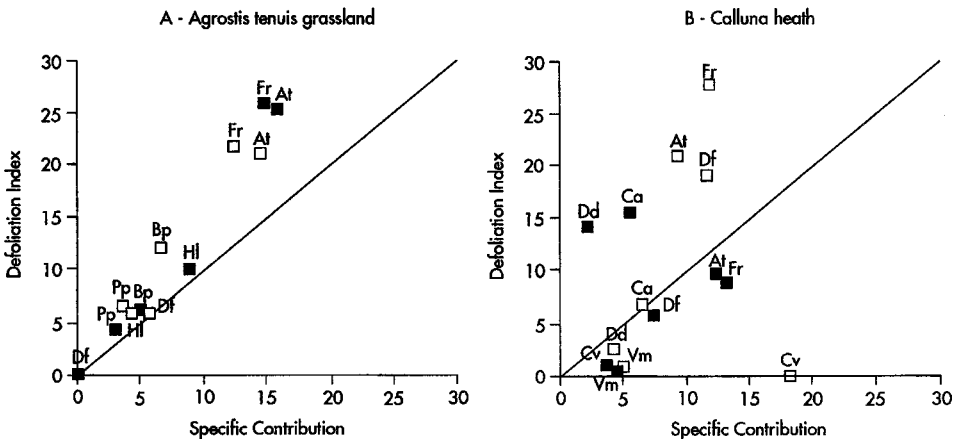


Figure 2. Relationship between defoliation index (defoliation of the species relative to the whole community) and specific contribution to the community in July 1996 for different species (At, *Agrostis tenuis*; Bp, *Brachypodium pinnatum*; Ca, *Carex* sp.; Cv, *Calluna vulgaris*; Dd, *Danthonia decumbens*; Df, *Deschampsia flexuosa*; Fr, *Festuca rubra*; Hl, *Holcus lanatus*; Pp, *Poa pratensis*; Vm, *Vaccinium myrtillus*) for *Agrostis tenuis* grassland (A) and *Calluna* heath (B), under cattle grazing (closed symbols) or mixed grazing by cattle and horses (open symbols). All species present in the communities are not shown. The line shows a 1/1 relationship.

size (weight and height) of individual grass tillers and N stimulation of tiller production [41]. Some aggregation in excretal distribution may occur; at a high sheep stocking density, the distribution of excreta followed a negative binomial distribution [46]. In models of grazed grass-legume systems, urine deposition prevented the establishment of species equilibrium within patches, but a spatially random distribution of urine stabilised field-scale oscillations of plant populations [55, 56]. This occurred because the N additions set the patches out of phase with the intrinsic grass-legume population cycle.

The increased quality and quantity of nutrients in herbage on urine patches means that these patches may be selectively grazed compared to unaffected areas [32]. In contrast, herbage around cattle dung patches tends to be avoided [27]. Thus, particularly at low grazing pressures, tall patches of low tiller density and poor nutritional quality develop and persist.

2.2.3. Gaps and gaps dynamics

Disturbances which create bare ground or gaps in the vegetation canopy provide opportunities for species composition or species arrangement to change [51], either through vegetative growth of species existing in the sward or seedling growth from the seed bank or outside the grazing system [64]. Gaps can be caused by many environmental factors but disturbances resulting from the activities of grazing animals are often the most important [51]. Defoliation, trampling, burrowing and excretal return can all cause plant damage or death and allow gaps to develop. The size range of gaps can vary from as little as 1–2 cm in diameter [57], through 10–20 cm in diameter, i.e., the scale of dung and urine patches [27], up to large disturbances of greater than 50 cm in diameter caused by burrowing [17]. Small patches have a higher edge to area ratio than bigger patches and plants on the edges can colonise these patches more

quickly by vegetative growth [2] whereas seedling colonisation and growth may be more successful in larger patches [21]. There may be significant positive relationships between the vegetation which has grown in gaps and that found in undisturbed areas [40], but in some cases stoloniferous and rhizomatous species can be more successful colonisers than tillering species [2, 50].

Any change in the numbers or species of grazing animals may alter the likelihood of gaps forming or change the spatial and temporal pattern, or the scale of pattern, and the longevity of gaps in the vegetation. For example, heavier grazing by sheep in summer increased the frequency of small gaps as well as the total area of gaps [58]. Gaps created in swards under a range of extensive management disappeared most rapidly in unfertilised, ungrazed swards and in grazed, fertilised swards, the most different treatments in terms of species composition and sward structure [40]. This was attributed to differences in canopy architecture as sward height increased in the ungrazed sward and to faster herbage growth rates in the fertilised sward.

Disturbance which creates open space in the vegetation canopy can affect both species richness and spatial heterogeneity of the community [18, 42], but changes in the vegetation can be short-lived [4]. Patch disturbances from pocket gopher activity in a short-grass prairie community created sites where there was relatively low competitive pressure and enabled less competitive dicotyledonous species to colonise [42]. In contrast, in a species-poor grassland, most rarer species of grass and dicotyledons were less frequent in the vegetation that colonised areas where vegetation had been removed (gaps) than in the undisturbed pasture; some of the common species increased in the gaps while others decreased [12]. Limited availability of seed as well as high competitive pressure from dominant grasses may explain the different response. The timing of gap creation on subsequent species composition

may be important because of seasonal differences in seedling germination and establishment [36], but this may be less relevant when colonisation relies mainly on vegetative growth.

3. SCALES AND PROCESSES OF THE PLANT-ANIMAL INTERFACE

Many recent grazing studies have adopted a reductionist approach to aid the development of thinking and methodology (e.g. [63]). Such studies satisfy their particular objectives, but they ignore scaling issues and measurements cannot be extrapolated to other scales by simply changing units. It is widely recognised that temporal and spatial heterogeneity is of importance at all scales from plant to plant interactions to landscape variation [1, 11, 31, 61].

Although herbivore foraging mechanisms are hierarchical [60], and integrated across spatial and temporal scales [34], our concepts of grazing do not always deal adequately with heterogeneity [15]. Often it is not clear whether a theory deals with averages across a heterogeneous sample or with a homogeneous sample at some smaller scale, and this creates confusion of scales [10, 15]. Meaningful measures of plant population responses to herbivores are different from measures of a single plant response [10]. In populations, it is appropriate to ask how herbivores affect the abundance, distribution and dominance of the consumed population, and how this influences plant reproductive output or fitness, whereas the severity and frequency of defoliation are important issues for the single plant. Likewise, relationships between jaw size, bite geometry and ingestive behaviour derived from short-term small-scale experiments [63], cannot predict how an animal utilises pasture of a defined average quality because in a single day an animal takes many bites from a wide variety of patch types. Equally, measurements taken at the field-scale, for

example the relationship between average sward height and average bite depth, cannot be 'scaled down' to tell us something about bite geometry. The interpretation of herbivore data is very strongly influenced by the way observations are made, and, because mechanisms and functional relationships are scale-dependent, it is useful to point out how the choice of unit and measurement affects the result [10].

There is widespread agreement that plant-animal interactions are multi-interactive phenomena, and it is difficult to separate causes from the effects. Our knowledge comes mainly from experiments which analyse the effect of one isolated factor (or pseudo-isolated factor), for example from experiments on artificial swards [35]. In the modelling process, such empirical data are used to generate functional relationships between the different factors of the system being modelled. This allows us to simulate (predict) the dynamics of the system relatively easily, when an empirical approach would require hundreds of experiments [7]. Comparison with empirical results allows a new research approach to identify the key factors in system functioning.

The need to explicitly take into account the spatial dimensions of grazing, and to consider grazing processes over scales of space and time has been emphasised by Laca and Demment [33]. At present, a major problem is that we do not know how phenomena at the 'bite scale' express themselves at the 'field-scale' or whether there is an interaction between phenomena at these different scales. Spatially explicit mechanistic models provide a way to understand these interactions and integrate across scales. The hypotheses of these models are generally established at the scale of the elementary cell of the model. Generally, they are well known, and validated under experimental conditions. The dynamics of mixed pasture can be understood on the basis of physiological and ecological concepts if there is integration across a range of scales: com-

petitive interactions occur at the patch-scale, dispersal at the between-patch scale and seasonal variations, such as winter mortality and fertiliser application in spring, at a field scale [56]. An important result is that unstable dynamics at the patch-scale can generate sustained and highly complex field scale dynamics [56] or can generate steady states for a given set of conditions [15]. This means that new properties emerge from the system, simply by taking into account the spatial dimension. In the case of the Schwinning and Parsons field-scale models [56] the stable pasture structure exhibited a pattern not previously shown by a purely physiological model [55].

Modelling also broadens perspectives. In very large-scale rangeland management, it is expensive and labour-intensive to record experimentally the distribution of animals over an area of many square kilometres and so few experimental observations are available [52]. Association between satellite imagery and model simulation allows the prediction of the impact of spatial distribution of cattle on vegetation dynamics, and could have output in management of rangeland systems [53]. The same goal exists in modelling vegetation dynamics under grazing, for predictive outputs which may be used in grassland management [7].

4. CONCLUSIONS

The role of vertical structure in competition mechanisms is relatively well known, from experimental studies and some models, but the role of horizontal structure is less well understood. However it is clear that taking account of the spatio-temporal dimension of sward dynamics opens up new perspectives about the functioning of systems. Firstly, measurements or events at a small scale cannot be directly extrapolated to a larger scale. Moreover, integration of small scale functions could result in counter intuitive results at the larger scale, e.g., plant

population dynamics under grazing may not be accurately represented by integration of physiological responses of individual plants to defoliation, because of selective defoliation. Experimentation to explore this topic is difficult and may not be the best approach. Models appear to be useful tools to explore complex spatio-temporal systems, increasing our knowledge of such systems, and generating new hypotheses. Models will also enable us to make predictions of system dynamics at different spatial and temporal scales, and so are useful in management and land use decision processes.

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