2. IMPACTS ON TERRESTRIAL ECOSYSTEMS

Fernando Valladares, Josep Peñuelas and Estanislao de Luis Calabuig

Contributing Authors

J. J. Camarero, M. Estiarte, I. Filella, C. Gracia, F. Lloret, E. Gutiérrez Merino, R. Ogaya, R. Pérez-Obiol, S. Sabaté, M. T. Sebastiá

Reviewers

I. Alonso, J. S. Carrión, P. Castro, J. Cortina, A. Escudero, M. Génova, F. Maestre, D. Morales, F. Ojeda, B. Peco, F. Pugnaire, F. Pulido, J. M. Rey-Benayas, S. Rivas-Martínez, F. Rodá, J. C. Rodríguez-Murillo, B. Sánchez, J. J. Sanz, M. Segur, J. Terradas, M. Vila, R. Zamora, M. A. Zavala

J. Pereira, P. Canadell

ABSTRACT

Spain presents a large variety of terrestrial ecosystems, many of them unique, and all of them offering a wide range of goods and services. These ecosystems have been subjected to intense climate change in the past, but the rhythm of these changes has accelerated in an exceptional manner as a consequence of the anthropogenic emission of greenhouse gases. Accelerated climate change is bringing about a series of direct and indirect effects which are accentuated by the interaction with other motors of global change (changes in land use, pollution, biotic exchange). The effects are different for the ecosystems of the Atlantic region, limited by temperature, and for those of the Mediterranean region, limited by water. Whereas productivity could increase with climate change in the former, it might possibly be reduced in the latter.

The ecosystems that are at their ecological or geographic limit (formations with zero water balance, ecosystems dominated by relic species from past climates, high-mountain ecosystems, certain formations in arid regions) are the ones that will be most affected by climatic change.

The areas and systems most vulnerable to climate change are islands in the broad sense (including edaphic islands and high-mountain ecosystems) and ecotones or transition zones between systems. The spatial situation of the latter could be used as an integrated indicator and as a possible early warning of climate change.

There is scientific evidence that climate change will affect the phenology and interactions between species, favour the expansion of invading species and pests, will cause changes in the dominance, structure and composition of the communities, and will increase the impact of disturbances such as fire. With climatic change, the capacity for sequestration of atmospheric carbon of the ecosystems will decrease and altitudinal and latitudinal migrations of species will occur, along with the extinction of local species.

However, it is currently unknown whether species will be capable of evolving and adapting to climate change in time, whether plants will increase their efficiency with regard to water use in times of drought and warming, and whether these processes will accelerate the biogeochemical processes.

The management of terrestrial ecosystems should involve society as a whole and ought to seek creative formulae for the funding of activities for the mitigation of effects, restoration and research. The conservation of terrestrial ecosystems in a scenario of climate change clashes with numerous human activities, especially in relation to the use of natural resources like water. This conservation is at odds with management aimed at maximising production or at sequestrating atmospheric carbon.

Noteworthy among the main research needs is the consolidation of long-term ecological follow-up networks, making as much use as possible of the existing ones and favouring the interdisciplinary participation of the scientific community, the study of interactions, both between environmental factors and between species and trophic levels, along with the determination of minimum tolerance levels (climatic, structural, functional) in systems vulnerable to climatic change.

2.1. INTRODUCTION

2.1.1. Human influence in terrestrial ecosystems: the multiple effects of a spreading species

At an increasingly faster rate, humans are modifying the spatial distribution and functioning of ecosystems. This modification is occurring at local, regional and global scale so that, currently, the vast majority of ecosystems present a certain degree of degradation or alteration attributable to human activities (Vitousek *et al.* 1997). Furthermore, these activities are changing the biophysical properties of the atmosphere and of the climate, and there is irrefutable proof that the ecosystems are responding to all these changes (Hulme *et al.* 1999, Hughes 2000). Although much of this proof is based on the responses of particularly sensitive species, there are more and more results that show effects at the level of the whole ecosystem. Although these effects are not easily appreciable, they generally have a temporal time scale of several decades and are frequently influenced by local conditions (Vitousek *et al.* 1997, Parmesan and Yohe 2003).

2.1.2. The diversity of Spanish terrestrial ecosystems

Very much due to its geographical position and complex orography, Spain presents a great variety of terrestrial ecosystems, one of the widest in Europe. Of the six biogeographical regions contemplated in the Directive Habitats, four are represented in Spain (the Atlantic, Mediterranean, Alpine and Macaronesian) encompassing 141 different types of terrestrial habitats from a total of 264. This extraordinary variety of terrestrial ecosystems together with the particular evolutionary history of Spain, has given rise to a great diversity of species, natural resources and unique biological systems, which have led to the protection of 536 natural spaces throughout the country. Approximately 20% of the country's 50 million hectares (Mha) corresponds to forest ecosystems in the broad sense (the figures oscillate depending on the definition of forest ecosystem). The Mediterranean region is the largest, with 43 Mha, of which 3 Mha are forests, 2.9 Mha are shrubland and heathlands, and 2.6 Mha are natural or semi-natural pastures. The Atlantic region takes up 5.5 Mha, including 1.1 Mha of shrubland and heathlands, and 0.5 Mha of forests. The Alpine region occupies 0.9 Mha and is dominated by natural and seminatural pastures (0.2 Mha) and by forests (0.2 Mha). The smallest region is the Macaronesian (0.7 Mha) and here, forests and shrubland total 0.1 Mha (Reyero 2002). Apart from climatic and biogeographic features, the degree and temporal extent of human intervention are other intrinsic characteristics that must be taken very much into account in the description of Spanish terrestrial ecosystems. The human intervention varies from intense and prolonged in the Mediterranean and Atlantic regions to moderate and relatively more recent in the Alpine and Macaronesian regions. The surface area of the Spanish Mediterranean region represents 17.3% of the whole Mediterranean region in the strict sense, which is distributed throughout 18 countries, and is only surpassed by Turkey (20.8% of the total).

Thus, Spanish terrestrial ecosystems are exposed to a great natural climatic variability, and are the result of a noteworthy topographic and lithological complexity and marked gradients in land uses and in water availability, and frequently accommodate a high level of biodiversity. As we will see, these and other characteristics make many of these ecosystems particularly sensitive to atmospheric and climatic changes. An understanding of the effects of climate change on terrestrial ecosystems is crucial in order to take the measures necessary to guarantee the multiple goods and services they provide us with, many of which are vital to our very existence.

2.1.3. Goods and services of the terrestrial ecosystems

From the anthropocentric point of view, terrestrial ecosystems are systems that fulfil three general types of functions: productive, environmental and social (Rodá *et al.* 2003). In their productive function, they provide renewable natural goods, such as food, medicines, timber products and non-timber products (pastures, cork, pine cones, game, fungi, etc.). Among the environmental and ecological functions are the ecosystem services provided free of charge, like the maintenance of biodiversity, regulation of atmospheric composition and of the climate, the regulation of biogeochemical cycles, soil conservation (e.g. prevention of erosion), the regulation of the water cycle and of carbon storage. Among the social functions, the most important ones are recreation, education and leisure uses, demonstrated health benefits, opportunities for research, the traditional cultural and emotional values, and functioning giving rise to important economic activities like tourism and hiking. It is clear that the alterations caused by atmospheric and climatic changes will have an impact on many of these goods and services, and consequently, an impact on the socioeconomic systems (Winnet 1998). Among the ecosystem functions and services, we can highlight atmospheric carbon sequestration and storage, because this is the basis of the plant production that sustains the ecosystems and because it has direct implications in the balance of atmospheric CO_2, one of the main agents of climatic change. Other ecosystem services include the provision of pollinators and pest control.

Terrestrial ecosystems are considered to be important regulators of both global and local climate, decisively influencing biogeochemical cycles and characteristics of the atmosphere. Certain terrestrial ecosystems like forests affect relative humidity and even local rainfall regimes, and can give rise to a feedback cycle in which the forest favours hydric conditions in order to maintain itself. Although it has been established on numerous occasions that when vegetation cover is high (when the leaf area index – LAI – increases), there is less water available in the ecosystem due to an increase in transpiration (Rambal and Debussche 1995), the forest can serve to capture water in certain Mediterranean conditions. Experimental data and numerical simulations indicate that the presence of tree masses on coastal mountain slopes significantly favours the formation of summer storms and the collection of water which, in the form of more or less dense fog, rises from the sea (Millán 2002). Although these local effects of the forest on microclimate and rainfall are evident and have been proven, their influence on regional climate (macroclimate) is less clear. In simulations of the effects of extensive deforestation in Spain and France, it has been found that the forest only favours rains when these occur in summer by means of vertically developed clouds, in whose formation forest transpiration can actively intervene (Gaertner *et al.* 2001).

2.1.4. Human impact on Spanish ecosystems

Intense human intervention is a characteristic typical of most Spanish terrestrial ecosystems. These ecosystems have been very much modified by man from the start of the Neolithic, specially since the Bronze Age, causing a general reduction of their original forest surface areas (Pons and Suc 1980, Reille and Pons 1992). Within this process of intervention, certain qualitatively new semi-natural and relatively stable ecosystems have been created, such as the *dehesas* of species of *Quercus* (Stevenson and Harrison 1992). Anthropic action over the last few millennia is a critical element that has determined radical changes in diversity and in tree and shrub cover, and, in short, in the structure and functioning of many terrestrial ecosystems. Carrión *et al*. (2003) reconstructed the history of the vegetation in the Sierra de Gádor mountain range in the Southeast of the Iberian Peninsula using a palaeo-ecological register. They showed significant changes in the abundance of plant species, with the replacement in dominance of deciduous *Quercus* by evergreen *Pinus* and *Quercus* around 3940 years BP, the maximum rise of *Pinus* to the detriment of the evergreen *Quercus* between 1760-1629 years BP, along with the diminished size of the forests accompanied by an increase in helophytes until 1160 years BP. Among the factors that resulted in vegetation change during the second half of the Holocene are the occurrence and frequency of fires, human activity, climate change and the interrelation between these. Since that time, climate and human activity have become inextricably interrelated.

Within a more recent temporal framework, in Spain at the beginning of the 20th century, large reforestation programmes were started for production purposes, which coincided with the rural crisis throughout the western world and the abandonment of the countryside, which was re-colonised by communities of woody plants. The abandonment of crops on poor soils, a common practice on the Iberian Peninsula, has led to a marked change in the structure and functioning of the ecosystems, with an increase in floristic and faunistic diversity, an improvement in the quality of the soil and of the hydrological cycle and reduced soil erosion. But the abandonment of many traditional practices also leads to the crisis of production systems of great natural value due to their high biodiversity, such as the *dehesa*, and to the ageing of the underwood containing species of *Quercus*, which, on not being managed lose vigour and become more sensitive to abiotic disturbances (drought and climatic extremes) and biotic ones (pests and diseases). In turn, the accumulation of biomass favours fires. The general forest area increased in the last third of the 20th century and there has been a rise in the number of protected natural spaces, resulting from the spread of an ecological vision of the forest and of terrestrial habitats. The natural recovery is observed of Holm oak forests and Cork oak forests in less dry, sub-Mediterranean marginal areas, but there is an increase in the environmental deterioration of the air and the waters, and in the rhythm of climatic change. There is little protection of natural spaces outside the mountainous areas or historic or emblematic sites, and the forests, shrublands and pastures become fragmented and disconnected (Costa *et al.* 1990, Valladares 2004a). Likewise, there are areas (certain abandoned crop fields, stipa-dominated grasslands) and shrublands affected by overgrazing) in which, in spite of the abandonment of traditional practices, the degree of degradation, combined with unfavourable climatic cycles, has considerably hindered the spontaneous recovery of the vegetation.

2.1.5. Changes in the carbon balance, cause and consequence of climate change

The carbon balance of terrestrial ecosystems is the result of processes that trap atmospheric CO_2 (e.g. photosynthesis) and processes that release CO_2 (e.g. respiration, fires). A vital aspect at the present time is to determine to what extent terrestrial ecosystems can act as carbon sinks thus attenuating global warming. But to make a detailed calculation of the carbon balance is not an easy task, especially when different scales of time and space intervene in the analysis. There is great uncertainty regarding how these affect the environmental conditions interacting with the diverse processes involved. Furthermore, in order to understand carbon flows, it is important to quantify the amounts of carbon existing in our ecosystems. For the aerial part, good databases are available, like those provided by forest inventories, although there is a lack of data on ecosystems not included in this initiative. The least known part corresponds to subterranean biomass, which is considerable in Mediterranean ecosystems and, in the case of a Holm oak forest, can account for 50 per cent of total biomass. To this carbon we must add the necromass accumulated on the ground, which frequently exceeds the total carbon of the biomass, although very little information is available in this respect.

Analyses based on national forest inventories reveal that, for much of the 20th century, Spanish forests have acted as carbon sinks and that all the Spanish regional autonomies accumulated carbon in their forests during the 1974-1987 period (Rodríguez-Murillo 1997, Rodríguez-Murillo 1999). This accumulation oscillated from 4.5 tons of carbon per hectare and year in Galicia (2.0 in the previous period) to 1.1 in Murcia (0.27 in the previous period). This effect is attributed to the reforestation carried out in the 1940's and to the most recent changes in agriculture and livestock farming uses which have contributed to the increase in tree cover and in the density of the forest masses (Rodríguez-Murillo 1999). With regard to the emission of greenhouse gasses (CO_2, CH_4, N_2O) from forest fires in the 1970-2001 period, the average value is $21.5*10^6$ tons for the whole country for direct emissions; delayed emissions are, on average, 3.8 time higher than these (Prieto and Rodríguez-Murillo 2003). Galicia was the regional autonomy that most contributed to the total emissions of greenhouse gasses as a consequence of forest fires. However, it must be pointed out that the data on the total estimated emissions of CO_2 only represent 1% of the total estimated emissions of this gas for Spain.

2.1.6. Methods of study of the effects of climate change

The study of the effects of climate change on our terrestrial ecosystems was carried out using five types of activities covering different time scales: (1) the palaeoecological study of datable sedimentary cores, with the use of biological and geochemical indicators (thousands of millions of years), (2) the study of different types of historic material, like, for example, specimens of herbarium, museum pieces, archives, tree rings (last few centuries), (3) the study of the ecophysiological, biogeochemical and demographic changes in our ecosystems in response to the changing climatic conditions (last few decades and years), (4) the experimental study of our ecosystems, under more or less controlled conditions, simulating the changes predicted for the next few decades by the climatic models and, lastly, (5) the modelling of past and future changes, in space and in time. Apart from using palaeoecological and historical tools to travel through time, the study of climate change and of its effects require to successively follow the spatial scale upwards, from the leaf to the ecosystem, the region and the whole planet, combining the modelling tools with those used for tele-detection. We must point out, however, that the influences of climate change are difficult to separate from those of the other components of global change, such as changes in biogeochemical cycles or changes in land uses.

2.1.7. Contents of the chapter and clarifications

Given the broad scope of aspects included in this chapter, a certain overlapping with other chapters is inevitable, especially with those dealing with forestry (Chap. 9), plant biodiversity (Chap. 5), animal biodiversity (Chap. 6), and edaphic resources (Chap. 8). In order to minimise this overlap, we have gone more deeply into the ecophysiological aspects of the vegetation and into processes operating at the levels of community and ecosystem. We will highlight the Mediterranean region, as it is the largest region of the Iberian Peninsula and because more information is available on its sensitivity to climatic change. Indeed, this region contains formations which have reached the limit of their possibilities, with hydric balances in which rainfall is equalled by evapotranspiration. The freshwater and coastal systems are dealt with in other chapters (Chaps. 3 and 11 respectively). By the term increased aridity, we refer jointly to the decrease in rainfall, which in turn is becoming more irregular, and to the temperature increase, which leads to an increased evapotranspiration.

2.2. SENSITIVITY TO THE PRESENT CLIMATE

2.2.1. History of climate change and of anthropogenetic influence in ecosystems

Our country, like the whole planet, is subjected to environmental change, a change that has been very spectacular in different phases of the history of the earth, but which is currently occurring at a particularly accelerated rhythm (IPCC 2001). European terrestrial ecosystems have undergone multiple and profound changes related to equally profound climatic changes accompanied in more recent times by alterations in the regime of disturbances (e.g. grazing, fire, charring and extraction of timber). It must be pointed out that the adaptational and competitive characteristics of the species and stochastic processes have been as important, if not more, as the conclusion of the glacial phases and the climatic changes of the Holocene with regard to the establishment of dominant species following each crisis (Carrión 2003).

The Iberian Peninsula and the Balearic Isles have been of great biogeographical value in the study of climatic changes during the last glacier-interglacial cycle. Following the so-called Riss-Würm interglaciation, between around 120,000 and 80,000 years before the present, the pollen registers suggest the expansion of steppe landscapes that responded to low rainfall and temperatures (Pérez-Obiol and Julià 1994). Nevertheless, during the last glacial crises, some mountain and coastal areas in the South of the Peninsula maintained a climate that was warmer and more humid which represented an important uniqueness in the peninsular environment and reflects a landscape that was eventually more wooded with the inclusion of mesophyll and thermophilic species (Carrión 2002, Carrión *et al.* 2003). The most noteworthy information on centennial and millennial pulses from the last glaciar-interglacial cycle comes from the period known as Lateglacial which began around 14-15,000 years ago. This period involved a global climatic improvement, concurrent with the deglaciation process, which favoured the development of tree and shrub formations in many regions of the Peninsula, although the nature of this colonisation is transgressive. Subsequently, between 11,000 and 10,400 years, a climatic anomaly occurred, which meant a step backwards by several centuries to the cold and arid conditions of the pleniglacial. We are referring to the recent Dryas (in reference to the alpine Rosaceae, *Dryas octopetala*). The end of the recent Dryas constitutes the start of the present interglacial (Holocene) which is characterised by a rapid increase in temperature and humidity reaching optimum level around 8,500-5,500 years before present. Between 5,000-4,500 years, climatic parameters acquire a Mediterranean character in the South, the East and in the Balearic Isles (Yll *et al.* 1997) and in many parts of Eastern Iberia, greater seasonality and a more xeric landscape are observed. In the West and North of the Peninsula, this climate change did not manifest itself in such an abrupt manner, but the bioindicators permit us to establish a reduction in rainfall. The last 3,000 years are characterised by phenomena of generalised deforestation, above all in the thermo-Mediterranean context, caused by the aforementioned synergy of climate and anthropic action.

Although most of the pollen sequences do not reach the adequate resolution to distinguish questions below multi-millennial change, some suggest that changes in vegetation may occur in very few centuries or even decades, as a consequence of abrupt climatic changes. On the Iberian Peninsula, only one Holocene pollen sequence revealed these dynamic plant responses to climate change, that of Cañada de la Cruz, at the upper forest limit of Sierra de Segura mountain range (Jaén) (Carrión *et al.* 2001). These changes have forced the relatively rapid altitudinal or latitudinal migration of different species. At even shorter temporal scales, the studies of herbarium material show that in the last two centuries, stomatic density has fallen by 21% and the discrimination of the ^{13}C by 5.2%, suggesting the influence of an adaptation process (increased efficiency of water use) as a response to variations in selective pressure determined by the warmer and more arid conditions of the present (Peñuelas and Matamala 1990, Peñuelas and Azcon-Bieto 1992).

It ought to be mentioned that in recent years, evidence has been found of a rapid biotic response (decades-centuries) to the abrupt climatic changes occurring at the heart of the glacial phases (the so-called Heinrich and Dansgaard-Oeschger events, which can be seen in the ice cores in the Antarctic and Greenland). These responses seem to include the continental vegetation of the Southern Peninsula, as has been seen in certain marine sequences in Alborán and on the Iberian Atlantic and North African coasts (D´Errico and Sánchez Goñi 2003). Very recently it has been proven that the sign of climate change also appears in the geochemistry of speleothemes (Genty *et al.* 2003). Given that the marine sequences provide a pollen rain of uncertain spatial control and that they have a complex taphonomy, we should wait for the appearance of continental records to confirm or reject the fact that the responses of vegetation to interglacial events have been equally brusque. The preliminary reports on European palaeovegetation during the Marine Oxygen isotopic stage 3 (*OIS 3 Project*) are not conclusive in this sense (Huntley *et al.* 2003).

Among the country's terrestrial ecosystems, forests and shrublands have spread over the last few decades as a result of the temperature rise, of the increased CO_2, and/or of the increase in fertilisers in the atmosphere (diffuse eutrophication), but above all as a result of two processes of anthropic origin: secondary succession based on pastures and abandoned crop fields, and the superposition of successive severe disturbances upon the terrestrial ecosystems (Mesa-Jimenez 2002, Costa *et al.* 1998). The different uses that humans have made of them have produced a mosaic of ecosystems with varying degrees of maturity, forming heterogeneous landscapes that favour the maintenance of diversity.

2.2.2. The "fingerprints" of climate change in the trees of the Iberian Peninsula

The growth rings in timber from trees reveal big inter-annual oscillations in response to the climatic changes of the last few centuries, although these oscillations differ among species. Species tolerant to drought, but which can make use of the phreatic water, such as the Holm oak (*Quercus ilex*), show less oscillation than the species that elude drought, and depend more directly on rainfall, like the Aleppo pine (*Pinus halepensis*) (Ferrio *et al.* 2003). Throughout the 20th century, trees, forests and ecosystems have been responding to effects of climate change like increases in CO_2, global warming and climatic variability. The response of the trees to these effects has been analysed in over 60 forests of conifers of different environmental characteristics throughout the whole eastern half of the Peninsula. Most of the dendrochronological variables (based on the thickness of the annual rings, their isotopic composition and changes in the anatomy and density of the wood) showed a growing variability during the second half of the 20th century, reflecting an increase in climatic variability and in the frequency of extreme events (Tardif *et al.* 2003, Camarero and Gutiérrez 2004). Climate change has restricted the possibilities for change of the trees, which show greater synchronisation in their growth, both among individual trees and among species. This means a reduction in the differences between sites due to local causes (slope, orientation, substrate, or influence of a determined type of climate), which have acquired secondary importance in the last few decades. These effects have been observed for different spatial and temporal scales. Among the changes detected are: a) an increase in intra-annual variability in growth in the thickness of Mediterranean tree species, in *Pinus halepensis*, related to the lengthening of the growth period; and b) an increase in the inter-annual and inter-decade variability in the series of ring thickness and of the isotopic composition in populations of sub-alpine trees at local and regional scale (Camarero and Gutiérrez 2004).

During the 20th century, two very contrasted periods have been described, based on the radial growth of Mountain pine *Pinus uncinata* in the central Pyrenees: (*i*) the first half of the last century showed a low frequency of wide and narrow growth rings, low average sensitivity and a low proportion of common variance among trees, whereas (*ii*) the second half presented the opposite characteristics (Tardif *et al*. 2003). The lower variability in growth between 1900 and 1950 has been associated with a "relaxation" of the altitudinal thermal gradient due to the greater regional warming observed during these decades and to a lower inter-annual climatic variability of the temperatures. Further up, at the upper limit of the forest, the recent increase in this climatic variability since 1950 has stopped the altitudinal limit of the tree from rising (Camarero and Gutiérrez 2004). In contrast, in the climatically warm and stable period from 1900-1950 a clear rise in the limit of the tree was observed. The increase in climatic variability since 1950 has slowed this rise, favouring an increase in density within the sub-alpine forest – alpine pastures ecotone.

2.2.3. Sensitivity to temperature and direct responses of organisms and systems

The activity of all living organisms is strongly influenced by temperature. Thus, we cannot expect anything other than alterations of this activity. And the first type of change provoked by warming is in the life cycles of plants and animals (Peñuelas and Filella 2001). These phenological changes have become the clearest symptom of the fact that climate change is now affecting life (Fig. 2.1). At individual level, the most direct physiological effect of the temperature increase is the rapid increase in the respiration rate. The respiration of the whole ecosystem, the main component of which is plant respiration, is the determinant process of carbon balance, at least in European forest ecosystems which have been studied with sufficient accuracy (Valentini *et al.* 2000). The high temperatures affect the photosynthesis of plants, but these are capable of becoming acclimatised and of growing even at extreme temperatures, provided that water is not a limiting factor. The high temperatures increase the deficit of vapour pressure, increasing the plants' transpiration. But the closing of the stomata, frequently exacerbated by the combination of high temperatures with drought and high levels of CO_2, can even make transpiration diminish (Kirschbaum 2004). The capacity of the plants to become acclimatised to different temperatures, particularly during their development, stops respiration from increasing as rapidly with temperature as could be expected, but in spite of the big impact of plant respiration on the productivity of ecosystems, there are still many physiological uncertainties (Atkin and Tjoelker 2003).

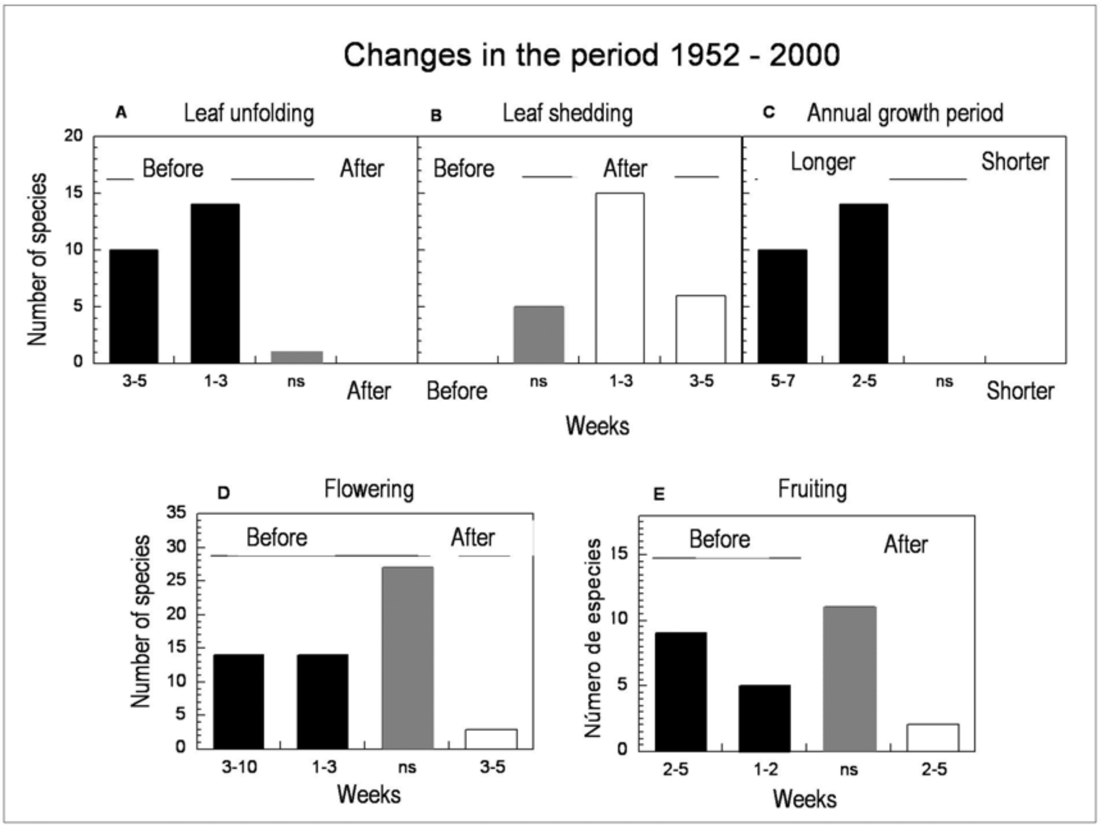

Fig. 2.1. Frequency of plant species with life cycles that have been altered in the last five decades (from 1952 to 2000) in Cardedeu (Vallès Oriental, Barcelona). Before and After refer to the moment of the event, that is to say, if this is advanced or delayed respectively during the period studied: ns = not significant. (After Peñuelas et al. 2002).

But it is not only organisms that are affected by warming, but also ecosystem processes. Given that biogeochemical processes depend on temperature, eutrophication, or enrichment in nutrients, is sensitive to warming, above all nitrates, a very worrying process at international level. Although eutrophication is generally associated with the occasional or diffuse contribution of nutrients (e.g. excess of cattle faeces, fertilisers), increased temperature and droughts have a great influence on the dynamics of nutrients, due to the fact that warming increases mineralisation, and that the drought impedes the use of nutrients by the plants and facilitates losses by the system with rain. Another similar biogeochemical alteration lies in the stimulation of the decomposition of organic matter by warming (see chapter on edaphic resources). The lack of water, conversely, retards this. It is therefore a situation in which two factors involved in climate change have different effects (even conflicting ones) on the cycle of the material and the functioning of our ecosystems (Emmet *et al.* 2004). In pastures in the Catalonian Pyrenees which are not limited in the hydric sense, it has been seen that warming increases productivity and accelerates the decomposition of organic matter (Sebastiá *et al*. 2004).

2.2.4. Phenological changes and desynchronisation between trophic levels in a warming world

Due to its situation and topography, Spain is one of the places in which the phenological changes are expected to be biggest. The biological cycle of many common plants, migrating birds and species of butterflies and other insects is changing significantly and climate change seems to be the main cause of this alteration (Fig. 2.1). In Catalonia, the leaves of the trees unfold, in general terms, 20 days earlier than fifty years ago. The leaves of the apple tree, the elm or the fig tree seem to sprout a month in advance and the almond tree and the poplar, fifteen days before, although some other trees, like the chestnut, seem impervious to changes in temperature due to being more dependent on other factors such as the photoperiod or water availability in the soil. Furthermore, plants are also flowering and fruiting an average of 10 days earlier than 30 years ago (Fig. 2.1). And the life cycles of animals have also been altered. For instance, the appearance of insects that go through the different larval states faster in response to warming, with an average advance of 11 days (Stefanescu *et al.* 2004). All this premature activity of plants and animals may endanger them by means of late frost episodes. But the frequency of these episodes has also changed, generally diminishing in an environment that is getting warmer and warmer. For example, in Cardedeu (Barcelona) there was frost around 60 times a year and now there are about 20 (Peñuelas *et al.* 2002). Similar responses in the advance of the phenophases of plants and animals (invertebrates, amphibians, birds....), by around 3-4 days in spring, have been recently described in many other parts of the world (Peñuelas and Filella 2001, Walther *et al.* 2002, Parmesan and Yohe 2003), so that this seems to be a generalised phenomenon, with the regional, local and specific variability typical of all biological phenomena. All these phenological changes are not simple indicators of climatic change. They are of critical ecological importance because they affect the competitive capacity of the different species, the conservation of these, and therefore, the structure and functioning of the ecosystems. As nature is not homogeneous, the responses to warming are different depending on the species and even on the individuals. Such heterogeneous responses to climate change may cause serious de-synchronisations in the interactions between species, for instance, between plants and their pollinators, as in the case studied by Santandreu and Lloret (1999), or between plants and herbivores, thus altering the structure of communities. A paradigmatic example of the desincronizaciones between trophic levels can be seen in what occurs with migrating birds. Given the advance in the flowering and fruiting of plants and in the appearance of insects, and therefore, the advance in the availability of food for birds, we can expect an earlier arrival of migrating birds. But this is not so, because the arrival of certain very common and popular birds like the nightingale, the swallow, the cuckoo or the quail is being retarded in certain areas by an average of two weeks in relation to thirty years ago (Peñuelas *et al.* 2002). This delay is surely determined by climate change in the place they emigrate from, the sub-Saharan regions, or in the regions they pass through on their migratory routes. However, studies already underway reveal a complex spatial pattern, with parts of the country where the birds arrive earlier (see chapter on animal biodiversity).

If we observe the phenological changes at global scale, we can see very important alterations such as, for example, the increase by 20% in the biological activity on our planet in the last 30 years, very much due to this phenological retardation of the productive period (Peñuelas and Filella 2001). We can appreciate this increase both in the pictures from the satellites for observation of the Earth, and in the data on atmospheric concentration of CO_2. The normalised data on the vegetation index (NDVI) corroborate the data from the observation of the Earth and show how in the last 20 years the growth season of plants has been lengthened by 18 days in Eurasia, which has led to an increase in green biomass, at least at latitudes 40º (Myneni *et al.* 1997). The increase in plant productivity in the last few decades which had been attributed to the fertilising effect of the CO_2 and to nitrogen depositions, may also be partly due to this temperature rise and to this lengthening of the growth season (vegetative activity). All of this is corroborated by the data on atmospheric concentration of CO_2, which show us an increase in the range of seasonal oscillation of CO_2 in the last few decades due to the greater springtime drop in the concentration of CO_2 (Keeling *et al.* 1996).

2.2.5. Another effect of warming: more emission of volatile organic compounds

The temperature increase has diverse direct effects on the activity of living organisms. One environmentally important one is the exponential increase in the biogenic emission of volatile organic compounds (VOC). These emissions affect atmospheric chemistry, not only in relation to the carbon cycle (emissions of around 1500 Tm C year^{-1}) and to the formation of aerosols, but also to the role they play in the oxidative balance of the levels of OH, NOx and O_3 (Peñuelas and Llusià 2001). Emissions of VOC are controlled by the factors that alter the tissue concentration of these compounds, vapour pressure and resistance to diffusion into the atmosphere. Temperature exponentially increases the emission of VOC on activating its enzymatic synthesis and its vapour pressure and on decreasing resistance to emission. Drought, however, reduces the emissions due to the lack of carbohydrates and ATP, and to the decrease in the permeability of the cuticle to the exchange of gasses. At the present time, it is difficult to estimate the final result of this antagonism between warming and drought. Other factors linked to global change, like the increase in tropospheric ozone also affect the emissions of VOC; these is a phenomenon of positive feedback from pollution by ozone, which requires greater attention in order to correctly understand it (Llusia *et al.* 2002). One of the most important apparent functions of some of these VOC, like isoprene and the terpenes, is to act as thermoprotectors. *Quercus ilex* seems to use these compounds as stabilisers of the cell membranes and also as deactivators of the of the oxidised radicals to protect itself from the high summer temperatures (Peñuelas and Llusia 2002). Furthermore, these emissions of VOCs could provide a negative feedback for the warming of the atmosphere itself, on acting as aerosols that decrease irradiance, although they could also provide positive feedback for warming by means of their direct greenhouse effect, by absorbing infrared radiation, and of the indirect one, that is, lengthening the life of methane and other greenhouse gasses (Peñuelas and Llusia 2003).

2.2.6. Sensitivity and response to drought

Hydric availability is a critical factor for evaluating the effects of climate change on most terrestrial ecosystems. Warming and drought should be considered simultaneously. Indeed, both the lengthening of the life of deciduous trees and the acceleration of the renovation of the leaves of evergreens, phenomena associated with temperature increase (Gracia *et al.* 2001, Sabaté *et al.* 2002), will lead to an increase in the water transpired which is added to the greater potential evaporation resulting from the temperature rise. In those places in which the forest avails of sufficient water to compensate for this greater hydric demand, forest production can be expected to increase. However, in the places subjected to hydric deficit, which represent most of the terrestrial ecosystems in Spain, changes can be expected which will range from a reduction in the density of the trees to alterations in the distribution of species (Sabaté *et al.* 2002).

Droughts can be moderate or extreme, chronic or acute, recurrent or sporadic, and the responses of one same species can vary depending on these characteristics and on the moment and speed with which the drought sets in. Predictions of climate change indicate an increase in the duration and intensity of droughts during the 21st century, associated with a more irregular rainfall regime and with more extreme and generally higher temperatures (IPCC 2001). The spatial heterogeneity of these variables, especially of those related to the rainfall regime, is high, and it is therefore currently difficult to make predictions for specific areas. This climate change will undoubtedly give rise to local extinctions and changes in species dominance in many terrestrial ecosystems. Drought limits plant growth and survival, acting as a selective stress filter of plants, according to their tolerance to hydric stress. It also negatively affects reproduction and alters the production rhythm of leaves, stems, flowers and fruits (phenology). In spite of the apparent recovery of tree cover following unusually intense droughts, there are indications that generalised droughts leave consequences that persist for several years (Peñuelas *et al.* 2000). The increasingly frequent repetition of drought episodes could accelerate these changes at community level (Valladares *et al.* 2004c).

In a comparative study of the hydraulic architecture of nine woody species, it was seen that whereas *Ilex aquifolium, Phillyrea latifolia* and *Juniperus oxycedrus* were resistant to the cavitation of the xylem caused by drought, *Quercus ilex, Arbutus unedo* and *Acer monspessulanum* were much more vulnerable (Martinez-Vilalta *et al.* 2002b). It was also observed that this different vulnerability to cavitation was correlated to the hydric potentials that each species showed in the field, confirming the existence of different hydric strategies that make the species growing together spend the summer drought with different stress levels and with different safety margins with regard to embolisms. Analogous differences have been observed in *Quercus coccifera* and *Pistacia lentiscus* (Vilagrosa *et al.* 2003).

We can learn about the effects of heat and drought from examples of hot, dry periods such as those of the summer of 1994. This summer severely damaged many forests and shrublands on the Iberian Peninsula (80% of the 190 peninsular sites studied presented damaged species, Peñuelas *et al.* 2001). The Holm oaks, for example, dried up in many sites (Lloret and Siscart 1995). In parts of the Iberian System mountain range in Aragón, intense defoliation was observed, along with drastic changes in anatomy and growth, but the Holm oaks recovered after the drought (Corcuera *et al.* 2004). Isotopic studies with ^{13}C and ^{15}N showed that in the following years these Holm oak forests continued to be affected, so that they presented less use of the water that was available to them, and the loss of soil nutrients was favoured (Peñuelas *et al.* 2000), a serious secondary consequence, if we take into account that these ecosystems are usually limited by nutrients (Rodá *et al.* 1999). The different severity of the effects on the different forests in the country was determined, among other factors, by 1) the orientation of the slopes (greater damage on the sun-facing slopes) (Peñuelas *et al.* 2000), 2) soil lithology (less damage in the deeper soils that were more penetrable by the roots, for example, soils on schists) (Lloret and Siscart 1995), 3) the dominant species (Peñuelas *et al.* 1998), and 4) forest management (thinned forests less affected than the dense ones) (Gracia *et al.* 1999). The degree of damage varied depending on the functional type and on the evolutionary history of the different species (Peñuelas *et al.* 2001). The genera, *Lavandula, Erica, Genista, Cistus* and *Rosmarinus*, that have diversified under the Mediterranean climatic conditions (i.e. after the 3.2 million years of the Pliocene) were initially more affected by drought than genera that had evolved previously (e.g. *Pistacia, Olea, Juniperus, Pinus* and *Quercus*), but recovered much better after several years of greater water availability. An non-native genus *Eucalyptus* was seriously damaged by the drought and did not recover in successive years. The post-Pliocene Mediterranean species, therefore seem to be more resistant to an environment that is difficult to predict, with great seasonal and inter-annual variability and subject to frequent droughts (Fig.

2.5). An understanding of these responses is important in order to predict the future composition of the communities in a scenario of climatic change.

2.2.7. The importance of disturbances and their interaction with climate

Many terrestrial ecosystems and in particular the Mediterranean ones, have been and are exposed to disturbances that may be episodic, such as intense drought and fires, or chronic, like overexploitation and herbivory. Fire, and subsequently, grazing, had a very significant influence upon the evolution of the vegetation during the second half of the Holocene. The increase in aridity was, in many cases, little more than a background influence. Given the frequency and intensity of the disturbances suffered by Mediterranean ecosystems, the differential sensitivity of the species to these is a very important mechanism in the composition and spatial and temporal dynamics of plant and animal communities. But climate can cause significant variations in the effect of the disturbances on the ecosystems. The effect of herbivory, for example, can cause drastic changes under more xeric conditions (Milchunas *et al.* 1988). In the short term, overgrazing generates the consumption of much of the primary production and accelerates soil erosion. In the long term, it may lead to an increase in the abundance of unpalatable species, apart from a generalised collapse in the regeneration of woody species. Damage by herbivory of woody plants depends on the amount of annual rainfall, and the impact is greater in the dry years (Zamora *et al.* 2004).

The hotter and more arid conditions, along with the increase in biomass and in the inflammability of this associated with the increase in CO_2, the changes in land use, such as the abandonment of crop fields followed by a process of forestation and accumulation of fuel, and the activities of a growing number of visitors to our forests, increase the frequency and intensity of forest fires. Mediterranean forests and shrublands, characterised by severe summer drought, are ecosystems prone to fires. Fires, which increased throughout the 20th century, now constitute one of the most serious disturbances in Mediterranean region (Moreno *et al*. 1998, Piñol *et al.* 1998). This increase is partly due to the abandonment of the countryside and to previous reforestation programmes using pine species that result in very inflammable forest formations. The vegetation-fire relationship, however, is a complex one (Moreno y Vallejo 1999, Moreno *et al* in press *a,* Ojeda 2001; see chapter 12). Fire causes intense disturbance of vegetation and landscape: at historic or evolutionary scale, it has acted as a selective filter of plant and animal species; at ecological scale, it creates open spaces, changes the structure of the habitat and the supply of food for the fauna, and determines spatial mosaics of regeneration which, depending on the spatial scale and recurrence of the fires, can generate greater diversity. The structural composition of the species, and therefore of the community as a whole, is modified, as has been seen in the response of Mediterranean plant species in the different conditions of fire recurrence simulated in the Garraf Nature Park in Catalonia (Lloret *et al.* 2003). Furthermore, the increased intensity and frequency of fires, the synergic effect of other severe disturbances, such as excessive herbivory, causes nutrient losses in the ecosystem, negatively affects species with strict forest requirements and those that have no suitable persistence or dispersion mechanisms, and can finally lead to a simplification of the composition and structure of the communities (Ojeda 2001).

2.2.8. Direct effects of increased atmospheric CO_2

All the aforementioned factors, water availability, temperature, fires, VOC and nutrients, interact with the main factor generating climatic change, the increase in atmospheric CO_2. Given that CO_2 is the substrate of photosynthesis, thousands of studies have been carried on the direct effects of the increase in atmospheric CO_2, mostly at short temporal scales, under controlled conditions and with young plants (Körner 2000). In general, an increase in photosynthesis rates has been observed, along with less tissue concentrations of N and a reduction of transpiration which leads to the more efficient use of water (Kirschbaum 2004). The final effect of the increase in CO_2 however, depends on the interaction with other environmental factors: temperature, radiation, drought, availability of nutrients or the presence of atmospheric pollutants. Responses to CO_2 are different depending on species, and even on genotypes (Castells *et al.* 2002), which could lead to changes at community level, as the concentration of this gas increases. It is still very unclear what may happen in the long term and even less under the real complex conditions of the ecosystems (Körner 1995, Körner 2000). For instance, the responses observed could be buffered in time; indeed, in some plants, acclimatisation of the photosynthesis and the disappearance of the reductions in concentrations of N have been observed after six years of growth at high CO_2 (Peñuelas *et al.* 1997). The increase in CO_2 could increase the synthesis of secondary metabolites in plants, which could provide protection against pests and pathogens, but on increasing the C/N relationship, consumption by herbivores may be stimulated and the quality of the organic matter in the soil could worsen (Sebastiá *et al.* 2003). In short, the tendencies to be expected in the photosynthesis rates with an increase in CO_2 have been confirmed in recent reviews, but not the tendencies related to primary production, which vary according to species (Poorter and Navas 2003) and interacts in a complex manner with other resources such as water and nitrogen (Nowak *et al.* 2004). In the scaling of ecosystems there is an increasing uncertainty caused by the diverse climatic factors operating together with the increase in CO_2 (Norby and Luo 2004).

2.2.9. Capacity of species to evolve and to adjust to phenotypical plasticity

From the evolutionary point of view, species tend to be quite conservative and to respond to disturbances by migrating rather than through adaptation. But migration in the currently fragmented landscape is quite unlikely. The slowness of certain ecological processes, like the natural regeneration of some species of the genus *Quercus*, compromises the long-term viability of the ecosystem, as one of the characteristics of climate change is the acceleration of change rates. Microevolutionary processes can occur on short time scales in dynamic systems such as temporary lakes, thus compensating for the negative effects of a very rapid environmental change rate. But these processes are not operative for long-lived, slow-growing species such as Holm oaks and other oaks, essential in many of our terrestrial ecosystems (Rice and Emery 2003). The capacity for ecophysical adaptation to local environmental conditions is noteworthy in most plant species, but the problem is the rapid rate of environmental change, above all for woody species, in which evolutionary adjustments require 200-1200 years in order to be effective, as has been estimated in *Pinus contorta* (Rehfeldt *et al.* 2001). If the plants cannot follow climate change by evolution, they can attenuate its adverse effects by means of short-term responses (acclimatisation, phenotypical plasticity). But plasticity has not generally been maximised during evolution in adverse systems (e.g. arid areas or ones poor in nutrients or subjected to climatic extremes), but rather the species in these areas tend to make conservative use of the resources involved in moderate plasticity (Valladares *et al.* 2002). It could therefore be thought that the capacity for physiological and morphological adjustment to new climatic conditions is initially limited for certain species or populations in Mediterranean areas and perhaps also for high-mountain species on oligotrophic soils.

2.2.10. Sensitivity of ecosystems to climate change within a framework of interactions

Ecosystems are, by definition, characterised by the existence of interactions both between biotic and abiotic factors and among the living organisms. If the information on sensitivity to climate change is deficient for many species, it is even more so if we want to take these interactions into consideration. These interactions are crucial, however, for interpreting the sensitivity of ecosystems. For example, if one determined species requires the intervention of another species to complete its life cycle (e.g. a pollinator for a plant), knowledge of the sensitivity of the former to climate change is of little use to us if we know nothing of the sensitivity of the latter.

Changes in the phenology and distribution of many species will contribute to separating in space and/or in time species that until now have coincided in the same habitats, but also to make contact between species that had had no interaction until now. That is to say, climate change is favouring both the rupture of interactions and the establishment of new ones. An example of new interactions is being observed in Mediterranean mountains in the behaviour of the pine caterpillar (*Thaumetopoea pityocampa*), a defoliator of diverse pine species (Hódar and Zamora 2004). The interactions are crucial for interpreting the sensitivity of ecosystems to climatic change, as in the case of the Scots pine, for example, the autochthonous populations of the endemic variety Sierra Nevada seem to be able to resist well recent climatic changes, but the rise in winter temperatures is causing the pine caterpillar to rise altitudinally, infesting the native populations of Scots pine situated further up the mountain (Hódar *et al.* 2003). Studies of the interactions among plants reveal a general pattern of change of sign from negative (competition) in favourable conditions to positive (facilitation or mutualism) in adverse conditions (Pugnaire and Luque 2001). In experimental reforestation carried out along a broad environmental gradient in Sierra Nevada, it has been found that the magnitude of the facilitation of pioneer shrubs towards seedlings of woody species increases at low altitude and in exposure to sun-facing slopes, where there is greater abiotic stress (Gómez-Aparicio *et al.* 2004). To the contrary, at greater altitudes and northern exposure, with lower temperatures during the summer and above all more rainfall, the facilitation of the shrubland is much less evident.

Recent studies show that the type of interaction can also be negative when the stress level is very high and not only when the conditions are favourable (Maestre and Cortina 2004) (Fig. 2.2). There is current evidence of temporal changes in the magnitude and sense of the interactions, for instance between *Pinus halepensis* and resprouting shrub species, which are probably related to the inter-annual variation in climatic conditions (Maestre *et al.* 2003). In any case, it is clear that climate change will affect the intensity and sign of the interaction between species and an additional source of evidence in this respect lies in the phenological studies of temporal phase differences between trophic levels, with profound but unpredictable consequences for the structure and functioning of ecosystems (Fig. 2.3).

Not only species interact, but also the factors influencing the processes. The two main climatic changes, temperature increase and reduced rainfall, interact, giving rise to synergies, when they both stop or accelerate a process, but more frequently to antagonisms, when the effect of one has a sign opposite to that of the other (e.g. in plant productivity or microbial activity of the soil, as, while temperature increases activity, drought reduces it). Other factors that interact and merit particular attention are, for instance, radiation and drought. With the abandonment of the countryside and the general darkening of the atmosphere by the increase in aerosols and cloudiness, there is increasingly less light available for the regeneration and growth of plants (Valladares *et al.* 2004a). The combination of this darkening with increased drought gives rise to a growing frequency of dry shades which imposes a double limitation on the regeneration of many plant species and about which we still know very little (Valladares and Pearcy 2002, Valladares 2003, Valladares *et al.* 2004b).

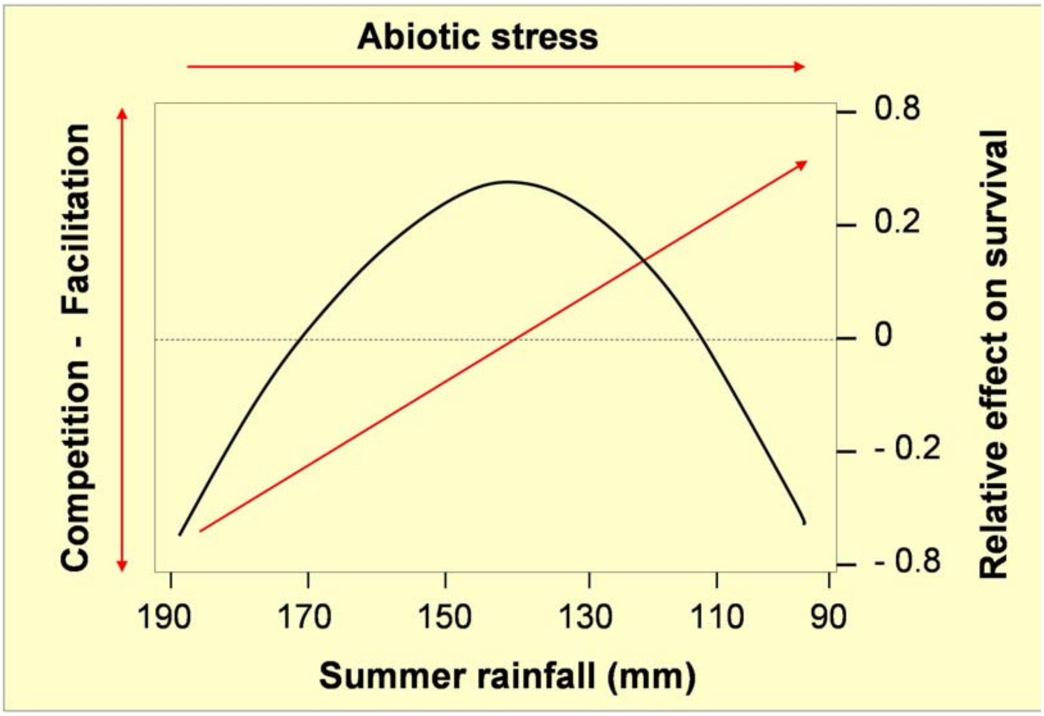

Fig. 2.2. *Interaction among species according to abiotic stress. Whereas different studies show that, as stress increases, the interaction among the different plant species of a community changes from competition to facilitation (red arrow), in conditions of intense stress there may be competition in conditions of little stress. The black line indicates the relative effect of* Stipa tenacissima *on the survival of seedlings of* Pistacia lentiscus *according to the amount of rainfall in spring and summer in the semiarid region of Alicante (After Maestre and Cortina 2004). Climate change therefore has effects which are not only quantitative but also qualitative in the interactions between organisms (sign of interaction).*

2.2.11. Sensitivity of terrestrial ecosystems of islands

The terrestrial ecosystems of islands are generally subjected to a higher risk of extinction and functional alterations than their continental homologues, and the smaller the island the greater this is. Spanish island ecosystems (mainly the Balearic and Canary Isles) are rich in endemic species, many of which are sensitive to brusque climatic changes. Some of these species, like *Rhamnus ludovici-salvatoris* on the Balearic Isles, present little tolerance to drought and a poor photosynthetic performance if compared with the non-endemic species with which they coexist, such as *R. alaternus, Quercus ilex, Q. humilis, Pistacia lentiscus* and *P. terebinthus*, which has been interpreted as a consequence of their relictic and recessive nature (Gulías *et al.* 2002).

The plant species of the cloud forests of the Canaries, an ecosystem that currently occupies small and fragmented areas, are relics from less arid climates, and their sensitivity to climate change is therefore initially high. Indeed, some species of the cloud forest such as *Persea indica* can be used as indicators of climate change (Larcher *et al.* 1991). Several of the main species of these formations have very little capacity to regulate water loss through transpiration, and are therefore very sensitive to a fall in hydric availability (Zohlen *et al.* 1995, Cermak *et al.* 2002). Intense land use changes, the pressure applied to the ecosystems by the development of tourism and the reiterated introduction of exotic species, many of which become invaders, are serious threats which make the terrestrial ecosystems of islands very sensitive to climatic change. Other island ecosystems which share, to a certain extent, the aforementioned features and sensitivities are systems that are isolated or fragmented in general and particularly those called edaphic islands. Among the latter, gypsum ecosystems, those of serpentine soils and brine basins should be mentioned. These systems are very valuable due to their richness in endemisms and constitute nature biodiversity reserves, which are under threat, not only due to the low level of protection, and the total lack of awareness of their importance, but also to climate change itself: these ecosystems are to a certain extent immobilised due to their edaphic dependence and they contain numerous species with inefficient dispersion (Escudero *et al.* 2000).

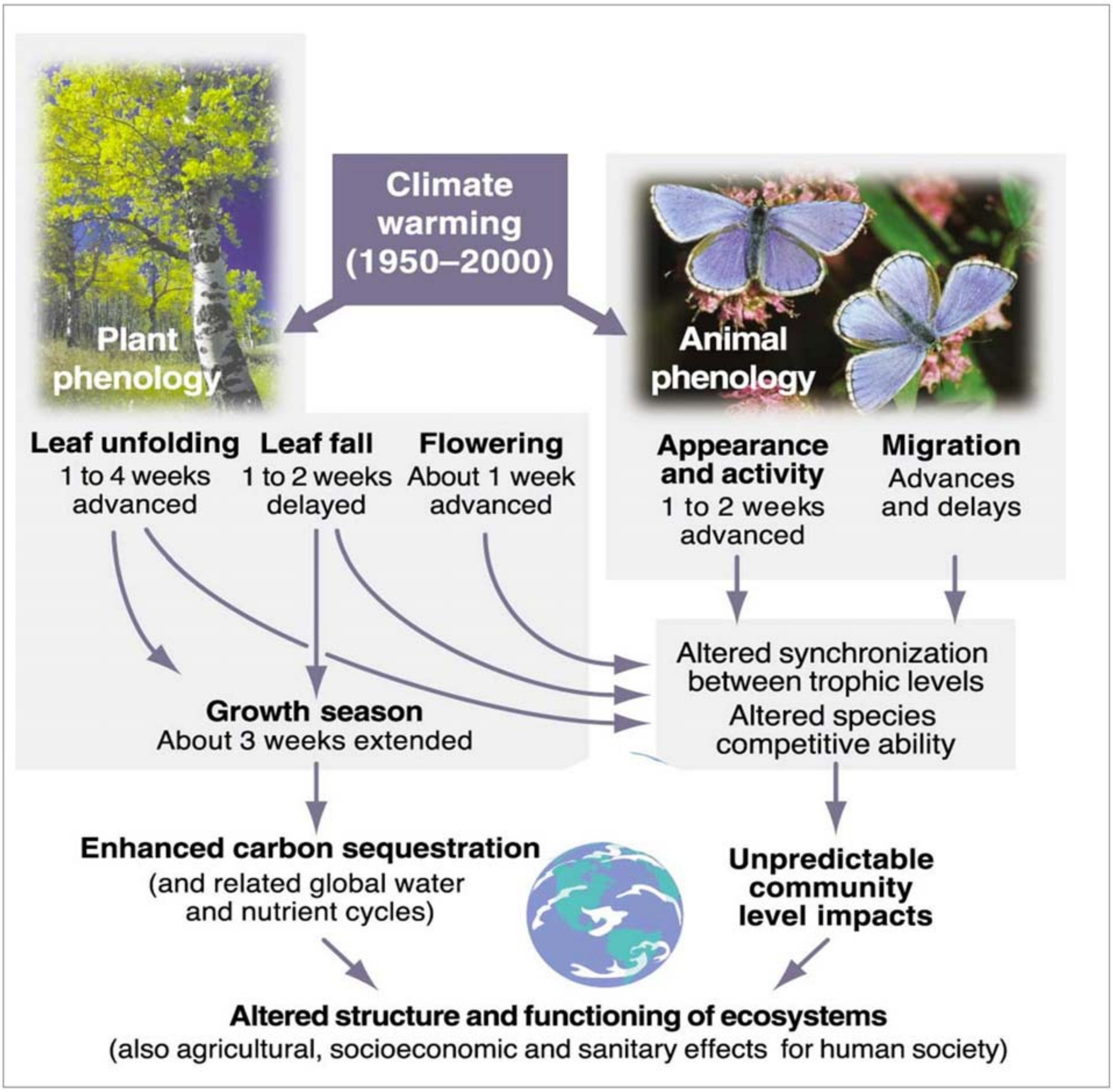

Fig. 2.3. *Ecological effects of the phenological changes caused by climate change (Taken from Peñuelas and Filella 2001)*

2.3. FORESEEABLE IMPACTS OF CLIMATIC CHANGE

2.3.1. Altitudinal and latitudinal migration

Europe's vegetation has migrated latitudinally and altitudinally in the different geologic periods as a response to the climatic changes registered. The main European woody species migrated latitudinally during the glaciations at rates of between 50 and 500 metres per year, and exceptionally, over one kilometre a year with the genera *Acer, Alnus, Carpinus* and *Ulmus* (Huntley and Webb III 1988). The upper limit of the forest, limited by temperature, advanced in the most favourable periods of the Holocene by between one and three centimetres a year and in the Central Pyrenees, advances have been recorded of between 20 and 80 centimetres a year during the last century (Camarero 1999). The predicted climate change would allow for the spread of thermophilic species, but the drop in rainfall would halt this advance, would harm those species that were not tolerant to drought and would negatively affect the lower limit of the forest (limited by hydric availability). Woody vegetation might spread towards the higher mountain areas and the communities already existing in these areas would become rarer or extinct. In many cases, the only possible migration is towards northern latitudes. But the migration rates would not be efficient in the current scenario of global change because, on one hand, the climate changes too fast, and on the other, the territory is very fragmented, which significantly restricts the real possibility of latitudinal or altitudinal migrations of the vegetation. It should also be pointed out that the Iberian Peninsula is the southern limit for the distribution of many species (e.g. *Pinus sylvestris*, *P. uncinata*) whose southern relictic populations are frequently isolated in mountain massifs.

In the mountains, species can respond to climate change by migrating vertically over short distances (for example, 500 metres is sufficient to counteract an increase 3°C). In Spain, and in general throughout the world, palaeoecological studies have shown numerous displacements from the distribution zones of certain species and plant formations in response to past climatic changes. But there still is not much evidence of responses to the present warming. Recently, the distribution of the vegetation in Montseny was compared with that of 1945 and the progressive substitution of temperate ecosystems (e.g. beech forests) by Mediterranean ones (e.g. Holm oak forests) was appreciated (Peñuelas and Boada 2003) (Fig. 2.4). Furthermore, beech forests have increased at maximum altitudes (1600-1700 m). Heathlands of *Calluna vulgaris* are also being replaced by Holm oak forests at medium altitudes, so that the Holm oak is now found at the unexpected height of 1400 m (Peñuelas and Boada 2003). Something similar has been observed in the Pañalara Massif, in the Guadarrama mountains, where the shrubs (*Juniperus* and *Cytisus*) are becoming increasingly abundant at altitudes at which pastures previously dominated (Sanz-Elorza *et al.* 2003) (Fig. 2.4). It must be remembered that in relation to the mountains, migration towards greater altitudes is accompanied by a reduction in the total area of each habitat, and the species with greater requirements related to area may become extinct. However, these observations of altitudinal migrations of key plant species in terrestrial ecosystems ought to be analysed with care, as the effects are not only attributable to climatic change. The decrease in cattle, with the consequent decrease in pressure by herbivores, and other changes in land uses, are to a certain extent involved in these migrations.

The analyses of the relationships between tree growth, the isotopic composition of the rings and climate indicate that the increase observed in the variability of this relationship is associated with an increase in the variability of meteorological oscillations at intra- and inter-annual, and inter-decade scale (Camarero and Gutiérrez 2004). The synchronic response of the trees to a lower number of environmental variables is seen as a reduction of the number of limiting climatic variables, which are in turn more stressful. The effect can also be seen in a lower level of successful establishment above the tree limit in places that have not been directly disturbed by anthropic activity. Thus, the negative relationship between the advance rate of the tree limit and the variability of temperatures in some months (e.g. march) suggests that the rise of the trees to greater elevations due to temperature increase (in specific parts of the Pyrenees for which no information exists) is limited.

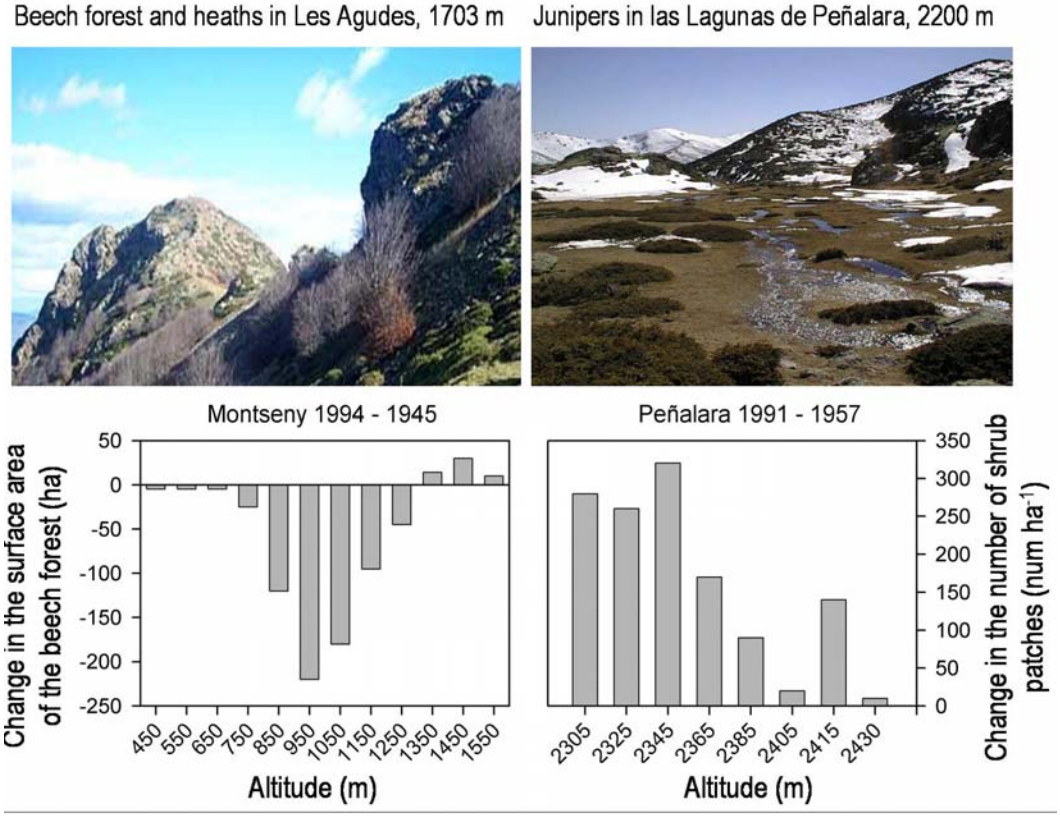

Fig. 2.4. *Altitudinal migration of plant formations in two mountains (Montseny Massif, Barcelona, and Peñalara, Sierra de Guadarrama mountains, Madrid) during the second half of the 20th century. In Montseny, the changes are shown in the area of the beech forests for a period of 49 years of progressive warming, along with changes in land uses (taken from (Peñuelas and Boada 2003), whereas in Peñalara the increase is shown in the number of patches of shrubs per hectare after 34 years (After Sanz-Elorza et al. 2003).*

2.3.2. Spread of pests and invasive species

Climate change will alter the interactions among species, bringing into contact many species that had hardly interacted previously. Some of these new interactions will involve parasitism, and the climate change will have a double impact (*per se* and through parasitism) in the host species. In the predicted scenarios of climatic change, certain thermophilic pests like the pine caterpillar could spread and in the case of the mountains reach species or populations that had never been affected by them. For instance, the impact of climate change in the autochthonous populations of Scots pine in certain Mediterranean mountains would be mediated by the pine caterpillar, typical of lower altitudes, and the interaction would therefore be more frequent, and not so much because of the direct effects of climate change itself on this species of pine (Hódar *et al.* 2003).

Invasive species are exotic species introduced voluntarily or involuntarily by man, and are capable of maintaining their populations in an independent manner, spreading and altering diverse key ecosystem processes (productivity, biogeochemical processes, etc.) (Mooney and Hobbs 2000). The invasive plant species have a great potential impact on the regeneration and natural dynamics of many terrestrial ecosystems, but there is little specific information on the impact that climate change could have on biological invasions (Valladares *et al.* 2004a). Evidence indicates, however, an increase in these invasions (Dukes and Mooney 1999).

Climatic alterations favour those invasive species that show a more plastic behaviour than their non-invasive homologues. It has been seen that certain invasive species or populations present greater phenotypical plasticity than the native species with which they coexist or than the non-invasive populations of these same species. This has been observed in comparisons of relictic populations of *Rhododendron ponticum* in southern Spain and invasive populations in Central Europe (Niinemets *et al.* 2003).

In certain populations, the climate change *per se,* and not the variability of this, would favour the invasive species. The spread of invasive plants can be predicted in clearings and underbrush, particularly under conditions of high CO_2 levels and/or high nitrogen levels. Many invasive plants are efficient colonisers of clearings and areas exposed to sunshine due to their high photosynthetic efficiency in direct sunlight, and they are capable of actively displacing the autochthonous species under these conditions (Pattison *et al.* 1998), whereas others efficiently invade the underbrush partly because they benefit proportionally more from an increase in CO_2 (Hattenschwiler and Korner 2003) or in soil nitrogen (Siemann and Rogers 2003) in shady conditions than the native species. The direct effects of climate change on invasions through ecosystem functioning could selectively favour the invaders over the native species, although there is very little available information. Tolerance to drought of certain invasive plants may also give them competitive advantages in dry shady conditions (Valladares *et al.* 2004a).

2.3.3. Changes in dominant species and reduction of productivity by drought

If the altitudinal and latitudinal movement of vegetation is unlikely, then drought and climatic extremes will cause change in communities and could lead to the local extinction of the worse adapted species. Changes in the dominant species of a community involve changes in its productivity, as has been seen in the productivity of herbaceous plants growing under different shrubs in semi-arid parts of the Iberian Peninsula (Pugnaire *et al.* 2004). These changes could therefore significantly affect carbon storage by plants. The progressive water crisis can already be seen in some Holm oak forests, and in pine forests and other Mediterranean forests at their hydric limit, with evapotranspiration rates equal to those of rainfall (Peñuelas 2001). In these forests, the worsening conditions of aridity during the summer could be the main reason or at least a factor of the mass decay of the trees. There are now clear indications that the increase in aridity and in temperature will not only negatively affect the net primary production of existing plant species, but will also lead to their substitution by other ones, more resistant to the new climatic conditions (Peñuelas *et al.* 2001, Martinez-Vilalta *et al.* 2002a). For instance, the increase in climatic aridity could compromise the survival of several populations of *P. sylvestris* in the Mediterranean basin (Martínez-Vilalta and Piñol 2002) and species like *Quercus coccifera* and *Q. ilex* could be gradually replaced by species that are more resistant to drought, such as *Pistacia lentiscus* and *Phyllirea latifolia* (Filella *et al.* 1998, Ogaya and Peñuelas 2003, Vilagrosa *et al.* 2003). Based on the hydric strategies of the main functional groups of Mediterranean woody plants, it has been suggested that the first local extinctions would threaten the relictic lauroid sclerophylls of the Tertiary (e.g. *Myrtus, Arbutus, Viburnum*), followed by arboreal sclerophyll plants (e.g. species of *Quercus*), whereas those that would be less affected or even favoured would be the chamaephytes (e.g. species of thyme *Thymus* spp.), the xerophytic malacophyllous plants (e.g. rock rose *Cistus* spp.) and in general the summertime deciduous shrubs (Fig. 2.5). In the zones of the Peninsula that are now at their climatic limit for plant formations like thyme and sage fields, climate change could involve the permanent disappearance of plant cover and desertification, like what can now be seen in semi-arid rosemary fields in Murcia, where no re-colonisation ahs been registered ten years after cutting down the vegetation (Castillo *et al.* 1997). In the short term changes in the relative dominance of the woody species of the forest are already being registered, which confirm the predictions.

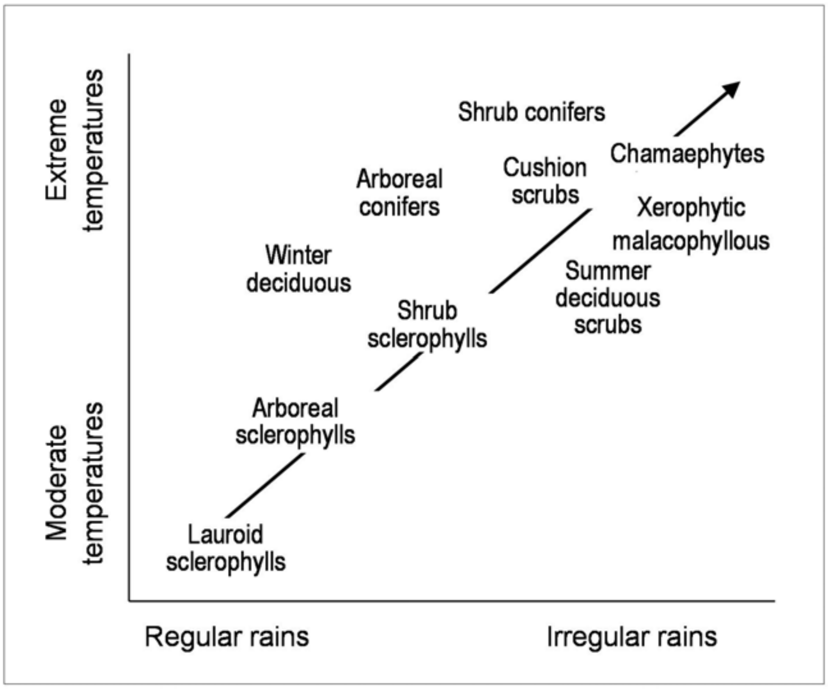

Fig. 2.5. *Distribution of the main functional groups of Mediterranean woody plants according to climatic conditions and impact related to climate change on their populations (arrow). The ordination of these groups according to the regularity of rainfall (correlated to aridity) and thermal extremes (continentality, heat waves) indicates that the lauroid sclerophyll plants (relics from the Tertiary) would be the first to be affected by climatic change, and would disappear, at least locally. However, the chamaephytes like thyme and malacophyllous shrubs like rock rose (which appeared following the establishment of the Mediterranean climate in the Pliocene) would be the least affected. In situations of cold winters, the sclerophyllous plants would be subjected to a proportionally greater impact than conifers and deciduous trees. (Reproduced from Valladares et al. 2004c).*

The experiments on drought and warming carried out in El Garraf (Barcelona) indicate that drought reduces the number of seedlings and their respective short-term species richness. This decrease also occurs, but in much lower proportions, in the treatment of warming in these same experiments. This effect occurs mainly in germination, and once the seedling has become established, its survival is affected little by the treatments. In general terms, the species that currently produce less seedlings are those that have more probabilities of disappearing in a drier climatic scenario (Fig. 2.6). When conditions are more severe, however, there are indications that the response of the species might be independent from the current abundance of their seedlings, that is, idiosyncratic (Lloret *et al.* 2004).

In an experiment consisting of the partial exclusion of rainwater and surface runoff, (15% decrease in soil humidity), different responses were observed among the dominant species, within the general tendency of growth reduction in drought in a forest dominated by Q*uercus ilex, Phillyrea latifolia* and *Arbutus unedo*. The drop in edaphic humidity retarded the cycles of water, of C, of N and of P, and affected the ecophysiology and demography of the species. Certain species are quite sensitive, like *Arbutus unedo* and *Quercus ilex*, whereas others like *Phillyrea latifolia* did not undergo any appreciable decrease in diametric growth (Ogaya and Peñuelas 2003, Ogaya *et al.* 2003). The death rate of the individuals showed a similar pattern, given that *Arbutus unedo* and *Quercus ilex* showed a higher death rate than *Phillyrea latifolia*. Under these drought conditions, the accumulation of total aerial biomass diminished by 42%, showing that under more arid conditions than the present ones, the growth rate of Mediterranean forests may be reduced to quite a great extent. Furthermore, considering that not all the plant species are equally affected, in the long run there could be a change in the specific composition of the forest, the drought-resistant species being more favoured. In this experiment the appearance and survival of new seedlings of *Quercus ilex* and *Phillyrea latifolia* were also studied. These species present different recruitment strategies in the forest studied: shoot and seed germination seedlings, respectively. The results indicate that the appearance of new seedlings of *Phillyrea latifolia* is more affected by the drought than the growth of new shoots of Holm oak. However these differences disappear with the development of the new plants, so that the survival of seedlings and shoots is similar not many years after. These results indicate that the effects of drought are greater in the initial development phases. Even so, the differences between species vary with the development phase: adult Holm oaks seem to be less resistant to drought than those of *Phillyrea latifolia*, but the models of recruitment are the opposite. Things become even more complicated if we consider that the survival of new seedlings of many of these species, like, for instance, the Holm oak, depends on finding conditions in which they are not excessively exposed to radiation, especially in the initial stages. If tree cover decreases much, as a result of climatic change, the areas in which the seedlings can become established may also decrease.

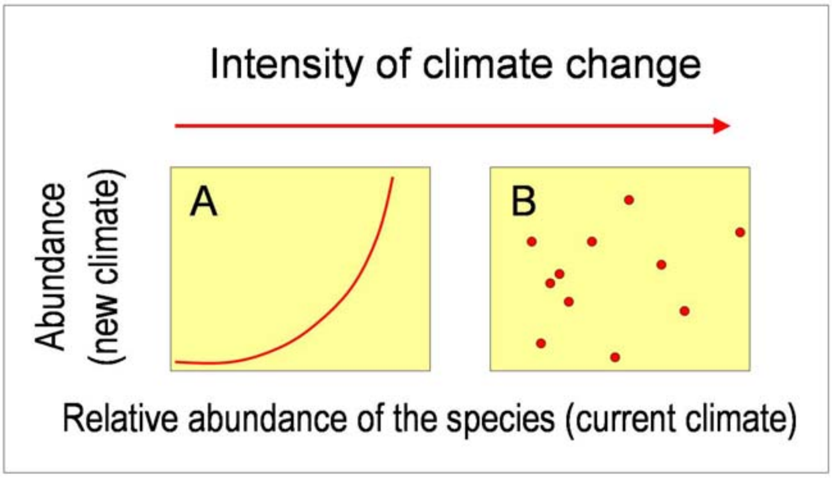

Fig. 2.6. *Effects of climate change on the diversity of seedlings in experimental simulations of drought and temperature increase in Mediterranean shrublands in El Garraf (Barcelona). The results after four years indicate that when climate change is moderate (A) the most abundant species in the present climatic conditions have more chance of survival than those less abundant, giving rise to a foreseeable impoverishment of communities, whereas when the change is more extreme (B) there is no relationship between abundance in the present climate and abundance in new climatic conditions (After Lloret et al. 2004).*

The studies based on rainfall reduction and passive nocturnal warming of the ecosystems reveal that the magnitude of the response to warming and drought is very different depending on the conditions of the study area. Cold and humid places, like Northern Europe, are more sensitive to warming, whereas our county, hotter and drier, is more sensitive to drought. It also depends on the season of the year: the processes are more sensitive to warming in winter than in summer, and once again, the responses also depend on the species, and even on the individuals (Peñuelas *et al.* 2004b). Drought will also have similar impacts on grasslands and herbaceous communities in general, in which the seasonality of rainfall is as important, if not more, than the amount of rain that falls in the year. It has been observed that drought, particularly in autumn, conditions the differential germination of species and leads to the impoverishment of grassland species, with similar effects in communities in different successional stages and topographic situations (Espigares and Peco 1995, Figueroa and Davy

1981). Modelling of tendencies and fluctuations in the diversity of Mediterranean annual herbaceous communities reveal that, although 33% of the species show successional behaviour, the vast majority respond to the temporal heterogeneity associated with rainfall, and to the spatial heterogeneity generated by the topography (Peco *et al.* 1998). The subalpine meadows in the Pyrenees will also be affected by climatic change. Recent studies reveal that warming impoverishes these communities, altering their function and inter-species competitive relationships, favouring changes in dominance and an increase in aerial, as opposed to subterranean, productivity (Sebastiá *et al.* 2004).

2.3.4. Maladjustment in biogeochemical cycles and in the hydric reserves of the soil

In spite of the fact that in the short term, drought retards the decomposition of the forest litter, its composition was not affected in the long term in experiments using rainfall reduction and passive nocturnal warming. The changes in temperature and humidity not only altered the carbon cycles, but also the N cycles and energy balances (Peñuelas *et al.* 2004b). The most complete simulations of the effects of climate change in Spanish forest systems were carried out in Mediterranean formations (mainly Holm oak forests) In Catalonia, with structural information on the forest obtained from the Catalonian Ecology and Forest Inventory (Gracia *et al.* 2000). In simulations for the next forty years, the net production of the ecosystem will vary little, in spite of the fact that there will be a considerable increase in its components (gross production in the year 2040 will increase by 56% compared with the present, and total respiration will increase by 58%). The increase in litter production, by 84%, contributes to the increase in respiration, partly as a consequence of the reduction of the average life of the leaves of evergreens, which will change from the current value of 2.6 years to a value of 1.9 years in the year 2040. These phenological changes involve important physiological change and, in particular, an increase in annual transpiration. As a consequence, the hydric reserve in forest soils, which is now 32 mm (l/m^2) if we consider the annual average at each point, drops to only 24 mm, which represents a decrease of 25% of hydric reserve; this is particularly critical in an environment with a summer hydric deficit, like the Mediterranean region at present. In spite of what has been revealed by eco-physiological studies at leaf level, the whole ecosystem's efficiency in the use of water diminishes with hydric stress, mainly due to the fact that decreases in carbon gain by around 90% during drought, as has been determined in different European Holm oak forests (Reichstein *et al.* 2002).

2.3.5. Decrease in the capacity for carbon sequestration

The estimation of the carbon balance of shrublands and forests becomes more complex due to the effect of drought, which radically alters diverse eco-physiologial processes and functions of the canopy. Experimentally induced droughts in Holm oak forests have shown that under more arid conditions than the current ones, Mediterranean forest will reduce to a great extent their growth rates and therefore, their capacity to sequestrate atmospheric carbon (Ogaya and Peñuelas 2003). In spite of the existing uncertainties, it seems clear that the efficiency in the use of water of Mediterranean forests will decrease with drought and that the carbon balance will tend to become positive (the forest becomes a source of CO_2 once again) not only in summer, but also in hot, dry years (Gracia *et al.* 2001, Joffre *et al.* 2001, Reichstein *et al.* 2002). Given the important role of the hydric and thermal conditions of the soil in the ecosystem's respiration, the net carbon balance during the dry periods will depend on the duration and intensity of the drought and on the amount of water available for the tree roots in the deep strata of the soil (Pereira *et al.* 2002). The results of the simulation of carbon balance in scenarios of climate change in the forests of Catalonia reveal that the role they play as the carbon sinks of our forest formations may be seriously threatened in the next few decades (see Chapter 9, Forestry Sector). But not only forests sequestrate carbon. Although forests have the greatest capacity to store carbon in their aerial parts, other formations, like grasslands, have great capacity to store carbon in their subterranean parts. In the case of the grasslands in the Pyrenees, it has been shown that the abandonment of traditional practices leads in a decrease in their capacity to sequestrate and store carbon (Casals *et al*. 2004).

2.3.6. Increased impact of disturbances

Disturbances, whether they be chronic or episodic, will have an increasing impact due to the fact that they will occur in ecosystems subjected to stress by climatic change. The higher frequency of episodic disturbance, like intense droughts, in combination with chronic disturbances, such as herbivory, will probably exacerbate the degradation of Mediterranean vegetation and accelerate erosion processes (Zamora *et al.* 2004). The disturbance for which most information is available and for which most models and predictions have been made on the Iberian Peninsula is fire. The climatic evolution towards hotter and more arid extremes, with an increases in biomass and in inflammability in response to the increase in CO_2, together with the abandonment of crop fields, forestation and the accumulation of fuel, will increase the intensity and, above all, the frequency of fires, restructuring the carbon balance (Peñuelas 1996). The capacity of plant species to respond to these changes in the regime of fires will determine to a great extent the alteration of the structure of the ecosystems and their response pattern to changes in climate and in the regime of disturbances. Although it could be said that many Mediterranean communities and plants are resistant to severe disturbances like fire or clearing (Cruz *et al.* 2003, Calvo *et al.* 2002), the capacity of the plants to respond varies greatly according to the type and duration of the fire, the basic type of regeneration of the constituting species (e.g. resprouters versus germinaters, Ojeda 2001) or the level of resistance of the individuals (resprouting species) and/or populations (germinating species) to very frequent fires or fires followed by stress from excessive herbivory (Ojeda 2001). Thus, an alteration in the regime of disturbance frequency could cause drastic changes in the composition and structure of communities that are apparently resistant to disturbances, as, apparently, has happened in oaks (formations of *Quercus pyrenaica*, a resprouting species (Luis-Calabuig *et al.* 2000) in the Duero basin, and as has been established through the experimental increase in the frequency of fires (Calvo *et al.* 2002). In general terms, the increase in the frequency of fires will increase the spread of purely germinating species and heliophilous ones, intolerant to shade, like the rock rose (Luis-Calabuig *et al.* 2000) and will reduce the presence of shade-loving species, forcing the communities into early successional stages (Terradas 1996). In short, although some Mediterranean plant communities may have evolved in the presence of recurring fires as a selective pressure, to the extent that fire has become an inherent element in the system, the increase in the frequency of fires as a consequence of climate change will have negative and drastic consequences for the biodiversity and structure of these communities (see chapter 12).

2.3.7. Increasing impact of extreme events

Extreme climatic events are difficult to predict, but are very important, as their ecological and evolutionary impact is very great (Gutschick and BassiriRad 2003). Both extreme droughts and heat waves have profound effects on ecosystems which are felt for years (Peñuelas *et al.* 2000, Groom *et al.* 2004). A recent review showed that extreme events are the ones that determine the evolution of many species through directional selection, and that the functional characteristics selected are not only those that provide tolerance to extreme events, but also those that optimise the harnessing and utilisation of resources (Gutschick and BassiriRad 2003). The concept of extreme event should, however, be contemplated from the point of view of organism, including the functional features and capacity for acclimatisation of this, and not from the environmental point of view, only considering the statistical rarity of a determined climatic event. Which means to say that, one same heat wave may have a notable impact on an organism that is active but not acclimatised to heat and a minimum impact on an organism in the resistance phase which is well acclimatised because this event was preceded by a period of progressive warming. The recurrence of extreme events (droughts and heat waves) has an accumulative effect, reaching threshold situations after which the impact of climate is disproportionately high.

2.3.8. Impact on the terrestrial ecosystems of islands

Climate change will have a foreseeably greater impact on island ecosystems than on their continental equivalents due to the limitation of regeneration and natural colonisation imposed by isolation. The aforementioned impacts on the tree and shrub ecosystems of the Mediterranean region can be applied to islands like the Balearic isles, but taking into account this multiplying effect due to isolation, which is directly proportional to the distance from the continent and inversely proportional to the size of the island. The Canary Isles maintain much of the current vegetation because of the Trade Winds which bring humidity and are trapped by the mountains on the islands with greater altitudes like Tenerife, Gran Canaria, La Palma and La Gomera. Climate change could compromise formations like cloud forests which are sustained by this orographic phenomenon involving the harnessing of humidity. Recent studies, however, reveal that the tendencies observed and the emerging predictions are contrary to what was expected: low clouds are increasing in frequency, which means that the potential area for cloud forest is spreading to lower altitudes (Sperling *et al.* 2004). Nevertheless, given that the low zones are densely populated, it is unlikely that the cloud forest will spread. The invasive species are particularly problematic in Spanish island ecosystems (Vilà and Muñoz 1999) and climate change could favour the spread of some of these (Dukes and Mooney 1999).

2.3.9. Corollary: predicting the unpredictable

Simulations of climate change in plants reveal big differences according to the functional group the species belongs to (Fig. 2.7). Both the natural climatic variability and that resulting from climatic change, along with the climate change itself, simulated as a scenario of a 25% reduction of rainfall and an increase in 4 °C, had effects that ranged from zero to very intense, depending on whether it was a Mediterranean sclerophyllous species (*Quercus coccifera*), a chamaephyte (*Thymus vulgaris*) or a perennial tussock grass (*Stipa tenacissima*), and these effects also depended on whether the response variable was reproductive biomass, leaf area index (LAI) or growth period (Fig. 2.7). Climate change *per se* and the climatic variability associated with this change had negative effects on the growth period of *Q. coccifera* whereas this parameter was hardly affected in the other species. The opposite occurred with LAI, which was barely affected in *Q. coccifera* whereas it varied greatly in *S. tenacissima*. Climate change had a very intense potential effect, reducing the reproductive biomass in *Thymus vulgaris* (Mulligan *et al.* 2004). However, the shortening of the growth period of two of the species contrasts with the phenological observations obtained for different species of trees and shrubs for which data are available (Peñuelas *et al.* 2002). These simulations, however, suggest profound effects of climate change in the plant component of ecosystems, effects which are manifested differentially in reproduction, eco-physiology or growth, and which depend on the species.

But in natural systems, the species are not alone. The complexity of effects and interactions between climate change and ecosystem processes makes it very difficult to predict the sense and intensity of the responses of terrestrial ecosystems to climatic change, although all the studies indicate that there will be important effects. What is certain is that any predictions of the conditions of Spanish terrestrial ecosystems in future decades requires better knowledge of their responses to climate change and of regionalised predictions of climate and land uses. This is still far from being available due to the inherent variability and unpredictability of the climatic system at regional level, and especially in the Mediterranean region. It must be remembered that it is very unlikely that the changes and responses will be simple linear ones. With the combination of climate change and changes in land use, we can predict that in coming decades there will be more ecosystems in early successional stages and with less ecological complexity. The decreases in plant productivity and in reproduction in response to drought (and to a lesser extent, also to warming) will be seen in a decrease in organic matter reaching the soil, and also in the recruitment of new plants and in soil cover, all of these phenomena that reduce its capacity to retain water. If the water content of the soil diminishes, plant productivity decreases, reducing even more the entry of organic matter in a vicious circle which feeds on itself (Peñuelas *et al.* 2003). Decreased water in the soil increases the risk of fire and decreased plant cover and organic matter in the soil also increase the risk of erosion.

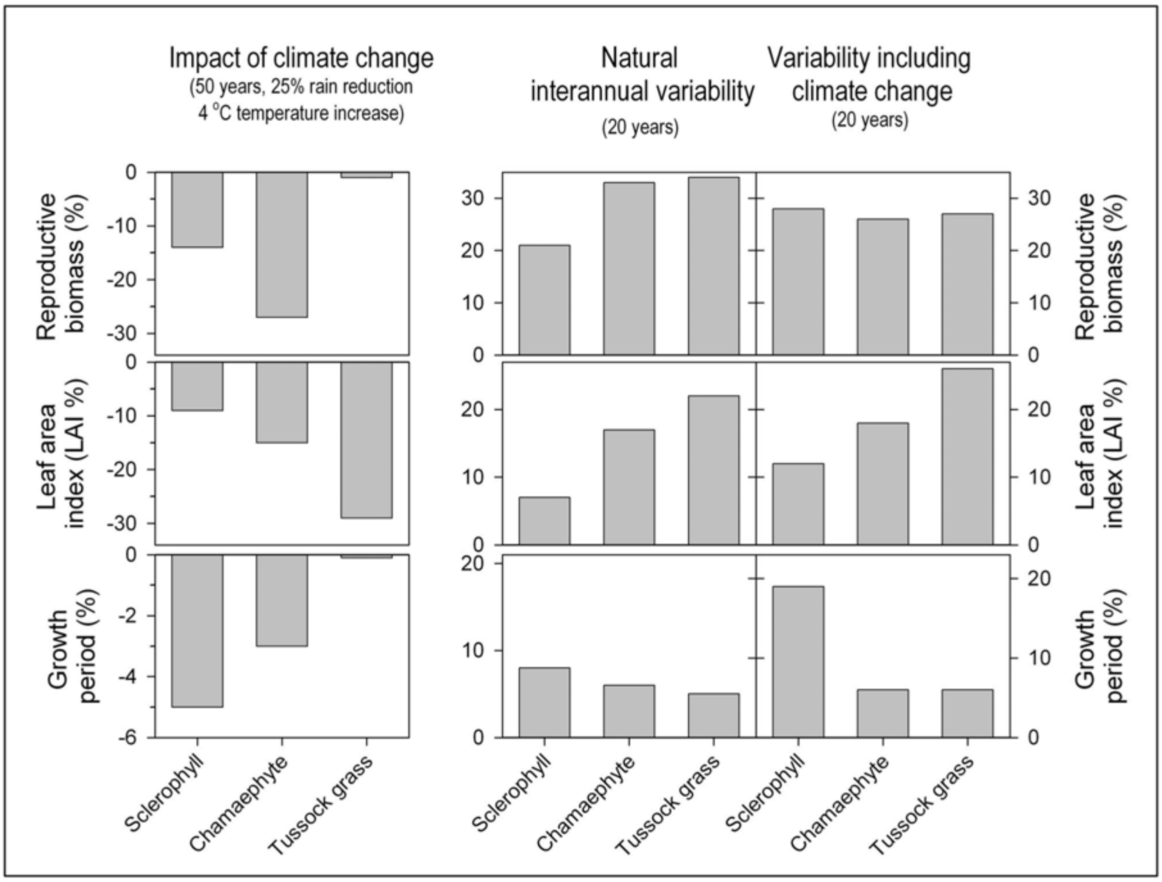

Fig. 2.7. *Impact of a simulated climate change (0.5% reduction of annual rainfall and annual increase of 0.08 ºC for 50 years) in reproductive biomass (Kg m-2), leaf area index (LAI, m2 m-2) and growth period (months year-1) in three plant species (Quercus coccifera – sclerophyll plant-, Thymus vulgaris – chamaephyte-, and Stipa tenacisima –perennial herbaceous-). The three graphs on the right show the effect of the natural inter-annual climatic variability and the variability including the climate change in a period of 20 years for these same parameters and species. The impact of climate change differs significantly among species with different forms of growth, although in general it provokes a decrease in reproductive biomass, in leaf area and in the duration of the growth period. The influence of climate change on inter-annual variability was also different among parameters and species, tending to cause an increase in the variability of the leaf area but a decrease invariability in the reproductive biomass; with climate change there is a noteworthy increase in variability in the duration of the growth period of the sclerophylous shrub. The values are expressed as a percentage and were calculated with the PATTERN model from the climatic data from the period 1940-1990 from La Alberca de Záncara and with the conditions and parameters recorded in Belmonte (Cuenca). (Data based on the tables in Mulligan et al. 2004).*

The more arid the area considered, the longer the vegetation takes to recover after multiple and prolonged droughts and/or fires, both because it takes a long time to create new biomass and because the soil often becomes degraded, especially if there is overexploitation during the dry periods or if there is a recurrence of the fires. Erosion is thus facilitated and, in extreme cases, desertification can occur, a problem that already exists in which the soils of the degraded ecosystems are incapable of retaining the water provided by the occasional storms and autumn extremes, which provoke flooding and more erosion. In areas with terracing for agriculture, erosion probably constitutes a less immediate threat than in similar areas without terracing. The burnt areas of the Levante are more susceptible to erosion because many of them are located in fields generally upon marlaceous substrates which are very sensitive to erosion, and where rainfall is limited (350–600 mm, or less) and mainly concentrated in autumn, and where, given the previous agricultural use, there is a lower number of resprouting species. These conditions would aggravate the direct conditions of the drought and would create more arid conditions in the ecosystem. The attraction of these systems for recreational activities like, for instance, the observation of nature or hunting could diminish, along with the amount of stored and absorbed carbon. This means that there could be a profound alteration of the goods and services provided by the ecosystems.

In order to lend a dimension to the role of climate change in terrestrial ecosystems, it is important to remember that all the changes described in the last few decades occurred in conditions of warming that were only a third or less of that predicted for the end of the 21st century.

2.4. MOST VULNERABLE AREAS

The Spanish areas and terrestrial ecosystems most vulnerable to climate change are the ecotones or contact areas between two or more systems, and islands in the broad sense (including isolated ecosystems like edaphic islands -–gypsums, serpentine soils and brine basins especially-, and high-mountain areas; (see section 2.2.11 for the vulnerability of island ecosystems). Logically, not all the species of a determined ecosystem are equally vulnerable. In studies of high-altitude grasslands in the Pyrenees of Catalonia, it has been observed that the boreo-alpine components are the ones most affected by warming (Sebastiá *et al*. 2004). The ecotones are vulnerable due to their great sensitivity to environmental conditions, although more than the ecotone itself, what is vulnerable to climate change is its geographic or topographic location. Given the fragmentation of the territory, however, any climatic tension applied to an ecotone cannot be alleviated by merely transferring it to other areas, as this mobility is very restricted in practice. Among ecotones, the lower limit of the forest, determined by aridity, is where the effects of climate change will be felt most rapidly. The responses observed at the upper altitudinal limit of the forest in the Pyrenees suggest that certain variables like recruitment or radial or longitudinal growth are more sensitive indicators of climate change than the altitudinal position of the forest limit (Camarero and Gutiérrez 2004). The variables to be measured in the ecotones should therefore be evaluated with care in order to detect climatic effects. The contact zones between biogeographic regions, particularly the transition zone between the Mediterranean region and the Atlantic or Eurosiberian, would also be affected very rapidly by climatic change, which would increase the area of the former at the expense of the latter. The oaks of *Quercus pyrenaica* would spread at the expense of oak forests and Atlantic forests, and the isolated fragments of the latter remaining dispersed throughout the Central System (Peña de Francia, Gredos, Guadarrama) would tend to disappear. The transitions between shrublands and Holm oak forests would undergo an analogous spread of the former at the expense of the latter.

Whereas the ecotones will generally suffer gradual changes, the island ecosystems and the riparian ones will most likely undergo brusque changes, or threshold-type changes. In the case of islands, the threshold will be determined by the minimum area, whereas in riparian ecosystems, this will be determined by flow or minimum phreatic level. Below these minimum thresholds, the ecosystems risk collapse, whereas above them, they might hardly show the effects of climatic change.

The different reviews by D.M. Richardson, P. W. Rundel, B.B. Lamont, among others, on the ecology of Mediterranean ecosystems in a scenario of global change appearing in the book by Arianoutsou and Papanastasis (2004) indicates that, contrary to what might be expected, Mediterranean ecosystems are very sensitive to climatic change. Decreased predictability of rainfall (estimated as the opposite to the seasonal or annual variance in rainfall) is reducing the diversity and the regeneration of determined Mediterranean ecosystems. Changes in the regime of fires (frequency and intensity) together with general climatic changes are already having profound consequences for these ecosystems and affect mostly strictly pyrophilous species (e.g. serotinal species) which only recruit after fire. Recent analyses of the fire regime in Mediterranean Spain have revealed that the increase in frequency and area burnt is associated with climate, so that the fires are bigger and more frequent in years of dry summers, and that rainy summers generate bigger amounts of fuel, giving rise to more catastrophic fires after two years on average (Pausas 2004).

2.5. MAIN ADAPTATIONAL OPTIONS

2.5.1. Actions involving keystone species

Evidence from diverse studies coincide in highlighting the progressive decline of keystone species in our terrestrial ecosystems, like, for instance, the Holm oak. The sensitivity observed in the Holm oak to climate change lies in its mediocre eco-physiological tolerance to severe droughts (Joffre *et al.* 2001, Martinez-Vilalta *et al.* 2002a), its poor efficiency in relation to water use during drought (Reichstein *et al.* 2002), the ageing of the masses of Holm oak and of the underwoods which are not managed through thinning and prunings, the episodes of “drought” of the Holm oak, the negative carbon balance during the summer, the long regeneration period of over 20 years of the carbohydrates used in resprouting after fire (Gracia *et al.* 1997, Gracia *et al.* 2001), and the results of Ogaya and Peñuelas (2003, 2003) which suggest the low level of competitiveness of this species in conditions of intense drought. This gradual hydric crisis can now undoubtedly be verified in some Holm oak forests, and also in pine forests and other Mediterranean forests, which are at their hydric limit, with evapotranspiration rates equal to those of rainfall (Peñuelas 2001).

In these forests, the worsening of aridity in the summer, together with unfavourable climatic periods, may be the main cause, or at least an important factor, of the mass decay of the forests. The recovery and application of the basic aspects of management of Mediterranean shrubland and forests, along with the implementation of new forestry techniques aimed at improving the efficiency of water use both of individual stands and of the ecosystem in general, are the main measures available for correcting the general downward and for preventing brusque, threshold-type responses to the increase in aridity and in the irregularity of rainfall (Gracia *et al.* 1997, Gracia *et al.* 2001, Joffre *et al.* 2001). The same type of analysis should be applied to other keystone species of our ecosystems, more example of which are provided in other chapters. However, actions involving one single species are quite inefficient if what we want is to conserve more than this determined species. In many cases, even for the conservation of this species, it is necessary to regenerate or conserve the environmental conditions that allow for its existence and the measures should be therefore taken at the level of the ecosystem, provided that this is possible.

2.5.2. Actions involving key systems

An important aspect in the attenuation of the impacts of climate change is to avail of suitable registers of the evolution of the different ecosystems over the years. But habitat loss confuses the effects of climatic change. It must be kept in mind that this loss of habitats gives rise to rapid changes in the distribution of frequencies of environmental conditions, both due to biophysical changes in the habitat and to the effects of sampling (Pyke 2004). These sampling effects are due to the fact that habitat loss is rarely random, so that the habitats that remain are a biased sample of the region's climatic conditions. Through the follow-up of these biased samples, one can overestimate or underestimate the effect of climate change if the samples are in the hotter and drier parts of the region, or in the fresher ones and wetlands, respectively. Thus, it is necessary to consider climatically underrepresented zones in the follow-up of any action, and to compensate for the tendency to protect and study small areas, unrepresentative of the general environmental conditions of a region.

There is a range of systems that merit particular attention, either because of the key role they play in the supply of goods and services or because of their endemic and relictic nature. These systems require actions to counteract the effects of climate change and to apply effective conservation therein. Among these we can highlight:

- Relictic forest formations from past climates (e.g. cloud forests of the Canary Isles, forests of *Rhododendron ponticum* in the "canutos" of Cádiz and Málaga, forests of *Prunus lusitanica* in Extremadura)
- Tree or shrub formations in arid areas like those presenting *Maytenus senegalensis, Ziziphus lotus, Tetraclinis articulata,* and *Whitania frustecens.*
- Fragmented or isolated formations like the birch forests and beech forests in central Spain, the yew forests, holly forests and isolated woods of conifers like *Pinus sylvestris* in Sierra Nevada, *P. uncinata* in the Iberian System, *Abies alba* in Montseny and those of *Abies pinsapo* in the Serranía de Ronda.
- The aforementioned vulnerable areas (ecotones, island and high-mountain systems)
- Holm oak forests and *dehesas* of Holm oak showing signs of poor regeneration and vulnerability to climatic change.

2.5.3. Integrated design of protected natural spaces

The design of new protected spaces and the restructuring of the existing ones should incorporate the concepts dealt with here, which in short would include good representation of both the size and the spatial distribution of the main ecosystems of a region, and would allow for the migration and for changes in the distribution of species and systems through the inclusion of altitudinal gradients and biological corridors between the different zones. More emphasis must be placed on the management of the environment in the broad sense, because the protected spaces may become obsolete, and the systems or species to be conserved or protected or may change or disappear, especially in scenarios of climate change (Harrison *et al.* (Eds.) 2001).

2.6. REPERCUSSIONS FOR OTHER AREAS OR SECTORS

The sensitivity of many Spanish terrestrial ecosystems to climate change means that the measures taken to conserve them have repercussions in different socio-economic sectors. Some important examples are:

- Good management of hydric resources, indispensable for the maintenance of many natural formations, conflicts with intensive tourism or the facilities of golf courses in arid areas.
- The conservation of high-mountain areas is incompatible with the mass and intensive use of

the ski season.
- Intensive greenhouse crops in arid areas do not allow for the good conservation of the natural systems or for good water use.
- The management of certain areas for big game hunting leads to systems with a high level of pressure by herbivores, which are poor in species and vulnerable to climate change and disturbances.
- Forestry based on single cropping threatens the functionality of the ecosystems, as well as their long-term sustainability.

The conclusions of this chapter have clear repercussions on aspects that are dealt with in other chapters (e.g. Forestry Sector, Edaphic Resources, Animal and Plant Biodiversity, among others).

2.7. MAIN UNCERTAINTIES AND KNOWLEDGE GAPS

Cox *et al*. (2000) have estimated that the increase in respiration caused by temperature increases could turn many ecosystems into sources, and not sinks of CO_2 by the year 2050. The effect of drought, however, has not been taken into account, and, as Reichstein *et al*. (2002) showed, this can profoundly alter the balances of carbon and water whose calculations are based on models that only consider the stomatal response of the vegetation. In general, interactions between both factors (e.g. temperature, water and light) and between species (networks of trophic interactions, mutualisms, etc.) increase very much our uncertainty of the effects of climate change on our terrestrial ecosystems. This fact, along with the lack of long temporal series makes the predictions of the effects of climate change on these systems very fragile. Furthermore, the low level of spatial accuracy of the predictions makes the uncertainty even greater at local level, in spite of the fact that many processes operate at this level (e.g. local extinctions). The lack of information on the eco-physiology of keystone species (e.g. tolerance to drought in interaction with shade, the capacity for acclimatisation of respiration at high temperatures, the global effects of volatile organic compounds) together with the lack of genetic and molecular data makes it very difficult to calculate the capacity for evolution of the species in a changing world. Besides, it is also difficult to isolate the effects of climate change from those of the simultaneous participation of other motors of global change. In order to do so, experimentation is needed, and not only observation and follow-up. Table 2.1 summarises the level of uncertainty in relation to the main impacts that climate change will have on Spanish terrestrial ecosystems.

2.8. DETECTING THE CHANGE

The effect of climate change on terrestrial ecosystems can be detected by means of different types of indicators, ranging from the follow-up of particularly sensitive species of flora and fauna to monitoring ecosystem variables in zones of special interest. With regard to the former, specific recommendations can be found in the chapters on plant and animal biodiversity. However, we must emphasise the suitability of the population viability analyses (PVA) in order to detect the effects of climatic change. These analyses are already being carried out in the case of rare or endangered species (e.g. almost 40 species of critically endangered plants within the framework of the Atlas of Endangered Flora under the auspices of the Ministry of Environment) and are enabling the detection of effects that can be attributed to a certain extent to climate change. Here we propose a series of variables the follow-up of which has permitted and will permit us to detect the effects of climate change in the functioning of ecosystems. The variables differ with regard to their cost, both in economic terms and with regard to the technical level required, and are valued according to this cost (C, costly, E, economical, E-C the cost depends on the measurement protocol).

Table 2.1. *Level of uncertainty of the most relevant effects of climate change on terrestrial ecosystems in Spain*

Certainty	Most relevant effects of climate change on terrestrial ecosystems in Spain
****	Changes in species phenology
****	Changes in the interactions among species
****	Expansion of invasive species and pests
****	Changes in the species dominance of a community
****	Changes in the structure and functioning of terrestrial ecosystems
***	Decreased productivity due to warming and drought
***	Altitudinal migrations of keystone species
***	Decreases nutritive quality of the plants
***	Decreased capacity to sequestrate carbon
***	Local extinctions
***	Increased impact of disturbances and extreme events
**	Tolerance of new conditions through the acclimatisation and plasticity of keystone species
**	Lengthening of the real growth period of the vegetation
**	Increased emissions of VOC
*	Tolerance of new conditions through the adaptation (evolution) of keystone species
*	Latitudinal migrations of keystone species
*	Increased efficiency of water use by plants
*	Collapse of trophic networks
*	Acceleration of biogeochemical cycles due to warming and drought
*	Readjustment of the ecosystems to the new climate

(** very high certainty, *** high certainty, ** medium certainty, * low certainty)**

Phenological variables

Production of flowers and fruits of keystone species (enlargement of the Meteorology Institute list to include representative natural and wild species; E), phenology of plant communities (estimate of general dormancy moments, maximum production, maximum flowering, etc.; E), appearance of insects and migratory birds species (enlargement of the Meteorology Institute list to include representative natural and wild species; E),

Abiotic variables

Thermal changes and changes in rainfall in extreme zones, ecotones and habitats of relict species or populations or those at the limit of their distribution (E), follow-up of erosion in zones such as the previous one (C), follow-up of the phreatic level in zones like the previous one (C), follow-up of soil temperature and humidity in zones representative of the main ecosystems (E),

Structural variables

Leaf area index (LAI; E-C), accumulation of biomass and necromass (C), root development (C), altitudinal movement of ecosystems (upper and lower forest limits, ecotones, altitudinal limits of keystone species; E), dynamic cartography of ecosystems (temporal follow-up of their area and spatial distribution; C)

Ecological and physiological variables

Net carbon exchange of the ecosystem (Eddy Flux covariance technique; C), productivity (E-C), reserve carbohydrates in plant tissues (starch, mobile carbon, particularly in resprouting species; C), mineralisation of organic matter (C), natural regeneration of keystone species (C), follow-up of the rhizosphere (diversity, productivity; C), experimental simulation of warming and drought (C), emissions of volatile organic compounds (VOC; C), follow-up of populations of invasive species (E-C), follow-up of pests and pathogens (E-C).

In the case of any of the variables referred to, follow-up should include long temporal time periods, due to the marked intra- and inter-annual oscillations both of the climatic variables and of the responses of the ecosystems to environmental change. To this end, in the first place, the initiatives existing in Spain ought to be used, and before any new action is initiated, it must be ensured that no similar temporal series already exists. By way of an example, of particular strategic value is the maintenance of the phenological observations by the National Institute of Meteorology, of the forest health follow-up network (Ministry of Environment) and initiatives like the RESEL network for the physicochemical follow-up and the follow-up of soil erosion (Rojo and Sánchez-Fuster 1996) (see chapter on edaphic resources). The power of the existing initiatives is their seniority, and the series of uninterrupted data for long temporal periods should be given priority. This support of existing series should also be completed with the support of more recent initiatives and even of new initiatives to fill the big knowledge gaps or the badly recorded geographic areas. Many of these series are backed by the collaboration of different scientific groups and have certain moderate logistic requirements, which favours their continuity. Special mention should be made of the follow-up stations of the carbon balance of ecosystems by means of “Eddy flux” covariance, like the one in El Saler (Albufera Nature Park in Valencia) under the auspices of the CEAM, and the experimental facilities for the study of the effects of climate change in Montseny and El Garraf (Barcelona) belonging to the CREAF. Unlike the aforementioned initiatives, these facilities are costly, but the information they provide is of great value. In order for these facilities to be valued, and for the information they provide to detect the effects of climate change in terrestrial ecosystems, it is not sufficient to keep them active for long periods of time, but rather they should be integrated into other networks in order to compare results with other systems (e.g. shrublands, grasslands) and with other regions.

2.9. IMPLICATIONS FOR POLICIES

2.9.1. The importance of social awareness

The introduction of multi-use strategies for the management and rehabilitation of terrestrial ecosystems requires much education and research, and effort by the government, too, in order to give hope to the future development of these terrestrial ecosystems and of their resources within the framework of current climate change and land uses. In order to inform the public in general of the problems related to climate change and its effects and interactions with terrestrial ecosystems, we have phenological change as an easy-to-use and popular tool which shows everyone how climate change can affect our lives. Use should also be made of events like the 1994 drought in order to make the public aware of the of water reduction on our ecosystems. In these terms, and in all those terms previously referred to, all the research activity should be disseminated through the media. The communication activities should also be supported, with the joint participation of the stakeholders involved in research and in the forest management of natural spaces.

2.9.2. Sustainable management of ecosystems, reforestation and ecological restoration

Management of terrestrial ecosystems and planning the type and intensity of human activity should be based on a balance between the global vision of ecosystem processes, regional knowledge and local action. The dynamics of our ecosystems, almost all of them semi-natural ones, can be understood as a series of anthropogenic degradations and subsequent regeneration. Indeed, both overexploitation and complete protection can lead to lower levels of scenic attractiveness and economic utility in many terrestrial ecosystems like Mediterranean forests and shrublands. These current Mediterranean formations cannot be understood without human intervention, and an obvious paradigm is constituted by savannah or *dehesa* systems. Although changes in climate and in the regime of fires and disturbances could mean that the *dehesas* are maintained through measures different from human uses, at present, both the *dehesas* and the diversity they contain depend on correct forest and livestock farming management (Díaz *et al.* 2003). The management of these systems involves the management of high levels of biological diversity, and although in themselves, they may not contribute to the sustainability of the system, they may very well contribute to its maintenance and conservation thanks to value given by society to these systems, which are rich in species (Blondel and Aronson 1995). In spite of the fact that the need for human intervention has been demonstrated in order to maintain the local coexistence between grasslands and forests in the *dehesa,* the processes and mechanisms have not yet been established through which human intervention can be seen as important for the maintenance of this coexistence (Marañón *et al.* 1999). The management of these systems should therefore be adaptational, and should be able to vary according to the evolution of the system and to the effects of the management applied in each case (Rojas 2001, Charco 2002, Valladares 2004b).

There is abundant evidence that in actions aimed at rehabilitating or restoring terrestrial ecosystems, the optimum action lies in helping nature to recover, accelerating the natural processes of ecological succession, and minimising intervention (Suding *et al.* 2004). These actions should consider the tendency towards climatic change, and not just apply classical protocols, adjusted to the predominant climatic conditions to date. Knowledge of the mechanisms of the ecosystems' resistance to stress enables us to understand the evolutionary processes involved in the adaptation of the different species to environmental changes and to predict, to a certain extent, their response to the increase in adversity associated with global change (Valladares 2004b). This knowledge should be incorporated into the restoration programmes, for instance by improving or selecting the characteristics of the plants to be used in reforestation or restoration projects. Knowledge of these mechanisms may also enable us to use sensitive species as bioindicators of the stress associated with climatic change.

The people managing our nature and our habitats, both rural and urban, should consider the properties related to the emission of volatile organic compounds by the different plant species if they aim to avoid the formation of secondary atmospheric pollutants. Indeed, while they must consider the high-emission species as candidates for the reforestation of arid zones with high temperatures, as they are the ones most resistant to these conditions, they will have to chose the species with the lowest emissions for the reforestation of urban and suburban areas, as well as industrial areas, subjected to high levels of anthropogenic pollution (for instance nitrous oxides) if they are to avoid the formation of secondary pollutants like ozone. With the current ecological and climatic information referring to the Mediterranean coasts, the correct reforestation of the slopes of these coastal mountains could be used to reactivate the trigger and feedback mechanisms of summer storms, thus guiding the system towards a configuration with more vegetation, stabilising some of the anticipated effects of climate change (Millán 2002). This could also be applied to other areas in which the vegetation significantly affects the local characteristics of the atmosphere. In short, the forest management of natural spaces must not ignore the role of forests and shrublands in the preservation of the atmosphere and as buffers against polluting environments rich in CO_2.

2.9.3. Carbon sequestration versus the biological diversity and functionality of ecosystems against desertification

The management of terrestrial ecosystems ought to consider the important role played by the emissions of gasses by plants in atmospheric chemistry and in local and global climate, and the role of plants as sinks of such important atmospheric gasses as CO_2. In order to mitigate climate change by greater harnessing and less loss of CO_2 forestation and reforestation can be used, with the aim in mind of lengthening the immobilisation of carbon in forest products and of protecting the soils. Forest management will also have to incorporate the change in environmental conditions at the moment of defining the intensity and frequency of interventions. For example, if we take into account the increasing conditions of drought, we will have to reduce the density of shoots in high-density forests, a strategy which has proven to be effective for reducing the impact of extreme droughts.

Almost 90% of carbon in the form of biomass is accumulated by forests, which is 50% of terrestrial organic carbon. However, Körner (2003) observed the temporal asymmetry caused by the slow growth of a tree and the brusqueness of the disturbances (fire, logging, herbivory, decay) which release a lot of carbon into the atmosphere. In the case of underwoods of Holm oak and oak, dominant in many parts of the Iberian Peninsula, industrialisation and rural depopulation led to a brusque change. The traditional use of these forests for timber and charcoal has been abandoned, with much longer periods between clear cuts. These aged underwoods show very slow growth, which may imply greater vulnerability to the effect of abiotic stresses (e.g. drought) or biotic ones (e.g. defoliating pests). An experiment carried out at small scale (Luis-Calabuig *et al.* 2000) attempted to determine if the thinning of the underwoods favoured the development of the tree shape of the oak (*Quercus pyrenaica*) from dense and continuous shrub formations promoted by repeated fires. No differences were observed in the growth of the oaks between the treatments applied to eliminate the shrubland and the original situation. In the thinning, however, we observed that an increase in trunk perimeter was favoured over the growth in height of the 10 shoots that remained, the competition for light having diminished. With more long-term treatment it would be possible to improve the structure of these ecosystems. The intense disturbance associate with traditional forestry treatments causes a rapid release of carbon, but if no treatment is applied, there is a risk that the poor growth rate of these aged forests and their greater vulnerability to stress situations may lead to an acute decay and a high death rate, and, once again, provoke the abrupt release of carbon. This paradox is currently insoluble due to our ignorance of the functioning of the underwoods, and poses serious doubts about the role of these formations of *Quercus* species as carbon sinks.

In general, the policies and actions aimed at increasing the sequestration of atmospheric carbon by vegetation are incompatible with the conservation of biodiversity or the sustainable exploitation of this. One of the few compatible solutions identified to date would be to select unproductive areas for the maintenance of high-biodiversity forests and formations capable of storing the sequestered carbon over long periods of time, and to use more productive areas for other uses (Huston and Marland 2003).

2.9.4. Nature conservation and protected natural spaces

Palaeoecological models establish that the main centres of European postglacial dispersion were the southern Iberian Peninsula, Italy and the Balkans (Willis and Whittaker 2000). Therefore, if a species of tree becomes extinct from southern Europe, the chance of continental extinction in the face of future climatic changes are much greater if the extinction affects the British Isles or Scandinavia (Carrión 2003). This is a solid argument to insist, both at national and community levels, on the conservation of our terrestrial ecosystems and the application of sustainable development policies.

With the foreseen climatic change, the vegetation could spread to the higher mountain zones, but the communities already existing in these high zones will become extinct (Peñuelas and Boada 2003). In many cases, the only migration possible is towards northern latitudes. But the migration rates would not be efficient in the current scenario of global change, as, on one hand, the climate changes too quickly, and, on the other, the territory is very fragmented, which significantly restricts the real possibility of latitudinal or altitudinal migrations by the vegetation. For this reason, when managing the protected natural spaces or selecting new spaces to be protected, it is necessary to maximise the connectivity between the different units and ecosystems in the zone in order to compensate for fragmentation. Besides, it is important to conserve processes and systems, and to establish suitable spatial scales for the ecological processes. In order to ensure efficient long-term conservation of many of these processes, we must incorporate zones with different levels and types of human intervention and with different levels of susceptibility to climatic change. The protected natural spaces should establish a “risk reserve”, a component created specifically to reduce the ecological risk associated with climatic change. Furthermore, the management of natural spaces should incorporate a landscape scale that contemplates the combination of different types of spaces, favouring a multiple and controlled use, but without suppressing the effect of disturbances like fire.

2.9.5. Need for co-ordination and a closer relationship between research and follow-up

It is necessary to bring together the organisms, institutions and human and technological teams dedicated to the follow-up of environmental change, along with those dedicated to research into its effects on terrestrial ecosystems. It is only possible to obtain reliable results related to these effects through scientifically rigorous analysis of very diverse data, resulting from a necessarily interdisciplinary approach, and this analysis is only feasible if these data (environmental, ecological, physiological, etc.) are collected and stored in an equally rigorous manner over long periods of time.

2.9.6. Corollary: the funding of the goods and services provided by ecosystems requires creativity and flexibility of policies for greater social compromise

Climate change will exacerbate in a foreseeable way the environmental crisis the nature of our country is undergoing in general terms, and the terrestrial ecosystems in particular. One of the main causes underlying the poor sustainability of the current management of Spanish terrestrial ecosystems is the unprofitability of many of them. When ecosystems are not profitable, no investment is made in them. And it makes no difference whether they are publicly or privately owned, as the surface area of terrestrial ecosystems is so great that not even the State manages them if a minimum level of profitability is not ensured. This is evident in the case of forest ecosystems, for which European policies are dominated by the timber-producing countries, whereas Mediterranean forests, in spite of their considerable area, are considered as marginal. Thus, Spain is the European country with the highest proportion of economically unproductive forest, due, on one hand, to the abundance of unprofitable shrublands, above all in the areas with a dry Mediterranean climate, and on the other, to the existence of protected spaces. Society at present, however, assigns to terrestrial ecosystems a series of functions which surpass by far mere production, and increasing value is being given not only to hydrological regulation and protection against erosion, but also to the recreational use, the conservation of biodiversity and landscape and carbon storage. All of these functions mean that society recognises the benefits provided by terrestrial ecosystems, although they do not provide direct economic ones. As the owners do not receive any income from these services, there are no sources of finance to invest in the social functions of the ecosystems. The scientists do not have the answer to this kind of problem, but the correction of the malfunctions that will be accentuated by climate change will only be made if the funding problem is solved. The administrations should therefore use their imagination to find new sources of resources. If the ecosystem provides services, these should somehow be paid for by the beneficiaries (sometimes society as a whole, sometimes specific groups or private individuals). If the forest produces clean water, the societies supplied by this water and the municipal authorities ought to become involved in forest management. If it used for conduits, so should the electricity companies. The same can be said of the housing estates, hotels and other tourism establishments making use of the landscape. Social involvement is needed to develop new forms of management, in accordance with the newly recognised services provided by terrestrial ecosystems (Peñuelas *et al.* 2004a). The solution cannot come from the economy of administrations or from the efforts of a few private owners, but rather from imaginative and flexible policies involving greater collective compromise in order for the ecosystems to be treated in accordance with the services they provide us with and with their intrinsic value.

2.10. MAIN RESEARCH NEEDS

New ecological studies constantly reveal new patterns, and modification and exceptions to the known responses of species and terrestrial ecosystems to increasing drought and warming. This shows that our knowledge is still very little and possibly insufficient to satisfy the urgent need for accurate predictions and recommendations for the management of terrestrial ecosystems in a changing world. From the vast amount of knowledge needs seen in this review, we have established the following main lines of research, which need to be reinforced:

1. Attainment of long temporal series in order to establish tendencies and to analyse the dynamics of responses and reactions. The long-term follow-up of ecosystems will enable us to detect:
   a. The physical bases of environmental change itself,
   b. The impact of climate change on the ecosystems,
   c. The results of the attempts to mitigate climate change and its effects.
2. Study of the interaction between climate change and changes in land uses. Development of experiments and manipulation to separate the effects of both factors.
3. Study of the interactions between climatic factors (temperature, light, water, CO_2) and their effects on ecosystems.
4. Study of the interactions between species and of the sensitivity of networks of interactions to climatic change.
5. Extension of ecological and ecophysiological studies to unknown ecosystems, not only those dominated by unique species (see section 12.5.2), but also Mediterranean Holm oak forests and shrublands situated outside Eastern Spain (e.g. moorlands and continental zones, high mountain).
6. Analysis of the indirect effects of climatic change. Cascade effects. Synergic reactions and autocatalytic cycles like, for example, the decrease in productivity, the increased attacks by pests and the rising risk of fire.
7. Analysis of the expression time lag of the effects, of the reaction by the ecosystems and of the adaptation and evolution in new scenarios.
8. Selection of early indicators of change.
9. Determination of minimum tolerance values (minimum area, minimum hydric availability, minimum size and structure of the network of interspecific interactions) in vulnerable systems, particularly in those with a propensity for threshold-type responses, like island and riparian ecosystems.
10. Effects of climate change on the spread of invasive species.
11. Study of subterranean processes (C sinks, dynamics of roots and edaphic microorganisms).
12. Implementation of complete carbon balances for the different terrestrial ecosystems through the optimisation and parameterisation of accurate models and estimates, not only of biomass (aerial and subterranean), but also of necromass.
13. Improvement of ecological restoration techniques for the recovery of plant cover and other functions and services of ecosystems in degraded areas.

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