



University of Kentucky
UKnowledge

International Grassland Congress Proceedings

XIX International Grassland Congress

Ecophysiology of Grasslands: Dynamic Aspects of Forage Plant Populations in Grazed Swards

G. Lemaire
INRA, France

Follow this and additional works at: <https://uknowledge.uky.edu/igc>



Part of the [Plant Sciences Commons](#), and the [Soil Science Commons](#)

This document is available at <https://uknowledge.uky.edu/igc/19/1/35>

This collection is currently under construction.

The XIX International Grassland Congress took place in São Pedro, São Paulo, Brazil from February 11 through February 21, 2001.

Proceedings published by Fundacao de Estudos Agrarios Luiz de Queiroz

This Event is brought to you for free and open access by the Plant and Soil Sciences at UKnowledge. It has been accepted for inclusion in International Grassland Congress Proceedings by an authorized administrator of UKnowledge. For more information, please contact UKnowledge@lsv.uky.edu.

ECOPHYSIOLOGY OF GRASSLANDS: DYNAMIC ASPECTS OF FORAGE PLANT POPULATIONS IN GRAZED SWARDS.

G. Lemaire
INRA, Department of Environment and Agronomie
86600 Lusignan, France.

Introduction

The aim of this paper is to review knowledge of the ecophysiological mechanisms influencing the dynamics of plant populations in grazed swards. Such an objective requires some definitions. Firstly, it is necessary to define “ecophysiology” as the study of the interactions between biological individuals (plants) with their own environment: how individuals perceive and react to any constraint and change of their environment, and how the functioning of plants as a population can modify their own environment. Such a definition implies a dynamic approach to plant population functioning as resulting from constant plant-plant interactions mediated by micro-environment modifications. In a grazed plant community, these plant to plant interactions are perturbed by spatially explicit defoliation events which have a direct effect on the functioning of defoliated plants and also an indirect effect via the modification of the micro-environment of the neighbour plants. Secondly, it is necessary to define more precisely what we mean by “dynamics of plant population”. Because this paper is restricted to “ecophysiology of grasslands” plant population dynamics are not entirely taken into account in the sense that invasion or recruitment processes of new plants through seed dispersion and seed banks in the soil are not explicitly included in our approach. So the dynamic aspects of plant population discussed in this paper are restricted to competition between individual plants, including ability for clonal reproduction, survival ability, and morphological adaptation to defoliation and neighbourhood interactions. These determine the dynamic evolution of both sward structure for a short term and botanical composition for a longer term in a sward subjected to a given management.

The analysis will focus on three main concepts of ecophysiology: (i) the mechanisms of competition among individual plants within a plant community and their consequences to sward structure dynamics, (ii) the adaptive morphogenetic mechanisms of plants to defoliation and the consequence to plant morphology and sward structure dynamics, and (iii) the interactions between these two types of mechanism for an overall understanding of the vegetation dynamics of a grazed plant community and its consequence for sustainable pasture management.

Individual plant or plant population functioning ?

The functioning of a sward (or a crop) can be studied at different levels of organisation: plant organs, individual plants and plant population. The classical approach developed for crop modelling considers the plant population as an overall entity which exchanges energy and mass with the environment. The functioning of such a system is therefore characterised by fluxes of energy (radiation, sensible heat) and mass (CO₂, H₂O, N, minerals...) between the overall plant population and the soil and atmosphere. Because these fluxes are expressed per unit soil area they do not have any direct significance to individual plant functioning. In these models (see Jones and Kiniry, 1986, for CERES-Model, or Brisson *et al.* 1999 for STICS-Model) these fluxes are influenced by the structural characteristics of

the overall plant population in term of size and spatial distribution of the exchange surfaces such as leaf area index and its geometrical distribution, on root architecture and distribution in soil...Nevertheless these fluxes between plant population and the external environment are also regulated by biological functions such as stomatal diffusion for CO₂ and H₂O, photosynthesis, respiration, nitrate absorption or nitrogen fixation...These biological functions are introduced in models of physical exchanges as “resistance” coefficients more or less empirically related to environmental parameters.

Such an approach provides useful tools for modelling the functioning of a plant population at equilibrium, when the structural characteristics of the plant population, which determine the rate of the different fluxes in response to the external environment are in steady state. However, the structure parameters of the plant population, such as the relative size of the different organs for resource capture (leaf and root surfaces), or for reserve storage, determining the exchange properties of the system, change continuously as the plant population develops. These changes in plant population structure are the consequence of (i) the modifications of the allocation pattern of assimilates within individual plants among their different organs (leaves, stems, tillers or branches, roots...) as affected by plant ontogeny and/or environmental constraints, and (ii) the modification in resource sharing among the different categories of individual plants which compose the plant population. In most of the crop models, this allocation of assimilate is empirically represented with a compartmental analysis using empirical coefficients. But this problem is far from satisfactorily solved in most of the models. Therefore, to obtain a more mechanistic model of plant population functioning, it appears necessary to introduce a complementary approach considering the plant population not only as an overall entity which exchanges mass and energy with the external environment, but also as a “collection” of individual biological units (plants) which interacts among themselves and whose integrated structure determines “emerging properties” for the functioning of the overall plant population (Lemaire, 1993).

In the case of a mono-specific plant population, if we assume that the parameters describing the structure of individual plants (size, height, leaf/stem ratio, shoot/root ratio,...) are normally distributed, then it could be possible to use the “average” plant structure to analyse the dynamics of the plant population. But obviously, asymmetric distributions of plant structure characteristics are more often observed than normal distributions, even in mono-specific stands. Moreover, Gosse *et al.* (1988) showed that within a lucerne stand it was possible to distinguish two morphological categories of shoot with different height distribution, leading to a hierarchical structure of the plant population resulting from intraspecific competition. In a plurispecific plant population, the dynamics of structure is the result of both (i) the changes in species demography in terms of birth and death of individuals, and (ii) the changes in structure of each species in response to the interferences between individual plants within the plant population. So the identification of the mechanisms of competition among individual plants within a plant population is a prerequisite for an analysis of the dynamics of plant population subjected to variable environmental constraints and to diverse perturbations as determined by herbivory.

Competition among plants within plant communities

In the great majority of ecosystems individual plants are subjected to competition by their neighbours, and plant species evolved under the selective pressure of competition for survival. For instance, de Candolle (1820) suggested that the first species to establish in an area tend to exclude other species. Weaver and Clements (1929) stated that “the struggle for existence in the plant world is between each plant and its environment”. Two plants do not

compete with each other as long as environmental resources necessary for their own demand are in excess. So competition can be more generally defined as the interactions between individual plants induced by the necessity to share limited resources, leading to a reduction of the number of survivors and/or a diminution of their growth (Begon *et al.*, 1986). According to this definition the ecophysiological mechanisms involved in competition are dependent on the nature of the resources, which limit the growth of the individual plants (light, water, nutrients) and therefore could be different under different environmental conditions. Moreover, the intensity of the competition is difficult to evaluate. In theory, for each condition of competition (nature of the limiting resource) the intensity of the competition should be proportional to the deficiency in the availability of the limiting resource for the two competitors relative to their own requirement. But it is difficult to evaluate the level of availability of the same resource shared between two competitors because it is necessary to make explicit the temporal variations and the spatial distributions of these resources. So, in practice, the intensity of competition has been evaluated only through its observed effects on the two competitors by the measurement of the reduction in their performance (growth or resource capture) relative to a performance in absence of competition. Different methods of calculation of indices of competition have been proposed and they can lead to very contradictory results (Grace 1995) because mechanisms of resource capture and resource use are not clearly identified, and also because the interactions between the different resources are not taken into account: the availability of one resource (i.e. water) can determine conditions for capture of another (i.e. nutrient).

In a sward, plants experience both intra- and inter-specific competition. Intuitively, competition between plants of the same species is expected to be much greater because they have the same demands for resources on both a temporal and a spatial basis. Very often inter-specific competition in mixed stands has been evaluated in comparison with pure monocultures according to the model proposed by De Wit and Van den Bergh (1965). The difficulty of such an approach is that any change in proportion between species in mixed stands corresponds to a substitution of inter-specific by intra-specific competition and vice-versa. The other difficulty is that any variation in density of individual plants leads to a variation in the intensity of competition, but without any clear relationship because the size of individual plants is also affected by variations in density according to size-density compensations (Matthew *et al.* 1995). So many attempts in the literature to analyse plant competition in binary mixtures failed to provide a basis for interpreting the observed results at the plant population scale and to predict the evolution of the composition of the mixture in a variable environment. More recently, some authors (Goldberg, 1990; Keddy *et al.* 1998) tried to identify two components of the competition: (i) the “competitor effect” which measures the aptitude of one species to depress the performance of its neighbours, and (ii) the “response to competition” which measures the aptitude of one species to avoid the competition of its neighbours. Nevertheless, because this approach does not allow the identification of the ecophysiological mechanisms underlying “effect” and “response” it is difficult to predict the issue of competition in a large gradient of environmental constraints.

Lemaire and Millard (1999) identified five steps for analysing the effect of plant competition by a mechanistic approach:

- (i) model resource acquisition and use by individual plants in the absence of competition;
- (ii) analyse the response of individual plants to depletion of resources, as induced by the presence of neighbouring plants;
- (iii) study the spatial distribution of the different physical resources as resulting from the presence of neighbouring plants, and how plants perceive these changes and develop an integrated response;

- (iv) analyse plant to plant signalling by other means than the quantitative depletion of physical resources;
- (v) integrate resource effects with non-resource effects in a more comprehensive model at the level of the plant stand.

Such an approach does not distinguish between intra-specific and inter-specific competition and should allow a more generic analysis through the identification of the environmental modifications the plants are able to perceive, and to adapt to, when they are growing in dense populations. As stressed by Turkington (1983) the dynamic aspects of competition have been rarely studied. Because of the interactive processes between the plant response to its own environment by changes in its growth pattern and the subsequent modifications of the environment of the neighbouring plants, a modelling approach appears necessary with the use of appropriate temporal and spatial scales. For that, it is therefore necessary to achieve coupling between 3D architectural plant models and process-based models as proposed by Fournier and Andrieu (1998, 1999) for maize plants. Such an approach allows the representation of a canopy as a set of individual plants with explicit 3D structure, and coupling with physical models to compute the effects of microclimate on this structure. In this way it should be possible to follow the different steps defined by Lemaire and Millard (1999) for analysing mechanistically plant competition within swards.

Resource sharing in plant populations

Plants growing in dense stands have to share resources to satisfy their own requirements for growth and maintenance. When these resources are depleted and are not immediately renewed at the same rate as their use, competition between plants occurs. So the ability of a single plant to capture one resource more rapidly or/and more efficiently than another should confer to this plant a higher competitive ability than its neighbours. To understand the competition relationships among individual plants it is therefore necessary to know the hierarchies between the different resources for plant growth and development under different environmental constraints. The different resources are classified in “above-ground” (light and CO₂) and “below-ground” (water, nitrogen and minerals). In natural environments the source of CO₂ is continuously renewed with a more or less constant concentration in air, and no real competition occurs among plants within populations for this resource. But in fact, the use of CO₂ by a single plant is determined by its level of light capture. CO₂ assimilated by plant provides not only C skeletons for plant growth, but also energy for maintenance and activation of all metabolic functions which determines in great part the uptake capacity of the plant for N and minerals. So, the level of light capture by a single plant should also determine its N and mineral uptake ability. Therefore competition for N and mineral resources in soil between two competing plants should depend on their specific ability to capture these resources (root architecture and absorption properties of root tissues) but should also be greatly influenced by their own hierarchical position within the plant population in relation to light capture. Lemaire and Millard (1999) reported that, in a dense stand of sorghum, the nitrogen nutrition status of individuals was lower for dominated plants which have limited access to light than in dominant plants, despite an abundant soil N availability allowing maximum growth rate of the plant population as a whole. So, as a plant population develops, competition for light between dominant and dominated plants increases, and the more shaded plants become unable to absorb soil N due to the lack of energy provided to their roots. In consequence small initial differences in light interception among individuals within a plant population are progressively emphasised by the inability of the shaded plants to satisfy their N demand for maximising leaf expansion for light capture. As shown by Lemaire and Gastal

(1997) the dynamic of N uptake at plant population level is linearly related to the dynamic of leaf area index expansion giving a more or less constant plant N per unit leaf area. But at the level of individual plants such an average ratio does not match because smaller plants accumulate less N per unit leaf area than taller plants because they are shaded. Therefore, the remarkably constant critical plant N per unit leaf area or, its equivalent, the constant critical plant N% dilution curve observed for a very large range of species (Greenwood *et al.* 1990), appears to be an “emerging property” of the plant population resulting from competition for light between individual plants. As canopy develops the distribution of N between leaves of the different layers follows the light extinction profile (Hirose *et al.* 1988; Lemaire *et al.* 1991) and therefore the high N content of dominant plants which develop their leaves in the upper layer of the canopy is progressively compensated by the low N content of the dominated plants. So, whatever the hierarchical segregation between dominant and dominated plants as the canopy develops, the “average plant” follows the same dynamics of N uptake in relation to its mass (W) or its leaf area (L):

$$N_{upt} = aW^b \quad (1)$$

or:

$$N_{upt} = kL \quad (2)$$

Lemaire *et al.* (1992) and Lemaire and Gastal (1997) demonstrated that the decline in plant N% for the “average plant” as resulting from equation (1) was also due to the decline in the leaf area ratio (LAR), as shown by the combination between equation (1) and (2):

$$L = a/kW^b \quad (3)$$

$$LAR = L/W = a/kW^{b-1} \quad (4)$$

So as plant mass (W) increases the proportion of leaf tissues declines, and for the “average plant” the coefficient *b* appears to be close to the value 2/3 indicating an isometric growth if we assume that L scales with plan area, and W with plant volume. But such an isometry cannot be observable at individual plant level because smaller plants have a lower LAR as resulting from a higher investment in growth of structural tissues with low N content, while taller plants have a higher LAR because they can maximise leaf area expansion in the well illuminated upper layer of the canopy. This is the reason why, when L is plotted against W for a set of individual plants within a plant population, we do not find any “isometric relationship” as stated by $b=2/3$ in equation (3). So “isometry” is a dynamic property of the plant population as a whole, and not a dynamic property of individual plants (Sackville-Hamilton *et al.*, 1995). Moreover, we can imagine a plant population with a bimodal distribution of plant size, in which the “average plant” follows an isometric growth pattern despite the fact that no individual plant follows such an isometry.

Such a concept has been developed for mono-specific plant populations (Lemaire and Gastal, 1997) and comparisons between species showed that coefficient *b* does not vary, while coefficients *a* and *k* only vary between C3 and C4 species reflecting their different photosynthetic pathways. These relationships has been demonstrated to match also for plurispecific swards (Duru *et al.* 1997; Cruz and Soussana, 1997) demonstrating that intraspecific and interspecific competitions are driven by the same mechanisms and have to be studied with the same approach and models. In a plurispecific stand, the “average plant” is only a virtual entity which allows a framework to analyse the mutual interactions between the different species according to their hierarchical position for light capture. Models for light

resource sharing among individual plants competing in dense canopies are now available in the literature (Sinoquet *et al.*, 1990; Sinoquet and Bonhomme, 1991). These models are based on explicit 3D plant architecture dynamics for each of the species considered in a plant population. These plant architecture dynamics can be obtained either by digitising a real canopy structure, or as an output of an explicitly 3D architectural model as discussed above.

The interaction between light capture and N uptake is very important to take into account for understanding the dynamics of grass-legume mixture. Cruz and Lemaire (1986) showed that in a *Medicago sativa* – *Dactylis glomerata* stand, when lucerne was dominant, cocksfoot was deficient in nitrogen, despite the ability of the legume species to fix nitrogen and to not compete intensively for soil mineral N. But in situations where cocksfoot is dominant, the N nutrition of lucerne is depressed due to its lower N₂ fixation capacity as a consequence of shading. Many studies showed that whatever the source of N (soil mineral N or N₂ fixation), the whole plant population behaves in the same way in adjusting N uptake dynamics to biomass accumulation (Lemaire *et al.*, 1992) and, as stated above, the sharing of N resources among grass and legume is constrained by hierarchical interactions for light capture that implies that any advantage taken by one species in N acquisition provokes a corresponding disadvantage for the other species in order to maintain the “average plant” dynamics at the whole plant population level. Soussana *et al.* (1999a,b) integrated such an interaction between light capture and N accumulation and repartition in their CANOPT model simulating the dynamics of *Lolium perenne* – *Trifolium repens* mixtures. The possibility for legume plants to obtain their nitrogen from two complementary sources (i) soil mineral N, and (ii) N₂ fixation, gives them a competitive advantage over grasses when soil N supply is low but, when a large supply of N occurs in soil, legumes are disadvantaged for light capture and light use efficiency, and their ability to fix N₂ declines. So changes in the balance between grass and legumes in swards will cause fluctuations in soil mineral N which in turn result in the complex dynamics of grass-legume populations characterised by cyclic dominance of one species over the other at patch level as stated in the models of Thornley *et al.* (1995) and Schwinning and Parsons, (1996a,b).

Similar approaches have been developed for P and K uptake in swards (Duru and Ducrocq, 1997; Duru and Thélier, 1997) demonstrating that, as for nitrogen, the uptake of minerals from soil is regulated at the whole plant population level. Nevertheless, for minerals with low mobility in soil like P and K, the uptake capacity of plants is directly associated to root growth, allowing the plants to exploit new micro-sites of soil (Caldwell, 1994). The aptitude of plants to form symbioses with mycorrhizal fungi allows them to explore a larger volume of soil. C exudation from roots is also very important to take into account for rhizosphere functioning (Bardget *et al.*, 1998) and the availability of insoluble chemical compounds of phosphorus (Macklon *et al.*, 1994). But the variations among grassland species (and ecotypes ?) for these characters are poorly documented, while they must play an important role in the vegetation dynamics of grasslands in low fertility soils. It is also important to consider that, as for mineral N in soil, the repartition of minerals like P and K is very heterogeneous, specially in grazed swards. So the foraging aptitude of plant species to exploit rapidly and intensively mineral rich patches through a very plastic root morphology should play an important role on the competition among species in a grazed community, except in situations where competition for light does not dominate.

Water is absorbed and transpired by a single plant in relation to the amount of solar energy intercepted so, as for N and mineral resources, competition for water among individual plants within a plant population is largely driven by competition for light. Moreover, water cannot be considered exactly as a “resource” for plant growth, but as a mean for dissipating the excess of solar energy received by leaves to avoid plant tissue desiccation and excess of temperature. So, in some circumstances, plants can derive benefice from

shading by their neighbours only by a decrease in their own water demand. But such a positive effect can not be maintained after the soil water resources are exhausted.

The most efficient way for an individual plant to maintain an advantage on its neighbours in dry conditions is to have a faster root development allowing (i) earlier water uptake from soil, and (ii) access to water resources in deeper soil horizons. Nevertheless, the results of Garwood and Williams (1967a,b) demonstrated that when the upper layer of the soil is dried, the growth of grasses can be impaired by reduction of the absorption of N and P-K, while the water consumption of the sward is maintained at an optimum level by absorption of water from deeper soil layers. Thus in dry conditions, the growth of plants having a deep root system can be reduced by a drought-induced N and P-K deficiency before a water stress occurs. A comparison between species having contrasting root development, (eg.. *Festuca arrundinacea* with deep roots poorly ramified in the upper soil layer and *Dactylis glomerata* with a shallow and very ramified root system) shows that, in dry conditions, the advantage of a deeper root system for water acquisition can be totally offset by the disadvantage of a less efficient acquisition of N and minerals from the upper soil layer (Lemaire and Denoix, 1987). The water use efficiency of *Dactylis glomerata* remains high even in dry conditions, while it declines rapidly for *Festuca arrundinacea* as the soil dries because water absorbed from deeper soil layers is not accompanied by an equivalent flux of nutrients. In fact, *D. glomerata* appears more drought resistant, not because of a higher “intrinsic” water-stress resistance, but only because of its ability to explore the upper soil layers more intensively and to continue to provide nutrients to its roots by maintaining a minimum mass-flow. Lemaire *et al.* (1997) found similar differences between maize and sorghum. So a part of “drought resistance” attributed to species can be largely re-examined in the light of this water-nutrient interaction in soil. This phenomenon can be greatly enhanced in permanent grazed swards where the restitution in N, P and K either by animal excreta or fertiliser applications are only concentrated upon the top 10 cm of soil. In these conditions, any short period of drought should disadvantage species which do not have a very dense root system in this soil layer. Grass roots form arbuscular mycorrhizae in most natural and agricultural ecosystems (Newman and Reddell, 1987). The role of mycorrhizae in providing plant rhizosphere in nutrient should play an important role in these conditions. It is also important to consider that we know virtually nothing of root-root interactions between different plants: are the different root systems inter-penetrating? or are they spatially exclusive? which role for root exudates and chemical signaling? Many further researches are necessary to answer these questions and to have a clearer view of the vegetation dynamics of complex plant communities in a large range of levels of intensification where soil constraints impose strong competition for nutrient resources.

After this short review, it appears clear that no resource can be considered independently of the others. In a dense sward, sharing of soil resources is largely driven by sharing for light. This dependence of root systems on energy captured by leaves imposes a strong hierarchy between competition for light and competition for soil resources among plants growing in dense canopies. As soon as all incident light is intercepted by a sward, plants have to compete for light and their hierarchical position within the canopy for light capture determines their further capacity for acquisition of nutrients from soil. But before this point of full interception of light is reached, the ability of each individual plant to acquire soil resources rapidly determines its own growth rate and its further light capture ability. With such a dynamic view of plant competition it is possible to reconcile the theory of Grime (1979) who postulated that competition for light was the most important phenomenon for vegetation dynamics, with the theory of Tilman (1982) who considered that nutrient acquisition and conservation by plants was the most important characteristic to consider for competition ability. In low soil fertility conditions, the rate of acquisition of nutrient is low,

and therefore plants grow very slowly and competition for light occurs very late or never. In these conditions, the competitive ability of individual plants for soil resources as determined by their root architecture and rhizospheric properties can be expressed. Tilman's theory indicates that in such a situation, the plants having the more efficient uptake capacity for the more limiting resource, and/or the ability to store and to conserve this resource by an efficient internal recycling, will dominate. But as the soil fertility increases, the competition for light begins earlier and is enhanced, and in these conditions the ability of plants to use nutrient resources efficiently for shoot growth in order to position their leaves in the illuminated layer of the canopy determines their competitive ability. So the study of the adaptive response of plants to shade appears very important for understanding the dynamics of competition during sward growth.

Adaptive response of plants to shading

Leaf Area Index (LAI) appears to be the major sward characteristic which determines the intensity of competition for light among individual plants. As the sward LAI reaches a value of 1, leaf areas overlap and some of the leaves become shaded. The first effect of shading for an individual plant is a reduction in C assimilation rate. As demonstrated by several experiments in controlled conditions, reduction in the level of light received by leaves leads to a preferential allocation of C assimilates to shoot growth at the expense of root growth (Ryle and Powell, 1976; Gastal and Saugier, 1986). Such a decrease in C supply of the plant has been demonstrated to depress N uptake capacity of the root (Gastal and Saugier, 1989), so such a response of plants to low irradiance can explain the effect of shading on N and P-K acquisition as discussed above. Moreover, this preferential allocation of C assimilates to shoot meristems can be interpreted as an adaptive response of plant which allows the shaded plants to develop faster their leaf area and stem internodes for further improving light capture. So plants can develop two different strategies for adaptation to shading in a dense plant community: (i) either a "shade tolerance" strategy that corresponds to a photosynthetic acclimation in response to low irradiance (Percy and Sims, 1994) and/or an increase in specific leaf area (Peace and Grubb, 1989) which allows the plant to minimise the reduction of its C supply, or (ii) a "shade avoidance" strategy that corresponds to an optimisation of allocation of C to shoot meristems in order to optimise the positioning of new leaf area in the less shaded layers of the canopy by mean of an increase in internode elongation, a reduced leaf:stem dry weight ratio and an increased shoot:root ratio (Ballaré *et al.* 1991a).

In the canopy, shade light is rich in far-red light and poor in blue light (Holmes and Smith, 1977). This spectral change is the consequence of preferential wavelength absorption by leaves (Varlet-Grancher *et al.*, 1993). Many studies (Morgan and Smith, 1981; Casal and Smith, 1989; Ballaré *et al.*, 1991b; Aphalo and Ballaré, 1995) have demonstrated that most plants are able to change their morphology and their allocation pattern of C in response to changes in light quality by means of photoreceptors sensitive either to the red:far-red ratio (phytochromes) or to blue light (cryptochromes). Robin *et al.* (1992) demonstrated in *Trifolium repens* that an enrichment in far-red light increased the lamina area and the petiole length of growing leaves. Far-red treatments also stimulated stolon internode elongation while branching rate was depressed. An ecological interpretation of these results can be given. *Trifolium repens* can be considered as a "shade avoiding" species with a colonising strategy composed of two elements: (i) "space exploring" through the modulation by phytochrome of the internode elongation rate and of branching, and (ii) "space exploiting" through the production and positioning of new leaf area by increased petiole length. Gautier *et al.* (1997, 1998) demonstrated that the decrease in blue light in the shade also has an influence on plant

growth habit by increasing petiole length and petiole angle from the horizontal, and by raising stolons above the ground surface allowing the growing points to reach more light. This high morphogenetic responsiveness of white clover to shading confers to this species a high competitiveness for light in a mixed sward (Davidson and Robson, 1985). Thus, as competition for light within the canopy increases and the red:far-red ratio and blue light lower in the canopy decrease, petiole length and lamina size increase while the emergence of axillary buds ceases and stolon internodes elongate more rapidly. The result of these changes in plant morphogenesis is that leaf surfaces are positioned in the well illuminated layer of the canopy, and the stolon growing points can escape the shaded area and perhaps encounter a patch with better illumination where branching could be re-activated for exploiting the local light resources (Simon *et al.*, 1989). These responses may be interpreted as “foraging” for improved habitat quality (Harper, 1977). Morphogenetic adaptation allows the plant to optimise its C supply, but is only beneficial if some stolon growing points reach an illuminated patch. As the plant avoids a shaded habitat, its C supply is low because the leaves are shaded and moreover a greater proportion of C is allocated to stolon internodes and petiole elongation, so the quantity of assimilate allocated to roots for their growth and maintenance and for nutrient uptake could be very low and insufficient to support shoot growth demand for a long period before the exploitation of a new illuminated habitat becomes possible. The stoloniferous growth habit of white clover gives this species the capacity to exploit spatially patchy environments (Lemaire and Chapman, 1996), but should lead to a rapid decline in plant population in a uniform shaded habitat when leaves cannot reach light either through vertical (petiole length) or horizontal (stolon internodes) strategy of shade avoidance.

For grass species light quality has also an effect on plant morphogenesis (Casal *et al.* 1987). Deregibus *et al.* (1983) shows that a decrease in red:far-red ratio within canopies provokes a reduction in tillering of *Lolium* spp..Gautier *et al.* (1999) demonstrated that both a reduction of the photosynthetic photon flux (quantity of light) and/or a reduction of red far-red ratio could have an effect on tillering of *Lolium perenne*, while a reduction in blue light has no effect. Tillering rate is the result of the leaf appearance rate, which determines the rate of appearance of new potential site for tillers (bud appearance), and site filling (Fs) which measures the rate of development of a bud into a tiller (Davies, 1974). Gautier *et al.* (1999) demonstrated that the quantitative effect of shading (reduction of the photosynthetic photon flux density alone, with a constant red:far-red ratio) reduced mainly the leaf appearance rate and slightly the site filling, while the qualitative effect of shading (reduction of red:far-red ratio with a constant photosynthetic photon flux density) has an effect mainly on site filling and no effect on leaf appearance rate. In other experiments Gautier and Varlet-Grancher (1996) demonstrated that a reduction in blue light with the same level of photosynthetic photon flux density has an effect on lamina and sheath size of *Lolium perenne* and *Festuca arundinacea* by means of an enhanced leaf elongation rate and/or an increase in leaf elongation duration. The investigations on responses of grasses to changes in light quality have been carried on only on tufted temperate grass species such as *Lolium* spp or *Festuca arundinacea*. Little is known about the response of stoloniferous grass species, but Cruz and Boval (2000) reported that in a *Digitaria decumbens* sward, stolon elongation rate increase drastically as the canopy closed with a LAI of 3. This result could indicate that, as for white clover, the stoloniferous grass species could have a “shade avoidance” strategy, but further investigations on a larger range of species are necessary.

The effect of shading on plant growth appears to be a very complex response of plants to several intimately inter-correlated signals all resulting from light extinction processes within plant canopies: reduction of the photosynthetic photon flux density which reduces the C supply of plants (trophic effect), change in light quality perceived by the plant through a

reduction in red:far-red ratio, and reduction in blue light (morphogenetic effects). Ballaré *et al.*, (1987) showed that plants are able to perceive the changes in light quality through the horizontal reflection of light by their neighbours before the quantity of light absorbed by the plant will be significantly reduced. So this “proximity” perception of their neighbours permits plants to make anticipatory responses by changes in the C allocation pattern before the C supply is too strongly affected by shading. The inhibition of branching and tillering by shading observed respectively in white clover and grass species, and the preferential allocation of C to the main shoot meristem, correspond to a change from a strategy of exploiting local light resources by horizontal colonisation of space through the proliferation of new vegetation units to a strategy of exploring more illuminated sites by vertical (sheath and petiole length) or horizontal (stolon) development. But such a supplemental investment in non-photosynthetic tissues can only be supported by a plant if its C supply is adequate. In a natural stand, the decrease in red:far-red occurs long before the decrease in photosynthetic photon flux density (PPFD) that prevents the development of tillers on grasses and axillary buds on white clover before any reduction in C supply, favouring the growth of the main tiller or stolon axis. Later, as the canopy develops, PPFD is reduced and a decrease in C supply may also affect tillering or branching. This shortage of C can lead to the mortality of emerging buds and of younger tillers and branches while the rapid extension of leaves on the main tiller or of internodes on the main stolon continue until the C supply of the plant becomes too low for root maintenance and nutrient acquisition. Then the plant will die, leading to self-thinning at the plant population level (Sackville-Hamilton *et al.*, 1995).

Part of the hierarchy developed between individual plants within a stand of vegetation for light capture and, therefore, for acquisition of soil resources, could be the result of such anticipated morphogenetic responses to light quality signals developed during the early stage of canopy development. The sensitivity in the perception of the presence of the neighbouring plants and the efficiency of the morphogenetic response to the signals could therefore play an important role in plant species competitiveness (Lemaire and Millard 1999). Further studies are necessary to define the inter- and intra-specific variability in photomorphogenetic response and to use this information in dynamic models of plant population.

Which plant traits for competitive ability?

Variations in the definition of “competition ability” by different authors (Goldberg, 1997) leads to differences in evaluation between species according to the environmental conditions (Aerts, 1999). Competitiveness of species is evaluated by different traits in situations where competition for light dominates the acquisition of soil resources and in situations where plants do not compete for light. According to Grime (1979) the intensity of competition increases as the soil resource availability increases corresponding to situations where plant growth capacities are enough to permit the whole plant population to capture most of the light resource. So the species with the higher competitive ability is that which develops more rapidly a more adapted architecture for light capture: a rapid leaf area expansion and a rapid colonisation of the upper layer of the canopy by sheath, petiole or stem internode elongation. Nevertheless, according to Tilman (1982) competition can be also intense in poor soil resource environments, and in these conditions the more competitive plant is that which has the lower requirement for the more limiting resource in the situation considered. Tilman’s theory is based on the concept of “resource conservation” within the plant: as the time of residence of one resource within a plant increase, this resource becomes more efficient and in consequence it can be acquired in lower quantity for maintaining the plant alive. This minimum resource demand for the plant, named R^* in Tilman’s theory, can be variable among plant species according to their ability to maintain their leaves alive during

a given period of time. Species with long leaf life span should have lower R^* values for N and P resources and therefore should persist better in a poor soil conditions than species with short leaf life span. Berendse and Elberse, 1990, and Berendse, 1994 reconciled Tilman's and Grimes' theories, indicating that in a fertile soil conditions the more competitive species are those having a high rate of acquisition of soil resources, enhancing shoot growth for a rapid light capture, while in poor soil conditions species with low growth rate associated with high degree of internal conservation of resource should dominate. Thus, for the majority of herbaceous plant species the ability for acquiring and conserving resources can be described by leaf traits (Poorter and Garnier, 1999). Such traits (i.e. specific leaf area, dry matter content of leaf, leaf N% and leaf life span) can be used to describe differences in functioning, allowing a rapid classification between "slow" and "fast" growing species (Garnier *et al.*, 1999). It is clear that even if these traits have a clear ecophysiological significance, they are not sufficient for characterising plant competitive ability. Other morphological traits such as leaf area ratio, or shoot:root ratio should have also an important role in optimising C allocation for light capture. But these traits are not only specific characteristics of plant species, but also they result from adaptive responses of plants to competition for light. As demonstrated above, plants dominated by their neighbours in a plant stand show a more rapid decline in their leaf area ratio and root:shoot ratio than dominant plants. So differences in these morphological traits observed at a given date between plant species of the same community may reveal more a difference in their hierarchical position within the stand than an intrinsic difference between species. Only dynamics studies using these morphological traits could allow a distinction between intrinsic competitive ability of one species and its response to given intensity of competition within a plant stand.

The ecophysiological approach of plant competition we develop here tends to consider competition for light as the more important mechanisms determining the sharing of other resources. But the aptitude of plants for nutrient acquisition in soil largely determines the success of these plants in competition for light and, as demonstrated above, plants, which have a dominant position in the canopy continue to have a large access to soil resources that reinforce their competitiveness. So there exists a strong interaction between competition for light and competition for nutrients in soil, any success in one type of competition reinforcing the chance of success in the other. In this way, as soon as a plant dominates its neighbours, its competitive advantage increases and the gap between dominant and dominated plant continuously increases, until the death of the more dominated individuals occurs when no more light can be captured at the plant population level. Then, as described many times for diverse plant species, the density of individual plants declines allometrically with increasing average plant mass with a coefficient of $-3/2$, indicating an isometric growth of the average plant population (Sackville-Hamilton *et al.*, 1995). So the self-thinning law, which describes the size-density relationship of a plant population having intercepted all the incident light, appears to be the final stage of the processes of competition for light which imposes a morphological adaptation of the plant population through the photomorphogenetic responses of individual plants. Such an evolution of the plant population can only be stopped or reversed by a disturbance such as a defoliation which allows the dominated plants to survive and possibly to recover.

Response and adaptation of plant to defoliation

Plants in grazed communities experience intermittent defoliations the severity and frequency of which mainly depend on grazing animals, stocking density and grazing management rules (Wade and de F. Carvalho, 2000). Each defoliation event represents for the plant a disturbance in its growth, and therefore will interfere with its competitive ability in

population dynamics. Plant responses to the disturbance of defoliation can be viewed as having the goal of restoring and maintaining homeostatic growth patterns where all resources are used in a balanced way for optimal plant growth (Lemaire and Chapman, 1996). But in a grazed community, defoliations does not affect only a single plant but also its neighbours, so the defoliation at patch level can also be viewed as a way by which competition for light is removed. Thus, the overall response of a single plant to defoliation in a grazed community appears to be a complex mechanisms depending not only on the severity and intensity of defoliation experienced by the plant itself, but also on the pattern of defoliation of its neighbours. So depending on the selective grazing behaviour of animals for different plant species, or different morphological types of plants, competitiveness of different plants within a complex grazed community could be greatly influenced by grazing management (Crawley, 1983; Louda *et al.*, 1990).

The response of plants to grazing can be studied by using the concept of grazing resistance (Briske, 1986). Briske (1996) considered that grazing resistance can be divided into “grazing avoidance” and “grazing tolerance”. Tolerance mechanisms are concerned with short-term physiological acclimatisation to the restriction of carbohydrate supply for plant growth resulting from removal of photosynthetic tissues and restoration of rapid regrowth, while tolerance mechanisms involve longer-term morphological adaptation allowing the plant to reduce the probability and severity of further defoliations.

Physiological responses of plants to defoliation

The first immediate effect of defoliation on a plant is to reduce its leaf area and therefore the light intercepted. The consequence of this reduction of light capture on C economy of the plant depends on (i) the proportion of plant leaf area removed, (ii) the degree of defoliation of the neighbouring plants, and (iii) the photosynthetic capacity of the leaf tissue remaining after defoliation. So a single lenient defoliation could lead to only a slight reduction of the C assimilation rate at whole plant level and even to a positive effect if it is accompanied by the removal of surrounding leaves of the neighbouring plants. As defoliation becomes more severe, the proportion of remaining leaf tissues is too low to ensure the C supply for the plant even though these tissues becomes exposed to full light. Previously shaded leaves are unable to readapt their photosynthetic machinery to high irradiance (Prioul, 1971, Woledge, 1973). So after a severe defoliation, the C supply of the plant becomes too low in comparison with C demand for maintenance and growth, and the C budget of the plant becomes temporarily negative, until a sufficient new leaf area, with high photosynthetic capacity is restored (Richards, 1993). So the main physiological adaptation of plants recovering from defoliation concerns preferential C allocation to shoot meristems (Ryle and Powell, 1975; Schnyder and de Visser, 1999) for maximising new leaf area expansion. Additional morphological adaptations of the new expanding leaves such as an increase in specific leaf area (SLA, $\text{m}^2 \text{g}^{-1}$) allow a more efficient leaf area expansion and exposure (van Loo, 1993). Such a preferential allocation of C to shoot meristems in a situation of low C supply, due to leaf area removal, inevitably provokes a strong C shortage in roots. Studies on numerous C3 and C4 grasses have demonstrated that root growth ceases after removal of 50% or more of the leaf area (Richards, 1993). Nevertheless Dawson *et al.* (2000) found that differences of response to defoliation exist between plant species within the same pasture community.

As mineral N absorption or N_2 -fixation seem to be related to the flow of current C assimilates in the roots (Lemaire and Millard, 1999), defoliation can provoke a temporary decrease in plant N uptake until the C supply of plant has been restored through new leaf area expansion, as demonstrated by Kim *et al.* (1991) on *Medicago sativa*. So the plant recovering

from a severe defoliation has a contradiction to solve: it has to use preferentially carbon assimilates for rapid leaf area recovery, but the root C deficiency prevents the acquisition of N resources necessary for rapid leaf growth. This contradiction can be solved by C and N reserve storage and utilisation, that represents an important physiological adaptation of plants to defoliation (Thornton *et al.*, 2000). Several authors have studied the dynamics of mobilisation of N reserves from stubble and roots of grasses to new expanding leaves (Ourry *et al.*, 1990; Millard *et al.*, 1990; Thornton *et al.*, 1994), demonstrating that nitrogen previously stored in stubble can be rapidly recycled within the plant and used for new lamina extension until a sufficient C supply is achieved for the restoration of the N uptake capacity of the plant. Avice *et al.*(1996) demonstrated that, on defoliated plants of lucerne, carbohydrates stored as starch in the tap root during the preceding growth period are not directly used for new leaf growth after defoliation but are respired for maintenance of the root system during the period of negative C budget for the plant. Avice *et al.* (1997) demonstrated also that the capacity of regrowth of a lucerne plant after defoliation was directly linked to its level of root N reserve and not to the level of its carbohydrate reserve. Moreover, Avice *et al.* (1997) demonstrated that the dominated plants within a lucerne stand had very low N reserves in their tap root. Because they were shaded during the preceding regrowth period they was unable to uptake enough N for reserve formation, and then, when defoliated, they regrew very slowly compared to the dominant plants. So even if defoliation allows the shaded plant to recover full light, the effect of competition for light experienced by plants during the period before defoliation plays an important role in the subsequent regrowth period giving an initial disadvantage to the dominated plants that should lead to increasing differences among plants within the stand. In this way it is possible to explain the gradual decrease in plant density of lucerne stands during successive cuttings (Gosse *et al.*, 1988). So, due to the strong interaction between light capture and N uptake capacity, if a plant has been severely shaded its capacity to recover after defoliation could be too low and it will experience stronger and stronger competition for light until it dies. In this sense, defoliation can be viewed as accelerating plant population dynamics. Such a result has been obtained on *Medicago sativa*, a species which is not morphologically adapted to defoliation in the sense that all the leaf area and all the shoot apices are removed by cutting. Thus the shortage of C supply is high and the delay for new leaf area expansion is long, because new axillary buds are to be activated before new leaves emerge. For grass species the intercalary meristems responsible for leaf expansion are enclosed in the basal 4 cm of the tube sheath and are not removed by defoliation (Schnyder *et al.* 2000). Schäufele and Schnyder (2000) show that a severe defoliation affects the activity of the leaf growth zone leading to an important but small transient reduction of the leaf elongation rate. Thus, grasses rapidly recover a minimum leaf area after defoliation. Schnyder and de Visser (1999) showed that 82% of the new exposed foliage at 2 days after defoliation was contributed by cut leaves which were actively expanding at that time, and that the current photosynthesis contributed to about 87% of the C incorporation in regrowing tillers. So for grass species, the protection of basal leaf meristems from defoliation allows a rapid refoliation of the defoliated plants and the restoration of a positive C balance within a few days. For these species, the refoliation process is a continuous meristematic activity largely initiated before defoliation and only slightly and temporarily disturbed by it. This morphological adaptation gives these species a considerable competitive advantage in grazing situations in comparison with species like lucerne for which the recovery of a positive C balance after a severe defoliation takes at least 10 to 15 days (Avice *et al.*, 1996) because a new meristematic activity has to be initiated.

Adaptation of plants to defoliation: morphological plasticity

As grass plants are defoliated they develop a more or less adapted morphology in order to maintain some green leaf area under the height of defoliation, thus minimising the impact of further defoliation and therefore optimising their refoliation dynamics. So, plants can develop phenotypic plasticity as a progressive and reversible modification of their morphological traits (Chapman and Lemaire, 1993). This phenotypic plasticity, linked to defoliation, cannot be separated from the photomorphogenetic responses because, as discussed above, according to severity and frequency of defoliation the light micro-environment of plant changes.

The diagram of plant morphogenesis developed by Chapman and Lemaire (1993) and represented in Figure 1 allows the identification of the major morphogenetic characteristics of grass plants which determine sward structure. On this diagram, the feedback effect of competition for light mediated by the sward LAI through photomorphogenetic responses is indicated. So, the first effect of a defoliation pattern in terms of frequency and severity, as determined by a grazing management programme, is to maintain variations in sward LAI between two extreme values. This determines the amplitude of the plastic response the plant has to develop, and also the time scale at which the plant has to adapt to its environmental change. Under frequent defoliation resulting from continuous stocking management with high stocking density, there is little competition for light due to the constant leaf area removal, so the plant can develop a photomorphogenetic response to a more or less constant full light micro-environment. Moreover, each defoliation event concerns only a part of the leaf tissues and the plant architecture is not deeply modified. In these situations, characterised by high red:far-red ratio and high blue light, plants develop short leaves and high tiller density (Mazzanti *et al.* 1994). In contrast, under infrequent defoliation as in strip grazing or cutting management, competition for light continuously increases during the regrowth period, and each defoliation event corresponds to (i) a rapid change in the light micro-climate of the plant, and (ii) a rapid change in its architecture as this type of defoliation is generally very severe. In these situations, the plants tend to develop long leaves and to have a reduced tillering rate. Several phenomenological studies have been developed to describe the process of these morphological adaptations, linking leaf size and tiller density (see the recent review of Nelson, 2000). As stated by Huber *et al.* (1999) the phenotypic plasticity responsible for morphological and architectural adaptation of the plant to its environment has to be clearly distinguished from ontogeny. Thus, the phyllochron (Ph), the reciprocal of the leaf appearance rate (LAR), is an ontogeny event which plays a strategic role in the morphological adaptation of plant to defoliation. According to the diagram in Figure 1, any change in LAR due to temperature or light quality will have an effect on (i) leaf size, (ii) maximum number of leaves per tiller, and (iii) tiller density. Lemaire and Agnusdei (2000) show the dependence of both the final leaf length (FLL) and the maximum number of living leaves (NLL) from the variations in LAR:

$$\text{FLL} = \text{LED} \cdot \text{LAR} \quad (5)$$

with:

$$\text{LED} = a \cdot \text{LAR} \quad (6)$$

and:

$$\text{NLL} = \text{LLS} \cdot \text{LAR} \quad (7)$$

with LER as Leaf Elongation Rate, LED as Leaf Elongation Duration, *a* as the number of growing leaves per tiller, and LLS as Leaf Life Span. Figures 2 and 3 show that these equations hold for several C3 and C4 species in a grazed community of the Humid Pampa in

Argentina. So, as shown by Bahmani *et al.* (2000) for different genotypes of *Lolium perenne*, any decrease in LAR resulting from changes in light quality in growing sward (see discussion above) leads to an increase in final leaf length resulting from an increase in both leaf elongation rate (LER) and leaf elongation duration (LED), the value of coefficient a being unaffected by shading. Durand *et al.* (2000) developed a model based on the ontogeny of development of successive leaves on grass tillers. This model states that the development of two successive leaves on a tiller is intimately co-ordinated through a signal perceived by the tip of the growing lamina when emerging in the full light at the top of the tube sheath of the preceding leaf. Using the basic knowledge on leaf growth zone dynamics (Durand *et al.* 1999; Schnyder *et al.* 2000) this model shows that the length of the tube sheath of a leaf should determine the length of the following emerging leaf which should have inevitably a little bit longer tube sheath, and therefore the ontogenetic increase in leaf size of grass plant can be easily explained by very simple rules for leaf development. Moreover, such a model seems able to account for the modification of plant ontogeny through its response to light quality: if the signal perceived by lamina tip is altered by changes in light quality (blue light or red:far-red ratio) then the response in term of co-ordination of leaf development can be delayed (or attenuated ?). That could explain the decrease in LAR observed in shaded situations and the correlated increase in leaf elongation duration and leaf elongation rate which, resulting in increased tube sheath length, should provoke an acceleration of the ontogeny dynamics of the plant. In the reverse case, any defoliation which artificially reduces the tube sheath length should avoid the ontogenetic increases in leaf size and should maintain the plant in conditions of production of small leaves. If such a defoliation is repeated at relatively frequent intervals, less than or equal to the phyllochrone, all the leaves successively produced should be short, as observed on frequently grazed swards. Duru and Ducrocq (2000a,b) verified that growth of successive leaves of *Dactylis glomerata* were affected by the tube sheath length of the preceding leaves. Such a result has also been obtained by Davies *et al.* (1983) when tube sheath length is manipulated artificially.

Tiller production by plants is severely down-regulated by the sward LAI (Simon and Lemaire, 1987). The progressive decreases in LAR as the sward canopy develops, resulting from plant response to change in light quality (see discussion above), is the first cause of the reduction of tillering rate. As shading becomes more severe, site filling or site usage (Skinner and Nelson, 1992) becomes also affected (Bahmani *et al.*, 2000). As discussed above, when shading affects also the C supply of plant, competition for C allocation between expanding leaves and axillary buds could emphasise the decreases in tillering rate as resulting from photomorphogenetic responses of plants, generating the overall correlation generally observed between tiller size and tiller density. But as developed extensively by Nelson (2000) the coordination between leaf growth and tiller appearance is strongly genetically determined, even if very sensitive to phenotypic adaptation in response to environmental modifications. So the integrated response of grass plants to frequent defoliations, which lead to sheath length being maintained just lower than the defoliation height, allows the plant to maintain some green photosynthetically active lamina protected from defoliation, and therefore to minimize effects of defoliation on C supply. Moreover, the reduced leaf growth as a consequence of tube sheath shortening avoids too high a competition within the plant for C and N allocation between elongating leaves and tiller buds, and thus allows the plant to maintain tillering rate close to its potential level as determined by maximum site usage. The tiller dynamics of grazed swards have been intensively analysed by Matthew *et al.* (1995) and Matthew *et al.* (2000). These last authors developed two conceptual parameters for analysing genetical and environmental determinants of tiller dynamics: (i) the morphological ceiling leaf area (MCLA) representing the maximum leaf area per tiller, together with the maximum number of tillers a sward can attain according to its morphological characteristics such as leaf size and

maximum number of leaves per tiller, and (ii) the environmental ceiling leaf area (ECLA) representing the maximum leaf area a given environment characterised by its level of light can support before all light is captured and any new leaf area produced provokes the senescence and death of existing leaves. When MCLA is less than ECLA new tillers can appear, while when MCLA becomes greater than ECLA, young tillers die leading to the self-thinning process. By this means it should be possible to develop a model for analysis of tiller dynamics of different plant species and cultivars according to variation in environment (seasons, N nutrition...) and grazing management, taking into account the specific parameters describing morphological co-ordinations between leaf and tiller development.

Even if this general model of plant morphogenesis and its mechanistic components at meristematic level are now well known for tufted temperate grass species (Nelson *et al.* 2000) very little is known about the genetical determinism of some of the parameters either between species or among ecotypes of the same species. Also, very little is known about the degree of generalisation of such a model for stoloniferous plants. It is clear that some small variation in the leaf-tiller development co-ordination pattern could confer great differences in competitive ability between plants submitted to different grazing managements.

Conclusion

This review has developed a limited concept of plant population dynamics in grazed communities. The approach developed was restricted to the analysis of morphological and physiological traits of individual plants for competition with their neighbours in their own environment. So the analysis was confined to the elements of plant population dynamics at patch scale that corresponds to the environment an individual plant is able to perceive. Obviously, scaling from patch to paddock or to grassland area requires more information that has not been discussed in this paper. Interference between plants at long distances are mediated by herbivores through their spatially explicit grazing behaviour and deposition of excreta that determine the spatial heterogeneity dynamics of the grazed area (see Parsons *et al.* 2000 and Laca, 2000). So the spatial heterogeneity created in a grazed area can diversify the ecological niches for maintaining a high diversity within a plant population. Implications for white clover grass mixtures have been shown by the model developed by Schwining and Parsons (1996a,b). Such a model could be extended for more complex grazed communities as in extensive grazing situations. The second aspect not taken into account in this paper is related to the dynamics of invasive species by means of either clonal or reproductive dispersion. For controlling the invasion of undesirable species, it is necessary to know not only their dispersal ability through seed and ramet multiplication and dispersion, but also their morphological traits for young plant recruitment and survival (Magda, 1998). These morphological characteristics should be analysed with the same conceptual basis as that developed for pasture species in this paper. In this way it should be possible to develop a more global approach of vegetation dynamics linking both ecophysiological and agronomical views with the more general concepts developed in ecology and plant population dynamics.

Acknowledgments

The author thanks Prof. John Hodgson for his help in revising and improving the manuscript.

References

Aerts, R. (1999). Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedback. *Journal of Experimental Botany* **50**: 29-37.

- Aphalo, P.J. and Ballare C.L.** (1995). On the importance of information acquiring systems in plant-plant interactions. *Functional Ecology* **9**: 5-14.
- Avice, J.C., Oorry A., Lemaire G. and Boucard J.** (1996). Nitrogen and carbon flows estimated by ^{15}N and ^{13}C pulse-chase labelling during regrowth of alfalfa. *Plant Physiology* **112**: 282-290.
- Avice, J.C., Oorry A., Lemaire G., Volenec J.J. and Boucard J.** (1997). Alfalfa intraspecific competition and the involvement of reserve ability. *Crop Science* **37**: 1187-1193.
- Bahmani, I., Hazard L., Varlet-Grancher C., Betin M., Lemaine G., Matthew C. and Thom E.R.** (2000). Differences in tillering of long- and short-leaved perennial ryegrass genotypes under full light and shade treatments. *Crop Science* (in press).
- Ballare, C.L., Sanchez R.A., Scopel A.L. and Casal J.J.** (1987). Early detection of neighbour plants by phytochrome perception of spectral changes in reflected sunlight. *Plant Cell Environment* **10**: 551-557.
- Ballare, C.L., Scopel A.L. and Sanchez R.A.** (1991a). Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. *Plant Cell Environment* **14**: 57-65.
- Ballare, C.L., Scopel A.L. and Sanchez R.A.** (1991b). On the opportunity cost of the photosynthate invested in stem elongations mediated by phytochrome. *Oecologia*, **86**: 561-567.
- Bardget, R.D., Wardle D.A. and Yeates G.W.** (1998). Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biology and Biochemistry* **30**: 1867-1878.
- Begon, M., Harper J.L. and Townsend C.R.** (1986). *Ecology, individuals, populations and communities*. Oxford: Blackwell Scientific.
- Beredense, F. and Elberse W.T.** (1990). Competition and nutrient availability in heathland and grasslands ecosystems. In: Grace J.B. and Tilman D. (eds) *perspectives on Plant Competition*; San Diego: Academic Press, pp 93-116.
- Beredense, F.** (1994). Ecosystem stability, competition, and nutrient cycling. In: Schulze E.D. and Mooney H.A. (eds) *Biodiversity and Ecosystem Function*, Berlin Heidelberg: Springer-Verlag, pp 409-431.
- Briske, D.D.** (1986). Plant response to defoliation: morphological considerations and allocation priorities; In: Joss P.L., Lynnh P.W. and Williams O.B. (eds) *Rangelands: A Resource Under Siege*. Cambridge University Press, Sydney, pp. 425-427.
- Briske, D.D.** (1996). Strategies of plant survival in grazed systems: a functional interpretation. In: Hodgson J. and Illius A.W. (eds) *The Ecology and management of Grazing Systems*. Wallingford (UK), CAB International, pp. 37-67.
- Caldwell, M.M.** (1994). Exploiting nutrients in fertile soil micro-sites. In: Caldwell M. and Percy R.W. (eds.) *Exploitation of environmental heterogeneity by plants. Ecological processes above- and below-ground*. San Diego: Academic Press, 325-347.
- Casal, J.J., Sanchez R.A. and Deregibus V.A.** (1987). The effect of light quality on shoot extension growth on three species of grasses. *Annals of Botany* **59**: 1-7.
- Casal, J.J. and Smith H. (1989). The function, action and adaptative significance of phytochrome in light-grown plants. *Plant Cell Environment*, **12**: 855-862.
- Chapman, D.F. and Lemaire G.** (1973). Morphogenetic and structural determinants of plant regrowth after defoliation. In: Baker M.J. (ed.) *Grassland of Our World*. SIR Publishing, Wellington, pp 55-64.
- Crawley M.J.** (1983). *Herbivory: The Dynamics of Animal-Plant Interactions*. Blackwell Scientific Publications. Oxford.

- Cruz P. and Lemaire G.** (1986). Analyse des relations de compétition dans une association de luzerne (*Medicago sativa* L.) et de dactyle (*Dactylis glomerata* L.). 2) Effets sur la nutrition azotée des deux espèces. *Agronomie* **6**: 735-742.
- Cruz P. and Soussana J.F.** (1997). The nitrogen requirement of major agricultural crops: mixed crops. In: Lemaire G. (ed.), *Diagnosis of the Nitrogen Status in Crops*. Springer-Verlag, Heidelberg, pp 131-144.
- Cruz P. and Boval M.** (2000). Effect of nitrogen on some morphological traits of temperate and tropical perennial forage grasses. In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press).
- Davidson, I.A. and Robson M.J.** (1985). Effect of nitrogen supply on the grass and clover components of simulated swards grown under favourable environmental conditions. *Annals of Botany*, **55**: 685-695.
- Davies, A.** (1974). Leaf tissue remaining after cutting and regrowth in perennial ryegrass; *Journal of Agricultural Science (Cambridge)* **82**: 165-172.
- Davies, A., Evans M.E. and Exley J.K.** (1983). Regrowth of perennial ryegrass as affected by simulated leaf sheaths. *Journal of Agriculture Science (Cambridge)* **101**: 131-137.
- Dawson, L.A., Grayston S.J. and Paterson E.** (2000). Effects of grazing on the roots and rhizosphere of grasses. In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press).
- De Candolle, A.L.** (1820). Essai élémentaire de géographie botanique.
- Deregibus, V.A., Sanchez R.A. and Casal J.J.** (1983). Effect of light quality on tiller production in *Lolium* spp. *Plant Physiology* **72**: 900-902.
- De Vit, C.T. and Van Den Bergh J.P.** (1965). Competition between herbage plants. *Netherlands Journal of Agriculture Science* **13**: 212-221.
- Durand, J.L., Schäufele R. and Gastal L F.** (1999). Grass leaf elongation rate as a function of developmental stage and temperature: morphological analysis and modelling. *Annals of Botany* **83**: 577-588.
- Durand, J.L., Gastal F. and Schäufele R.** (2000). Dynamic model of leaf length for investigating the response of feeding value of grass swards to cutting height, cutting frequency and temperature. In: Soegaard K., Ohlson C., Sehested J., Hutchings N.J. and **Kristensen T.** (eds.) *Grassland Farming. Balancing environmental and economic demands*. European Grassland Federation, Grassland Science in Europe, Aalborg, Denmark, pp182-184.
- Duru, M., Lemaire G. and Cruz P.** (1997). The nitrogen requirement of major agricultural crops: grasslands. In: Lemaire G. (ed.), *Diagnosis of the Nitrogen Status in Crops*. Springer-Verlag, Heidelberg, pp 59-72.
- Duru, M. and Ducrocq H.** (1997). A nitrogen and phosphorus herbage nutrient index as a tool for assessing the effect of N and P supply on the dry matter yield of permanent pastures. *Nutrient Cycling in Agroecosystems*, **47**: 59-69.
- Duru, M. and Thelier L.** (1997). N and P-K status of herbage: use for diagnosis of grasslands. In: Lemaire G. and Burns I. (eds.) *Diagnostic procedures for crop N management*. INRA Editions Paris, pp 125-138.
- Duru, M. and Ducrocq H.** (2000a). Growth and senescence of the successive grass leaves on a tiller. Ontogenic development and effect of temperature. *Annals of Botany* (in press)
- Duru, M. and Ducrocq H.** (2000b). Growth and senescence of the successive leaves on a cocksfoot tiller. Effect of nitrogen and cutting regime. *Annals of Botany* (in press).
- Fournier, C. and Andrieu B.** (1998). A 3D architectural and process-based model of maize development; *Annals of Botany* **81**: 233-250.

- Fournier, C. and Andrieu B.** (1999). ADEL-Maize: an L-system based model for integration of growth processes from organ to the canopy. Application to regulation of morphogenesis by light availability. *Agronomie* **19**: 313-327.
- Garnier, E., Farrar J.F., Poorter H. and Dale J.E.** (1999). *Variation in Leaf Structure. An Ecophysiological Perspective*. Cambridge: Cambridge University Press.
- Garwood, E.A. and Williams T.E.** (1967a). Soil water use and growth of a grass sward. *Journal of Agricultural Sciences Cambridge* **68**: 281-292.
- Garwood, E.A. and Williams T.E.** (1967b). growth water use and nutrient uptake from subsoil by grass swards. *Journal of Agricultural Sciences Cambridge* **69**: 125-130.
- Gastal, F. and Saugier B.** (1986). Alimentation azotée et croissance de la fétuque élevée. 1)- Assimilation du carbone et répartition entre organes. *Agronomie* **6**: 157-166.
- Gastal, F. and Saugier B.** (1989). Relationships between nitrogen uptake and carbon assimilation in whole plants of tall fescue. *Plant Cell Environment* **12**: 407-418.
- Gautier, H. and Varlet-Grancher C.** (1996). Regulation of leaf growth by blue light. *Physiologia Plantarum* **98**: 424-430.
- Gautier, H., Varlet-Grancher C. and Baudry N.** (1997). Effects of blue light on the vertical colonisation of space by white clover and their consequences for dry matter production. *Annals of Botany* **80**: 665-671.
- Gautier, H., Varlet-Grancher C. and Baudry N.** (1998). Comparison of horizontal spread of white clover (*Trifolium repens* L.) grown under two artificial light sources differing in their content of blue light. *Annals of Botany* **82**: 41-48.
- Gautier, H., Varlet-Grancher C. and Hazard L.** (1999). Tillering response to the light environment and to defoliation in population of perennial ryegrass (*Lolium perenne* L.) selected for contrasting leaf length. *Annals of Botany* **83**: 423-429.
- Goldberg, D.E.** (1990). Components of resource competition in plant communities. In: J.B. Grace and J; Tilman, eds. *Perspectives on plant competition*, San Diego: Academic Press, 27-49.
- Goldberg, D.E.** (1997). Competitive ability: definitions, contingency and correlated traits. In: Silverstone J., Franco M; and Harper J.L. (eds) *Plant Life Histories*, Cambridge: Cambridge University Press, pp283-306.
- Gosse, G., Lemaire G., Chartier M. and Balfourier F.** (1988). Structure of a lucerne population (*Medicago sativa* L.) and dynamics of stem competition for light during regrowth. *Journal of Applied Ecology* **25**: 609-617.
- Grace, J.B.** (1995). On the measurement of plant competition intensity . *Ecology* **76**: 305-308.
- Greenwood, D.J., Lemaire G., Gosse G., Cruz P., Draycott A. and Neeteson J.J.** (1990). Decline in percentage N of C3 and C4 crops with increasing plant mass. *Annals of Botany* **66**: 425-436.
- Grime, J.P.** (1979) *Plant Strategies and Vegetation Processes*. London: Willey.
- Harper, J.L.** (1977) *Population Biology of Plants*. Academic Press, London.
- Hirose, T., Werger M.J.A., Pons T.L. and van Rheenen** (1988). Canopy structure and leaf nitrogen distribution in stand of *Lysimachia vulgaris* L. as influenced by stand density. *Oecologia* **77**: 145-150.
- Holmes, M.G. and Smith H.** (1977). The function of phytochrome in the natural environment. 2) The influence of vegetation canopies on the spectral energy distribution of natural daylight. *Photochemistry and Photobiology*, **25**: 539-545.
- Huber, H., Lukacs S. and Watson M.S.** (1999). Spatial structure of stoloniferous herbs: an interplay between structural blue-print, ontogeny and phenotypic plasticity. *Plant Ecology* **141**: 107-115.

- Jones, C.A. and Kiniry J.R.** (1986). CERES-Maize, a simulation model of maize growth and development. T&M University Press, College Station, USA.
- Kasperbauer, M.J., Hunt P.G. and Sojka R.E.** (1984). Photosynthate partitioning and nodule formation in soybean plants that received red or far-red light at the end of the photosynthetic period. *Physiologia Plantarum* **61**: 549-554.
- Keddy, P., Fraser L.H. and Wisheu I.C.** (1998). A comparative approach to examine competitive response of 48 wetland plant species. *Journal of Vegetation Science* **9**: 777-786.
- Kim, T.H., Ourry A., Boucard J. and Lemaire G.** (1991). Changes in source-sink relationship for nitrogen during regrowth of lucerne following removal of shoots. *Australian Journal of Plant Physiology* **18**: 593-602.
- Laca, E.A.** (2000). Modelling spatial aspects of plant-animal interactions. In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press)
- Lemaire, G. and Denoix A.** (1987). Croissance estivale en matière sèche de peuplements de fétuque élevée et de dactyle dans l'Ouest de la France. 2) Interaction entre les niveaux d'alimentation hydrique et de nutrition azotée. *Agronomie* **7**: 381-389.
- Lemaire, G., Onillon B., Gosse G., Chartier M., Allirand J.M.** (1991). Nitrogen distribution within a lucerne canopy during regrowth: relation with light distribution. *Annals of Botany* **68**: 483-488.
- Lemaire, G. Khaithy M., Onillon B., Allirand J.M., Chartier M. and Gosse G.** (1992). Dynamics of accumulation and partitioning of N in leaves, stems and roots of lucerne (*Medicago sativa* L.) in a dense canopy. *Annals of Botany* **70**: 429-435.
- Lemaire, G.** (1993). Ecophysiological approaches to intercropping. In: Sinoquet H. and Cruz P. eds. *Ecophysiology of Tropical Intercropping*, INRA Edition, Paris, pp 9-25
- Lemaire, G. and Gastal F.** (1997). N uptake and distribution in plant canopies. In: G. Lemaire (ed.) *Diagnosis of the Nitrogen Status in Crops.*, Springer-Verlag, Heidelberg, pp 3-44.
- Lemaire, G. and Chapman D.** (1996). Tissue flows in grazed plant communities. In: J. Hodgson and A.W. Illius (eds), *The Ecology and Management of Grazing Systems*, CAB International, Wallingford (UK), pp 3-36.
- Lemaire, G., Hebert Y. and Charrier X.** (1997). Nitrogen uptake capacities of maize and sorghum crops in different nitrogen and water supply conditions. *Agronomie* **16**: 231-246.
- Lemaire G. and Millard P.** (1999). An ecophysiological approach to modelling resource fluxes in competing plants. *Journal of Experimental Botany* **50**: 15-28.
- Lemaire, G. and Agnusdei M.** (2000). Leaf tissue turn-over and efficiency of herbage utilisation. In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press)
- Louda, S.V., Keeler K.H. and Holt R.D.** (1990). Herbivore influences on plant performance and competitive interactions. In: Grace J.B. and Tilman D. (eds) *Perspectives on Plant Competition*, San Diego: Academic Press, pp. 414-443.
- Macklon, A.E.S., Mackie-Dawson L.A., Sim A., Shand C.A. and Lilly A.** (1994). Soil P resources, plant growth and rooting characteristics in nutrient poor upland grasslands. *Plant and Soil* **163**: 257-266.
- Magda, D.** (1998). Effects of grassland extensification on the population dynamics on the invasive species *Chaerophyllum aureum*. *Journal of Vegetation Science* **9**: 409-416.
- Matthew, C., Lemaire G., Sackville-Hamilton N.R. and Hernandez-Garay A.** (1995). A modified self-thinning equation to describe size/density relationships for defoliated swards. *Annals of Botany* **76**: 579-587.

- Matthew, C., Assuero S.G., Black C.K. and Sackville-Hamilton N.R.** (2000). Tiller dynamics in grazed swards. In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press)
- Mazzanti, A., Lemaire G. and Gastal F.** (1994). The effect of nitrogen fertilisation upon herbage production of tall fescue swards continuously grazed with sheep. 1) Herbage growth dynamics. *Grass and Forage Science* **49**: 111-120.
- Millard, P., Thomas R.J. and Buckland S.T.** (1990). Nitrogen supply affects the remobilization of nitrogen for the regrowth of defoliated *Lolium perenne* L.. *Journal of Experimental Botany* **41**: 941-947.
- Morgan, D.C. and Smith H.** (1981). Non-photosynthetic responses to light quality. In: Lange O.L., Nobel P.S., Osmond C.B. and Ziegler H. (eds), *Physiology and Plant Ecology, Encyclopedia of Plant Physiology*. Springer-Verlag, Berlin, pp 109-134.
- Nelson, C.J.** (2000). Shoot morphological plasticity of grasses: leaf growth vs. tillering. . In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press).
- Newman, E.I. and Reddell P.** (1987). The distribution of mycorrhizae among families of vascular plants. *New Phytologist* **106**: 745-751.
- Ourry, A., Boucard J. and Salette J.** (1990). Partitioning and remobilization of nitrogen during regrowth in nitrogen-deficient ryegrass. *Crop Science* **30**: 1251-1254.
- Parsons, A.J., Carrere P. and Schwinnings S.** (2000). Dynamics of heterogeneity in a grazed sward. In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press)
- Peace, W.J.H. and Grubb P.J.** (1989). Interaction of light and mineral nutrient on the growth of *Impatiens parviflora*. *New Phytologist* **90**: 127-150.
- Pearcy, R.W. and Sims D.A.** (1994). Photosynthetic acclimation to changing light environments: scaling from leaf to whole plant. In: Caldwell M.M. and Pearcy R.W. (eds) *Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Below-Ground*. San Diego: Academic Press, pp 175-208.
- Poorter, H. and Garnier E.** (1999). Ecological significance of inherent variation in relative growth rate and its components; In: Pugnaire F.I. and Valladares F. (eds) *Handbook of Functional Plant Ecology*, New York: Marcel Dekker Inc, pp 81-103.
- Prioul, J.L.** (1971). Réaction des feuilles de *Lolium multiflorum* à l'éclaircissement pendant la croissance et variation des résistances aux échanges gazeux photosynthétiques. *Photosynthetica* **5**: 364-375.
- Richards, J.H.** (1993). Physiology of plants recovering from defoliation. In: Baker, M.J. (ed.) *Grassland for Our World*, Wellington: SIR Publishing, pp. 46-54.
- Robin, C., Varlet-Grancher C., Gastal F., Flenet F. and Guckert A.** (1992). Photomorphogenesis of white clover (*Trifolium repens* L.): phytochrome mediated effects on ¹⁴C-assimilate partitioning. *European Journal of Agronomy*, **1**: 235-240.
- Ryle, G.J.A. and Powell C.E.** (1975). defoliation and regrowth in the graminaceous plant: the role of current assimilate. *Annals of Botany* **39**: 297-310.
- Ryle, G.J.A. and Powell C.E.** (1976). Effect of rate of photosynthesis on the pattern of assimilate distribution in the graminaceous plants. *Journal of Experimental Botany* **27**: 189-199.
- Sackville-Hamilton, N.R., Matthew C. and Lemaire G.** (1995). Self-thinning: a re-evaluation of concepts and status. *Annals of Botany* **76**: 569-577.

- Schaufele, R. and Schnyder H.** (2000). Cell growth analysis during steady and non-steady growth in leaves of perennial ryegrass (*Lolium perenne* L.) subject to defoliation. *Plant Cell Environment* (in press).
- Schnyder, H. and De Visser R.** (1999). Fluxes of reserve-derived and currently assimilated carbon and nitrogen in perennial ryegrass recovering from defoliation. The regrowing tiller and its component functionally distinct zones. *Plant Physiology* **119**: 1423-1435.
- Schnyder, H., Schaufele R., De Visser R. and Nelson J.** (2000). An integrated view of C and N uses in leaf growth zone of defoliated grasses. In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press).
- Schwinning, S. and Parsons A.J.** (1996a). Analysis of the coexistence mechanisms for grasses and legumes in grazing systems. *Journal of Ecology* **84**: 799-813.
- Schwinning, S. and Parsons A.J.** (1996b). A spatially explicit population model of stoloniferous N-fixing legumes in mixed pastures with grass. *Journal of Ecology* **84**: 815-826.
- Simon J.C. and Lemaire G.** (1987). Tillering and leaf area index in grasses in the vegetative phase. *Grass and Forage Science* **42**: 373-380.
- Simon, J.C., Gastal F. and Lemaire G.** (1989). Compétition pour la lumière et morphologie du trèfle blanc (*Trifolium repens* L.): émission des feuilles et des ramifications. *Agronomie* **9**: 383-389
- Sinoquet, H., Moulia B., Gastal F., Bonhomme R. and Varlet-Grancher C.** (1990). Modeling the radiative balance of the components of a well-mixed canopy: application to a white clover-tall fescue mixture. *Acta Oecologica* **11**: 469-486.
- Sinoquet, H. and Bonhomme R.** (1991). A theoretical analysis of radiation interception in a two species plant canopy. *Mathematic Biosciences* **105**: 23-45.
- Skinner, R.H. and Nelson C.J.** (1992). Estimation of potential tiller production and site usage during tall fescue canopy development. *Annals of Botany* **70**: 493-499.
- Soussana, J.F., Teyssonnyere F. and Thiery J.** (1999a). Un modèle dynamique d'allocation basé sur l'hypothèse d'une co-limitation de la croissance végétale par les absorptions de lumière et d'azote. In: Bonhomme R. and Maillard P. (eds), *Fonctionnement des Peuplements Végétaux et Environnement*. INRA Editions, Paris, pp 87-116.
- Soussana, J.F., Teyssonnyere E.F. and Thiery J.** (1999b). Un modèle simulant les compétitions pour la lumière et pour l'azote entre espèces herbacées à croissance clonale. In: Bonhomme R. and Maillard P. (eds), *Fonctionnement des Peuplements Végétaux et Environnement*. INRA Editions, Paris, pp 325-352.
- Thornley, J.H.M., Bergelson J. and Parsons A.J.** (1995). Complex dynamics in a carbon-nitrogen model of a grass-legume pasture. *Annals of Botany* **75**: 79-94.
- Thornton, B., Millard P. and Duff E.I.** (1994). Effects of nitrogen supply on the source of nitrogen used for regrowth of laminae after defoliation of four grass species. *New Phytologist* **128**: 615-620.
- Thornton, B., Millard P. and Bausenwein U.** (2000). Reserve formation and recycling of carbon and nitrogen during regrowth of defoliated plants. In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press).
- Tilman, G.D.** (1982). *Resource Competition and Community Structure*. Princeton, New Jersey: Princeton University Press.
- Turkington, R.** (1983). Leaf and flower demography of *Trifolium repens* L. 1) Growth in mixture with grasses. *New Phytologist* **93**: 599-616.
- Van Loo E.N.** (1993). On the relation between tillering, leaf area dynamics and growth of perennial ryegrass (*Lolium perenne* L.). Doctoral Thesis, Wageningen Agricultural University, The Netherlands.

Varlet-Grancher C., Moulia B., Sinoquet H. and Russell G. (1993). Spectral modification of light within plant canopies: how to quantify its effects on the architecture of the plant stand. In: Varlet-Grancher C., Bonhomme R. and Sinoquet H. (eds) *Crop Structure and Light Microclimate: Characterisation and Applications*. Science Update, INRA Editions, Paris, pp 427-451.

Wade, M. and de F. Carvalho P.C. (2000). Defoliation patterns and herbage intake on pastures. . In: Lemaire G., Hodgson J., Moraes H., Nabinger C. and de F.Carvalho P. (eds) *Grassland Ecophysiology and Grazing Ecology of Natural Grasslands*, Wallingford (UK): CAB International, (in press)

Weaver, J.E. and Clements F.E. (1929). *Plant Ecology*. McGraw-Hill Book Co., New York, 520 pp.

Woledge, J. (1973). The photosynthesis of ryegrass leaves grown in a simulated sward. *Annals of Applied Biology* **73**: 229-237.

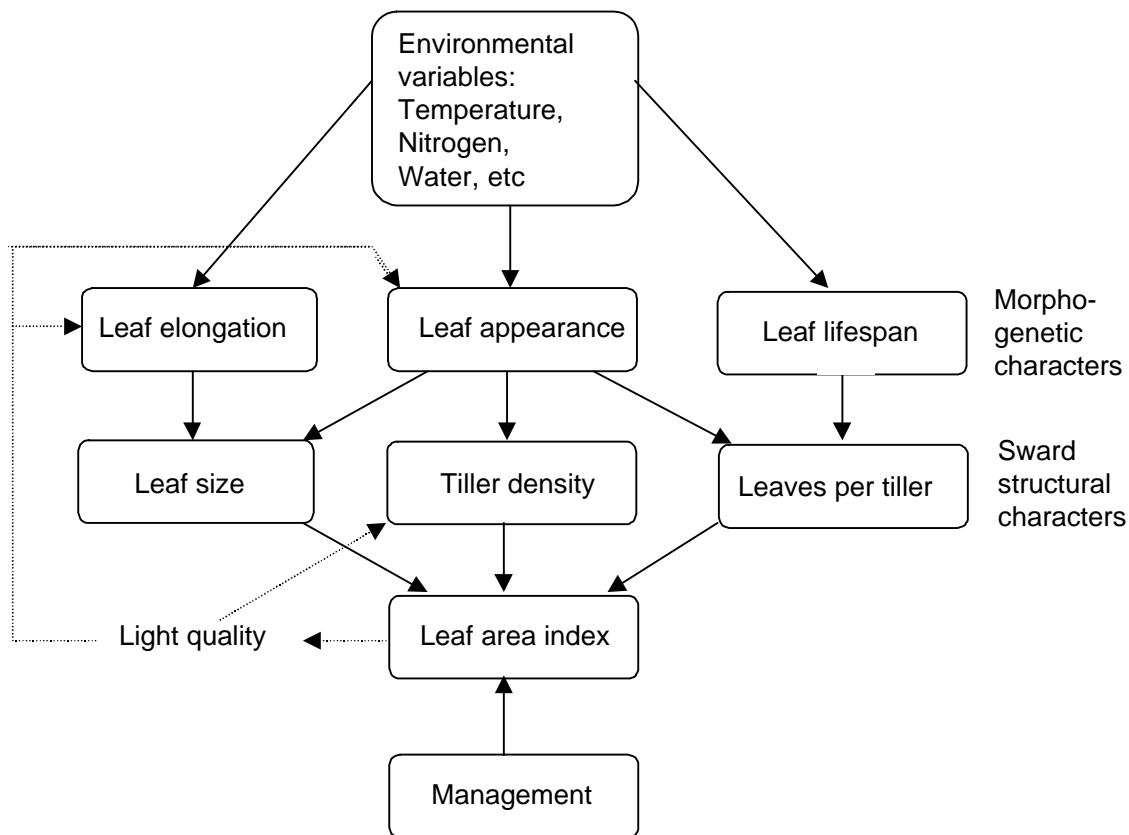


Figure 1 - Relationship between morphogenetic variables and sward structural characteristics (after Lemaire and Chapman, 1996).

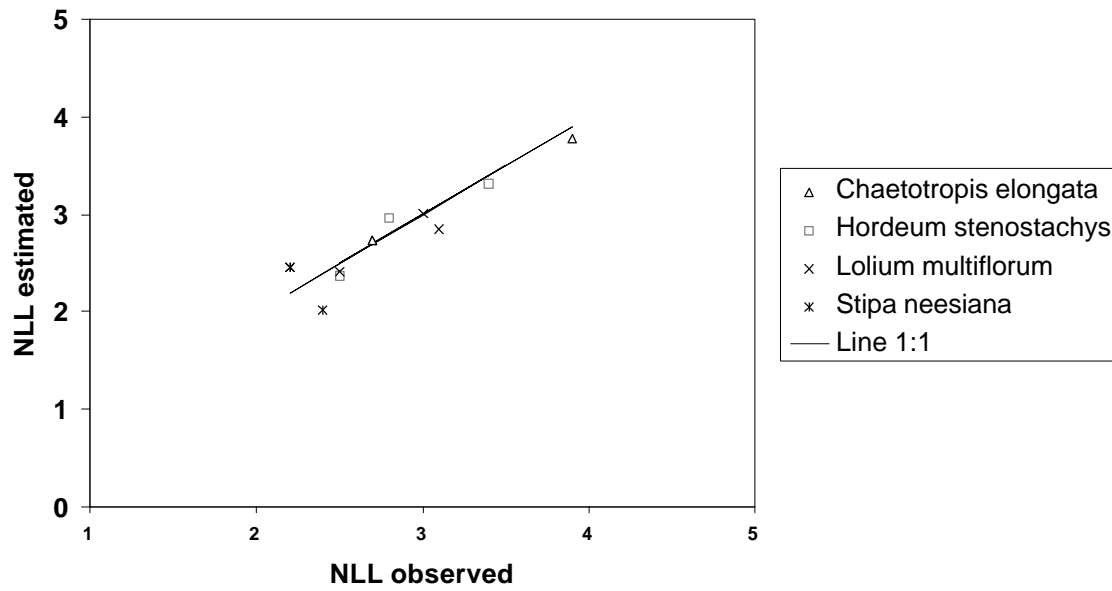


Figure 2 - Relationship between the number of living leaves per tiller (NLL) estimated by Equation 7 and the observed values at different seasons for different species of a grazed community of the Pampa in Argentina (after Lemaire and Agnusdei, 2000).

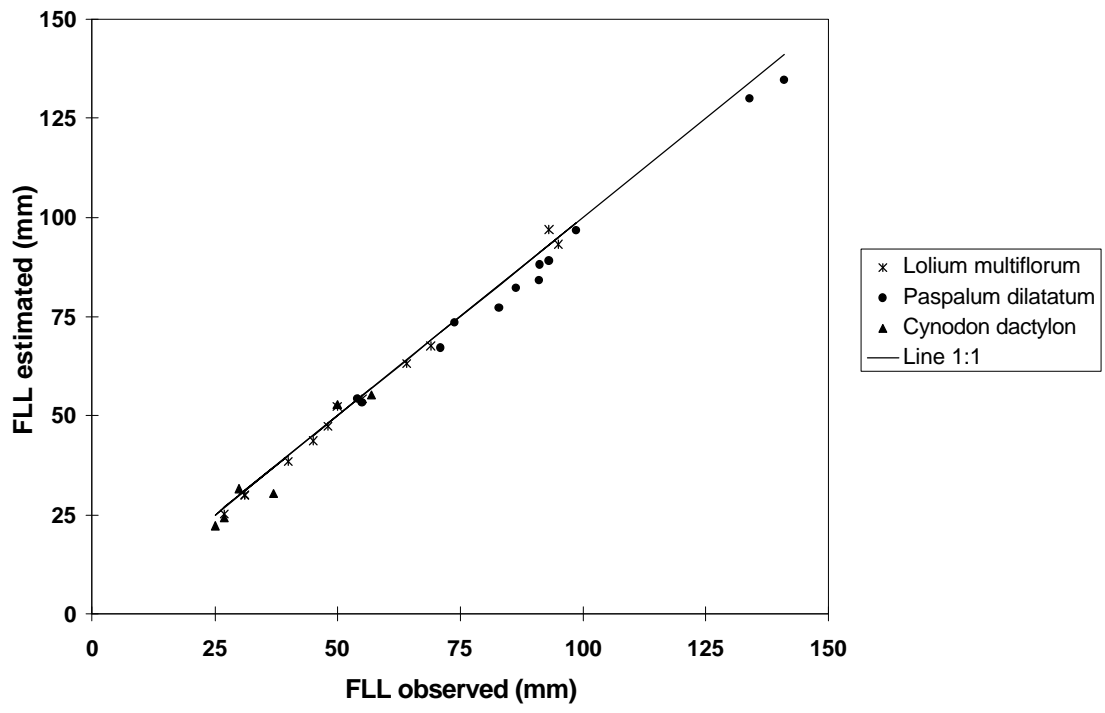


Figure 3 - Relationship between the final leaf length (FLL) estimated by means of Equations 5 and 6 and the observed values for different species of a grazed community of the Pampa in Argentina (after Lemaire and Agnusdei, 2000).