Orsis 11, 1996 **165-175**

Overview on current and past Global Changes in the Mediterranean ecosystems

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Manuscript received on November 1995

Abstract

Atmospheric increases in CO_2 and other greenhouse gases are the basis of Global Change. The effects on ecosystems are not yet well known. Effects on Mediterranean ecosystems are even less known. Some of the current knowledge on direct and indirect (through climate changes) effects on Mediterranean ecosystems is presented. Recent data from historical plant material are highlighted to discuss the biological changes already produced after several decades of Global Change.

Key words: Global Change, CO_2, Climate Change, Mediterranean ecosystems, evapotranspiration, water-use efficiency, nitrogen, secondary metabolites, growth, fires, vegetation degradation.

Resum. *Passeig pels canvis globals actuals i passats als ecosistemes mediterranis*

Els increments en les concentracions atmosfèriques de CO_2 i d'altres gasos hivernacle constitueixen la base de l'anomenat *canvi global*. Els efectes sobre els ecosistemes no són encara ben coneguts, i encara ho són menys els efectes sobre els ecosistemes mediterranis. Aquí es presenta una part dels coneixements actuals sobre els efectes directes i indirectes (a través dels canvis climàtics), i es destaquen les dades recents sobre material vegetal històric per discutir els canvis biològics ja ocorreguts després d'unes quantes dècades de canvi global.

Paraules clau: canvi global, CO_2, canvi climàtic, ecosistemes mediterranis, evapotranspiració, eficiència en l'ús d'aigua, nitrogen, metabolits secundaris, creixement, focs, degradació de la vegetació.

Global Change and Mediterranean ecosystems

Atmospheric increases in CO_2 and other greenhouse gases are the basis of Global Change, including climate changes (Houghton et al., 1992; Peñuelas, 1993). Global temperature, precipitation, frequency of extreme events such as fires, the sea level, and soil chemistry, all interrelated factors, are also expected to change (Houghton et al., 1990). Their change would be unprecedented in human history, e.g. the five degree warming since the last ice-age 18000 years ago would take effect between 10 and 100 times faster (Schneider, 1989). Although certain direct effects of higher CO_2 concentrations like an increased biomass or a change in plant tissue quality and several indirect effects on natural ecosystems through climate change are anticipated, great uncertainties are associated with the magnitude and direction of these effects, especially at the regional level. The Mediterranean ecosystems are even less well known than other temperate regions because they are regionally very diverse and have been less studied. Here I present some of the current knowledge on biological effects of increased atmospheric CO_2 and associated changing climate in the Mediterranean region of Europe. I pay special attention to recent data from historical plant material such as herbaria specimens with the aim of studying the biological changes already produced after decades of Global Change.

Direct effects of CO_2 increase

In CO_2 enriched experiments, enhanced CO_2 levels usually increase plant photosynthetic rates, plant biomass and yield (Kimball, 1983) at least in short term experiments. In some species these effects level off with time (Bazzaz, 1990). Other general accompanying features are reduced transpiration rates and higher water use efficiency (g biomass assimilated per kg water transpired) because increases in CO_2 levels reduce stomatal conductance (Allen, 1990; Parry, 1992). Therefore high CO_2 would stimulate growth in water-limited Mediterranean environments. Yet, the total water used by a community is unlikely to be altered with CO_2 alone, because plants tend to develop leafier canopies (Woodward et al., 1991) and to increase relative root size (Idso & Kimball, 1992; Callaway et al., 1994), especially when other resources are scarce (Peñuelas et al., 1995a).

The ultimate effect of an increased CO_2 level depends on the interaction between other Mediterranean environmental conditions like warm temperatures, high light levels, reduced summer soil moisture, and nutrient availability (Bazzaz, 1990; Peñuelas et al., 1995a). In particular, the currently increased levels of gaseous pollutants toxic to plants may also affect the response to high CO_2 levels. To a large extent, phytotoxic gases are presumed to penetrate through stomata and to be taken up in dissolved form. Thus as stomata tend to close in response to CO_2, this may facilitate plant tolerance to some air pollutants. On the contrary, the generally high humidities in Mediterranean coastal zones tend to increase stomatal conductance and thus to favor pollutant entrance. Because of this and because climatic conditions, mainly high solar radiation, contribute to ozone formation, ozone is currently an important pollutant problem in some areas of the Mediterranean coast (Peñuelas et al., 1995b), where there is a high level of industrialization and population density that increases the generation of trace gases that lead to ozone formation, and where ozone importation from the sea might also be important (Gimeno et al., 1989; Martin et al., 1991). Hence ozone injuries on several crops (watermelon, beans, and soybean) and trees (e.g. alepo pine) have been reported along the Spanish Mediterranean litoral (Salleras et al., 1989; Reinert et al., 1992; Gimeno et al., 1992, 1992b). The interaction between increased levels of both CO_2 and ozone and other trace gases should be studied widely in Mediterranean ecosystems.

The effects of atmospheric changes in CO_2 and other trace gases like ozone are not the same for all plant species. When direct response to elevated CO_2 varies between species (Zangerl & Bazzaz, 1984; Peñuelas & Matamala, 1990; Poorter, 1993), plant-plant interactions, population dynamics, and competitive relationships between plants are altered. Increased CO_2 could also affect plant-animal interactions, i.e. herbivory, through changes in tissue quality. For example, lowered N concentration (Peñuelas & Matamala, 1990) seems to increase herbivore feeding rate to compensate for decreased protein content (Scriber & Slausky, 1981). This has not, however, been found in some studies of Mediterranean taxa (Estiarte et al., 1994). The relationships between plants and microbes may also be affected. For example, C/N ratios of plant tissues have been found to increase (Curtis et al., 1989). There is experimental evidence that tissues with high C/N ratio decay more slowly (Bazzaz, 1990). However, decomposition rates generally increase with temperature and precipitation in well drained areas. The result is that the few community experiments performed at elevated CO_2 suggest little changes in the rate of nutrient cycling (Woodward et al., 1991). It is thus not clear whether N cycling will be accelerated by higher C availability or not.

Biological indirect effects through climate change

Precipitation and evapotranspiration

The 3-4 °C increase in average temperature predicted for the Mediterranean area by Global Circulation Models could lead to an increase in potential evapotranspiration of 200-300 mm per year within the first half of the next century (Imeson & Emmer, 1988). Considering that several Mediterranean regions receive less than 500 mm of precipitation per year, it might be concluded that a 10% increase in annual average precipitation would not be enough to compensate for the higher evapotranspiration rates. The drier conditions this forecasts for Mediterranean areas can cause plant water stress. Increased water stress can reduce photosynthesis, but this might be alleviated in the short term by elevated CO_2. Under water stress, the biochemical composition of plants also changes. The concentrations of amino acids, alcohols, and other potential insect attractants tend to rise (Rubenstein, 1992) again changing plant-animal interaction. There is, though, great uncertainty regarding the magnitude of these effects.

The Mediterranean climate is characterized by summer drought, so that most Mediterranean plants are adapted to summer soil moisture shortage. However, decreases in wet season rainfall can lead to the gradual degradation of the vegetation and soil, and ultimately desertification. This is already a growing problem in some Mediterranean areas, e.g. in Southeastern Spain. The soils of degraded ecosystems are unable to retain water supplied by the ocassional high intensity storms that occur typically at the beginning of autumn. Thus, scarce water is not used efficiently, and flooding and erosion ensues. Another important characteristic of the Mediterranean region is the vulnerability of the soils to salt accumulation. Where rainfall is insufficient to leach out salts from soils, these become concentrated at particular locations on slopes and in drainage basins (for example in inland Eastern Spain). Water will thus decrease both its availability and its quality. The implications of this for water supply and agriculture are obvious.

Temperature

It is well known that all living organisms are strongly affected by temperature (Margalef, 1974). The physiological processes of plants and animals proceed at a rate dependent upon ambient temperature. Plant respiration is more responsive than photosynthesis at higher temperatures, what could result in a reduction in net carbon uptake by plants (Woodwell, 1987). However, plant respiration decreases with increasing atmospheric CO_2 (González-Meler, 1995). Temperature and moisture also affect the timing of development and senescence. In fact, plant distribution is correlated with growing season length, absolute lowest annual temperature, and total precipitation (Woodward, 1992). Several animal functions are affected with changing temperature: the behavioral pattern of parents, especially critical when food and water resources are scarce; reproductive processes including fertility and fecundity, intensity and duration of estrus and egg production; adult birds ability to maintain proper temperatures for embryos and chicks; and sex determination in reptiles are among them (Dawson, 1992). Parasites and diseases, for example, may do well in a warmer world; decreased development times will enable extra generations to occur (Cammell & Knight, 1992).

Fire

The expected increase in biomass and its flammability, and the expected climate induced changes could increase periodicity and intensity of fires (Brubaker 1986). Despite the complexity of the fire-vegetation system, the effects of fire on population are often easy to predict. For instance, fire should increase the range of expansion and local population growth for shade-intolerant species which require large openings for establishments. On the other hand, the spread of shade tolerant, late succesional species may be slowed if fires are frequent enough to keep most stands in early succesional stages (Brubaker, 1986).

Adaptation, migration or extinction?

On an individual level, the ability to adjust to environmental changes would depend upon the physiological plasticity; whereas, on a population level, this ability would also be determined by the species potential for rapid evolution of new traits, and therefore by genetic heterogeneity and generation time.

The potential for evolution is generally regarded as insufficient in comparison to the rates at which Global Change is occurring. Paleoecological evidence of the response, especially of plants, to past climate changes seems to indicate that evolutionary adaptation has played only a minor role as a response to climate change (Huntley, 1991). Species would have responded to climate changes not by evolution, but by migration (Bradshaw & McNeilly, 1991; Huntley, 1991). However, there are also many other results of historical plant material (Woodward, 1987; Peñuelas & Matamala, 1990; Beerling et al., 1993) indicating the contrary: a significant role of evolutionary adaptation.

The extent of migration depends upon factors such as severity of environmental conditions, ability to disperse, and generation time, with evident more rapid response for animals than for plants. Thus, trees, with their long generation time, would be rather slow in responding to climate change (Ford, 1982).

In Mediterranean mountainous areas such as Pyrinees, species may repond to climate change by migrating vertically over relatively short distances: they may have to ascend only 500 m to compensate for a three degree temperature rise. Grabherr et al. (1994) have described that even recent moderate warming of this century has induced species migration in Alps mountains. However, migration to higher altitudes leads to a concomitant reduction in the total area of any habitat type, so species with larger area requirement may go extinct (Dobson et al., 1989).

Another major obstacle comes from habitat destruction due to human activities that will prevent many species from colonizing new habitats when their old ones become unsuitable. The sinergy between climate change and habitat destruction would threaten many more species than either factor alone (Peters, 1991).

Studies of the recent past

Studies of CO_2 effects on vegetation have been conducted in controlled environment chambers, in greenhouses, open top chambers, and free air fumigation systems (Kimball, 1983; Eamus & Jarvis, 1989; Estiarte *et al.*, 1994; Peñuelas et al., 1994). New studies must be developed in order to overcome the several drawbacks of most of these current Global Change experimental studies. There are large differences in plant response due to genetic differences inside species (Dirzo & Sarukhan, 1984). Observations at the leaf and plant scale may not be easily translated to the canopy scale (Jarvis & McNaughton, 1986). Experiments conducted on a few plants grossly oversimplify what will happen within complex vegetation. For example, the plants themselves influence the microclimate and the behaviour of other plants. Because we still know very little about these and other interactions, it is impossible to say how entire tracts of vegetation will respond to the increase in atmospheric CO_2. Most of these studies are conducted for relatively short periods of time (less than 12 months). They are likely to be reporting on short-term acclimatory response more than long-term physiological adaptation (Jarvis, 1989). Only long-term whole-ecosystem experimentation that considers the complex multifactorial interactions between environment and organisms can help to model ecosystem response. These kinds of experiment are difficult and expensive to perform. A promising alternative is the study of natural environments close to CO_2 vents (Migglieta & Raschi, 1993) or the examination of plants stored in herbaria (Woodward, 1987; Peñuelas & Matamala, 1990), tree rings (LaMarche et al., 1984; Graumlich, 1991), and relict tree stumps rooted in present-day lakes, marshes and streams (Stine, 1994). The study of these historical plant materials is a very interesting approach because they correspond to actual and natural long-term environmental conditions. They also have drawbacks. Among them, the lack of control or knowledge of growth environmental conditions is outstanding.

Graumlich (1991) has studied tree rings from Sierra Nevada and arrived at the conclusion that there is no strong evidence in support of the theory of enhanced tree growth by CO_2 fertilization since the onset of the Industrial Revolution as it had been previously suggested by results of LaMarche et al. (1984). No greater stimulations of elevated CO_2 were either found for plants originating from high altitude at lower CO_2 partial pressures (Woodward, 1993). However, some important changes such as a decrease in stomatal density have been reported in herbarium specimens collected during the last three centuries in England (Woodward, 1987).

In the Mediterranean area, stomatal density of herbarium specimens of 14 species (trees, shrubs, and herbs) collected over the last 250 years in Catalonia (N.E. Spain) has also decreased 17% (Peñuelas & Matamala, 1990). This reduction could be due to many environmental factors; nevertheless, in the laboratory the same response can be simulated by changes in CO_2 alone (Madsen, 1973; Woodward & Bazzaz, 1988), with an increase in CO_2 up to about 320 ppm causing a reduction in stomatal density. Interestingly, further increases in CO_2 mole fraction were found in some instances to exert no effect on stomatal density both in herbaria and experimental data (Woodward & Bazzaz, 1988; Peñuelas & Matamala, 1990; Radoglou & Jarvis, 1990; Estiarte et al., 1994). A decrease of 5.2% in carbon isotope discrimination $\Delta^{13}C$ has also been reported in the mentioned herbarium material (Peñuelas and Azcón-Bieto 1992) suggesting an increase in carbon assimilation or a decrease in stomatal conductance, and, hence an increase in water use efficiency over the last decades. Moreover, herbarium leaf nitrogen content has decreased 31% (Peñuelas & Matamala, 1990) and leaf contents of Al, Ca, Cu, Sr, Fe, P, Mg, Mn, K, Na, S, and Zn were always lower in the present than in any other period of the last three centuries (Peñuelas & Matamala, 1993). The carbon/nitrogen ratio would thus have increased, implying possible important consequences on herbivores, decomposers, and ecosystems.

Although there are several problems in using herbarium material to arrive to reliable conclusions on Global Change effects, mainly because of the associated variability and the many environmental factors interacting (Woodward, 1987; Peñuelas & Matamala, 1990), all these results mirror experimental results obtained submitting plants to different CO_2 concentrations under controlled conditions (Lemon, 1983; Strain & Bazzaz, 1983; Woodward & Bazzaz, 1988; Overdieck, 1993) where steeper biological changes have been found in the initial increase in CO_2 atmospheric levels. These results indicate that human activities are influencing Mediterranean vegetation, might be through short-term phenotypic responses within the present period of rapid global changes. The rise in atmospheric

CO_2 concentration over the past 200 years is outstanding among these changes. Besides direct effects on vegetation, it would have had indirect effects through higher temperatures and lower precipitations in the studied Mediterranean area (Burgueño, 1989). Over longer terms of CO_2 increase, a genotypic adaptation could also be likely, as has been reported for the stomatal density of fossil leaves of *Salix herbacea* L. extending back over 140 thousand years ago (Beerling et al., 1993), or for the possible increase in water use efficiency suggested by changes in carbon isotope discrimination in grain cereals from the mentioned North-Western mediterranean basin during the past seven millenia (Araus & Buxó, 1993). Paleological evidence of variations from the beginning of the agricultural activity 7000 BP onwards to the Iron Age and Roman Period (Burjachs, 1990) agrees with the influence of aridity conditions that could explain progressive decrease in $\Delta^{13}C$ and progressive increase in WUE since the Neolithic. This increase in WUE has coincided with increases in atmospheric CO_2 concentration. If the improvement is sustained and even increased as CO_2 continues to accumulate in the atmosphere, significant consequences for the distribution of Mediterranean plants, such as spreading into droughted areas, might be expected.

Conclusions

Mediterranean ecosystems are characterized by scarce water availability for several months and frequent and recurrent fires. Current and future increased atmosp-

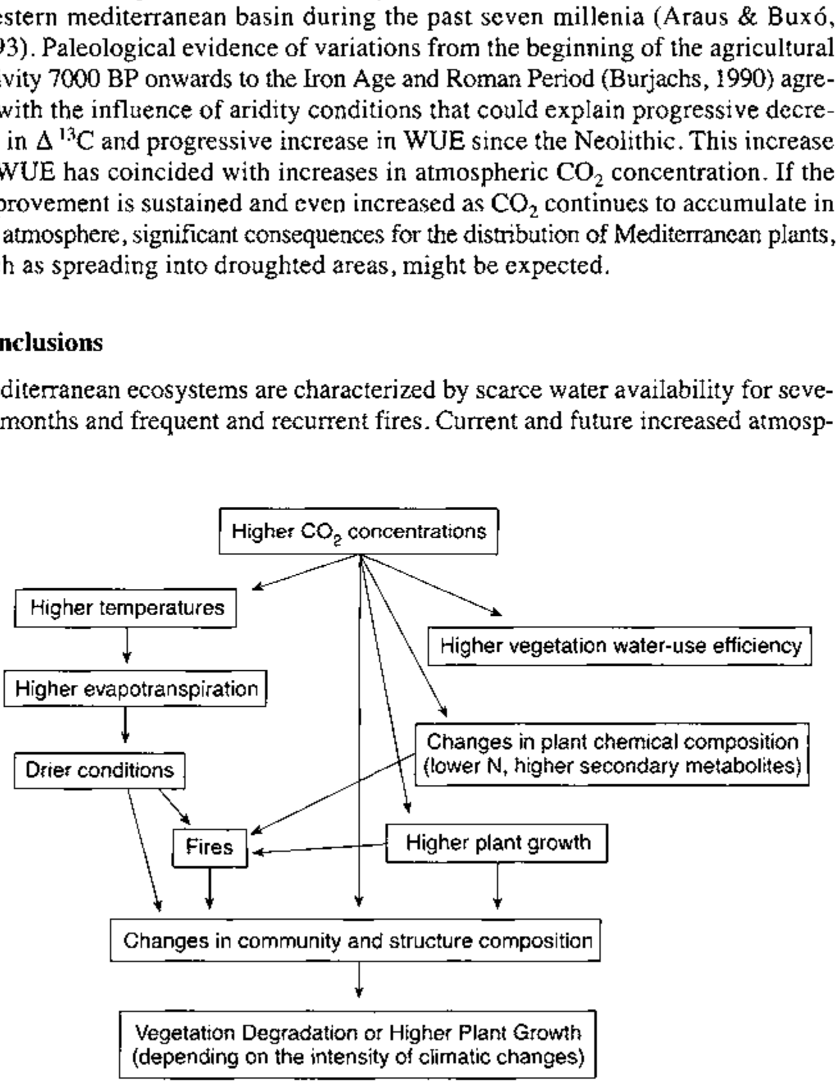

Figura 1. Summary of the global change effects on Mediterranean ecosystems.

heric CO_2 concentrations may importantly change functioning and structure of Mediterranean communities and ecosystems through both direct effects and interactions with temperature, water and fires. It is likely that dry Mediterranean ecosystems respond more than other temperate ecosystems because of an increase in plant water use efficiency (Peñuelas & Matamala, 1990; Peñuelas & Azcón-Bieto, 1992; Araus & Buxó, 1993). The expected increase in leaf area and roots (Kimball, 1993; Peñuelas et al., 1994) may alter overall water use so that it will interact with hydrology of the system. The expected increase in biomass (Kimball, 1983) and flammability may also shorten the periodicity and increase the intensity of fires and thus, change species composition and the structure of the community developed after the fire. The current and expected changes in plant tissue chemical composition (carbohydrates, nitrogen, phenolics, other secondary metabolites) (Peñuelas & Matamala, 1990; Estiarte et al., 1994; Peñuelas et al., 1996) might likely change plant-animal and plant-microorganisms interactions. The climate change associated to the increase of CO_2 and other gases (higher temperature and lower water availability for most of the Mediterranean area) may reinforce these effects. However, if the drier conditions become too extreme, vegetation may degrade and erosion and desertification may ensue (Fig. 1).

Acknowledgements

This research was supported by grants CICYT AMB94-0199 and INIA SC94-011 (Spain), and CIRIT-1994 (Catalonia).

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