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ECOLOGICAL BASIS OF LIVESTOCK GRAZING IN MEDITERRANEAN ECOSYSTEMS

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Modelling the impact of grazing on vegetation in the Mediterranean: the approach of the ModMED Project*

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Summary

The vegetation of the Mediterranean has been shaped by several thousand years of land use. Grazing by domestic animals and the associated burning of vegetation have been powerful factors in the evolution of species composition, structure and dynamics of the present plant communities. The last few decades, however, have seen rapid changes in land use with desertion of many marginal areas resulting in reduced fire frequency and successional change in the vegetation, but increased grazing levels elsewhere. Predicting the effects of changes in grazing pressure on landscapes requires an understanding of the processes of vegetation change and the response of vegetation to fire and grazing. The ecosystem can be considered at a range of spatial and organisational scales. For example, the intensity of grazing depends on the dispersal of animals at the landscape scale in response to attractiveness and accessibility of the vegetation. At the community scale, offtake by animals will vary depending on the choice of plant species available. At the individual scale different plant species will show particular patterns of resistance and resilience to grazing damage. At all levels, burning of the vegetation will alter the behaviour of both plants and animals. The objective of the ModMED project is to understand these processes that have shaped the present vegetation and to provide a modelling tool for investigating the likely development of landscapes following changes in grazing pressure and altered fire frequencies. This paper reviews the information that is required to model vegetation dynamics and the effects of changed management. The potential value of the modelling approach is discussed in the context of research priorities for quantifying grazing impacts.

Keywords: grazing, vegetation dynamics, modelling, Mediterranean ecosystems, landscape ecology.

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* Invited paper

Introduction

The Mediterranean landscape has evolved over several thousand years of land use by cutting, burning, grazing and agriculture, but the pattern of land use has been changing rapidly over the last few decades. In some areas there has been continuing intensification of grazing due largely to grazing subsidies (e.g. Lyrintzis, 1996), while in other areas there has been abandonment of the marginal land on the less fertile soils. Increased grazing pressure has lead to progressive degradation of the vegetation while abandonment has permitted successional development of the vegetation from degraded scrub to dense evergreen woodland. The ModMED project ('Modelling Mediterranean Ecosystem Dynamics', EC Environment Programme, ENV4-CT95-0139) is working to understand the processes of vegetation change in response to changes in land use including the effects of changes in grazing patterns and burning regimes.

Modelling provides a valuable tool for studying complex dynamic systems such as those including the interactions between vegetation and grazing. Models provide a conceptual framework that is valuable for co-ordinating the research effort, for illustrating the current status of our knowledge about processes, and for exposing gaps in our understanding. Modelling also imposes a constraint on complexity which focuses the research effort onto those processes that are considered truly critical to the functioning of the system.

This paper reviews the modelling approach to the interactions between grazing and vegetation that is being taken by the ModMED Project and discusses the potential contribution of this approach to an understanding of the dynamics of Mediterranean systems.

State of the art

There has recently been a great interest in the modelling of grazing systems, largely based on the theory of optimal foraging and the 'Ideal Free Distribution' (IFD) (Fretwell & Lucas, 1970). This theory suggests that animals will disperse themselves in a complex environment such that all individuals have access to a similar amount of resources. Habitat matching (or input matching) is one example of an Ideal Free Distribution in which the local density of animals tends to become proportional to the local availability of resources (Kennedy & Gray, 1993). While most of the papers published before the 1980's seemed to support the Ideal Free Distribution concept (Kennedy & Gray, 1993), those published more recently seem to emphasise the inadequacies of habitat matching to explain animal distributions (e.g. Milinski, 1994).

Ideal Free Distribution models are mostly based on the assumptions of identical, free-ranging animals with a perfect knowledge of the distribution of resources and predict the equilibrium distribution of animals given a continuous input of resources. However, grazing systems in the Mediterranean commonly comprise mixed flocks of sheep and goats which are shepherded by day and corralled at night. Although the average grazing pressure will be dispersed over a wide area it will be concentrated around the corral and will be highly aggregated at any one time. The resources are not then continuous because the vegetation must re-grow before the patch can be revisited. The pattern of dispersal is determined largely by the shepherd who may direct flocks according to factors other than simple resource availability, resulting in overmatching (e.g. by concentrating on the better quality sites) or undermatching (e.g. through an inadequate knowledge of habitat quality resulting in more grazing on the low-quality patches than predicted by the IFD). The distribution will certainly not be 'free' and will probably be less than 'ideal'. Equally, with a strongly seasonal climate and a movement of animals between different vegetation types at different times of year, the system is unlikely to be at equilibrium.

The literature is rich in functional and quantitative models of vegetation dynamics in boreal and tropical forests, for example those based on gap models (Urban & Shugart, 1992). These are mostly demographic models based on empirical relationships or the physiological responses of plants to the changing physical environment (light, water) as succession proceeds. However, in Mediterranean systems the dominant forces in determining vegetation structure and dynamics have been the impact of grazing animals and disturbance caused by periodic burning or cutting. The vital attribute approach of Noble & Slatyer (1980) provides a qualitative model of vegetation response to fire for Australian vegetation, but there have been few attempts to create quantitative functional models that relate patterns of vegetation succession to fire and grazing impacts, and, to our knowledge, no such studies have been completed for Mediterranean vegetation.

The ModMED approach

The ModMED modelling approach is both hierarchical and modular. This has permitted the development of a flexible and user-friendly modelling environment which gives the user considerable control over the structure of the model using a graphical Windows interface.

The modular approach (McCown et al., 1996) enables each ecological process to be represented as a discrete part of the model which is simple to modify, or to replace with a different representation, without needing to re-write large sections of code. The modular structure also enables the user to select modules from a 'library' of different components to construct a wide range of different and unique models each suited to particular objectives. In ModMED, modularity has been achieved through object-oriented programming.

The representation is hierarchical in the sense that we recognise that different ecological processes are dominant at different spatial and organisational scales (Levin, 1992; Laval, 1995). We have therefore distinguished the landscape, community and individual levels (Fig. 1). The landscape comprises a collection of grid-based maps containing landscape-scale data and also a grid of community-level vegetation models. Each community-level model is a discrete module which can therefore be removed and exchanged for a different module from a library. At present we are working on both qualitative, rule-based community-level models, and detailed individual-based simulation models in which individual plants are represented spatially within a 'community'. Individuals interact through shading and competition for water resources. It is an underlying principle of this approach that an understanding of the fine-scale processes can be used to make predictions of patterns at the coarser scale (see for example With & Crist, 1996).

Distribution of grazing animals at the landscape level

Prediction of the impact of grazing animals on vegetation requires information on grazing intensity including the amount of time that animals will spend in any particular patch, how frequently they will return and how much biomass will be removed at each visit. Levels of grazing intensity, however, are often stated as overall stocking rates (number of animals per unit area) that give little indication of the impact those animals will have on a particular patch of vegetation.

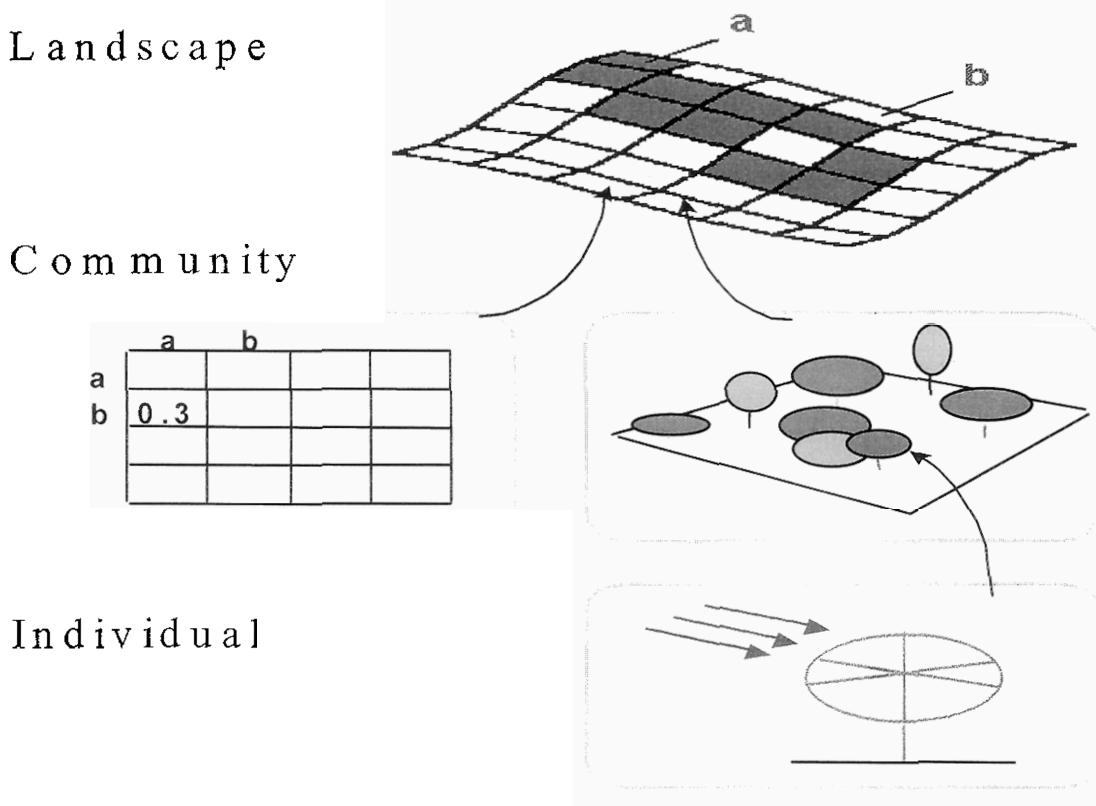

Figure 1. The hierarchical and modular structure of the ModMED modelling environment. The modular structure permits several alternative community-level models to be used in the same landscape. Equally, several different individual-level models can be represented in the same community.

In reality, the amount of time that an animal spends grazing in a particular patch depends on many factors. Accessibility to the site is determined by the steepness of slope and distance from 'gathering points' such as places where the animals are corralled at night, or sources of water that must be visited at least daily. For shepherded animals the distance from roads and tracks may also be important. In addition, the quality, quantity and accessibility of alternative food sources available elsewhere in the landscape will influence animal behaviour. These are all properties of the landscape and are independent of the individual patch of interest.

Different species of animal have different ecological characteristics which will influence distributions. Thus goats will forage on much steeper slopes than cattle and will be attracted to different types of vegetation. If the model is to be extended to wild animals, then predator defence (e.g. in rabbits, *Oryctolagus cuniculus* L.) and territorial behaviour (e.g. roe deer, *Capreolus capreolus* L.) may also influence distribution.

Finally, the quantity and quality of food present in each patch ('pastoral value') and accessibility of the vegetation in terms of vegetation height and penetrability will influence animal presence. These are all properties of the individual patch of vegetation concerned. They are also dynamic properties that will change seasonally, or as the vegetation develops, and they may be modified by the grazing animals themselves as biomass is removed.

In the ModMED landscape, now modelled within the Landlord modelling environment (D. Heathfield, unpublished), the spatial data (e.g. topography, locations of gathering points) are handled as a collection of maps (Fig. 2).

These are stored in a format compatible with a standard GIS and can be derived for any site. The properties of the each patch of vegetation can be obtained from the community-level models nested within the landscape and represented as maps. These maps are then combined to generate new maps showing derived data. For example, maps of pastoral value could be used to generate an Ideal Free Distribution of animals using simple habitat matching. A simple way to incorporate factors such as accessibility (slope, penetrability of vegetation and distance from gathering points) in this model would be to modify the pastoral value of each patch with an estimated 'energetic cost' (e.g. Grand & Dill, 1997) of access. These modified values for resource availability could then be incorporated in the habitat matching calculations.

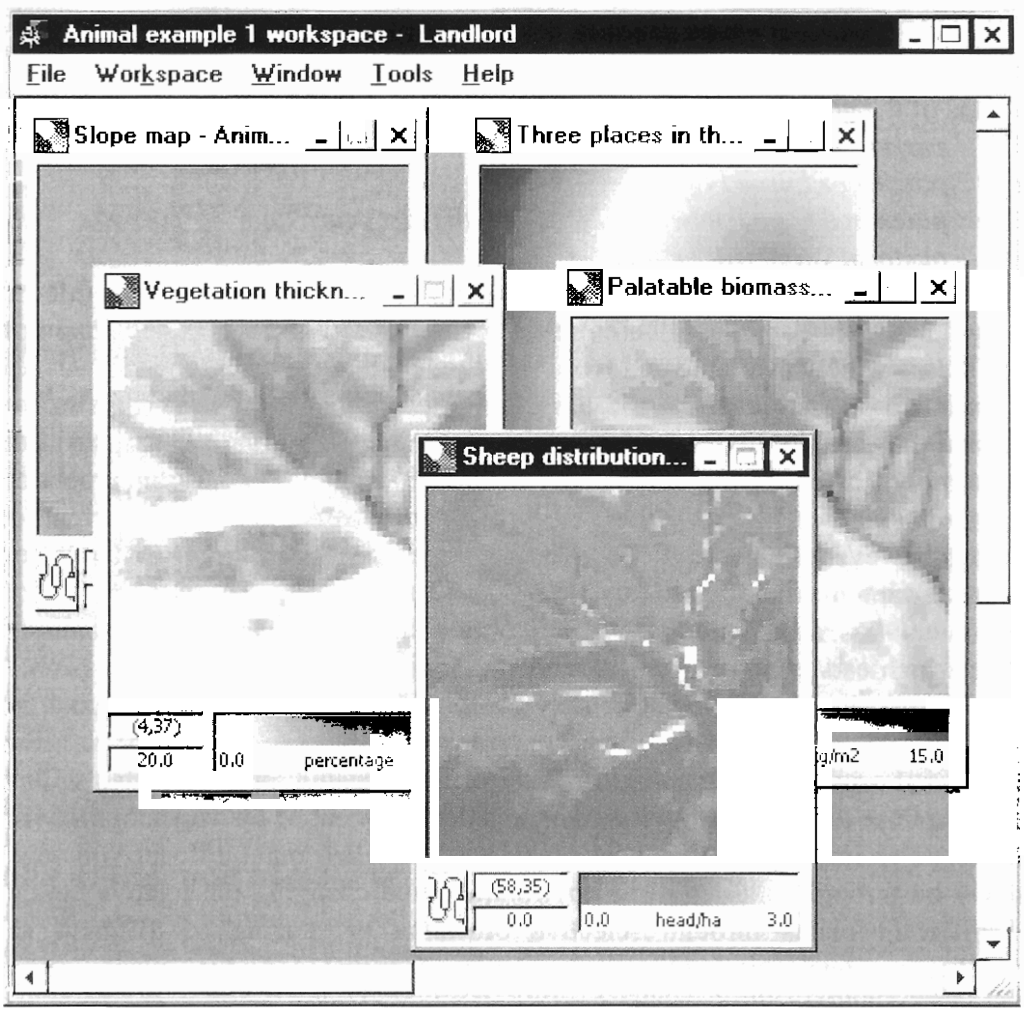

Figure 2. Screen display from Landlord software showing a collection of maps that might be used in the prediction of distribution of sheep in a landscape. These represent the slope, the distribution of gathering points, thickness (penetrability) of the vegetation, and palatable biomass.

The modular approach means that more complex formulae can be applied where necessary. For example, Bautista et al. (1995) note that overmatching occurs when resources are plentiful, but undermatching may occur when the population approaches or exceeds carrying capacity. The degree of overmatching or undermatching could therefore be included as a function of the number of animals present in the landscape relative to the total amount of resources available. There would also be scope for inclusion of an individual-based grazing model in which each animal or each flock is treated as a separate object in the landscape This is similar to the approach currently being developed at the Macaulay Land Use Research Institute in Aberdeen, UK (K. D. Farnsworth, pers. comm.)

Grazing at the community level

While the landscape model determines the total amount of grazing that will occur in a particular patch of ground, it is the community-level model than must determine the response of the vegetation. The community-level model then determines the dynamic patch characteristics such as pastoral value and vegetation thickness (penetrability) that are required by the landscape-level model.

The rule-based community-level model provides information on pastoral value using a set of simple rules of the general '*IF ... THEN ...*' type. For example, a rule might be:

IF *current vegetation type is maquis*
AND *patch was burned two years ago*
AND *patch has not been heavily grazed in the last year*
THEN *pastoral value will be high*

Although this type of rule is qualitative, it does represent valuable ecological information. The rule-based modelling approach therefore enables us to capture a considerable amount of information that is widely available and frequently used by ecologists and land managers and incorporate it into a predictive model at the landscape level. Rule-based models also have the advantages that they are simple for the land manager to understand and to modify or develop, they are extremely flexible in that almost any form of information can be incorporated, and they are computationally efficient. While rules can capture something of our current level of understanding, however, more detailed simulation models of the community will be more valuable as research tools and for quantitative predictions.

Each individual-based community-level model is a simulation model of a small stand of vegetation in which each shrub or herb is modelled individually (Fig. 3). Succession can be represented through the establishment of new plants and through mortality. Plants interact through shading and competition for water resources. Water availability may be influenced by soil quality and organic matter content. These are all dynamic properties that will change with time in response to changing environment and development of the vegetation.

Herbivores are an important component of this system. Their main influence on vegetation dynamics will be through modifying the environment and changing the relative competitive ability of different plants through selective browsing or grazing of different species. Prediction of how much biomass will be removed from individual plants requires a knowledge of the relative attractiveness or palatability of each species available and the proportions of different species that will be selected by the animal. There have been numerous published studies of the nutritional value of different shrub species in Mediterranean vegetation and the proportions of different species taken in by domestic animals (e.g. Papachristou, T. G.,1997; Papachristou, T. G. and Nastis, A. S.,1996; Papachristou, T. G. and Papanastasis, V. P.,1994; Papachristou, T. G. and Papanastasis, V. P.,1997). However, the value of different species changes with season. A suggested ranking of palatability of some common Mediterranean species for sheep and goats at different seasons is given in Table 1. Fire plays a crucial role in determining the age and stage of development of vegetation by removing indigestible woody material and encouraging a flush of young, palatable and nutritious shoots which are easily accessible to the animals.

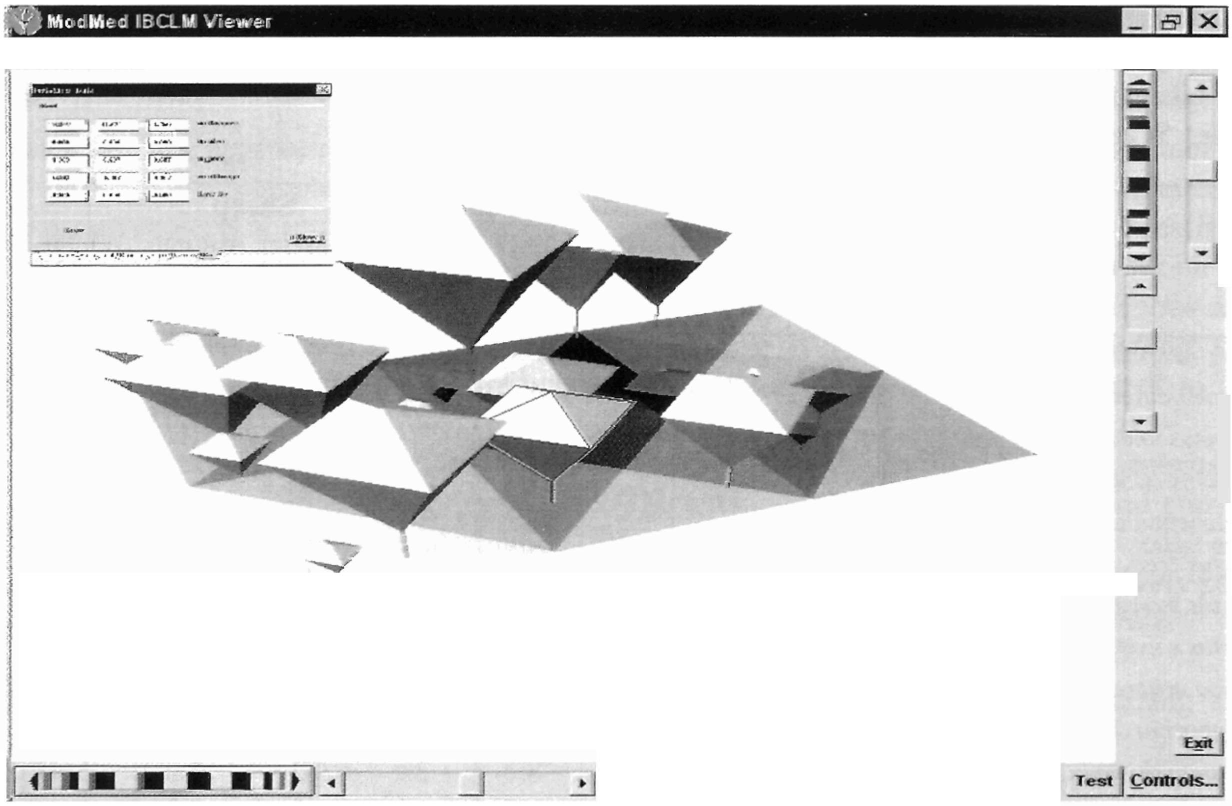

Figure 3. Screen display of the ModMED individual-based community-level model showing individual plants. The inset window displays the properties of one individual selected from within the community.

The community-level model, therefore, needs to be able to model the offtake of biomass from each individual plant, given the total intake of grazing animals in that patch and the quantity and quality of food available from each individual plant within that patch.

Domestic animals also influence the system at the community level through trampling damage which causes direct damage to plants, but also causes soil compression. Together with dunging this may have significant effects on the soil quality within the patch. The colonisation of new species brought into the patch in dung may also be a critical part of the successional process.

Grazing at the individual level

Each plant in the individual-based community-level model grows according to a physiological model based on light and water availability. Plants respond to browsing by the production of new sprouts. However, the sprouting ability depends on the status of the plant and the rules determining the allocation of resources to the different components of root, shoot and reproduction. The allocation patterns will vary with season and will depend on the ecological characteristics of the particular species.

The research priority at the individual level is therefore to try to understand the way different species allocate resources to different functions within the plant, and how this responds to different environmental conditions and disturbances such as defoliation or browsing damage. Although there has been some work published on the re-sprouting ability of plants following browsing damage (e.g. Tsiouvaras, 1988), we still have little understanding of the processes that determine the root : shoot : reproduction allocation patterns of major crop species, let alone the native Mediterranean plants.

Table 1. Preferences of sheep and goats to some common Mediterranean species. Data are rankings of the degree of utilization of the species for each season. Blank indicates species not taken in that season; ? insufficient data; * seed heads may be eaten; ~ eaten only very little; $ eaten when dead; + seedlings and young plants eaten.

	Goats				Sheep			
	Spring mid Mar-May	Summer June-Aug	Autumn Sept-Oct	Winter Nov-mid-Mar	Spring mid Mar-May	Summer June-Aug	Autumn Oct-Sept	Winter Nov-mid-Mar
Acer neapolitanum	8	2	14		10	2	19	
Ampelodesmos mauritanica	?	*	?	?	22~			
Arbutus unedo	19	12	19	15		13	15	15
Brachypodium ramosum	16	21	11	10	12	8	7	7
Brachypodium sylvaticum	22	21		11	21~			
Cistus creticus	20	18	21	22			17	19
Cistus monspeliensis								
Cistus salvifolius	20	18	21	22			17	19
Erica arborea	23	20	20	16	20	18	16	16
Euphorbia dendroides		25						
Festuca drymeia	1	5	8	8	3	10	5	5
Festuca heterophylla	1	5	8	8	3	10	5	5
Fraxinus ornus	4	2	14		9	2	19	
Hyparrhenia hirta	18	15	10		13	9		
Hyppocrepis unisiliquosa					6		1~	1
Lathyrus cicera	5		12	11	1		1~	1
Laurus nobilis	24	23	21	19				
Medicago poymorpha					1		1~	1
Myrtus communis	24	24	21	19				
Olea europea	11	9	1	1	16	5	8	8
Ostrya carpinifolia	12	10	14		11	6	19	
Phyllirea angustifolia	9	7	2	2	14	12	9	9
Phyllirea latifolia	9	7	2	2	14	12	9	9
Pinus brutia	24	24	21	16			24	16
Pinus halepensis	24	24	21	16			24	16
Pistacia lentiscus	17	16	6	14		16	13	14
Quercus coccifera	15	17	2	2	19	17	9	9
Quercus ilex	13	13	5	6	17	14	12	12
Quercus pubescens	3	4	14		7	4	19	
Quercus rotundifolia	7	10	14		8	6	19	
Quercus suber	14	14	6	7	18	15	13	13
Rosmarinus officinalis	24	24	21	19				
Vicia sativa	5	1	12	11	5	1$	1+	1

Browsing also changes the canopy structure of shrub species, both by direct removal of shoots and by promoting branching (Escos et al., 1997) and sprouting from the base. In addition to altering the three-dimensional structure of the vegetation this can, for example, alter the ability of plants to withstand fire.

Conclusions

Modelling as a framework for research

The modelling approach as used in the ModMED project has proved to be a valuable tool for co-ordinating a complex research programme. The project includes many apparently disparate subjects spanning a wide range of spatial, temporal and organisational scales from the mapping of vegetation and land use by remote sensing, down to physiological work on the growth response of individual plants to light and water stress. The field observations and ecological understanding of the Mediterranean ecologists have driven the planning and development of the modelling environment and the modelling work has contributed to the planning and execution of the field research.

The modelling process provides a clear framework for understanding the mechanisms of succession. For example, attempting to model the interaction between vegetation and grazing animals quickly highlights the information that is required and the gaps in our knowledge and understanding. Table 2 lists some of the processes for which there is at present relatively poor understanding, or for which additional data are required before predictions can be made.

Table 2. Some of the research priorities for understanding the effects of grazing and browsing on vegetation dynamics in the Mediterranean.

Landscape Level

- Factors determining the distribution of grazing pressure
  - Relative attractiveness of different vegetation types
  - Importance of accessibility - slope, distance from gathering points, etc
  - Distribution patterns of shepherded flocks
  - Dispersal characteristics of different animal species

Community Level

- Relative palatability of different plant species
  - Seasonal variation in palatability of different species
  - Variation in palatability due to stage of development following fire
  - Relative 'cost' of reduced accessibility of foliage
- Grazing characteristics of the animal
  - Factors determining which species will be eaten
  - Differences between shepherded flocks and free-ranging animals
- Role of animals in seed dispersal
- Effect of trampling and dunging on soils

Individual Level

- Type of damage caused
  - How much shoot material is removed by different animal species
  - Which shoots are removed - e.g. browsing height of different animals
- Response of plant to damage
  - Re-sprouting ability
  - Response through allocation of resources to root, shoot and reproduction
  - Change in branching behaviour and crown geometry

Models as predictive tools

It is clear from Table 2 that much more research is required before precise predictions can be made of the impact of domestic animals on Mediterranean vegetation. However, the rule-based modelling approach demonstrates that even relatively simple models based on the wealth of qualitative knowledge already available from ecologists and land managers can be used to make useful predictions. As more data become available the precision of the predictions will increase and as research increases our understanding of the ecological processes, so the generality of models will improve.

Even at the this stage, the models that are being developed as part of this project provide valuable tools for exploratory investigations into the potential effects of management practice. For example, models of plant growth provide information on biomass accumulation which could be used to explore the possible effects of reduced grazing pressure on fire hazard. Conversely, the use of prescribed fire for improving the management of grazing systems could be investigated. Although predictions will not be perfect, the modelling approach can reveal emergent properties of the system and can indicate some of the potential unforeseen consequences of different management options.

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