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Review. Impact of grazing on plant communities in forestry areas

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Abstract

The depopulation of mountainous areas and the accompanying reduction in livestock that has traditionally grazed on the spontaneous vegetation of these areas, has led to the uncontrolled growth of shrubs and a significant increase in the risk of fire due to the increased availability of combustible fuel. The reintroduction of extensive grazing may be a viable way of ensuring a sustainable ecosystem compatible with the economic and social life of these areas. Modifications to native plant communities as a result of grazing, however, may lead to directional changes in their structure and composition. Thus, knowledge of animal-plant relationships is essential if foresters are to make appropriate management decisions. Current knowledge of these animal-plant interactions is here reviewed, with special attention paid to tolerance mechanisms, the effects of grazing and plant community dynamics.

Key words: herbivory, grazing tolerance, morphological alterations, vegetation dynamics.

Resumen

Revisión. Impacto del pastoreo sobre la vegetación en áreas forestales

El despoblamiento de las áreas de montaña y con él la disminución del censo ganadero que aprovechaba los recursos vegetales de estas áreas ha dado lugar a una progresiva degradación del pasto y a una invasión incontrolada de la vegetación arbustiva, con el consiguiente incremento de la masa combustible y del riesgo de incendios. La reorientación de la actividad hacia sistemas ganaderos extensivos surge como una alternativa viable para asegurar un ecosistema sostenible y compatible con el mantenimiento de la vida económica y social de estas áreas. Sin embargo, el conjunto de modificaciones que acontecen en la cubierta vegetal, como consecuencia del pastoreo, pueden dar lugar a cambios direccionales en la estructura y composición de la comunidad vegetal. En consecuencia, la comprensión de las relaciones entre animales y plantas es esencial para que el gestor de espacios forestales pueda tomar las decisiones de manejo oportunas al objetivo propuesto. En este trabajo se revisa la información generada sobre la respuesta de la vegetación a la acción del ganado, prestando especial atención a los mecanismos de tolerancia, efectos del pastoreo y dinámica de la comunidad vegetal.

Palabras clave: herbivoría, tolerancia al pastoreo, alteraciones morfológicas, dinámica vegetal.

Introduction

The depopulation suffered by the mountainous regions of Spain in recent decades has led to a drastic reduction in the number of livestock animals that make use of their plant resources (Revilla, 1987). The abandonment of grazing in these areas has led to the progressive degradation of pasture, the appearance of plant species of little forage value, an increase in the amount of dead material in the bottom layer of forest understories, and the uncontrolled invasion by bushes and shrubs. This has resulted in a significant increase in the amount of fuel material available and therefore of the fire risk in forested areas, as well as a parallel loss of landscape quality in a territory where tourism is now of undoubted economic and social importance.

Previous attempts at bush control in different habitats, either by mechanical procedures or by fire clearing, has frequently been found unsatisfactory (Fernández Santos *et al.*, 1992; Currás *et al.*, 1995) or economically or physically inadequate. As an alternative to these ecologically aggressive techniques, the use of grazing herbivores could be an efficient way to control shrub growth and reduce the risk of fire

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(Tsiouvaras *et al*., 1989; Magadlela *et al*., 1995; Ferrer *et al*., 1997b).

The impact of grazing on different plant species appears to depend on what use different herbivores make of them, the efficacy of the tolerance mechanisms to herbivory that each species develops, and the competitive interactions between different plants (Briske, 1991; Herms and Mattson, 1992). Therefore, the recovery of forested areas and their use by grazing livestock requires knowledge of plant-animal interactions and of the impact of grazing on vegetation. Without such knowledge, forestry managers will find it hard to make appropriate decisions.

The impact of grazing on vegetation refers to modifications to plant morphology and physiology resulting from direct effects, such as defoliation and trampling, and indirect effects, such as the alteration of growth conditions. The combination of these direct and indirect effects (outlined in Fig. 1) can cause the destabilisation of competitive interactions between plants. In time, this can alter the dynamics of plant populations via the impact on species natality, density and mortality, and eventually may cause directional changes in the structure and composition of plant communities (Archer and Smeins, 1991).

This work reviews the information available on the modifications suffered by plant communities as a result of the direct and indirect effects of grazing. Particular attention is paid to mechanisms of tolerance to grazing, the effects of grazing on plants, and the dynamics of plant communities.

Direct effects of grazing on vegetation

The direct effect of herbivory on vegetation includes modifications to plant growth, reproduction and architecture. The importance of ligneous species in now abandoned mountainous areas requires special mention be made of the modifications they suffer through grazing.

Growth

The main effect of grazing on plant growth is the reduction of photosynthetic capacity associated with the loss of leaf area. This reduces the supply of assimilated compounds to roots, seeds, developing fruits and growing shoots (Willard and McKell, 1973; Donaghy and Fulkerson, 1997). Consequently, the success of plants faced with herbivory depends on the efficacy of their morphological and physiological adaptations for replacing consumed biomass (Roundy and Ruyle, 1989; Herms and Mattson, 1992; Edenius *et al*., 1995). The mechanisms that could potentially compensate for herbivory include complex responses and physiological inter-relationships of difficult interpretation (Paige and Whitham, 1987; Briske, 1991). Whitham *et al*. (1991) proposed a model for analysing compensation mechanisms in which they considered the plant to be a balanced system of «sources and sinks». The plant is divided into «source» organs, i.e.,

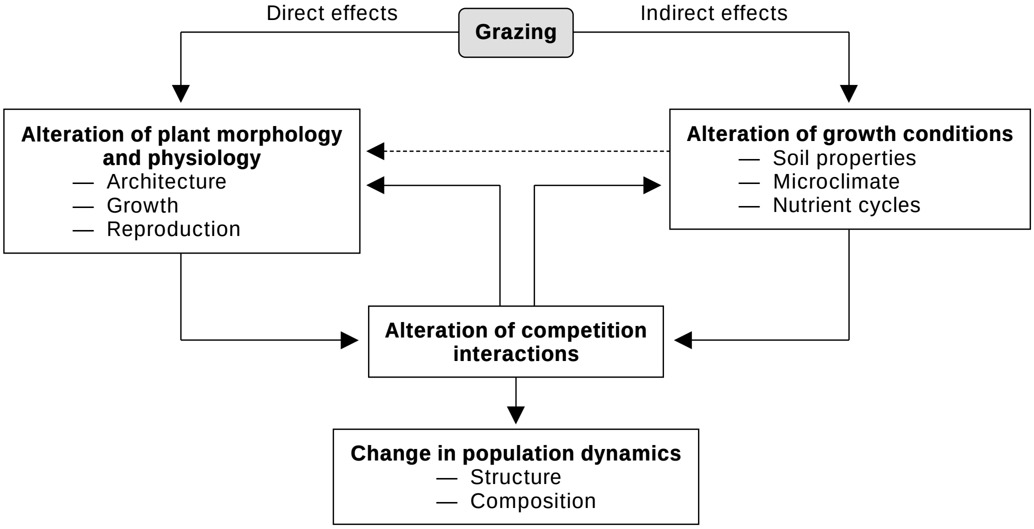

Figure 1. Relationships between the direct and indirect effects of grazing on vegetation.

those parts specialised in the net gain of carbon (photosynthetic and storage organs), and «sink» regions, specialised in growth and reproduction (growing meristems, flowers and fruits). According to this model, plants can physiologically compensate for the damage caused by herbivory through an adequate response of either the source or sink organs. The source organs undamaged by herbivores could respond by increasing the supply of photoassimilated compounds to the sink organs via increased photosynthetic efficiency (compensatory photosynthesis) as a result of the elimination of older, less active tissue, because of the increasing amount of light reaching lower tissues, or due to the increased efficiency of water use associated with the reduction in transpiring surfaces (McNaughton, 1979; Nowak and Caldwell, 1984). The response to defoliation by the «sink» organs would be an increase in the number of growing points (Whitham *et al*., 1991) caused by the elimination of the dominant apical meristem and the subsequent «activation» of lateral buds growth (Briske, 1991; Shepherd, 1992).

The ongoing debate between those who suggest that herbivory is bad for plants (Belsky, 1986) and those who believe its effects might be beneficial by increasing productivity and biological success (Paige and Whitham, 1987) is owed mainly to the different morphological and physiological characteristics of plants. Indeed, the resistance of different ecological groups to grazing has been ordered according to their morphophysiological adaptations (Whitham *et al*., 1991). While apical and intercalary meristems in herbaceous monocotyledonous plants are less vulnerable to large herbivores because of their basal location, the sprouting shoots of herbaceous dicots' are found in terminal or lateral positions, increasing the likelihood of damage by grazing animals (Briske, 1991). The lack of grasses preponderance in some parts of the world has actually been linked to an absence of large herbivores (López González, 2003) since these plants are well adapted to the conditions such animals help produce. Many ligneous species, however, particularly evergreens, are far less efficient in replacing the photosynthetic surfaces removed by these animals, and frequently rely on defence rather than tolerance mechanisms to combat grazing. Consequently, those plants that suffer the effects of herbivory most are shrubs, while equal growth or overcompensation is generally seen among annual and biennial species (Paige and Whitham, 1987; Lambert *et al*., 1989; Whitham *et al*., 1991).

Numerous studies support the idea that grazing is an efficient way of managing vegetation to prevent invasion by shrubs and bushes (Loiseau and Merle, 1988; Sabiiti and Wein, 1991; Ferrer *et al*., 1997b). While both ovines (Harradine and Jones, 1985) and bovines (Kosko and Bartolomé, 1983) contribute to a reduction in the growth of ligneous species, the greater browsing ability of caprines suggests that goats might be the best choice for clearing the shrub layer (Allan *et al*., 1994; Magadlela *et al*., 1995; Osoro *et al*.,1996).

Though ligneous species are, in general, more susceptible to herbivory than herbaceous species, their response to browsing is varied as a result of the interaction of many factors. Knowledge of how these factors affect the physiology of plants and of regrowth is vital for manipulating either individual plants or plant communities. However, research into the response of vegetation to grazing has mainly focused on the influence of grazing intensity and grazing season: two factors easily manipulated by grazing management.

Influence of grazing intensity

Increasing the intensity of grazing can either reduce the productivity of plants (Buwai and Trlica, 1977), increase it (Provenza *et al*., 1983) or have no effect at a certain level of use (Tsiouvaras *et al*., 1986). In addition, shrubby vegetation production may be increased or maintained up to a certain degree of defoliation, while more intense use can cause a fall in production (Willard and McKell, 1978; Grant *et al*., 1982; Schmutz, 1983). This is in agreement with the hypothesis of optimisation of herbivory for herbaceous plant communities (McNaughton, 1979, 1983; Briske and Heitschmidt, 1991). This suggests that optimal grazing intensity can increase the primary production of a previously non-grazed system, while high stocking rates generally lead to reduced production through defoliation and damage caused by trampling (King *et al*., 1979; Binnie and Chestnutt, 1991). Several authors have recommended usage levels for shrubs of around 50% of the total weight of the plant (Schmutz, 1983) or of annual growth (Roundy and Ruyle, 1989) to stimulate the production of shoots or maximise net growth respectively.

The effect of successive years of herbivory must also be taken into account. The accumulated effects of even moderate use can cause a decrease in regrowth in some bushy species (Garrison, 1953; Wright, 1970).

Influence of grazing season

The time of grazing with respect to the phenological stage of the plants consumed has been proposed the most important external factor affecting post-herbivory compensatory growth (Whitham *et al*., 1991; Danell *et al*., 1994). The defoliation of plants during critical periods of their development can reduce their vigour and their capacity to maintain their growth. One of the most susceptible periods in development is the seedling stage. Until they have established their root systems and photosynthetic apparatus, plantlets are extremely vulnerable to herbivory. Older plants, however, are less affected because of their ability to compensate or to increase their defences (Whitham *et al*., 1991).

The compensatory response, however, becomes weakened as herbivory extends into the growth season (Grant *et al*., 1982; Gregory and Wargo, 1986). This has generally been attributed to effects on the level of non-structural carbohydrate reserves (Willard and McKell, 1973): defoliation during the time when reserves are accumulated can reduce regrowth in the next growth season (Grant *et al*., 1978). Trlica and Cook (1971) observed a reduction in carbohydrate reserves in the autumn as the time between defoliation and quiescence (vegetative rest) became shorter. They also report a direct relationship between total autumnal carbohydrate levels and post-defoliation regrowth in five shrub species and two desert grass species.

Other factors, however, may also be involved in the response of plants to the defoliation season, such as the time of formation of vegetative buds. This means that, in ligneous species, the response to defoliation time is not always the same. Shepherd (1992) and Valderrábano and Torrano (2000) observed a greater number of new vegetative buds in *Pseudotsuga menziesii* and *Genista scorpius* when these plants were consumed early in the growth season than when consumption occurred later and the buds had already differentiated. This also led to significant differences in shrub volume. However, the use of *Atriplex halimus* by livestock during the fruiting season (autumn-winter) did not affect the plant's response in the following season (Valderrábano *et al*., 1996) since bud differentiation occurs in spring.

Influence of other factors linked to the plant and the environment

The different responses of plants to herbivory are the result of the interaction of many factors since they involve a variety of morphological and physiological changes depending upon the tissue consumed (Alonso *et al*., 1993; Danell *et al*., 1994), the size of the plant, and its stage of growth (Bryant *et al*., 1991, 1992). Responses also differ between plant species (Wright, 1970; Buwai and Trlica, 1977; Clark and Medcraft, 1986) and even between individuals (Urness and Jensen, 1983), and could depend on factors such as growth conditions. The availability of water and light and competition interactions can affect the general status of a plant, and therefore its compensatory response (McNaughton, 1983; Shepherd, 1992). Plants damaged by herbivores could become more vulnerable to further attacks by other herbivores or to pathogens (Fedde, 1973). As a consequence, the interaction of numerous factors leads to a gradient of compensatory responses dictated by morphological and physiological limitations and ecological conditions (Whitham *et al*., 1991). The plants most affected by herbivory should therefore be woody perennials with few reserve meristems and slow growth. Their compensatory abilities are reduced in situations of intense competition, low availability of water, light and nutrients, and when herbivory is maintained until the end of the growing season (Table 1).

Architecture

Animals clearly modify the structure of the vegetation they make use of. If protected and grazed areas are compared, the difference in the height of plants

Table 1. Growing conditions and plant traits important in determining a plant's probable compensatory response (Whitham *et al.*, 1991)

Equal to overcompensation	Undercompensation
Herbivory early in season	Herbivory late in season
Abundant water, light and nutrients	Low water, light and nutrients
Low competition	High competition
No meristem limitation	Meristem limitation
Fast growth	Slow growth
Annuals and biennials	Woody perennials

is one of the most noticeable features. When grazed, plant communities generally acquire a more homogeneous, shorter appearance with more prostrate growth characteristics (Clark and Medcraft, 1986; Alonso *et al*., 1993). The way in which herbivores alter the architecture of plants, however, depends on numerous factors such as the species consumed, the intensity of grazing and the season when this occurs (Danell *et al*., 1994).

Grazing-induced variations in the structure of the vegetation can have important consequences from the point of view of animal/plant interactions. By changing the architecture of plants, herbivores can modify their food resources (Grant *et al*., 1978; Danell *et al*., 1994); the structural characteristics of plants, and consequently the accessibility of resources, have great influence over the feeding behaviour of herbivores.

Reproduction

Measuring the biological success of perennials is difficult because their reproductive effort is accumulated over the multiple bouts of reproduction that occur during their lifetimes (Whitham *et al*., 1991), because of their different survival strategies (Sabiiti and Wein, 1991; Vera and Obeso, 1995; Ceballos *et al*., 1997), and because of the difficulty in comparing the ecological and evolutionary value of sexually formed seeds and asexually derived offspring (Whitham *et al*., 1991). However, the majority of bushy species produce great quantities of seeds (Kosco and Bartolomé, 1983), and it has therefore been suggested (Archer and Smeins, 1991) that grazing strategies for limiting invasion by woody plants should be focussed on the reduction of seed production and dispersal. From this perspective, grazing generally contributes to the reduced reproductive success of woody plants through the consumption of floral buds (Milton, 1995a), a reduction in the flowering rate (Roundy and Ruyle, 1989) and a corresponding fall in the production of fruits and seeds (Schmutz, 1983; Urness and Jensen, 1983). The drastic reduction in the number of flowers on individuals of *G. scorpius* browsed in the previous grazing season (Valderrábano and Torrano, 2000) suggests that, as a result of defoliation, the reserves of these plants are insufficient to drive the development of flowering buds (Bernier *et al*., 1993). They respond to herbivore damage by giving priority to vegetative growth over flower production as a way of ensuring survival.

Indirect effects of grazing on vegetation

The indirect effects associated with grazing include the modification of the microclimate, the physical and hydrological properties of the soil, and the redistribution and transformation of nutrients.

Hydrology, microclimate and soil

Through plant consumption and trampling, grazing reduces the accumulation of litter in the soil (Tsiouvaras *et al*., 1989; Severson and Debano, 1991) and can reduce plant cover. This leads to an increase in the amount of bare ground (Ferrer *et al*., 1997a, c). The result can be a warmer, drier and more extreme environment (Milton, 1995b) plus an increase in the wind speed at ground level that could reduce soil humidity by increasing evaporation and transpiration. The resulting environment would facilitate the instalment of annual and short-lived perennials, as well as xerophytes adapted to such conditions (Archer and Smeins, 1991).

The impact of rain on the soil, plus its compaction by trampling, could reduce the amount of infiltration that occurs, and therefore increase erosion and run-off (Thurow, 1991; Pell, 1999). The long-term success of any grazing management strategy therefore depends on its capacity to maintain or improve the soil and its hydrological conditions.

Despite these negative effects of herbivory, some plant communities, especially conifer forests, could benefit from grazing activity. These populations usually accumulate a considerable amount of acidic litter resistant to decomposition. A clearing of the pine litter as a result of animal consumption and trampling (Torrano and Valderrábano, 1999) would not only increase the chances of plants emerging, but also help the germination of species inhibited by the acidity of the soil (Ratliff *et al*., 1991). From the point of view of fire prevention, the clearing of the litter would reduce the probability of ignition occurring in these communities, which otherwise would be at considerable risk (Tsiouvaras *et al*., 1989).

Nutrient cycles

Large herbivores influence the speed at which nutrients are recycled as well as their redistribution through two primary mechanisms: the elimination of plant biomass and its associated nutrients, and the deposition of nutrients.

The consumption of leaves diverts the aerial biomass accumulated as litter and modifies the microclimate, which in turn affects the microbial activity of the soil (Archer and Smeins, 1991). In addition, defoliation alters root growth and morphology (Donaghy and Fulkerson, 1997; Arredondo and Johnson, 1998) which can affect the soil nutrient exchange pool.

The cycling of nutrients through grazing animals is important and can favour or maintain the fertility of the soil (Parsons *et al*., 1991; Pell, 1999). Grazing increases mineralisation through the reduction of the size of plant particles (chewing and rumination), and the creation of an environment favourable to microbial activity. This in turn favours the maintenance of a pool of rapidly mineralisable organic nutrients close to the soil surface (Floate, 1981; Chapin *et al*., 1995), which translates into increased pasture production (Williams and Haynes, 1995). The greater concentrations of nutrients in the vegetation of grazed than in non-grazed systems supports the idea that grazing accelerates the recycling of nutrients (Detling, 1988; Thomas *et al*., 1990). This might be due, however, to other factors such as enhanced uptake of nutrients by defoliated plants (Ruess, 1984), an increase in nutrient availability due to increased microbial activity associated with higher humidity and soil temperature (Jones and Woodmansee, 1979; Parton and Risser, 1980), or the different ages or phenological stages of plants when the modifications to their structure occur (Binnie and Chestnutt, 1994).

Modifications in microbial activity and the distribution, form and abundance of nutrients at the local level may show feedback, intensifying the response of plants to defoliation and contributing to changes in botanical composition. In the long-term, this could affect the quality and the quantity of litter as well as the dynamics of its decomposition (Rittenhouse, 1991). The speed and the direction of plant succession when grazing stops would not only depend on the degree to which microbial activity, structure and fertility of the soil had been altered, but also on the combination of these with climatic factors (Archer and Smeins, 1991; Briske and Heitschmidt, 1991). In the long-term, however, excessive grazing or the concentration of nutrients in particular excretion areas could increase ammonia volatilisation and cause the net transport of nutrients to particular sites (Thomas, 1992; Williams and Haynes, 1995). The result could be a reduction in global fertility and an increase in the heterogeneity of primary production.

Dynamics of plant communities

The combination of the direct and indirect effects of grazing on vegetation will determine the competitive interactions between plants, and therefore the dynamics and composition of plant communities.

Competition

Plants do not respond to grazing as isolated individuals, but rather as members of a population and plant community. They compete with nearby plants for light, nutrients, water and space (Braun-Blanquet, 1979).

The capacity of a plant species to compete is mainly associated with measurable genetic characteristics that maximise the capture of resources (Grime, 1977). This author proposes a model of plant evolution based on the development of three main strategies as a result of two major categories of external factors that reduce plant biomass. The first of these categories, *stress*, includes conditions that restrict production through the lack of light, water or nutrients, suboptimal temperatures or the presence of toxic compounds. The second, *disturbance*, is associated with the partial or total destruction of plant biomass through the action of herbivores, pathogens, wind, frost, desiccation, erosion or fire. Using these concepts, Grime suggested that, of the four combinations of high and low stress with high and low disturbance, only three are viable since, in greatly altered habitats, intense stress would impede the recovery of vegetation. This author also associated each of these three viable combinations with a different type of primary strategy, each identifiable from morphological traits, resource distribution, phenology and stress responses (Table 2). The competitive strategy prevails in productive and relatively undisturbed vegetation. Tolerance to stress is associated with limited production conditions and evergreen vegetation with slow growth rate and low palatability – a result of the natural selection of defence mechanisms against herbivory (Bryant *et al*., 1991, 1992). The ruderal strategy is characteristic of plants adapted to intensely disturbed but potentially productive areas; a large proportion of their photosynthetic products goes towards making seeds (Table 2).

Table 2. Some characteristics of competitive, stress tolerant and ruderal plants (Grime, 1977)

	Competitive	**Stress tolerant**	**Ruderal**
Shoot morphology	High dense canopy of leaves; extensive lateral spread above and bellow ground	Extremely wide range of growth forms	Small stature, limited lateral spread
Leaf form	Robust, often mesomorphic	Often small or leathery or needle-like	Various, often mesomorphic
Litter	Copious, often persistent	Sparse, sometimes persistent	Sparse, not usually persistent
Maximum potential relative growth rate	Rapid	Slow	Rapid
Longevity of leaves	Relatively short	Long	Short
Phenology of leaf production	Well-defined peaks of leaf production coinciding with period of maximum potential productivity	Evergreens with various patterns of leaf production	Short period of leaf production during periods of high potential productivity
Phenology of flowering	Flowers produced after (or more rarely, before) periods of maximum potential productivity	No general relationship between time of flowering and season	Flowers produced at the end of the temporarily favourable season
Proportion of annual production devoted to seeds	Small	Small	Large
Response to stress	Large and rapid changes in root:shoot ratio, leaf area and root surface area	Morphological changes slow and often small in magnitude	Rapid restriction of vegetative growth with diversion of resources towards seed production

The effects of herbivory on plant species depends on their competitive interactions with other plants (Whitham *et al.*, 1991). However, herbivory can modify these interactions (Fig. 2) through the grazing of different plants with different degrees of tolerance to defoliation (Estell *et al.*, 1994; Allan and Holst, 1996). Species grazed less severely (those with efficient defence mechanisms), those capable of growing rapidly after defoliation (those with efficient tolerance mechanisms), or those which possess a combination of these two resistance mechanisms, have a competitive advantage in the community. These species, via their possession of greater aerial mass, can assimilate more carbon to increase the size of their root systems, and therefore more effectively explore the soil profile in search of resources (Briske, 1991; Donaghy and Fulkerson, 1997).

When grazing is only light, the composition of plant species may not be appreciably modified since growth is not altered and competitive interactions are unchanged. However, differences in plant use and growth intensify as the stocking rate and defoliation increases, leading to changes in competitive interactions that contribute to the replacement of certain species (Archer and Smeins, 1991). Further, the herbivore species —or combination of herbivore species— will affect the frequency, intensity and seasonality of grazing within plant communities depending on the animals' preferences and behaviour. Environmental factors could also greatly modify the competitive interactions between species, inducing a range of plant responses (Briske, 1991).

When shrubby vegetation invades plant communities, the penetration of light is inhibited and there is competition for soil moisture and nutrients (Harrington, 1979; Goby *et al.*, 1994). It might be expected that the clearing performed by livestock would allow the recovery and growth of herbaceous plants (Riggs and Urness, 1989; Magadlela *et al.*, 1995), but some authors (Severson and Debano, 1991) record only an increase in annual plants as a response to the reduction of shrubs. Undoubtedly, the degree of pressure exerted by livestock on the herbaceous layer also influences the response to the clearance of ligneous species (Grant *et al.*, 1982). The use of other clearing techniques (mechanical or chemical) is not always effective

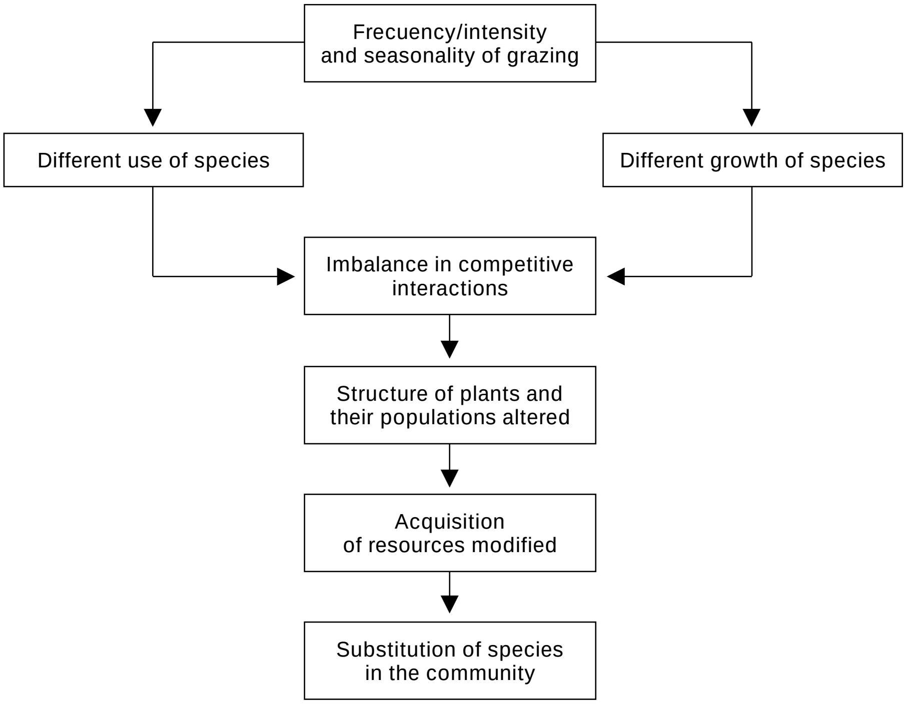

Figure 2. Cause-effect relationship between grazing-induced competitive interactions and modified plant and population structure as it may regulate species composition at the community level (Briske, 1991).

at increasing the density of herbaceous plants (Morton and Melgoza, 1991; Bartolomé *et al*., 1994; Nolte and Fulbright, 1997) either due to the influence of topo-edaphological (Archer and Smeins, 1991) and climatic factors (Bozzo *et al*., 1992; Bartolomé *et al*., 1994), and to the influence of the dominant shrubby vegetation (Ratliff *et al*., 1991) on the response of herbaceous plants to shrub control.

Diversity

An increase in the diversity of plants with grazing has been recorded in numerous studies (Collins, 1987; McNaughton, 1993; Ferrer *et al*., 1997a; Torrano, 2001). This appears to be the result of a reduction in the competitive capacity of the dominant species and the appearance of bare areas that can be occupied by other species (Huston, 1979; Naveh and Whittaker, 1980). In addition, livestock also contribute to increased plant diversity through selective grazing, the use of certain areas, the unequal distribution of manure, and through their role as dispersion vectors of seeds - both through endozoochory (Arrieta and Suárez, 2001; Castro and Robles, 2003) and exozoochory (de Pablos and Peco, 2003). This would seem to be more important than traditionally believed, and causes the appearance of small mosaics of vegetation in the landscape (Archer and Smeins, 1991; Fulbright, 1996).

Above certain frequencies or intensities, however, disturbance can reduce diversity. The phenomenon of diversity increase at moderate disturbance levels –known as the hypothesis of intermediate disturbance (Conell, 1978)– has been reported in communities subjected to different grazing intensities (Patón *et al*., 1995; Willoughby and West, 1996; Pueyo *et al*., 2003). Fulbright (1996) indicates the importance of intermediate disturbance frequencies and intensities in the production of a wide range of habitats allowing the coexistence of more species.

The diversity of plant communities has important implications for grazing management, and its conservation is desirable (Marañón, 1997). It has been shown that the stability and primary productivity of more diverse plant communities are more resistant (and flexible) to disturbances than species-poor communities (Frank and McNaughton, 1991). This greater stability-productivity of richer communities might reflect an ability of mixtures of species to use resources more efficiently than monocultures, or perhaps that the existence of disturbance-resistant species in such communities is more likely (Tilman and Downing, 1994).

Society more highly values the heterogeneity of natural resources (Fulbright, 1996). In addition, heterogeneity has positive consequences for wild animals (Bryant *et al.*, 1981; LaGory *et al.*, 1985; Ngugi *et al.*, 1992) as well as for the diets of livestock since it improves the value of *a priori* more mediocre pasture through synergic effects among different pasture types that stimulate the consumption of large quantities of low quality forage (Meuret *et al.*, 1994).

Fluctuation and plant succession

In grazing systems, sustainable productivity and the long-term survival of plants depends on reproductive success and the establishment of new generations. Herbivores affect the productivity, composition and stability of plant communities through their influence on germination, establishment and mortality.

With respect to plant succession, plants have been classified as either decreasers, increasers or invaders depending on their response to grazing (Dyksterhuis, 1949). Those plants that make up a large proportion of the community but become reduced in number through grazing are known as decreasers. Those that increase in number, either because of their greater tolerance to defoliation or because they are less used by herbivores than other plants, are known as increasers. If grazing pressure is maintained, any bare patches formed could be occupied by herbaceous annuals, unpalatable perennials or shrubs that were previously absent or limited in number. These plants, known as invaders, are undesirable for livestock production because they displace more acceptable species, are of lower nutritive value, and have erratic or very seasonal production patterns. Where grazing is intense, it has been suggested that plants with adequate defence mechanisms and which are not very acceptable to herbivores will dominate the plant community (Bryant *et al.*, 1991, 1992). The most common result seen in pastures used by animals that browse infrequently is the progressive invasion of shrubs (Estell *et al.*, 1994; Allan and Holst, 1996). The substitution of species could modify the quantity, quality and variability of biomass production, altering the initial uptake and eventual flow of energy through the ecosystem. This could lead to new modifications in the botanical composition of the pasture (Fig. 2).

In the plant dynamics of pastureland, three types of change can be appreciated: fluctuation, regression and progression. Fluctuation refers to reversible changes in the dominance of species within a community in equilibrium, while progression and regression are directional changes in plant composition and dominance which might be irreversible (Margalef, 1998). When the composition of species changes and their contribution to overall production moves away from the climax vegetation, the condition of the pasture is reduced through regression. Grazing or changes in environmental conditions could cause regression which, over time, and if favoured by rain- and wind-driven erosion, could lead to a loss of diversity, net primary production and even total plant cover (Braun-Blanquet, 1979). Regression therefore implies degradation, and in pasture management this term is used to describe the substitution of perennial species by annuals, or that of palatable by unpalatable species (Allan and Holst, 1996; Goby *et al.*, 1997).

Progressive directional changes —progression— occur in the opposite direction and represent the recovery of ecosystem structure after disturbance. A feature of progression in natural vegetation is the dominance or incursion of larger plants; at each stage of succession, the main components of the plant biomass are usually the species with the largest life forms (Grime, 1977). However, when grazing pressure is reduced or eliminated, the rhythm of succession towards the area's previous state, as well as the importance of plant strategies in this succession, will depend on the degree to which the productivity of the area, the seed bank, and the regeneration potential have been altered. On many occasions, succession following the cessation of grazing does not lead to the re-establishment of the initial vegetation. After a certain threshold, systems may not be able to return to their original state (Braun-Blanquet, 1979; Margalef, 1998) even if large investments in energy and nutrients are made (Archer and Smeins, 1991).

Conclusions

The information available on the modifications that occur in plant communities due to grazing permits the conclusion that the use of pasture resources by livestock in mountainous areas would not be harmful. Under certain management conditions it could even contribute towards improving the diversity of plant resources and the prevention of fires. Managers of natural resources need efficient methods for predicting plant responses to stock raising practices which allow them to plan the use of these areas in accordance with social demands. Such practices would ensure a sustainable ecosystem through the maintenance of the diversity and productivity of its main functional groups (Chapin *et al.*, 1996). All users of these areas should be conscious of the value and fragility of such heritage and its need to be defended.

The grazing process used to gather food can be described as a hierarchical system of diet selection interacting with the animal's physiological needs resulting in a unique pattern of use across a given landscape. The characteristics of the land and the configuration of pasture resources interact with the needs of animals to determine the overall impact of the animal population on the vegetation. The reaction of plants to grazing pressure gives rise to short-term responses that might suggest the need to correct grazing practices. In the long-term, this could modify successional trends.

Despite the numerous studies performed on the impact of grazing on vegetation, many questions remain, and a better understanding of the relationships between grazing animals and plants is required if we are to develop managements practices that will maintain sufficiently rich and abundant pasture (Roguet *et al.*, 1998). Grazing systems are management tools designed to improve and stabilise stock production over time. However, because of the many interactive processes that regulate the composition of species and the productivity of natural systems, it is difficult —and often confusing— to propose norms for vegetation management. It is therefore essential that we acquire a functional knowledge of the basic ecological process underlying natural systems, and develop flexible management strategies within the limitations imposed by soil and climatic conditions.

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