Analysis of the production stability of mixed grasslands I: A conceptual framework for the qualification of production stability in grassland ecosystems

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Abstract

The increased use of white clover in grasslands has led to new management challenges, as mixed pastures have been associated with unstable herbage production. The stability of mixed pastures depends on a complex of intrinsic ecosystem properties, on the variability of the environment, and on the spatial and temporal scale at which it is studied. In this paper, intrinsic ecosystem properties and processes are explored and illustrated using a simple dynamic simulation model of grass and clover interactions. Competition for light, the delayed availability of nitrogen fixed by white clover, grazing per se, preferential grazing for clover, and cutting were identified as destabilising processes. Instead, niche-differentiation, nitrogen dependence of grass and clover, and plant mechanisms to 'escape' from grazing, were identified as stabilising processes. The intrinsic stability of mixed swards depended on the balance of, and the interactions between these processes. Including the temperature as an environmental variable into the model, unstable ecosystems were stabilised by seasonal temperature fluctuations, and were either further destabilised, or stabilised by stochastic temperature fluctuations. Stable ecosystems were always destabilised by these stochastic fluctuations. It is explained how spatial heterogeneity can stabilise ecosystems, which oscillate at patch scale. Heterogeneity can be maximised by increasing the incidence of small-scale disturbances and by minimising large-scale disturbances. Finally, three concepts of stability are presented. The actual stability is defined as the stability of grasslands as measured in the field, i.e. subjected to both seasonal and stochastic environmental fluctuations. The extrinsic stability presumes the presence of seasonal, yet the absence of stochastic environmental fluctuations. The intrinsic stability represents the stability of yields in a hypothetical constant environment. It is explained how these concepts of stability can bridge the gap between experimental and theoretical studies. It is demonstrated that long-term experiments are required for the experimental analysis of grassland stability, and it is argued that the development of spatially and environmentally explicit simulation models is a prerequisite for the prototyping of management systems for mixed grasslands.

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1. Introduction

Recent years have shown a renewed interest in the use of legumes in pastures, in particular of white clover (Trifolium repens L.), as a more sustainable alternative to fertiliser nitrogen (Parsons et al., 1991a,b; Laws and Newton, 1992; Schwinning and Parsons, 1996a). Whereas the herbage production of grass monocultures under a fertiliser regime can be controlled to some extent by fertiliser inputs and grassland management strategies, the maintenance of stable and productive mixed swards has been a challenge to date. Fluctuating performances of mixed pastures have frequently been reported (Curll et al., 1985a,b; Evans et al., 1990; Orr et al., 1990; Laws and Newton, 1992; Schwinning and Parsons, 1996a,b; Fothergill et al., 2000). The reliability of herbage production is a prerequisite for the managerial decision making by individual farmers. Hence the production stability of mixed pastures over several years is as important to the livestock industry as is the level of production itself (Curll, 1982; Fothergill et al., 2000).

Grassland ecosystems can be studied either in agronomic experiments, or by using ecological models. To date most experimental agronomic studies have focussed mainly on the level of production. Unfortunately, the duration of these experiments is commonly limited to a maximum of 4 or 5 years, which is too short to allow an analysis of the stability of production (Mitchell and Csillag, 2001). One of the exceptions to this rule is the Park Grass Experiment (Collins, 1995), in which yields of a large number of experimental plots have been recorded for well over a century (e.g. Silvertown, 1980; Silvertown and Dodd, 1994; Dodd et al., 1995).

In these agronomic studies, grassland stability is frequently defined as the inverse of the variation of yields among years. However, this variation depends both on intrinsic ecosystem properties, and on the variability of the environment during the observation period. For example, a grassland system observed during a period of transient drought, heat, rain and frost, is bound to show a high variability of yields. Although the impacts of intrinsic properties and environment on yield can sometimes be separated (e.g. Barthram et al., 1992; Silvertown and Dodd, 1994), the discrimination of their respective impacts on the stability is highly complex. Due to the dependence of the observed stability level on environmental fluctuations, this level is restricted to a limited environment during a limited period, disabling a fair comparison of the stability of ecosystems, which are separated in either time or space.

Stability has received more attention in theoretical ecological studies, in which the behaviour of ecosystems is analysed using mechanistic models. In a now classical publication, Noy-Meir (1975) transformed the predator–prey model by Rosenzweig and MacArthur (1963) into an ecological model, applicable to agricultural grassland ecosystems. Recently, increasing computer power has enabled the development of increasingly complex dynamic simulation models, in which pasture processes are simulated over time (e.g. Grenfell, 1988; Thornley and Verberne, 1989; Parsons et al., 1991b, 1994; Schwinning and Parsons, 1996a,b; Thornley et al., 1995; Thornley, 1998; Brereton and McGilloway, 1999). These models can simulate numerous possible ecosystems in various hypothetical environments, thus allowing a mechanistic analysis of the processes regulating ecosystem stability. Nevertheless, this approach, too, has serious limitations.

Firstly, the predictions on stability largely depend on the structure of the model itself. For instance, Schwinning and Parsons (1996a) reported that the predictions on stability changed fundamentally when they simplified their grass–clover model from eight to four state variables. In their following paper (Schwinning and Parsons, 1996b) an even more drastic change was observed when spatial (lateral) interactions were included in the model. In an earlier model, Parsons et al. (1991b) simulated competition between grass and
clover under various defoliation regimes. This model did not include nitrogen fixation by clover, and therefore, its long-term predictions were mostly biased towards a high ryegrass content and clover extinction. In these cases the boundaries and the structures of the models had a definite impact on their predictions.

Secondly, simulation models commonly analyse the intrinsic ecosystem properties in isolation of the environment, presuming either constant (e.g. Noy-Meir, 1975; Grenfell, 1988; Parsons et al., 1991b) or sinusoidally fluctuating (e.g. Thornley, 1998) environmental variables. However, the impact of stochastic environmental events is decisive for both the level and the stability of production. Nonhebel (1994) studied the effect of using average weather data (ten-daily, monthly, or seasonally) instead of daily weather data in a wheat growth simulation model, and found that the use of the former led to yield overestimates of less than 15% in wet conditions, and to underestimates up to 50% in dry conditions. These differences arose from non-linear responses of the system to environmental variables such as temperature and precipitation. However, the growth period of wheat did not exceed 6 months in any case, which limited the accumulation of under and overestimations. Larger discrepancies caused by using average instead of daily weather data may be expected in grassland simulations, which may cover growth periods up to 10, 100, or even 1000 years (e.g. Thornley, 1998). More recently, Mitchell and Csillag (2001) reported on the importance of rainfall variability on the productivity and stability of northern mixed grass prairie. In this study, complex interactions were observed between temperature, the amount of rainfall and its variability.

Finally, ‘stable’ grassland systems are often associated with systems in equilibrium, i.e. systems in which all state variables remain constant (e.g. Noy-Meir, 1975), or return to their initial values each year, in case environmental seasonality is incorporated into the model (e.g. Thornley, 1998). System stability is then implicitly defined as the capacity to remain in equilibrium in the face of environmental perturbations (e.g. Matsinos and Troumbis, 2002). In fact, stability is here confused with the combined resistance (reluctance to change) and resilience (recovery capacity) of the system (see also Sun and Yang, 1999). In contrast, real ecosystems are continuously exposed to stochastic environmental events, and are therefore, constantly ‘pushed out of’ their equilibria. Moreover, the positions of the equilibria are largely defined by environmental variables, which may change too rapidly for the ecosystem to respond and to return to its equilibrium. A rather spectacular example of the latter phenomenon is given by Thornley (1998), who examined a modelled grazing system of Noy-Meir (1975). Noy-Meir’s original system was discontinuously stable, showing two equilibria, one at a low and one at a high Leaf Area Index. When this system was reproduced at a higher temperature (20 instead of 10 °C), this bifurcation disappeared, resulting in an ecosystem with only one equilibrium. Such a change of temperature can readily be achieved within 1 day in temperate climates, and therefore, the existence of either of the equilibria is only of academic significance.

Summarising, there are two schools of thought in the study of grassland ecosystem stability. The first one is based on experimental research, where the stability of the total yield between years is the primary focus. Unfortunately, the experimental data are limited and dependent on both internal system properties and environmental factors. Their influences are hard to separate, and contain a large amount of ‘noise’. The second school of thought is based on theoretical ecological studies. These can analyse the underlying processes of the stability or instability of grassland ecosystems in isolation of the environment. Nevertheless, the direct applicability of their results into farm practice is questionable, considering the large impact of stochastic environmental fluctuations on the stability of real ecosystems (Mitchell and Csillag, 2001; companion paper, Schulte, 2002). Both approaches complement rather than exclude each other.

In this paper a conceptual framework for the analysis of grassland stability is presented, which incorporates both the intrinsic properties of grassland ecosystems in isolation, and their responses to the variable environment. This framework is based on a review of the experimental and modelling
studies available in the literature. The objective of this study is to derive a universally applicable definition and quantification of grassland stability. The emphasis in this paper will be on the interaction between white clover (T. repens L.) and perennial ryegrass (Lolium perenne L.), which will generally be referred to as ‘clover’ and ‘grass’. However, extrapolation of the main interactions to other legume and grass species with similar properties is easily envisaged.

First the intrinsic properties and interactions of a grass–clover sward will be summarised. Secondly, the impact of the environment will be taken into account, and finally, the effect of the spatial scale studied on the system stability will be conceptually explored, leading to a qualification of grassland stability. The resulting concept of stability will be quantified and tested against long-term experimental data in the following paper (companion paper, Schulte, 2002).

2. Intrinsic ecosystem properties and processes regulating stability

2.1. Materials and methods

First a concept is presented of the impact of the intrinsic properties and processes of the ecosystem which regulate stability. This concept is based on the insight into the behaviour of mixed pastures, produced by ecological models. Wherever these findings have been confirmed by empirical data, these will be referenced. To clarify the various stabilising and destabilising processes, these will be exemplified by the step-by-step construction of a simple simulation model, from a monoculture of perennial ryegrass growing under a cutting regime and under constant environmental conditions, to a grazed mixture of grass and clover in a variable environment. Pro temp. the herbage mass is assumed to be distributed homogeneously across the field, both vertically and laterally. This model is in fact an alteration and simplification of the model presented by Schwinning and Parsons (1996a). Its mere purpose is to graphically illustrate the stabilising and destabilising ecosystem processes that will be dealt with. To avoid the illusion that it would have any quantitative accuracy, its output is, sensu Noy-Meir (1975), only presented relatively, i.e. on a scale from 0 to 1, to the maximum instantaneous herbage mass of a perennial ryegrass monoculture under optimal conditions (for reference purposes only, 1 unit corresponds to ca. 7000–10 000 kg DM ha$^{-1}$). Nevertheless, the model has been constructed in such a way that its predictions agree qualitatively with the results of the far more sophisticated and preferable simulation models which have been produced to date.

2.2. Growth and senescence

The starting point is formed by an ecosystem consisting of a grass monoculture only, under an unlimited nutrient supply. This system is here defined by just one state variable, i.e. the total mass of live herbage per unit area. Riedo et al. (1998), Thornley (1998) needed 41 and 44 state-variables, respectively, to describe this grass monoculture with reasonable accuracy, which underlines the simplicity of the model presented here. The two processes regulating the productivity and stability of this monoculture, which are highlighted here are growth and senescence. Growth is modelled with a well-known saturation function, sensu Thornley et al. (1995), and based on empirical evidence by Bircham and Hodgson (1983):

$$p_i = \frac{p_{\text{max}, i}}{H_i + k_{p_i}} \text{ (1)}$$

in which $p_i$ is the growth rate; $p_{\text{max}, i}$, the maximum growth rate; $H_i$, the total amount of herbage; and $k_{p_i}$ is a parameter indicating the amount of herbage at which the growth rate is half of its maximum rate. The suffix $i$ takes the value of 1 to indicate grass, and will take the value 2 to indicate clover. In this function the relative growth rate ($p_{\text{max}}/H_i$) is maximal at low herbage, and progressively reduced by intra-specific competition, as the herbage accumulates. Simplifying Schwinning and Parsons’ (1996a) model, senescence is assumed to be linearly related to the total amount of herbage as:
\[ s_i = d_i H_i \] (2)

in which \( s_i \) is the senescence rate, and \( d_i \) is the relative senescence rate.

The effects of growth and senescence were dynamically simulated over time by numerical integration (Euler’s method) of Eqs. (1) and (2), with an integration step of 0.02 years. The initial herbage mass of grass was set at 0.1 units, and each year the herbage mass was reduced by a fraction \( c_i = 0.9 \) to simulate the cutting of the sward. Fig. 1 illustrates the pattern of the herbage mass over 20 years. This figure shows the progressive annual mean herbage mass, as the yearly cutting of the sward led to a high variability within years of the latter. The irregularity during the first year reflects the first cutting event. Note that (virtual) parameter values have been chosen, which in absence of cutting lead to a maximum amount of herbage of 1 unit in more or less half a year (see Appendix A).

The growth function is a positive feedback function, as the growth is accelerated as the amount of herbage increases. In contrast, senescence is a negative feedback process, decreasing the amount of herbage and thereby reducing its own rate. Predictably, growth in absence of senescence would lead to forever growing, and therefore, unstable systems. The result of growth and senescence stabilises the grass system into an equilibrium, at which growth equals senescence.

2.3. Competition for light

If clover is introduced into this grass monoculture, and if all soil factors (nutrient and water status) are assumed to remain unlimited during growth, then these two grassland species will primarily compete for light. Simplifying Schwinning and Parsons’ (1996a) approach, the growth of either species can be described by:

\[ p_i = p_{\text{maxi}} \frac{H_i}{H_1 + H_2 + k_i} \] (3)

where the suffix \( i \) takes the value of either 1 (grass) or 2 (clover). Adding \( H_1 \) and \( H_2 \) proportionally in the denominator, in fact implies that the intra-specific and the inter-specific competition have identical effects on the growth of either species. This unlikely situation can only arise when both species use an identical set of resources, i.e. show no niche-differentiation. Fig. 2, produced by numerical integration of Eqs. (2) and (3), shows that under an unlimited supply of other plant resources, the competition for light per se (i.e. in absence of other processes) leads to a rapid extinction of the least competitive species, i.e. clover. The initial values of both \( H_1 \) and \( H_2 \) were set at 0.1 units, and each year the herbage mass of both species was reduced by fractions \( c_1 = c_2 = 0.9 \).

Wolledge and Dennis (1982) found identical instantaneous CO2 assimilation rates for grass and clover leaves. However, Schwinning and Parsons (1996a) suggested that even when mineral

Fig. 1. Progressive annual mean herbage mass of grass during 20 years, as a result of growth and senescence only.

Fig. 2. The effects of competition for light on the progressive annual mean herbage masses of grass and clover during 20 years. Thin line, clover; single line, grass; bold line, total herbage mass.
nitrogen is not limiting growth, clover will continue to invest metabolic energy into the nitrogen fixing bacteria, thereby compromising its energy investment in growth. Curll (1982) stated that under lenient grazing clover is unable to raise its leaf canopy to the same height as the grass canopy, resulting in a lower light incidence for clover. Therefore, the current model follows the approach by Schwinning and Parsons (1996a), who attributed grass with a competitive advantage for light.

The destabilising effect of light competition is confirmed by experimental data from the Park Grass Experiment (Silvertown and Dodd, 1994). These show that at plots receiving nitrogen, grasses competed successfully with legumes for light. The same observation was made by Nassiri (1998), who studied the regrowth of grass and clover under yearly nitrogen applications of 150 kg N ha⁻¹. He showed that asymmetric competition for light between perennial ryegrass and clover was small at the early regrowth stages after a cutting event, when individual leaves of both species may be assumed to be light saturated. However, under a nitrogen regime, clover performance was progressively compromised during the regrowth period. The destabilising effect was also observed by Parsons et al. (1991b), who modelled grass–clover competition for light under continuous grazing, but in the absence of the biological nitrogen fixation by clover, and in absence of competition for nutrients. They consequently stated that mixtures (under these conditions) are intrinsically unstable and tend to lead to stable monocultures.

2.4. Niche-differentiation

Niche-differentiation compromises the use of (partially) different resources by individual grassland species. The resource usages of two species can be separated either in time, e.g. mixtures of early and late species or varieties (e.g. Culleton et al., 1986) or in space, e.g. mixtures of species with different rooting patterns (R.P. Collins, pers. comm.). But the most important niche-differentiation in grass–clover swards is beyond doubt the separated nitrogen sources of both species, resulting from the fixation of atmospheric nitrogen by clover. However, if clover is supplied with mineral soil nitrogen, e.g. after a fertiliser application, its soil nitrogen uptake will reduce the nitrogen fixation, and eventually exceed it (Schwinning and Parsons, 1996a). Hence the extent of the niche-differentiation is variable, and depends on the management regime.

Niche-differentiation for nitrogen was modelled mechanistically by Schwinning and Parsons (1996a), who to this purpose included an organic soil nitrogen and a mineralised soil nitrogen pool into their model. Nitrogen uptake by both species, and nitrogen fixation by clover depended dynamically on the size of these pools. However, the dependence of grass on clover for its nitrogen supply, and the soil processes involved in the nitrogen mineralisation also depended on the dynamics of these nitrogen pools. Therefore, their approach does not allow a formal discrimination of the effects of niche-differentiation, dependence, and delayed dependence, which are dealt with below.

In fact niche-differentiation implies that the mutual interference between individuals of one species exceeds the interference between individuals of different species, i.e. the intra-specific competition exceeds the inter-specific competition. Therefore, sensu Spitters (1983), a parameter for niche-overlap is included in the model here, \( n_i \), ranging between 0 and 1, which scales the inter-specific competition relative to the intra-specific competition:

\[ p_1 = p_{\text{max}1} \frac{H_1}{H_1 + n_1 H_2 + k_{p_1}} \]  
\[ p_2 = p_{\text{max}2} \frac{H_2}{n_2 H_2 + H_2 + k_{p_2}} \]

![Fig. 3. The effects of niche-overlap on the progressive annual mean herbage masses of grass and clover. (a) \( n_2 = 0.9 \) (default value); (b) \( n_2 = 0.5 \). In both graphs, \( n_1 = 1 \). Legend as in Fig. 2.](image)
For grass–clover it is assumed that \( n_1 = 1 \), which means that all resources of grass (e.g. mineral N) are also used by clover. However, \( n_2 < 1 \), as only part of the resources used by clover is also used by grass.

Fig. 3 shows that niche-differentiation can lead to stable mixtures, in case its stabilising effect compensates for the destabilising effect caused by competition for light, i.e. when the niche-overlap \( n_2 \) is below a critical value. Note that niche-differentiation may only lead to an increase of the total yield when certain criteria are met, such as a similar production level of both species in monoculture (see Van den Bergh, 1968).

Empirical evidence for the stabilising effects of niche-differentiation was again found in the Park Grass Experiment (Silvertown, 1980). In spite of the fluctuating performances of individual leguminous species, the total fraction of the herbage consisting of legumes remained remarkably stable through time in each plot, indicating a niche for the nitrogen fixating legumes. The size of this niche depended on the fertiliser regime. However, it should be kept in mind that this stability of the botanical composition is not necessarily an indicator of production stability.

2.5. Dependence

In absence of fertiliser nitrogen or other external nitrogen inputs, the grass in grass–clover mixtures will largely depend on the fixation by clover for its nitrogen supply. This is referred to as the dependence of grass on clover. It is assumed that the amount of nitrogen fixed by clover is linearly related to its total herbage yield. In fact the relation between clover growth, defoliation, and nitrogen fixation is complex, and extensively explored by Ryle et al. (1989). They concluded, however, that the rate of nitrogen fixation is regulated to meet the plant’s requirement for nitrogen; hence the simplified assumption here, of a linear relationship between the nitrogen fixation rate and the clover herbage mass. The growth response of ryegrass to available nitrogen is still the subject of debate (Thornley, 1998). Thornley and Verberne (1989) assume a linear response of the maximum photosynthetic rate to the tissue nitrogen content. In a later publication, Thornley (1998) adds a ceiling level to this function. Lantinga et al. (1996) (their Figure 3) showed that this response depends additionally on the nitrogen application rates. Sheldrick et al. (1990) present a complex function with a single maximum, relating total ryegrass yield to the fertiliser nitrogen rate. Here the approach of Schwinning and Parsons (1996a) is modified. They related grass growth to the mineral nitrogen level using a simple saturation function. Considering the assumed linear relationship between clover production and nitrogen fixation, here the mineral nitrogen level is replaced by the total amount of clover herbage. Pro temp. this simplification purposely ignores all soil processes involved in the decomposition of nitrogen in senescent tissue into available soil nitrogen, which will be dealt with below. The grass growth rate is now modified to:

\[
p_i = p_{\text{max}} \frac{H_1}{H_1 + n_2 H_2 + k_{\text{dep}}} \frac{H_2}{H_2 + k_{\text{dep}}} \tag{5}
\]

in which \( k_{\text{dep}} \) is a parameter indicating the amount of clover (and therefore, N\(_2\)-fixation) needed by grass to achieve its half-maximal growth rate. The default value of \( k_{\text{dep}} \) is set at 0.02, which corresponds with field data from Wind et al. (1993). They monitored yields and the botanical composition of grazed plots where nitrogen applications had ceased, but P and K applications continued. Annual dry matter production dropped from around 9 tonnes ha\(^{-1}\) per year under nitrogen

![Fig. 4](https://example.com/fig4.png)

Fig. 4. The effects of the dependence of grass on clover for its nitrogen supply on the progressive annual mean herbage masses of grass and clover. (a) \( k_{\text{dep}} = 0.02 \) (default value); (b) \( k_{\text{dep}} = 0.1 \) (strong dependence, a clover monoculture remains). Legend as in Fig. 2.
applications to around 4.5 tonnes ha\(^{-1}\) per year within 3 years, while the annual white clover production stabilised at around 0.225 tonnes ha\(^{-1}\) per year. Therefore, the ratio between the white clover yield leading to half maximum herbage yield (as opposed to half maximum growth), and the maximum herbage yield equalled 0.025.

Fig. 4a illustrates the stabilising effect of this dependence per se (ignoring the time delay between nitrogen fixation and nitrogen availability) on the stability of the mixture. As the growth rate of grass is progressively inhibited by lack of nitrogen, when the clover content decreases, this dependence now supplies clover a permanent place in the pasture. Note that this dependence and the resulting stability presume the absence of fertiliser nitrogen. This was confirmed by Schwinning and Parsons (1996a), whose model showed that at high fertiliser applications combined with low nitrogen losses, the stabilising effect of dependence is not strong enough to counteract the destabilising effect of competition for light, eventually leading to a grass monoculture. In cases where the dependence of ryegrass on clover is unusually high \((k_{dep} = 0.1; \text{ Fig. 4b})\), the system may be destabilised into a clover monoculture. This was also predicted by Schwinning and Parsons’ (1996a) model in absence of fertiliser inputs combined with a high relative leaching rate of mineral nitrogen.

The stabilising effect of dependence is indirectly confirmed by the data from the Park Grass Experiment; Silvertown and Dodd (1994) reported that the variability of yields, caused by the competition for light, was more pronounced on plots receiving fertiliser N. More conclusive evidence was given by Curl et al. (1985a). They found that in swards continuously grazed with sheep, the clover content declined to under 10\% within 1 year after reseeding, when nitrogen fertiliser was applied at a rate of 200 kg ha\(^{-1}\) per year, whereas clover was maintained at higher levels between 15 and 50\% on unfertilised plots. Barthram et al. (1992) found that nitrogen applications reduced branching of clover, leading to lower densities of growing points in mixed swards grazed by sheep. Similar conclusions were drawn by Nassiri (1998), who studied grass–clover competition under a cutting regime, on both fertilised (150 kg N ha\(^{-1}\) per year) and unfertilised plots. Both in spring and summer, the clover, which did not receive nitrogen outperformed the clover on the fertilised plots.

2.6. Delayed responses

Delayed responses are an important feature in a wide range of ecosystems. They are well documented and most pronounced in systems where animal species with discrete, non-overlapping generations, e.g. many insect species, play a major role (May, 1976). However, delayed responses have also been reported in grassland studies. Schwinning and Parsons (1996a) mention seed dormancy and maturity effects as possible causes of delayed responses, but emphasise the role of nutrient pools with a slow turnover-rate. In the absence of grazing, nitrogen fixed by clover will only become available when the clover material ages and decomposes. In addition, in their model the slow mineralisation rate of the organic nitrogen pool in the soil profoundly delayed the response of ryegrass to the nitrogen fixation by clover. Delayed responses are destabilising and in most cases lead to damped or sustained oscillatory system behaviour. Schwinning and Parsons (1996a) found sustained fluctuations of grass and clover yields with a periodicity of 4–7 years, this periodicity increasing with slower mineralisation rates. Even in absence of legumes, Thornley’s model of a grass monoculture produced biennial oscillations which were related to the interaction between plant and soil water status (Thornley, 1998). In ‘real’ ecosystems (as opposed to ‘model’ systems) most of these fluctuations will be either ‘hidden’ behind the noise of environmental variability (see Section 3 of this paper), or compensated by neighbouring patches fluctuating ‘out of phase’ (see Section 4 of this paper). However, some evidence of a delayed response is again available from the Park Grass Experiment. Silvertown (1980) detected no regular or irregular cycles in the composition of botanical components. Nevertheless, in a more recent publication (Silvertown and Dodd, 1994) a significant and positive correlation was found between the total herbage mass on the one hand,
and the fraction of the herbage mass made up by grass species in the following year, on the other. Dodd et al. (1995) reported on the occurrence of individual increases and declines of grassland species, as well as periodic oscillations of the presence of species in the same experiment. They related these, however, to the reproductive strategies of the species involved, rather than to the existence of nutrient pools with a slow turn-over rate. Fothergill et al. (2000) reported on 3–4 year cycles of clover content under continuous grazing. Finally, in a grazing experiment by Curll et al. (1985b), stocking rates and nitrogen application had significant effects on the production levels and botanical composition the following year, when all plots were treated identically, indicating delayed responses, or a ‘system memory’.

The current illustrative model focuses merely on the delayed response of ryegrass to the nitrogen fixation by clover. To enable exploration of the effects of delay per se, this is implemented crudely, sensu Thornley et al. (1995), the production of ryegrass is now directly related to the amount of clover \( t_{delay} \) years earlier (compare Eqs. (5) and (6)):

\[
p_1 = \frac{p_{max}}{H_1} \times \frac{H_2(t - t_{delay})}{H_2(t - t_{delay}) + k_{dep}} \tag{6}
\]

in which \( t \) represents the time in years, and \( t_{delay} \) the formally imposed delay period. Fig. 5 illustrates that this delayed dependence causes the simulated system to oscillate, with oscillations being damped when the delay is relatively short, i.e. 1 year (Fig. 5a). However, if the delay is doubled to its default value of 2 years, this results in sustained oscillations of both the yield and the botanical composition of the system (Fig. 5b). Note that the 7.5-year periodicity of the fluctuations in Fig. 5b exceeds the imposed delay of 2 years, as this periodicity is dependent on both the delay and the actual growth and senescence rates.

### 2.7. Grazing

Grazing is arguably the most complex factor in the maintenance of grassland stability, as it involves selective removal of plant tissue, accelerated recycling of nutrients, and dynamic interactions between plants and animals. The effect of grazing per se, i.e. the unselective removal of leaf material, has mostly been studied by the use of simulation models. In ‘real’ pastures, grassland plant species may almost by definition have ‘escape mechanisms’ (see below), while grazing animals are bound to show preference for particular species. Therefore no empirical data were found on the effects of grazing per se.

The herbage intake rate is a function of sward properties such as the vertical and horizontal dispersion of plant material, as well as of animal properties such as bite area, bite depth, handling time, maximum grazing time and grazing strategy (e.g. Parsons et al., 1994; Brereton and McGilloway, 1999; Hutchings and Gordon, 2001). In general, the animal intake rate increases with larger amounts of available herbage, to a maximum intake level, which is limited by animal numbers, handling time, maximum grazing time (Parsons et al., 1994), or constraints on the digestive capacity (Hutchings and Gordon, 2001; Owen-Smith, 2002). Here the grazing function of Schwining and Parsons (1996a) is modified into equations which give the intake rates of grass \( g_1 \) and of clover \( g_2 \), in the absence of escape mechanisms and preference, and which replace the annual cutting of the sward:

\[
g_1 = g_{max} \frac{H_1}{H_1 + k_g} \left( 1 - 0.5 \frac{H_2}{H_2 + k_g} \right) \tag{7a}
\]
in which \( g_{\text{max}} \) is the maximum intake rate of all animals, which is dependent on both the physically maximum intake rate per animal and the stocking rate (i.e. number of animals per ha). \( k_g \) is the total herbage mass at which the total intake rate is half maximal. The fraction 0.5 in both equations indicates the absence of animal preference for either species.

Fig. 6 shows the destabilising effect of grazing in the absence of preference and escape mechanisms on the herbage masses of grass and clover. In this case, even at a maximum intake rate \( (g_{\text{max}}) \) as low as 1 (default), corresponding to the maximum intake rate of approximately 1.4 livestock units per ha, grazing per se leads to the extinction of the dependent species, i.e. the ryegrass (Fig. 6a, in which clover recovers after ryegrass collapses). Only at extremely low stocking rates \( (g_{\text{max}} < 0.3) \) can the growth of ryegrass compensate for the tissue removal (Fig. 6b).

Using a much more sophisticated model, which did not include niche-differentiation or dependence, though, Parsons et al. (1991b) came to similar conclusions. In their model grazing per se led to monocultures of clover at all stocking rates. However, in their case this was the result of the higher specific leaf area which had been applied to clover, rather than by the dependence of grass on clover, as is the case in the current model. Noy-Meir (1975) studied the effect of grazing intensity on monocultures, and although his model did not include a temporal dimension, he found that in the absence of escape mechanisms (see below), higher stocking rates increased the probability of a 'system collapse' as a result from overgrazing.

In 'real' pastures grazing per se will usually be accompanied by plant escape mechanisms and animal preference. Therefore, no experimental data were found in the available literature to confirm its destabilising effect as predicted by the model.

2.8. Escape mechanisms from grazing

As explained above, the effects of grazing per se are only of academic interest, as most grassland plants show mechanisms to escape from being grazed to extinction. These mechanisms involve substrate reserves in roots, stolons, or bulbs, a prostrate morphology (Noy-Meir, 1975), or unpalatable plant components (Hutchings and Gordon, 2001). These keep at least part of the tissue or substrate material out of reach from the grazing animal. At very low herbage amounts, the grazing intensity is then reduced asymmetrically to the amount of herbage. Fig. 7 (after Noy-Meir, 1975) shows that stronger escape mechanisms lead to increasingly sigmoid grazing functions, with virtually no grazing at very low herbage densities. These sigmoid functions can be produced by adding an escape parameter \( q_{\text{esc}} \) to Eqs. (7a) and (7b), resulting in (modifying Schwinning and Parsons, 1996a; but see also Parsons et al., 1991b):

Fig. 6. The effects of grazing per se on the herbage masses of grass and clover. (a) \( g_{\text{max}} = 1 \) (default); a clover monoculture remains after grass collapses. (b) \( g_{\text{max}} = 0.25 \). Legend as in Fig. 2.

Fig. 7. The response of the intake rate to the total herbage mass under three levels of escape: thin line, \( q_{\text{esc}} = 1 \) (no escape); single line, \( q_{\text{esc}} = 2 \) (default); bold line, \( q_{\text{esc}} = 3 \).
Fig. 8. The effects of escape mechanisms and maximum intake on the stability of the system. (a) $g_{\text{max}} = 1$ (default); (b) $g_{\text{max}} = 2$; (c) $g_{\text{max}} = 0.25$. $q_{\text{esc}} = 2$ for all cases. Legend as in Fig. 2.

$$g_1 = g_{\text{max}} \frac{H_{1}^{\text{esc1}}}{H_{1}^{\text{esc1}} + k_{g}^{\text{esc1}}} \left( 1 - 0.5 \frac{H_{2}^{\text{esc2}}}{H_{2}^{\text{esc2}} + k_{g}^{\text{esc2}}} \right)$$

$$g_2 = g_{\text{max}} \frac{H_{2}^{\text{esc2}}}{H_{2}^{\text{esc2}} + k_{g}^{\text{esc2}}} \left( 1 - 0.5 \frac{H_{1}^{\text{esc1}}}{H_{1}^{\text{esc1}} + k_{g}^{\text{esc1}}} \right)$$

Fig. 8 shows the stabilising effect of the plant escape mechanism on the grassland system when for both species $q_{\text{esc}}$ is set at its default value of 2 (Schwinning and Parsons, 1996a, but see also Parsons et al., 1991b). It also shows an important interaction between the escape mechanism and the grazing intensity, as expressed in $g_{\text{max}}$: an increase in grazing intensity does not simply decrease system stability anymore. Instead, both an increase (Fig. 8b) and a decrease (Fig. 8c) of the maximum intake tend to stabilise the system. This is further illustrated by Fig. 9, where the average variability of the system as well as the average actual intake rate, are shown for a range of maximum grazing intensities. Ecosystem variability was quantified as the coefficient of variation of the average yearly herbage mass over a 10-year period (companion paper, Schulte, 2002). Both the variability and the animal intake show a function with a single maximum. This agrees qualitatively with results by Noy-Meir (1975) (his Figure 10), who found low total animal intake rates at both low and high stocking densities, when escape mechanisms were included. At intermediate stocking levels, his model produced a discontinuously stable system which is in equilibrium at either a high or a low herbage mass (see also Thornley, 1998). Using Eqs. (8a) and (8b), the current model does not show any discontinuities, yet shows the same phenomena, i.e. a high total animal intake and low stability at intermediate levels of the maximum intake rate.

Empirical responses of total intake to maximum grazing rate are well documented (e.g. Curll et al., 1985a), and generally show an optimum stocking level at which total animal intake (or growth) is maximal. However, no long-term data were available on the response of the system stability to stocking density, as the duration of stocking rate experiments rarely exceeds 3 successive years. Some evidence for the effectiveness of escape mechanisms is given by Evans et al. (1992), who studied clover varieties differing in leaf size under various management regimes. Under continuous sheep grazing, and low herbage masses, small leaved clover varieties were far more persistent than the large leaved varieties.

2.9. Selective grazing

Selective grazing of animals entails the discrepancy between the botanical composition of the sward and that of the diet ingested. This is a complex area, as it involves both within-species selectivity for lamina tissue over sheath and stem tissue (Brereton and McGilloway, 1999), and between-species selectivity for a particular species (e.g. Milne et al., 1982; Grant et al., 1985; Binnie
and Chestnutt, 1994). It is important to discriminate ‘apparent’ selectivity from ‘real’ selectivity, apparent selectivity may simply arise when the botanical composition of the grazed sward stratum differs from the composition of the entire sward (Milne et al., 1982). Real selectivity involves the intrinsic preference hierarchy of animals for particular plant species. However, this preference may be limited by the total herbage mass, the horizontal and vertical species distribution, as well as by animal factors such as handling time and searching time. Assuming that animals attempt to optimise their daily energy and nutrient balances, their intrinsic preferences may be compromised by the need to maximise their daily intake (Parsons et al., 1994).

Although spatially explicit models, such as presented by Parsons et al. (1994), are required to simulate the extent and effects of selectivity satisfactorily, here Schwinning and Parsons (1996a) is followed and expanded. They attributed fixed fractional preferences of 0.3 and 0.7 to grass and clover, respectively. Here, the fractional preferences of 0.5 for both species, used in Eqs. (7a), (7b), (8a) and (8b), are replaced by the parameters $f_1$ and $f_2$ for grass and clover, respectively. The intake of either species is then given by:

$$g_1 = g_{\text{max}} \frac{H_{\text{max}}}{H_1 \text{max} + k_g H_{\text{max}}} \left(1 - f_2 \frac{H_2 \text{max} + k_g H_{\text{max}}}{H_2 \text{max} + k_g H_{\text{max}}}ight)$$

$$g_2 = g_{\text{max}} \frac{H_{\text{max}}}{H_2 \text{max} + k_g H_{\text{max}}} \left(1 - f_1 \frac{H_1 \text{max} + k_g H_{\text{max}}}{H_1 \text{max} + k_g H_{\text{max}}}ight)$$

Fig. 10 shows that a fractional preference for clover of 0.7 (default value) has a destabilising effect on the grassland system (compare Fig. 10a with Fig. 8a). Conversely, if the preference would have been reversed in favour of perennial ryegrass, this would stabilise the system into a stable, non-oscillating mixture (compare Fig. 10b with Fig. 8a).

Field observations show a larger extent of selective grazing by sheep than by cattle, both in grass–clover mixtures (e.g. Evans et al., 1992) and in multi-species mixtures, in which sheep showed a stronger between-species preference for forbs and a stronger within-species preference for life tissue, which is possibly related to the smaller mouth areas of sheep (Grant et al., 1985). Evans et al. (1992) tested the performance of five clover varieties with different leaf sizes under continuous grazing by sheep, under rotational grazing by sheep and by cattle, and under a cutting regime. He found that none but the small-leaved varieties were persistent under continuous grazing by sheep during a 3-year period. The persistence of all varieties was found to increase progressively when they were instead managed under regimes of rotational sheep grazing, rotational cattle grazing, and cutting.

Finally, the interaction between grazing pressure, escape mechanisms, selective grazing, and time is highly complex. Where diet composition is initially the result of spatial availability, total herbage mass, and animal preference, over time it is progressively more dependent on the turnover rates of the grassland species. Eventually a clover-rich diet may only be sustained if clover has a higher growth rate under the present sward conditions (Parsons et al., 1991b; Schwinning and Parsons, 1996a). This may lead to paradoxes, where an increased preference for clover may eventually lead to a smaller herbage and clover intake (paradox of imprudence), as shown by the data of Evans et al. (1992), mentioned above.

The complexity of the interactions between grazing pressure, escape, and selectivity are exemplified in Fig. 11, where the average clover content of the sward, the average total intake, and the average system variability (quantified in the companion paper, Schulte, 2002) over a 50-year time period are presented for a wide range of maximum intake rates (stocking rates), animal preference.
preferences for clover, and escape mechanisms for clover.

In spite of the simplicity of the current model, Fig. 11 shows at least qualitatively how selective grazing, and its interaction with the maximum intake rate and escape mechanisms, has a decisive impact on the average clover content of the sward. At the default settings of the grazing parameters ($g_{\text{max}} = 1$, $q_{\text{esc1}} = q_{\text{esc2}} = 2$, $f_2 = 0.7$; left front corner of Fig. 11d), the average clover content of the sward is close to its minimum, whereas it accumulates with an increasing maximum intake rate. The latter is caused by the progressively reduced herbage mass at higher stocking rates, reducing both clover and grass growth. However, as this also reduces nitrogen fixation (Ryle et al., 1989) and availability, grass growth is not only compromised by grazing, but also by a limited nitrogen supply. Moreover, Schwinning and Parsons (1996a) found that higher stocking rates lead to an accelerated concentration of nitrogen in urine and manure patches, and therefore, to a nitrogen depletion at field scale, creating favourable conditions for clover growth.

Total animal intake appears nearly insensitive to clover preference, which is again in line with Schwinning and Parsons (1996a) (their Figure 10 d–f). However, total intake shows the same single maximum response to the stocking rate as earlier observed in Fig. 9.

Most strikingly, Fig. 11f reveals that at the default parameter settings, the ecosystem shows a high variability of production. Both an increase in stocking density or a decrease in clover preference would stabilise the system into a stable mixture. Alternatively, a stronger escape mechanism for
clover ($q_{esc} = 2.5$, Fig. 11i) would stabilise the system for all stocking rates and preferences, which explains the higher persistency of small-leaved clover varieties under continuous sheep grazing (Evans et al., 1992). Note that this stronger escape mechanism does not affect total animal intake at low stocking densities, even though it leads to a somewhat lower clover content in the sward (compare Fig. 11d and e with g and h). Conversely, a weaker escape mechanism for clover increases the sward clover content at low stocking densities, yet does not affect the total animal intake. Nevertheless it leads tot an increased instability of the system over time (Fig. 11a–c).

The variety of responses to grazing observed here, could possibly offer an explanation for the often conflicting results from field experiments. Whereas Curll et al. (1985a) found a negative relationship between stocking rate and clover content, both Orr et al. (1990), Parsons et al. (1991a) reported on an experiment in which higher clover contents were found on swards grazed ‘hard’ at 3 cm than on swards grazed ‘lenient’ at 6 or 9 cm. Both experiments involved continuous grazing by sheep. However, Curll et al. used the large-leaved clover cultivar Blanca, whereas the small-leaved cultivar Huia was used in the other experiment. If Fig. 11a represents large-leaved clover, with a weak escape mechanism due to its erect morphology, it shows that the average clover content decreases with stocking rate for at least a range of low stocking rates (i.e. the negative response of the clover content to maximum intake rates between 1 and ca. 2). However, the clover content is positively related to the stocking rate, for all stocking rates in Fig. 11g, representing small-leaved clover with a prostrate morphology.

3. The effect of structured and stochastic environmental variability

3.1. Structured versus stochastic variability

So far the stabilising and destabilising factors have been identified in a constant environment. In temperate climates however, ‘real’ grassland ecosystems are confronted with alternating favourable and unfavourable environmental conditions (e.g. Mitchell and Csillag, 2001). Temperature and precipitation are the two most obvious variables regulating plant growth (but see Thornley, 1998). Most environmental variables show a seasonal trend, which is to some extent perturbed by stochastic variation (Fig. 12). The magnitude of both this trend and of the stochastic variation may vary between climates and between variables: whereas temperature shows a strong seasonal trend with relatively small random variations in most temperate climates, rainfall tends to show a stronger stochastic pattern in comparison to its

Fig. 12. (a) Temperature and (b) rainfall patterns in Wageningen, The Netherlands, from 1993 to 1997. Single lines, monthly average values, bold lines, monthly values, averaged over 40 years. Data from the Department of Meteorology and Air Quality, Wageningen University, The Netherlands.
seasonal trend. Fig. 12a and b illustrate the fluctuations of temperature and rainfall measured in Wageningen, The Netherlands. Barthram et al. (1992) presented similar graphs for central Scotland (their Figure 1). It will be shown here how structured (seasonal) variation and stochastic variation have different impacts on the stability of grassland ecosystems.

3.2. Impact of structured environmental variability

The seasonal trends of temperature and rainfall are given by their daily, weekly, or monthly values, averaged over a large number of years. The structured variation can then be quantified by the variance among these average values. The seasonal trend and its variance are constant between years for any particular climate (ignoring possible climate changes).

First the effects of temperature fluctuations on the stability of grass and clover growth will be explored, whereas all other environmental variables (e.g. rainfall, radiation) are assumed to remain constant. The structured seasonal trend of the temperature $T$ is, sensu Thornley (1998), modelled as:

$$T = 1 + a_{\text{struc}} \sin(2\pi t)$$  \hspace{1cm} (10)

where $t$ is the time in years, and $a_{\text{struc}}$ the amplitude of the structured fluctuations. Note that the average temperature equals 1 unit, which is the (constant) value implicitly used in the constant environment of Section 2.

The effect of temperature on the CO$_2$ assimilation rates of perennial ryegrass and clover leaves was documented by Woledge and Dennis (1982), who found a non-linear relationship for both species. The responses of the CO$_2$ assimilation rates to temperature were also affected by the light intensity and by the temperature at which the plants had grown previously. No major differences were observed between the responses of grass and clover. Ignoring light intensities and previous temperatures, the effect of the temperature on the growth of both species is here modelled as:

$$p_1' = p_1 T^{q_{\text{temp}1}}$$ \hspace{1cm} (11a)  
$$p_2' = p_2 T^{q_{\text{temp}2}}$$ \hspace{1cm} (11b)

where $p_1'$ and $p_2'$ are the temperature dependent growth rates, $p_1$ and $p_2$ are the temperature independent growth rates of Eqs. (6) and (4b), respectively, and $q_{\text{temp}1}$ and $q_{\text{temp}2}$ are parameters indicating the linearity of the response of the photosynthesis to the temperature. These functions ensure that the production of both species equals 0 when the temperature is zero, and that the production is unaffected when the temperature is 1, for all values of $q_{\text{temp}}$ (Fig. 13). For the default
values of $q_{\text{temp}1}$ and $q_{\text{temp}2}$ (0.3 for both species), the responses agree well with the temperature responses found by Woledge and Dennis (1982) under high light intensities.

The senescence rate is also dependent on the temperature, which is modelled here as a linear relationship, sensu Johnson and Thornley (1983):

$$s'_i = s_i T$$

(12)

where $s'_i$ is the temperature dependent senescence rate of grass ($i = 1$) and clover ($i = 2$), and $s_i$ the independent rate. Again the senescence rate equals 0 when the temperature is zero, and is unaffected at the average temperature of 1. Note that a minimum level of 0 has been applied to both production and senescence of both species to prevent negative growth and senescence rates at temperatures below zero ($T < 0$), which would otherwise arise in case $s_{\text{struc}} > 1$.

The effect of structured environmental fluctuations on two of the modelled grassland ecosystems is studied: (1) an intrinsically unstable system, showing sustained oscillations in a constant environment. This system is simulated by setting all parameters at their default values. (2) An intrinsically stable system, which is obtained at default parameter settings, yet without the time delay of the dependence of grass on clover ($\tau_{\text{delay}} = 0$ in Eq. (6)).

Fig. 14 shows the effect of the structured variation of temperature (Eq. (10)) on the stability of the intrinsically unstable system. In absence of these fluctuations, the total herbage mass shows sustained oscillations (Fig. 14a). Obviously, the seasonal temperature fluctuations lead to a strong variability of the herbage mass within the year, the intra-annual variation (Fig. 14b). This will be referred to as the direct effect of the temperature on the system stability. However, when the progressive yearly average herbage mass is plotted over time, it shows that the variation between years, i.e. the inter-annual herbage mass is plotted over time, it shows that the variation between years, i.e. the inter-annual variation, is effectively reduced when large structured fluctuations are imposed (Fig. 14c and d). This will be referred to as the indirect effect of the temperature fluctuations.

Fig. 15 shows the indirect effect of structured temperature variation on the intrinsically stable grass clover mixture. This system remains stable, as the mean yearly temperature is constant and equals 1 for each year. However, the annual mean herbage mass is reduced, as a result of the non-linear response of plant growth to temperature. Due to this non-linear response, the extent to which herbage production is reduced at temperatures $<1$ exceeds the extent to which it is accelerated at temperatures $>1$, as a result of which the annual mean herbage mass is reduced.

Similar effects of structured environmental fluctuations were observed by Schwinning and Parsons (1996b), Owen-Smith (2002). In Schwinning and Parsons’ model, system oscillations were reduced when a fixed mortality rate was imposed on clover each winter. Owen-Smith’s herbivore-vegetation model was stabilised when herbage growth was abruptly terminated for 26 weeks, annually. Similar to the observations above, in both models this stabilisation resulted from the interference between the intrinsic ecosystem oscillations and the imposed environmental periodicity.
3.3. Impact of stochastic environmental variability

To simulate the impact of stochastic variability of an environmental variable, the temperature $T$ in Eq. (10) is now replaced by:

$$T = 1 + a_{\text{stoch}}$$  \hspace{1cm} (13)

where $a_{\text{stoch}}$ is a random number between $a_{\text{stoch, max}}$ and $-a_{\text{stoch, max}}$, which set the upper and the lower limits of the amplitudes of the stochastic variability.

Fig. 16 shows that the response of an intrinsically unstable system may now be rather unpredictable, even when $a_{\text{stoch, max}}$ remains unchanged. In Fig. 16a, the system is destabilised by the stochastic temperature pattern (compare with Fig. 14a). However, when the model is rerun for the same parameter values, changing the timing of individual high and low stochastic fluctuations yet for the same value of $a_{\text{stoch, max}}$, the system may be stabilised (Fig. 16b). Apparently the times at which high and low temperatures occur is critical in magnifying or counteracting the intrinsic oscillations.

The system which is intrinsically stable (Fig. 15a) is destabilised by stochastic fluctuations (Fig. 17). This is caused by the mean annual temperature, which is no longer constant, but instead changes from year to year, depending on the stochastic temperature regime.

Similar observations were made by Schwinning and Parsons’, when they imposed a variable winter mortality rate of clover, that sustained the intrinsic ecosystem oscillations. By contrast, the prairie grass ecosystem, modelled by Mitchell and Csillag (2001), was stabilised by a moderate increase of the stochastic rainfall variability. However, this stabilisation did not stem from the compensatory interaction between the rainfall variability and one or more intrinsic ecosystem cycles. Instead, an increase of rainfall variability resulted in both ‘drier’ and ‘wetter’ years. Since growth was already limited in dry years, the increased severity of droughts did not affect plant production, whereas the latter was stimulated during the increased number of wet years. As a result, in their model the incidence of years with a low productivity declined with a moderate increase of rainfall variability.

3.4. Impact of both structured and stochastic environmental variability

As discussed above, environmental fluctuations will generally consist of both a structured (seasonal) and a stochastic (daily, weekly or monthly) component. It is assumed here that these two components do not show any interaction, i.e. the daily stochastic variation is as large in winter as it is in summer. The temperature $T$ can then be simulated by adding both components (Eqs. (10) and (13)):

$$T = 1 + a_{\text{struc}} \sin(2\pi t) + a_{\text{stoch}}$$  \hspace{1cm} (14)

Fig. 18 presents the effect of a large structural component ($a_{\text{struc}} = 1$) and a moderate stochastic component ($a_{\text{stoch, max}} = 0.5$) on the stability of
both an intrinsically oscillating system (Fig. 18a) and an intrinsically stable system (Fig. 18b). The regime of stochastic fluctuations was kept identical for both systems. Now the identical behaviour of both systems over time is remarkable ($R^2 = 0.98$), considering the largely contrasting behaviours of these systems under constant average environmental conditions. This underlines the importance of including both structured and stochastic environmental fluctuations into simulation models, in order to predict realistic results. In the companion paper (Schulte, 2002) it will be shown that this identical behaviour of contrasting systems can also be found in empirical field data.

4. Effects of scale and disturbances

4.1. Effect of spatial scale

So far the intrinsic ecosystem properties have implicitly been modelled in absence of spatial heterogeneity and external disturbances. These simulations represent the processes on a patch-scale, i.e. on a spatial scale at which the herbage of each species may be assumed to be distributed homogeneously, and at which all individuals of one species hence may be assumed to show identical responses over time. However, the literature suggests that the stability of a system depends to a large extent on the scale on which it is studied (Collins, 1995; Matsinos and Troumbis, 2002). The interaction between the dynamics on a patch scale and on field scale have been explored extensively by Schwinning and Parsons (1996b), using a spatially explicit model, which allowed for the heterogeneity and the active interaction between patches. They concluded that systems, which show oscillating yields on a patch-scale may turn into stable mixtures when studied on field scale, provided that the patches oscillate ‘out of phase’. On a somewhat larger spatial scale, the grazed ecosystem by Owen-Smith (2002) was stabilised when heterogeneity of habitats was introduced, since animals ‘smoothed’ their annual intake pattern by grazing high quality habitats during the growing season, and the remaining poor habitats during the dry season.

In Section 2 it has been shown how individual patches may be stabilised by increased niche-differentiation, dependence of grass on clover, and management. However, using the default parameter values, representing continuous grazing under the low stocking rates commonly applied on clover-driven pastures, the system shows oscillating behaviour on a patch scale. The same results were found by Schwinning and Parsons (1996a). Setting these patches out of phase may provide an additional management tool to ensure stability at field level.

Schwinning and Parsons (1996b) distinguished four types of patches, based on the relative contributions of grass and clover, and on the soil mineral nitrogen status, (1) clover dominance; (2) grass dominance; (3) pure grass at high soil N; and (4) pure grass at low soil N. When all patches show oscillatory behaviour, the clover dominant phase and the grass dominant phase alternate on each patch. When local clover extinctions and invasions are included, patches may in time move through all four phases periodically and irregularly. The authors came to the conclusion that the ‘patchiness’ of pastures, which occurs when patches are out of phase, is a desirable feature in the maintenance of the stability of pastures, in other words, spatial and temporal heterogeneity on a small scale leads to stability on a large scale.

Strikingly, the same observation was made by Oldeman (1990), studying forest ecosystems. He stated that

“it is the fluidity of the eco-unit (patch) development itself that guarantees the inflexibility of their mosaic (pasture), because interaction between eco-units (patches) is open and erases the effects of small or somewhat larger diversifying forces”.

4.2. Effect of disturbances

Oscillating patches may be set either ‘in phase’ or ‘out of phase’ by ‘disturbances’, depending on the spatial scale of these disturbances. Small and frequent local disturbances, such as faeces and urine deposition and local tissue removal by grazing animals, are destabilising on a patch scale
Nevertheless, these set the patches out of phase, and are therefore, stabilising on a field scale. These disturbances will here be referred to, sensu Oldeman (1990) as ‘buckshot events’. Large-scale disturbances, such as reseeding, the stitching-in of clover, and environmental disturbances (Section 3), affect all patches in an identical manner, and are therefore destabilising on a field scale. These large-scale disturbances will be referred to, again sensu Oldeman (1990), as ‘sweeping events’. Disturbances may also be classified on a scale of ‘hardness’. ‘Hard’ disturbances, such as faeces deposition and reseeding, instantly mark the end of an existing patch or of multiple patches, and the start of new patches with changed properties. ‘Soft’ disturbances, such as urine depositions (in absence of urine scorch) or a cutting event, may change the patch properties over a time period, as they affect its properties in a more subtle way, e.g. by changing the soil mineral nitrogen balance (Curll, 1982). Fig. 19 summarises this two-dimensional classification of disturbances.

If a pasture is fluctuating on a patch scale, yet stabilised on a field scale by the occurrence of buckshot events, which set the patches out of phase, then it is doubtful whether this situation can still be referred to as a ‘steady state’. Oldeman (1990) proposed the term equilibrium (from eco-equilibrium) to describe situations where forest ecosystems are stabilised by fluctuations and disturbances on a small scale, and this seems to be equally applicable to grassland ecosystems:

“The proportions of eco-units (patches) have reached an equilibrium with the local regime of shifting events (disturbances). The existence of an equilibrium stage presupposes that there is a regular regime of shifting events (disturbances) (...) Not only is this rarely taken into account in forest (pasture) management plans, but (moreover) vegetation types, including forest (pasture) types, are correlated with average, long-term climatological features only’ (Oldeman, 1990).

For a more detailed account of the effect of disturbances on patches and field scale, see Schwinning and Parsons (1996b), Matsinos and Troumbis (2002).

5. Classification of stability

Most theoretical ecosystem studies have focussed implicitly on the stability of ecosystems under constant environmental conditions (e.g. Noy-Meir, 1975; Grenfell, 1988; Parsons et al., 1991b, 1994). At most, sinusoidal environmental fluctuations are implemented (e.g. Thornley, 1998), and in nearly all studies stochastic fluctuations are ignored, as these ‘obscure’ the intrinsic
ecosystem properties (but see Mitchell and Csillag, 2001). However, it has been shown in the previous section how both structured and stochastic fluctuations may have a profound impact on the stability of grassland ecosystems. Including the effects of these fluctuations in a qualification and quantification of system stability may be a prerequisite for applicability for both farmers and agronomists.

In contrast, in most empirical studies an attempt is made to explain yield differences between years by the variability of environmental factors. It is interesting to note that yields are commonly linked to rainfall (e.g. Barthram et al., 1992; Silvertown and Dodd, 1994), which is an environmental variable with a strong stochastic component. Its stochastic nature causes variability of rainfall between years, making rainfall an obvious candidate to explain yield differences between years. The effects of temperature are commonly ignored, as its fluctuations are strongly structured, leading to a constant mean yearly temperature between years. Nevertheless it has been demonstrated in Section 3 that in spite of this constant mean yearly value, structured fluctuations of temperature within years may have a large impact on the system stability between years.

In this section an attempt is made to come to a classification of grassland stability which allows for the effects of both intrinsic system properties and for the effects of structured and stochastic environmental variability. First, output variables are identified which represent the entire ecosystem, and the dynamics of which could serve as indicators of system stability. Next, both the spatial scale and the temporal scale at which these variables should be studied are defined. Finally, three concepts of ecosystem stability are proposed.

5.1. Identification of relevant variable

It is essential to identify an output variable of the system which represents the entire system, yet is also of direct importance to farmers. Noy-Meir (1975) found that the total herbage mass was a more reliable indicator of system stability than was total animal intake and performance, as the latter may be high even when the system is on the verge of a collapse. Total herbage mass, or related variables such as the total Leaf Area Index or the fraction of herbage cover, are also used by other authors (e.g. Parsons et al., 1991b; Schwinning and Parsons, 1996b; Thornley, 1998; Mitchell and Csillag, 2001; Matsinos and Troumbis, 2002), as the total herbage mass is the central state variable of most grassland models. However, three limitations in its use should be kept in mind; firstly, there is a tendency to base pasture rotations on 'sward surface heights' (e.g. Bircham and Hodgson, 1983; Orr et al., 1990; Evans, 1992; Laws and Newton, 1992), rather than using 'fixed rotations' (e.g. Curril et al., 1985a). The sward surface height is strongly related to herbage mass. Whenever this management type is applied, the stability of the herbage mass may depend primarily on the farmer’s skills to maintain the desirable height, rather than on system or environmental properties. Secondly, when the stability is studied in conjunction with production, herbage mass may be a poor indicator of agronomic productivity; e.g. understocking will lead to higher total herbage masses, whereas it may result in a lower total animal production. Finally, cutting grassland for conservation will cause a variable herbage mass within the year regardless of the system’s stability properties. In these cases the annual yield, the annual production, or total annual animal intake may be more appropriate output variables, bearing in mind their restrictions mentioned above.

In some studies the clover content, expressed as a percentage of the total herbage mass is used to study the system stability (e.g. Laws and Newton, 1992; Schwinning and Parsons, 1996b). However, care should be taken in this approach, as a fluctuating clover content does not necessarily lead to a fluctuating herbage mass, nor does a constant clover content implicitly indicate system stability.

5.2. Identification of relevant temporal scale

It is essential to discriminate within year (intra-annual) stability from between year (inter-annual) stability. It has been shown in Section 3 how structured environmental fluctuations will automatically lead to an increased variability of grass-
land production within individual years, yet may increase stability of production between years. Relevance to farmers should be the criterion for the choice whereas inter-annual stability is arguably most relevant to cattle and sheep producers, the intra-annual stability is just as important to dairy producers. In either case, long-term data are required to provide an indication of stability, as in most short-term data, stability properties are ‘obscured’ by stochastic environmental fluctuations. Moreover, Schwinning and Parsons (1996b) found intrinsic system fluctuations between 4 and 7 years in the steady state. In the Park Grass Experiment, botanical equilibrium was not reached until 40 years after the imposition of fertiliser treatments (Silvertown and Dodd, 1994). In an extensification experiment, Wind et al. (1993) reported that yields continued to decline for 4–7 consequent years after nitrogen treatments ceased in 1968, and that stability of the botanical composition has not yet been reached to date.

5.3. Identification of relevant spatial scale

It has been laid out in Section 4, that a satisfactory study of system stability requires a spatial dimension beyond the patch size, as spatial scale may have a definite impact on system stability. Ideally, the stability of production at farm level should be the focus of attention (e.g. Laws and Newton, 1992), as this is the scale at which farmers operate. It is conceivable that wherever regular reseeding is required to maintain pasture productivity, resulting in oscillating pastures (Section 4), that stability at farm level may be maintained by setting these entire pastures ‘out of’ phase. Alternatively, a stable animal production may be achieved from unstable pastures by increasing the conservation and outdoor feeding of herbage.

5.4. Identification of relevant stability concept

It has been shown in Section 4 that both structured and stochastic environmental fluctuations may have a profound impact on the stability of grassland ecosystems. These external factors tend to obscure the intrinsic system properties in field data. This complicates the analysis and comparison of different grassland systems in different climates, measured during different time courses, as the observed output variability may be a reflection of the environmental variability rather than of system properties. To overcome this problem, it is proposed here to define three concepts of stability:

1) Actual stability: the observed stability of herbage mass, yield or animal intake in an environment showing both structured and stochastic fluctuations. In fact this is the inverse of the coefficient of variation of the yields between years, measured in field experiments. The level of this actual stability is limited to a particular climate and to a particular time period, as it is highly dependent on the (coincidental) stochastic fluctuations during that observation period. A different level may be observed when the same ecosystem is studied under different weather conditions, i.e. at another location, or during another period (e.g. compare Fig. 16a and b). Nevertheless, the actual stability level is of direct relevance to farmers.

2) Extrinsic stability: the observed stability of herbage mass, yield or animal intake in an environment which shows structured yet no stochastic fluctuations. The level of this extrinsic stability is limited to a particular system in a particular climate (structured environment), yet remains the same for each observation period (presupposing no change of climate). This means that the extrinsic stability level of an ecosystem (e.g. an experimental plot) will remain constant between distinct observation periods. However, a different level may be expected when an identical ecosystem is studied in another climate (e.g. compare Fig. 14c and d). Although the extrinsic stability is independent of the large impact of stochastic environmental fluctuations, at least it incorporates the climate in which the ecosystem is studied.

3) Intrinsic stability: the observed stability of herbage mass, yield or animal intake in a hypothetical constant environment, as applied
in most simulation models. The level of this intrinsic stability is limited only to a particular system, and is identical for all climates and observation periods. This means that ecosystems with identical botanical components, on identical soils, with identical fertiliser and management regimes will show identical levels of intrinsic stability, irrespective of the climate and the period during which it is observed. However, the intrinsic stability level of a grassland ecosystem may profoundly differ from the stability of yields, as measured in the field.

Of these three stability concepts, the actual stability represents most accurately the yield fluctuations experienced by farmers. It may be used to compare the short-term stability performance of ecosystems, measured at the same location, during the same time course, e.g. two plots of an experiment. However, it should be kept in mind that the levels of actual stability which are found, may be profoundly different or even be reversed when both ecosystems are observed during a different period, i.e. under a different regime of stochastic fluctuations. Therefore, it is proposed here, to use the extrinsic stability levels for these comparisons instead, as these will remain constant over time. In fact, the extrinsic stability could bridge the gap between the stability properties observed in modelled ecosystems, i.e. the intrinsic stability, and those observed in experiments, i.e. the actual stability.

Additionally, a comparison of the actual and the external stability of an ecosystem will reveal its response to the regime of stochastic environmental fluctuations. Similarly, the effect of structured environmental fluctuations can be deduced by a comparison of the external and the intrinsic stability.

When using system simulation models, the extrinsic and the actual stability can be derived from the intrinsic stability relatively simply, by subsequently imposing structured and stochastic environmental fluctuations, as shown in Section 3. Conversely, the intrinsic and extrinsic stability can be derived from the experimentally measured actual stability. This rather complicated procedure requires large amounts of long term data. This procedure will be explained in the companion paper (Schulte, 2002).

6. Discussion

Due to the simplicity of its structure, the model presented in this paper should not be regarded as explanatory, nor should its predictions be considered conclusive. Quantitative interactions between perennial ryegrass and white clover at patch level have been modelled more satisfactorily by Parsons et al. (1991b), Thornley et al. (1995), Schwinning and Parsons (1996a). However, the higher complexity of their models complicates the discrimination of the effect of individual ecosystem properties and processes, which regulate stability. In contrast, the transparency of the model presented here enabled the identification and illustration of the impacts of these individual processes, and of their interactions.

It has been demonstrated that the stability of yields which is observed in the field depends on a complex of three components, the intrinsic ecosystem properties; the environmental variability; and on the degree of spatial heterogeneity.

Of the intrinsic ecosystem processes, competition for light, delayed responses, grazing per se, preferential grazing for clover and cutting were all identified as destabilising, whereas niche-differentiation, nitrogen dependence, and escape mechanisms were found to stabilise the ecosystem. To some extent, the stabilising processes may compensate for the instability caused by the destabilising processes. However, interactions between both process types were observed, which complicate this compensation. For instance, a strong clover preference destabilised the modelled ecosystem at low stocking rates, yet did not affect stability at higher animal densities. Moreover, the stability level was independent of clover preference at all stocking rates, when clover was attributed with a stronger escape mechanism (Fig. 11).

On top of these interactions among intrinsic ecosystem processes, matters are further complicated by structured and stochastic environmental fluctuations. It has been argued in Section 3.2 that
ecosystems which are unstable in temperate climates with small structured fluctuations, may show stable behaviour in more continental climates, in which structured environmental fluctuations are strong. Furthermore, stochastic environmental fluctuations may lead to drastic changes in the stability level between observation periods. Especially in intrinsically unstable systems, the timing of high and low temperatures was found critical to the actual stability level of the ecosystem. Therefore, it is well conceivable that an ecosystem, which appears to be stable during a 5 year experiment, would show unstable behaviour when observed at a different date (Fig. 16). In the companion paper (Schulte, 2002), it will be demonstrated that when stochastic fluctuations are strong, intrinsically stable systems may in fact show a larger variability of yields than intrinsically unstable systems.

Finally it was suggested that the picture may be further obscured by interactions between intrinsic ecosystem processes and environmental fluctuations on the one hand, and spatial heterogeneity on the other. It was put forward that even when the ecosystem is unstable at a patch scale, it may show a stable level of production at field scale, when the oscillating patches are set ‘out of phase’. Whether patches oscillate ‘out of phase’ or ‘in phase’ depends again on the management imposed. However, the same stability level may be observed when the individual patches are stabilised. Therefore, management factors affect the system stability through two pathways, i.e. by changing the balance of intrinsic processes, and by defining the spatial heterogeneity. It was shown, for instance, how preferential grazing under low stocking rates leads to instability at patch scale. At the same time, manure and urine depositions under grazing may act as ‘buckshot’ events, which increase pasture heterogeneity and therefore, stability at field scale.

Considering the complexity of all these interactions within and between intrinsic processes, spatial heterogeneity and environmental fluctuations, the prototyping of management systems for mixed swards is fraught with complications, when based on short-term experiments which establish the system responses to single management factors. In fact this complexity may well explain the large variety of responses of grass and clover to single management factors, as observed in the literature cited. Experimental designs, which take all processes and all interactions into account, are hardly conceivable. The companion paper (Schulte, 2002) demonstrates how the effect of some single management factors may be extracted from data on long-term experiments, with durations from 40 up to 150 years. However, the number of conclusions contrasts sharply with the huge resources required for these experiments. Therefore, the use of simulation models will remain indispensable in the analysis of grassland ecosystem stability.

Bearing in mind the limitations of simulation models mentioned in the introduction, a satisfactory simulation model of mixed swards should incorporate all three components which regulate stability. Primarily it requires an accurate description of the intrinsic system properties and processes, which allows for their mutual interactions. Such a description for grass monocultures has already been presented by Thornley (1998), Riedo et al. (1998). Although clover is formally included in the latter model, its dynamics are reduced to a most basic level: the fractional clover cover is entered as an initial and constant value, which linearly defines the nitrogen fixation rate in interaction with temperature. Conversely, models which satisfactorily simulate the dynamics of both perennial ryegrass and white clover (e.g. Parsons et al., 1991b; Thornley et al., 1995; Schwinning and Parsons, 1996a), have not yet achieved the same level of accuracy and detail in the description of plant physiology and soil processes.

Secondly, in order to produce results which reflect ecosystem behaviour under field conditions, the simulation model should include both structured and stochastic environmental fluctuations. It was demonstrated that even under moderate stochastic fluctuations, the yield patterns of an intrinsically stable and an intrinsically unstable system were nearly identical over time, in spite of the largely contrasting behaviour of both systems in a constant environment (Fig. 18). In such cases, the system response to environmental fluctuations...
makes the balance of all other intrinsic processes nearly irrelevant. Using a model which includes environmental variability, it is conceivable that ecosystems are no longer classified by the intrinsic stability level, but instead by either the extrinsic stability level, or by the probabilities of actual stability levels, e.g. the number of simulation runs in which a range of stability levels were exceeded.

Finally, considering the decisive impact of spatial heterogeneity on system stability at field scale, a simulation model of mixed swards should explicitly locate all processes in a three-dimensional space. This could be achieved by simulating a large number of patches, which all consist of a number of sward layers, and which interact directly with neighbouring patches. Parsons et al. (1994), Schwinning and Parsons (1996b), Matsinos and Troumbis (2002) have already presented two-dimensional (lateral) simulation models of mixed swards. However, in each of these models the simulation of intrinsic plant processes was reduced to a most basic level. Brereton and McGilloway (1999) presented a three-dimensional model to study the effects of sward structure on animal intake during short rotational grazing periods. In their model, plant processes were absent, and patches only interacted passively, i.e. through the selection between patches by the grazing animals.

Apart from drastically increasing the number of required calculations, the dynamic simulation of detailed plant processes and of plant-animal interactions in a three-dimensional space would require an adequate description of grass and clover morphology. Schulte and Lantinga (2002) presented a mechanistic model of the vertical distribution of perennial ryegrass and white clover tissue. Connecting these plant morphological and plant physiological models requires the explicit simulation of tiller dynamics, as exemplified by the morphogenesis model of perennial ryegrass by Van Loo (1993). For white clover, this remains a challenge.

It is envisaged that such a simulation model as described above, combined with data from long-term experiments, could bridge the gap between intrinsic ecosystem properties, which have been revealed by simulation models to date, and actual ecosystem behaviour, as reported from experimental studies. The definitions of the intrinsic, extrinsic, and actual stability levels presented in this paper, may aid the interpretation of model output in practical terms, and the deduction of intrinsic processes from field data, which would improve the information flows between both approaches. This would not only aid the understanding of grass–clover dynamics, but could also prototype entire management systems for grass-clover mixtures, taking into account all intrinsic, environmental and spatial processes and interactions involved.

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Appendix A.

Table of state variables, rate variables and parameters used in the model

<table>
<thead>
<tr>
<th>Type</th>
<th>Symbol</th>
<th>Description</th>
<th>Introduced in equation</th>
<th>Default value (parameters)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time variable</td>
<td>$t$</td>
<td>time since start of simulation</td>
<td>Eq. (6)</td>
<td></td>
</tr>
<tr>
<td>Plant state variable</td>
<td>$H_i$</td>
<td>Herbage mass</td>
<td>Eq. (1)</td>
<td></td>
</tr>
<tr>
<td>Plant rate variables</td>
<td>$p_i$</td>
<td>Herbage growth rate (temperature independent)</td>
<td>Eq. (1)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p_i'$</td>
<td>Temperature dependent herbage growth rate</td>
<td>Eqs. (11a) and (11b)</td>
<td></td>
</tr>
</tbody>
</table>
References


Riedo, M., Grub, A., Rosset, M., Fuhrer, J., 1998. A pasture simulation model for dry matter production, and fluxes of